Public Workshop (10/1-2/12)
Bay-Delta Workshop 2
Deadline: 9/14/12 by 12 noon

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Additional Scientific Information Related to Salmonids, Recommended Changes to the Bay-Delta Water Quality Control Plan, and Recommendations to Address Scientific Uncertainty and Changing Circumstances

Workshop 2: Bay-Delta Fishery Resources

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&
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Submitted to the State Water Resources Control Board on behalf of:
Trout Unlimited
The Bay Institute
Natural Resources Defense Council
Pacific Coast Federation of Fishermen's Associations

September 14, 2012

I. Response to Question 1: Additional Scientific Information and Recommended Changes to the Bay-Delta Water Quality Control Plan Regarding Salmonids

The State Water Resources Control Board (State Water Board) is requesting information related to the comprehensive Phase 2 review and update to the 2006 Water Quality Control Plan for the San Francisco/Sacramento-San Joaquin Delta Estuary (Bay-Delta Plan). Specifically, the State Water Board seeks scientific and technical information that was not addressed in its 2009 Staff Report or its 2010 final report on "Development of Flow Criteria for the Sacramento-San Joaquin Delta Ecosystem" (hereafter 2010 Delta Flow Report or SWRCB 2010). We recognize that many different public trust resources are impacted by the conditions in the Sacramento-San Joaquin Delta (Delta); however this submittal focuses on new scientific and technical information related to anadromous species that rely on the Delta, mainly Chinook salmon (*Oncorhynchus tshawytscha)*.

Anadromous fish utilize the Delta for a number of critical functions including spawning, rearing, migration (both upstream as adults and downstream as juveniles) and foraging. However, they also utilize upstream riverine habitats to complete essential life functions. Therefore, Delta flow requirements (both inflow and outflow) must be sufficient to provide the contiguous habitat that is necessary to support the life cycle of Chinook salmon and other anadromous species. To truly understand what flow requirements are sufficient, it is necessary to understand not only the in-Delta requirements of Chinook salmon life history but also the upstream relationships between flow and Chinook salmon survival. The characteristics of inflow to the Delta are positively correlated with flow characteristics in the upstream watershed. Therefore, a range of flow characteristics in the upstream watershed drive a variety of processes that promote sustainable conditions for salmon and other anadromous fish species as well as the overall ecological health of the Delta.

The current Delta hydrograph has been dramatically altered over time by both water exports from the Delta and diversions throughout the watershed. These alterations have resulted in the significant deterioration of the ecological health of the Delta and the Public Trust resources it supports, including salmonids. Habitat alterations in the Delta limit salmon and steelhead production primarily through reduced survival during the outmigrant (smolt) stage. Decreased flow can delay juvenile migration events resulting in their increased exposure to unsuitable water temperatures, predation or entrainment. These lower survivals are associated with decreases in the magnitude of flow through the estuary, increases in water temperature, and water project diversions in the Delta.

An extensive amount of scientific information supports the concept that the magnitude, duration, frequency and timing of flow is critical to the restoration of natural anadromous fish resources in the Central Valley watershed. In addition to survival being higher with higher flows, Chinook salmon abundance has also been found to be higher with greater Sacramento River (and San Joaquin River) flow. Therefore, adequate freshwater flow both into the Delta and through the Delta is an absolute prerequisite to increasing salmon survival rates and restoring natural salmon production in the Central Valley.

Scientific literature and other technical information that has become available since 2010 strongly supports the State Water Board's 2010 Delta Flow Report finding that "*the best available science suggests that current flows are insufficient to protect public trust resources.*" (2010 Delta Flow Report, p.2). In the context of anadromous fish, the information reinforces the finding that Chinook salmon have diverse life histories and life cycles that require suitable conditions in the upper and lower watersheds, Delta and ocean. The information also supports the finding that the drastic changes to the quality and characteristics of historic salmonid habitat, largely caused by water diversion activities, have resulted in decreased Sacramento Valley Chinook salmon and steelhead stocks. Salmonids are adapted to the seasonally variable stream flows and diverse habitats of Central Valley rivers. Water management and diversion activities have helped create a system that deviates from these historical conditions. This deviation and associated decrease in the dynamism of the system has degraded habitat and created an environment conducive to alien species that compete with juvenile salmon for prey or predate upon them.

In this written submission, we review and summarize the findings of new publications, studies, and data and conclude that these new studies and publications support the following findings:

1. California's native fish communities are experiencing rapid decline with the majority at risk of extinction and trends in decline having accelerated markedly over the last three decades.
2. All Central Valley Chinook salmon populations as well as Central Valley steelhead populations are now sufficiently impacted to be endangered or at least vulnerable to extinction, with the most significant mechanisms of their decline being loss of access to upstream tributary spawning and downstream floodplain rearing habitats and large-scale flow alterations.
3. Delta inflow levels and patterns exert a strong influence over the growth, survival, movement, and life history diversity of migratory species that rely on them. Juvenile Central Valley Chinook salmon, specifically, are reliant on and affected by flow levels in the Delta.
4. The scientific literature strongly suggests that restoring floodplain connectivity and restoring flow regimes in both the Delta and its watershed are the restoration actions below major dams most likely to result in direct benefits to salmon and other species, by ameliorating flow and temperature changes (including effects of climate change), increasing habitat diversity and population resilience, improving juvenile survival and transport to marine environments, and facilitating efficient and timely return of adult salmonids to upstream spawning habitats.
5. Increased flows, improved habitat quality and connectivity, and increased access of fish to improved channel and floodplain habitat can all, individually and in concert, have a positive effect on survival.

These new studies and publications also support the State Water Board's findings in the 2010 Delta Flow Report that:

1. Existing flows are inadequate to protect Public Trust resources.

2. Winter/Spring inflows should be substantially increased, using a percentage of unimpaired flows approach.
3. Releases from upstream sources should be made proportionally to each stream and watershed to preserve ecological connectivity between the Delta and upstream watersheds, increase the spatial distribution (and hence, distribution of risk) of salmon spawning populations, and avoid concentrating impacts on a subset of source areas.
4. Limitations on reverse flows in Old and Middle River (OMR), closures of the Delta Cross Channel gates, inflow: export restrictions, and other objectives are necessary to provide adequate migratory pathways through the Delta for juvenile and adult salmonids.

The State Water Board should complement these changes to the Bay-Delta Plan objectives with the adoption and implementation of a clear, transparent, and fully-defined adaptive management strategy that establishes specific, measureable, achievable, relevant and time-bound targets for protection of fish and wildlife beneficial uses.

A. POPULATION STATUS OF CENTRAL VALLEY CHINOOK SALMON AND STEELHEAD RUNS

Overall, populations of important Delta anadromous fisheries have been greatly reduced from historic levels, are currently in decline, or both. They all remain highly vulnerable to collapse in response to short-term disturbances, as evident in the collapse of the Sacramento River fall run Chinook salmon in 2008-09, which resulted in the complete closure of the salmon fishery for the first time in California history, and which was attributed to poor oceanic conditions in combination with significantly depressed freshwater conditions. Populations of anadromous fish species (Chinook salmon, steelhead, and green and white sturgeon) remain severely depressed since the State Water Board published its Delta Flow Report (SWRCB 2010). Population responses to improved environmental conditions during their juvenile (freshwater) life stages among Chinook salmon runs are only evident 2-3 years later when these fish return to spawn; thus, flow improvements (relative to those at the end of the last decade) in 2010 and 2011 would only manifest as improved salmon escapement in 2012 and subsequent years. The current anticipated rebound of the fall run Chinook population reinforces that anadromous fish are also very sensitive to positive environmental conditions and have the potential for recovery.

1. New Information on the Risk of Extinction for Native Species

A recent quantitative protocol has determined that all runs of Sacramento Valley Chinook salmon are vulnerable to extinction within the next century and identifies estuary alteration and major dams as the two most significant impacts on anadromous populations.

> [Moyle, P.B., J.V.E. Katz, R.M. Quiñones. 2011. Rapid decline of California's native inland fishes: A status assessment. Biological Conservation (144) 2414–2423]

Moyle and others (2011) applied a quantitative protocol to assess conservation status of all 129 freshwater fishes native to California. Their results indicated that 83% of California's freshwater fishes are extinct or at risk of becoming so, representing a 16% increase since 1995 and a 21% increase since 1989. Additionally, of 31 species officially listed under federal and state endangered species acts (ESAs), 17 (55%) were rated as endangered by their criteria, while 12 (39%) were rated vulnerable (including Central Valley fall, winter and spring run Chinook salmon). Conversely, of the 33 species that received endangered rating by Moyle and others, only 17 (51%) were officially listed under the ESAs. This latter finding points to the insufficiency of the ESA listing as an indicator for collapse in fish populations and the urgent need for actions to promote their recovery.

> [Katz, J., P. B. Moyle. R.M. Quiñones, J. Israel and S. Purdy. 2012. Impending extinction of salmon, steelhead, and trout (Salmonidae) in California. Environ Biol Fish. DOI 10.1007/s10641-012-9974-8]

Katz et al (2012) developed a quantitative protocol to determine conservation status of all salmonids native to CA. Results indicate that if present trends continue, 25 (78%) of the 32 taxa native to California will likely be extinct or extirpated within the next century. As a component of this analysis, results classified Central Valley Late Fall Run Chinook Salmon populations as Endangered and all other Central Valley Chinook Salmon (Fall, Winter, Spring) and Steelhead populations as “Vulnerable” to extinction. Katz quantitative analysis identified major dams (43%) and estuary alteration (43%) as the two most significant (“Critical High”) impacts on anadromous populations.

2. New Information on Population Status of Central Valley Salmon and Steelhead runs

Based on information from the sources identified below, the population status of Central Valley salmon and steelhead runs remain severely depressed.

> [Kormos, B., M. Palmer-Zwahlen, and A. Low. California Department of Fish and Game. March 2012. *Recovery of Coded-Wire Tags from Chinook Salmon in California’s Central Valley Escapement and Ocean Harvest in 2010*. Fisheries Branch Administrative Report 2012-02. Available at: https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=44306]

> [National Marine Fisheries Service. February 10, 2012. Biological Opinion for the Department of Water Resources 2012 Georgiana Slough non-physical barrier study. File # 151422SWR2011SA00060 (TN 2011/05837). Available at: http://swr.nmfs.noaa.gov/bo/Georgiana_Slough_Barrier_Study_021012.pdf. (“NMFS 2012a”)]

> [National Marine Fisheries Service. August 2011. *5-Year Review: Summary and Evaluation of Sacramento River Winter-run Chinook Salmon ESU*. Available at: http://swr.nmfs.noaa.gov/psd/fyr/Final_Winter-run_Chinook_5-year_Review_Report_082211.pdf (“NMFS 2011a”)]

> [National Marine Fisheries Service. January 26, 2012. *Letter from Maria Rea to Ron Milligan regarding Winter Run Chinook JPE during water year 2012*. (“NMFS 2012b”)]

[National Marine Fisheries Service. *Annual Report of Activities October 1, 2010, to September 30, 2011, Delta Operations for Salmonids and Sturgeon (DOSS) Technical Working Group.* October 2011. Available at: http://deltacouncil.ca.gov/sites/default/files/documents/files/DOSS_Annual_Report_10_18-11_final.pdf ("NMFS 2011b")]

[National Marine Fisheries Service. *Delta Operations for Salmonids and Sturgeon (DOSS) Working Group. Presentation for the Independent Review Panel, 11-8-11, by Bruce Oppenheim (NMFS) and Thuy Washburn, USBR.* Available at: http://deltacouncil.ca.gov/sites/default/files/documents/files/OCAP_2011_presentations_09_DOSS_ann_rev_11_7_11.pdf ("NMFS 2011c")]

[National Marine Fisheries Service. March 2012. Abundance-based Ocean Salmon Fisheries Management Framework for Sacramento River Winter-Run Chinook. Supplemental NMFS Report 2 to the Pacific Fishery Management Council. Available at: http://www.pcouncil.org/wp-content/uploads/G4c_SUP_NMFS_RPT2_MAR2012BB.pdf ("NMFS 2012c")]

[Pacific Fishery Management Council. April 2012. Preseason Report III: Council Adopted Management Measures and Environmental Assessment Part 3 for 2012 Ocean Salmon Fishery Regulations. Available at: http://www.pcouncil.org/wp-content/uploads/Preseason_Report_III_2012.pdf]

i. Winter Run Chinook Salmon

In recent years, escapement of winter run Chinook peaked in 2006 (the highest level since 1994), but since then, "*escapement estimates for 2007, 2008, 2009, 2010, and 2011 show a precipitous decline in escapement numbers based on redd counts and carcass counts*." (NMFS 2012a: 20). Brood year 2011 marked the fifth consecutive year of declining juvenile numbers and the fifth consecutive year in which the cohort replacement rate[1] was less than 1, indicating a negative growth rate and declining abundance. (NMFS 2012b: 1, NMFS 2012a: 20-21; *see* Fig. 1-2). The Department of

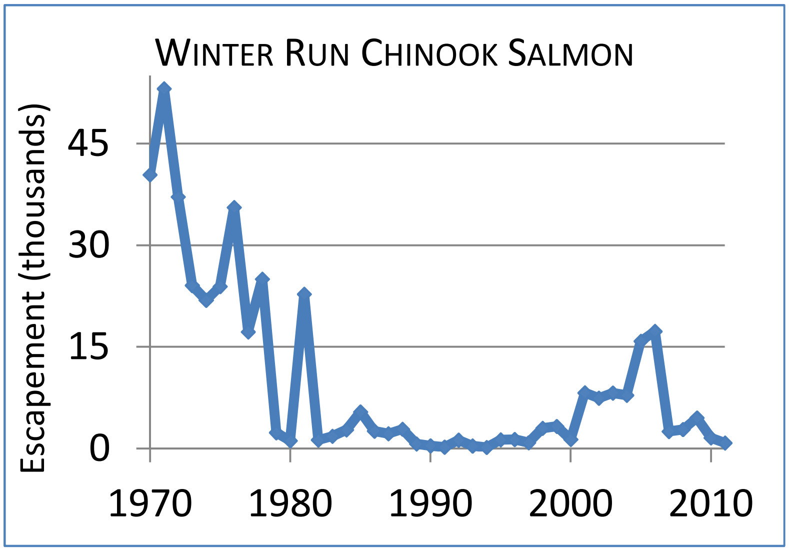

Fig. 1

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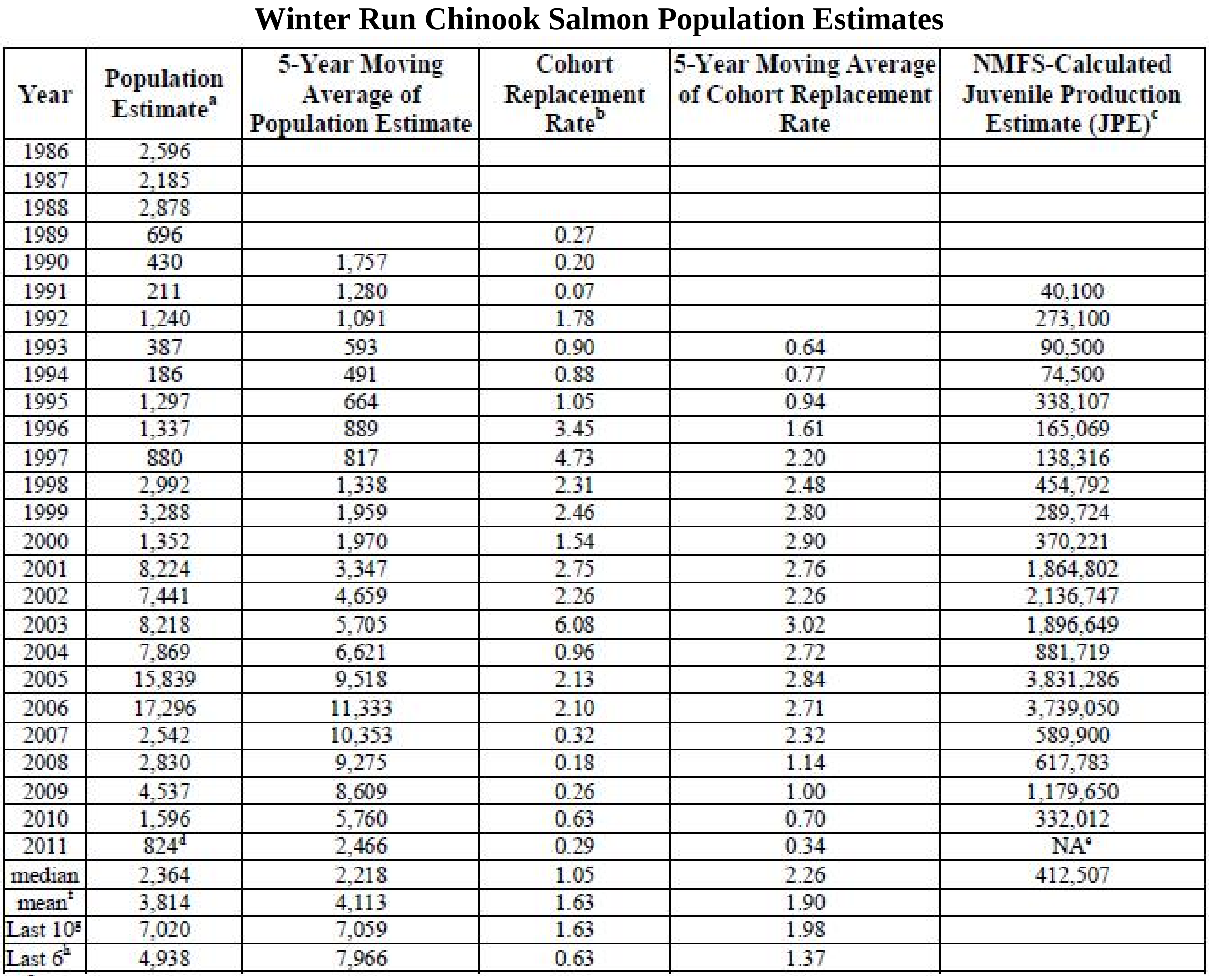
[1] The cohort replacement rate is a measure of whether the population is increasing or decreasing. Because the majority of winter run spawners are three years old, the CRR is estimated by using the current brood year escapement divided by the escapement 3 years prior.

Fish and Game (DFG) estimated that adult winter run escapement in 2011 was only 824 spawners, including fish spawned at the hatchery. (NMFS 2012b: 1) This is the lowest level since 1994.

The National Marine Fisheries Service (NMFS) has suggested that the low 2011 escapement resulted from operations of Shasta Reservoir and dry conditions in 2008. (*See* NMFS 2011a: 20, 29-30). NMFS has also noted that the low abundance in recent years occurred despite the complete closure of the ocean fishery in 2008 and 2009, and very limited fishing season in 2010. (NMFS 2012: 30) Indeed, DFG concluded in a recent report that only 2 winter run Chinook salmon with coded wire tags were caught in the 2010 ocean fishery from brood years 2004, 2005, 2006, 2007, and 2008 (expanded count of 6). (Kormos et al 2012: 6 and Table 7)



Winter Run Chinook Salmon Population Estimates

Year	Population Estimate[a]	5-Year Moving Average of Population Estimate	Cohort Replacement Rate[b]	5-Year Moving Average of Cohort Replacement Rate	NMFS-Calculated Juvenile Production Estimate (JPE)[c]
1986	2,596				
1987	2,185				
1988	2,878				
1989	696		0.27		
1990	430	1,757	0.20		
1991	211	1,280	0.07		40,100
1992	1,240	1,091	1.78		273,100
1993	387	593	0.90	0.64	90,500
1994	186	491	0.88	0.77	74,500
1995	1,297	664	1.05	0.94	338,107
1996	1,337	889	3.45	1.61	165,069
1997	880	817	4.73	2.20	138,316
1998	2,992	1,338	2.31	2.48	454,792
1999	3,288	1,959	2.46	2.80	289,724
2000	1,352	1,970	1.54	2.90	370,221
2001	8,224	3,347	2.75	2.76	1,864,802
2002	7,441	4,659	2.26	2.26	2,136,747
2003	8,218	5,705	6.08	3.02	1,896,649
2004	7,869	6,621	0.96	2.72	881,719
2005	15,839	9,518	2.13	2.84	3,831,286
2006	17,296	11,333	2.10	2.71	3,739,050
2007	2,542	10,353	0.32	2.32	589,900
2008	2,830	9,275	0.18	1.14	617,783
2009	4,537	8,609	0.26	1.00	1,179,650
2010	1,596	5,760	0.63	0.70	332,012
2011	824[d]	2,466	0.29	0.34	NA[e]
median	2,364	2,218	1.05	2.26	412,507
mean[f]	3,814	4,113	1.63	1.90	
Last 10[g]	7,020	7,059	1.63	1.98	
Last 6[h]	4,938	7,966	0.63	1.37	

Figure 2 (reprinted from NMFS 2012a)

In 2010, NMFS issued a new biological opinion on the effect of the ocean salmon fishery on winter run salmon, and new measures to constrain take of winter run in the fishery were imposed. In 2011, NMFS released an analysis of the impacts of the fishery on winter run (O'Farrell 2011, Winship *et al* 2012) and its Winter Run Harvest Model to guide development of fishery measures to constrain impacts. NMFS concluded that ocean fishing is not adversely affecting winter run when populations are stable or increasing, but that measures were needed when the population was otherwise declining or at very low levels. (NMFS 2012c:1-2) The management strategy evaluation and life cycle model that it was based on found that, "*the most influential factors in winter-run population dynamics are related to variation in juvenile survival rates in the fresh water and marine environments (survival prior to age-2).*" (NMFS 2012c: 5) NMFS has also observed that "*Lindley et al. (2009) concluded that late-fall, winter and spring Chinook salmon in the Central Valley were not as strongly affected by recent changes in ocean conditions as the Sacramento River fall-run Chinook salmon*." (NMFS 2011: 30).

Since 2009, entrainment of winter run Chinook has been limited by the NMFS biological opinion, including OMR restrictions and an incidental take limit of entrainment at the CVP and SWP to less than 2% of the Juvenile Production Estimate (JPE). While entrainment has not exceeded this incidental take limit since 2009, incidental take of winter run exceeded 1% of the JPE in 2011. (NMFS 2011c: 50) In its presentation to the independent peer review panel organized by the Delta Science Program, NMFS examined the use of Smolt to Adult Ratios (SAR) to estimate the effect of juvenile incidental take on the abundance of adult winter run three years later, and estimated that the take in 2011 could be expected to reduce adult winter run populations in 3 years by 16-25%. (NMFS 2011d at 23; see Fig. 2)

Analysis of the population level effect of winter run losses at the Central Valley Project (CVP) and State Water Project (SWP) are ongoing.[2] However, in 2012 the independent peer review of the BDCP effects analysis cautioned against simply normalizing salvage to adult populations three years later:

> *A process to normalize observed salvage to mean population abundance of the species was described in order to account for some of the year to year variability in salvage associated with fish abundance.* ***Given the large and variable effect of survival at sea on adult salmon abundance, it seems that normalization of the juvenile salvage data to mean adult salmon abundance could introduce considerable error.*** *Was adult run size lagged back to the appropriate smolt year? Both normalized and non-normalized values of entrainment were provided, which is good.*

[Parker 2012: 41][3] (emphasis added)

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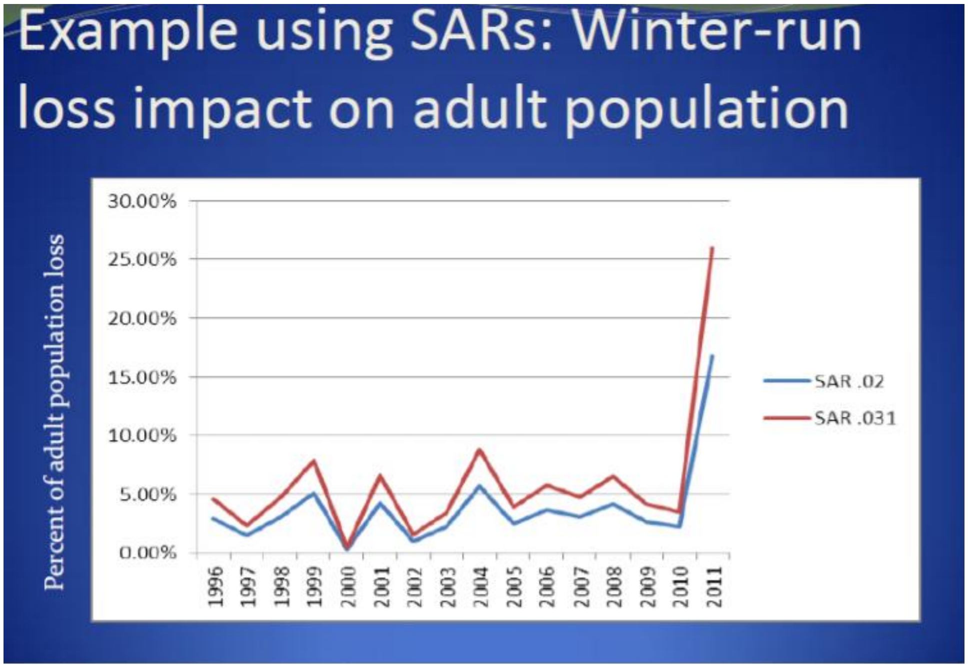
[2] Part of the debate over impacts focuses on the total number of fish impacted because run-identification of salvaged fishes is uncertain and because the number of fish salvaged is unquestionably only a small (though undetermined) fraction of the number of fish that are negatively impacted before they reach the SWP and CVP fish screening facilities.

[3] This peer review of the BDCP effects analysis was cited in the TBI et al submission for Workshop I:
[Parker, A., Simenstad, S., George, T., Monsen, N., Parker, T., Ruggerone, G., and Skalski, J. 2012. Bay Delta Conservation Plan (BDCP) Effects Analysis Phase 2 Partial Review, Review Panel Summary Report. Delta Science Program. Available at: http://deltacouncil.ca.gov/sites/default/files/documents/files/BDCP_Effects_Analysis_Review_Panel_Final_Report_061112.pdf]



Example using SARs: Winter-run loss impact on adult population

Fig. 3 (Reprinted from NMFS 2011c)

Furthermore, there is reason to believe that proportionate impacts of salmon entrainment that are expressed as a proportion of juvenile production would also significantly underestimate the population level effect of entrainment on Chinook salmon populations. DFG and NMFS have not updated the estimated survival to the Delta in the JPE calculation to account for recent acoustic tag data on survival to the Delta. (NMFS 2012b: 7) For instance, recent studies of late fall run Chinook salmon released in 2007-2007 with acoustic tags found that the average survival rate was only 3.9% for the migration from Battle Creek / upper Sacramento River release site to the ocean and that survival from the release site to the Delta was below 40% in all three years and was below 20% in 2007. (Michel 2010: 8 and Fig. 4)[4] Thus current estimates of entrainment at the pumps may substantially underestimate the fraction of the population that is taken, as well as the population level effects of this entrainment.

ii. Spring Run Chinook Salmon

Escapement of spring run Chinook salmon has been declining since 2005 in the Sacramento River basin and in most of the tributaries; since 2006, the cohort replacement rate has been less than 1 (indicating a negative growth rate and declining abundance) in the tributaries, and the CRR has been less than 1 in the basin since 2004. (NMFS 2012a: 26-27; *see* Fig. 4-5) Higher water temperatures and lower flows in 2007-2009 are generally associated with lower salmon abundance and may have contributed to recent declines.

The 2009 biological opinion does not establish an incidental take limit for spring run Chinook salmon based on observed salvage of spring run at the CVP/SWP. There currently is not a juvenile production estimate (JPE) for spring run, and there are difficulties in distinguishing spring and fall run fish in salvage. Currently, NMFS' biological opinion uses estimated salvage

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[4] Michel 2010 is discussed in detail on page 20 of this submission.

of a few releases of late fall run hatchery salmon as surrogates for spring run take. (*See* NMFS 2011b: 51) There are substantial problems with this approach.

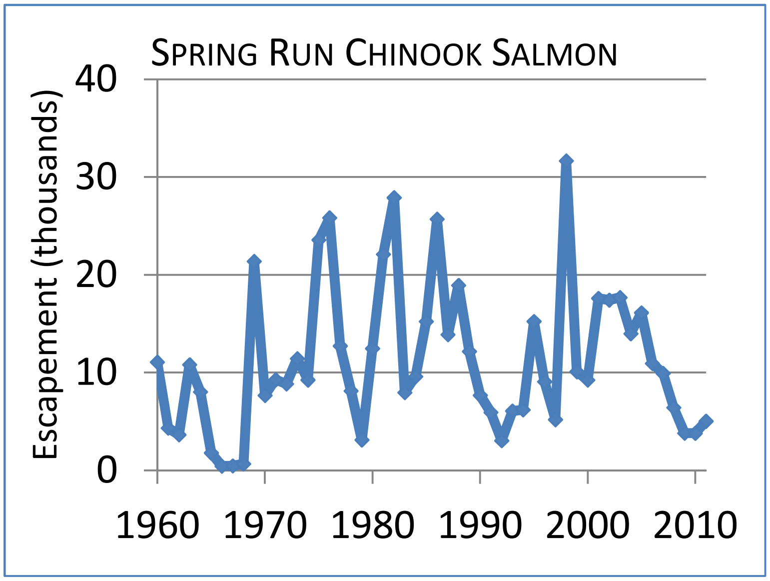
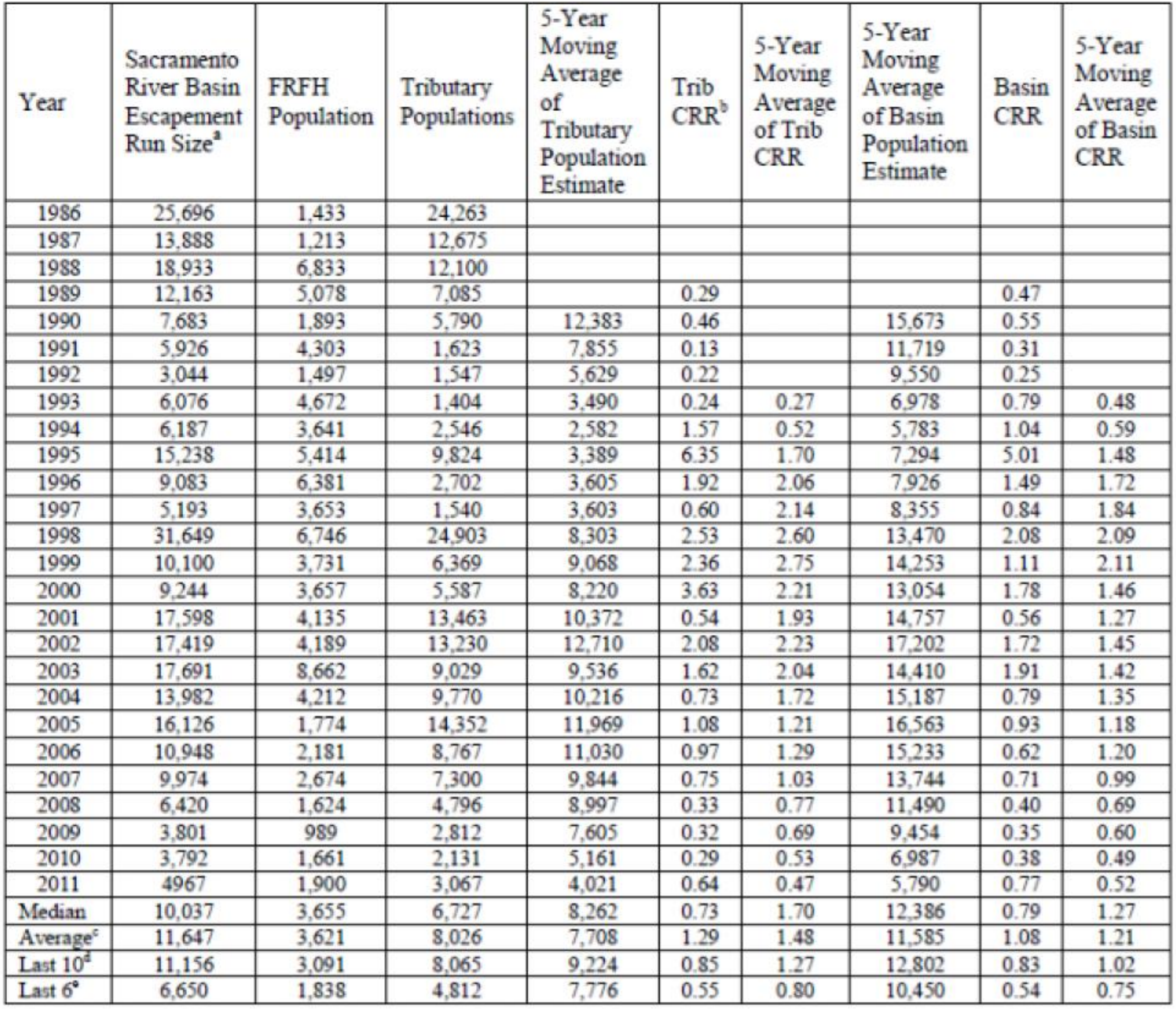


Fig. 4

Population numbers reveal only a part of the spring run's conservation status. Like winter run Chinook salmon, the spring run's geographic spawning range is severely restricted, making this unique species extremely susceptible to geographically isolated catastrophes (e.g. forest fires, mudslides, disease outbreaks). Geographic range restrictions represent a significant threat to fish populations (Rosenfield 2002) and to salmonids, in particular (McElhany et al 2000). Thus, current efforts to restore spawning populations of spring run Chinook salmon to watersheds in the San Joaquin River basin are considered essential to this species' persistence (NMFS 2008) in addition to the need to improve conditions and habitat availability in the Sacramento River basin waterways that support spring run spawning or could support it in the future.

Spring Run Chinook Salmon Abundance Estimates



Year	Sacramento River Basin Escapement Run Size[a]	FRFH Population	Tributary Populations	5-Year Moving Average of Tributary Population Estimate	Trib CRR[b]	5-Year Moving Average of Trib CRR	5-Year Moving Average of Basin Population Estimate	Basin CRR	5-Year Moving Average of Basin CRR
1986	25,696	1,433	24,263						
1987	13,888	1,213	12,675						
1988	18,933	6,833	12,100						
1989	12,163	5,078	7,085		0.29			0.47	
1990	7,683	1,893	5,790	12,383	0.46		15,673	0.55	
1991	5,926	4,303	1,623	7,855	0.13		11,719	0.31	
1992	3,044	1,497	1,547	5,629	0.22		9,550	0.25	
1993	6,076	4,672	1,404	3,490	0.24	0.27	6,978	0.79	0.48
1994	6,187	3,641	2,546	2,582	1.57	0.52	5,783	1.04	0.59
1995	15,238	5,414	9,824	3,389	6.35	1.70	7,294	5.01	1.48
1996	9,083	6,381	2,702	3,605	1.92	2.06	7,926	1.49	1.72
1997	5,193	3,653	1,540	3,603	0.60	2.14	8,355	0.84	1.84
1998	31,649	6,746	24,903	8,303	2.53	2.60	13,470	2.08	2.09
1999	10,100	3,731	6,369	9,068	2.36	2.75	14,253	1.11	2.11
2000	9,244	3,657	5,587	8,220	3.63	2.21	13,054	1.78	1.46
2001	17,598	4,135	13,463	10,372	0.54	1.93	14,757	0.56	1.27
2002	17,419	4,189	13,230	12,710	2.08	2.23	17,202	1.72	1.45
2003	17,691	8,662	9,029	9,536	1.62	2.04	14,410	1.91	1.42
2004	13,982	4,212	9,770	10,216	0.73	1.72	15,187	0.79	1.35
2005	16,126	1,774	14,352	11,969	1.08	1.21	16,563	0.93	1.18
2006	10,948	2,181	8,767	11,030	0.97	1.29	15,233	0.62	1.20
2007	9,974	2,674	7,300	9,844	0.75	1.03	13,744	0.71	0.99
2008	6,420	1,624	4,796	8,997	0.33	0.77	11,490	0.40	0.69
2009	3,801	989	2,812	7,605	0.32	0.69	9,454	0.35	0.60
2010	3,792	1,661	2,131	5,161	0.29	0.53	6,987	0.38	0.49
2011	4967	1,900	3,067	4,021	0.64	0.47	5,790	0.77	0.52
Median	10,037	3,655	6,727	8,262	0.73	1.70	12,386	0.79	1.27
Average[c]	11,647	3,621	8,026	7,708	1.29	1.48	11,585	1.08	1.21
Last 10[d]	11,156	3,091	8,065	9,224	0.85	1.27	12,802	0.83	1.02
Last 6[e]	6,650	1,838	4,812	7,776	0.55	0.80	10,450	0.54	0.75

Fig. 5 (Reprinted from NMFS 2012a)

iii. Central Valley Steelhead

There is currently no abundance estimate for Central Valley steelhead. However, according to NMFS, the available evidence suggests a decline in the population of wild steelhead since 2005:

> *The most recent status review of the California Central Valley steelhead DPS (NMFS 2011c) found that the status of the population appears to have worsened since the 2005 status review (Good et al. 2005), when it was considered to be in danger of extinction. Analysis of data from the Chipps Island monitoring program indicates that natural steelhead production has continued to decline and that hatchery origin fish represent an increasing fraction of the juvenile production in the Central Valley (see Figure 14). Since 1998, all hatchery produced steelhead in the Central Valley have been adipose fin clipped (ad-clipped). Since that time, the trawl data indicates that the proportion of ad-clip steelhead juveniles*

> *captured in the Chipps Island monitoring trawls has increased relative to wild juveniles, indicating a decline in natural production of juvenile steelhead. In recent years, the proportion of hatchery produced juvenile steelhead in the catch has exceeded 90% and in 2010 was 95% of the catch. Because hatchery releases have been fairly consistent through the years, this data suggests that the natural production of steelhead has been declining in the Central Valley*.

(NMFS 2012a: 33) NMFS also found that salvage at the CVP and SWP indicated a decline in natural production, and they found that while small numbers of wild steelhead consistently return to the Coleman fish hatchery (200-300 fish per year), the number of hatchery fish has fluctuated significantly and have declined in recent years. (NMFS 2012a: 33-34)

Entrainment and low survival rates through the Delta remain a concern for steelhead from the San Joaquin River basin, Sacramento River basin, and eastside tributaries. Although there is no population estimates for Central Valley steelhead, the 2009 NMFS biological opinion continues use of an incidental take limit of 3,000 wild steelhead that is not based on a measure of steelhead abundance. (NMFS 2011b at 53-54) Salvage of wild steelhead in 2011 (738) was lower than in 2010 (1,029), with the highest monthly salvage of wild steelhead observed in June 2011. (NMFS 2011b: 54, 68) The seasonal salvage for hatchery steelhead in 2011 was the lowest observed in the past 11 years. (NMFS 2011b: 54)

iv. Fall Run Chinook Salmon

The Pacific Fishery Management Council (PFMC) has forecast that the 2012 Sacramento River Index is 819,400 adult Central Valley Fall run Chinook salmon, with escapement estimated at 245,820 spawners. (PFMC 2012:9-10) This is higher than the SI forecast of 729,900 fish in 2011, but the forecast of escapement in 2011 was substantially higher than actual escapement. (PFMC 2012:9) The PFMC adopted revisions to the fishery management plan until the stock is rebuilt, which includes an annual management target of 122,000 natural and hatchery adult spawners at moderate abundance, and lower fishing rates at low abundance. (PFMC 2012:4).

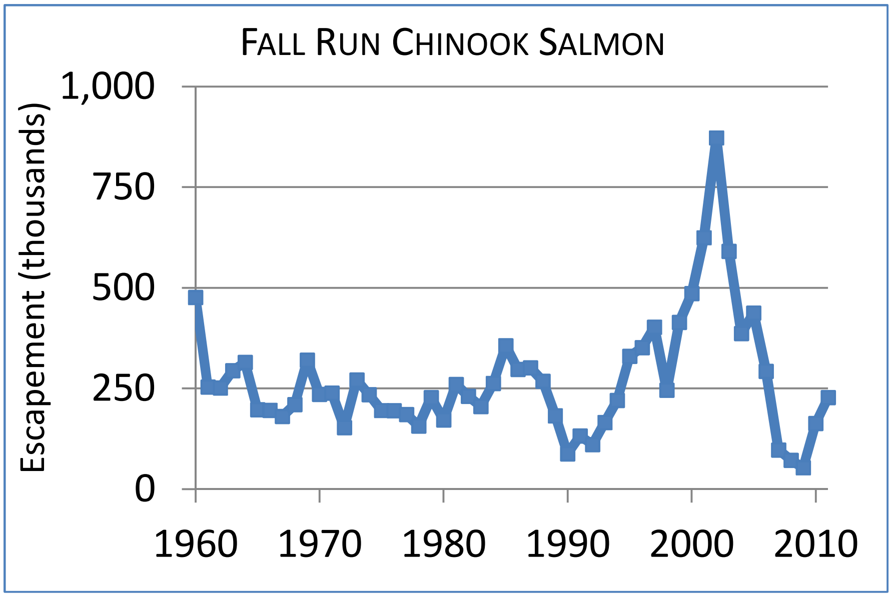


Fig. 6

The Central Valley Constant Fractional Marking Program (CFM) was initiated in 2007 to estimate in a statistically valid manner the relative contribution of hatchery production and to evaluate the various release strategies being employed in the Central Valley. Beginning with Brood

Year 2006 fall run Chinook, the program has marked and coded-wire tagged a minimum of 25 percent of releases from the Central Valley hatcheries each year. In 2012, biologists with the Department of Fish and Game released a report (Kormos et al (2012), *Recovery of Coded-Wire Tags from Chinook Salmon in California's Central Valley Escapement and Ocean Harvest in 2010*) which evaluates the 2010 CV fall, spring, winter and late fall run Chinook CWT recovery data in an attempt to answer the following four questions with this first essentially complete year of recovery data:

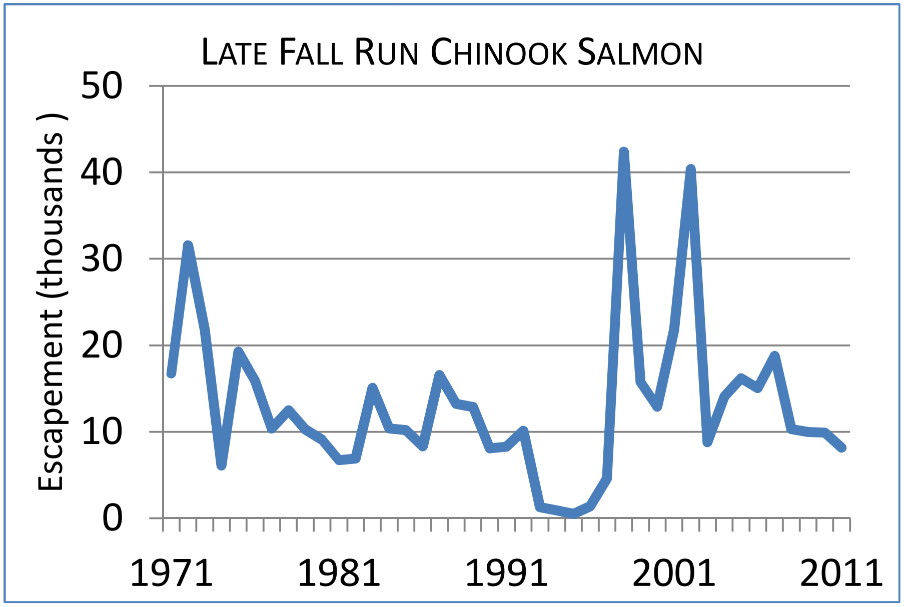


Fig. 7

1. What are the proportions of hatchery and natural-origin fish in spawning returns to CV hatcheries and natural areas, and in ocean harvest? Of the hatchery proportions, what proportions originated from in-basin versus out-of-basin CWT recoveries?
2. What are the relative recovery and stray rates for hatchery fish released in-basin versus salmon trucked to and released into the waters of the Carquinez Straits? The latter includes salmon acclimated in net pens that are pulled for several hours into San Pablo Bay before fish are released.
3. What are the relative recovery rates for fish acclimated in net pens and released in the bay versus salmon released directly into the waters of the Carquinez Straits?
4. What are the relative contribution rates of hatchery fish, by run and release type, to the ocean harvest?

General Recovery rates and age classes
Based on the findings presented in the report, during 2010, almost 27,000 CWTs were recovered from ad-clipped Chinook sampled in Central Valley natural area spawning surveys, at CV hatcheries, in CV river creel surveys, and in California ocean commercial and recreational fisheries. Almost all of the fall run Chinook CWTs recovered in the CV were tagged as part of the CFM program since most CV fish return at ages two, three, or four. Age five Chinook made up a very small fraction (0.01%) of the total CV fall run escapement in 2010.

24,838 valid CWTs recovered in the CV during 2010 were CV Chinook releases, with the majority originated from brood year 2006 through 2008. The specific breakdown of recoveries included more than 84% from fall run Chinook, followed by spring run (10%) and late fall run (6%). No Sacramento River winter run Chinook CWTs were recovered in 2010.

California ocean harvest recoveries in 2010 included 1846 of CV origin. Approximately 62% of all CWTs in the ocean harvest were fall run Chinook, followed by late fall run (30%), spring run (3%), and winter run (<1%). Only 2 winter run with CWTs (for an expanded count of 6) were caught in the ocean fishery in 2010.

Proportion of hatchery origin fish
Results indicate that the proportion of hatchery-origin fish on spawning grounds varied throughout the CV and by run. The lowest hatchery proportion (1%) was observed in the Butte Creek spring run Chinook mark-recapture survey, while the highest proportion (78%) was observed in the Feather River fall/spring run Chinook mark-recapture survey. The hatchery proportion of fall run Chinook returning to CV hatcheries ranged from 79% to 95%. Spring run Chinook return to FRH was 82% hatchery-origin fish whereas the late fall run return to CNFH approached 100% hatchery-origin. The majority of fish returning to spawn in the San Joaquin Basin and the Feather River were hatchery-origin, whereas the majority of fish returning to spawn in the Sacramento River were not.

Relative recovery and stray proportions for hatchery-origin Chinook released in-basin versus hatchery-origin Chinook trucked and released into the waters of the Carquinez Strait (includes Chinook salmon acclimated in net pens and released into San Pablo Bay).
Results on relative recovery and stray proportions of in basin vs. trucked and released hatchery-origin fish were limited due to “lack of consistency” and “problem releases” among CV hatcheries. As a result, the report only presents results from direct comparisons for in a limited number of release groups. Overall results indicate that, Chinook that were trucked and released directly into the waters of Carquinez Strait or acclimated in bay area net pens had higher relative recovery rates than their respective in-basin releases (often at a 2:1 ratio or more). These releases also had higher stray proportions than their paired in-basin counterparts.

Though based only on a single year of recovery data, and so not necessarily indicative of larger scale trends in population dynamics, results from this report reinforce other research findings pointing to a) the severe impact of low juvenile outmigration survival rates on subsequent abundance, b) the increase in straying resulting from the alternative strategy of ocean release, c) the severely imperiled condition of winter run stocks and need for immediate action to recover them, d) the dominance of hatchery origin returns in the CV. This program should provide very useful information to managers in the future.

B. IMPORTANCE OF SACRAMENTO INFLOWS INTO THE DELTA

The magnitude, timing, duration, and frequency of Delta inflows[5] from source streams has changed dramatically from historical condition, particularly during the winter and early spring months. These reductions in flow have diminished the Delta's ability to support the viability of anadromous resources that rely on the Delta for food, habitat and migration.

1. The importance of a natural flow regime

New Information Summary:

Flow is a critical determinant of native fish success. Altered flow regimes, due to water management facilities and operation, are a significant cause of native fish declines. In addition, altered flow regimes are a significant predictor of spring run Chinook extirpation.

> [Nislow, K. H. and J. D. Armstrong. 2011. Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. Fisheries Management and Ecology. DOI: 10.1111/j.1365-2400.2011.00810.x]

Nislow and Armstrong review the state of science concerning the influence of flow regime on juvenile salmonids and their habitats. Their findings indicate that a key consideration in the stage-specific impacts of flow is the extent to which flow-related losses or gains during early developmental stages can be compensated by increased growth or survival later in juvenile life history. Their recommendations include targeting specific aspects of flow regimes critical to multiple life-history stages, which can then serve as a basis for interim flow prescriptions and subsequent adaptive management. Findings from their assessment point not only to the importance of flow as a critical determinant of juvenile salmon success, but to the need for a management approach that integrates flow management in the upper and lower watershed as well as other factors promoting increased growth and survival access to productive floodplain habitat.

> [Zeug, S.C. 2010. Predictors of Chinook Salmon Extirpation in California's Central Valley. Fisheries Management and Ecology 18: 61-71.]

Zeug 2010 examined the relative strength of predictors for probability of extirpation of Chinook salmon in Central Valley streams and found that altered flow regime, habitat loss, and migration barriers were all significant predictors for extirpation of spring run Chinook salmon.

> [Mount, J., W. Bennett, J. Durand, W. Fleenor, E. Hanak, J. Lund, and P. Moyle. 2012. Aquatic Ecosystem Stressors in the Sacramento–San Joaquin Delta. Public Policy Institute of California, San Francisco, CA. 24p. Available at: http://www.ppic.org/content/pubs/report/R_612JMR.pdf]

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[5] Because San Joaquin River inflows are being addressed in another Board proceeding, this submission focuses primarily on Sacramento River inflows.

This report synthesizes the stressors acting on the Delta into five key categories of like process and consequence relevant to management and decision-making:

> 1. ***Discharges****: Land and water use activities that directly alter water quality in the greater Delta watershed by discharging various contaminants that degrade habitat, disrupt food webs, or cause direct harm to populations of native species.*
> 2. ***Fisheries management****: Policies and activities that adversely affect populations of native species through harvest (commercial and sport) or hatcheries.*
> 3. ***Flow regime change****: Alterations in flow characteristics due to water management facilities and operations, including volume, timing, hydraulics, sediment load, and temperatures.*
> 4. ***Invasive species:*** *Alien (non-native) species that negatively affect native species by disrupting food webs, altering ecosystem function, introducing disease, or displacing native species.*
> 5. ***Physical habitat alteration****: Land use activities that alter or eliminate physical habitat necessary to support native species, including upland, floodplain, riparian, open water/channel, and tidal marsh. (p. 8)*

Additionally, the report explains that none of these stressors is entirely independent of the others, with significant interactions amplifying or suppressing the negative effects each has on native populations. As an example, Mount et al 2012 points to water operations that reduce flow intensifying the effects of agricultural and urban discharges that, in turn, promote conditions favorable to invasive species that alter food webs and ecosystem functions.

> [Moyle, P., W. Bennett, J. Durand, W. Fleenor, B. Gray, E. Hanak, J. Lund, and J. Mount. 2012. Where the Wild Things Aren't: Making the Delta a Better Place for Native Species. Public Policy Institute of California, San Francisco, CA. 55p. Available at: http://www.ppic.org/content/pubs/report/R_612PMR.pdf]

Moyle et al 2012 attributes harm to native species living in or passing through the Delta as well as the degradation of water quality and habitat to key stressors working singly and in combination. These stressors include alteration of flows, channelization of waterways, discharge of pollutants, introduction of non-native species, and the diversions of water from the system. Their analysis identifies five core premises that have strong scientific support including that the most restrictive physical and biological constraints on the system include limits on the availability of fresh water, and the domination of the ecosystem by invasive species. The report recommends five key components of a strategy for recovery and reoperation of the delta, the first of which is that natural processes place limits on all water and land management goals.

> [Miller, J.A., A. Gray, and J. Merz. 2010. Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. Marine Ecology Progress Series 408:227–240].

This study documented contributions of three different life-history types to subsequent adult populations but noted that management activity is often disproportionately focused on particular life history strategies (e.g. big or fast-growing juveniles). They note:

> *The contribution of all 3 migratory phenotypes to the adult population indicates that management and recovery efforts should focus on maintenance of life-history variation rather than the promotion of a particular phenotype.* (Miller et al. 2012: 227).

This finding reinforces the need to identify the full seasonal duration of flows that benefit different fish species as flows constrained to narrow durations and particular calendar dates tend to reduce migratory species' viability by eroding natural life history diversity (McElhaney 2000). Miller et al (2010) is also quite valuable in that it demonstrates the potential to measure the differential migration success of various life-history types post-hoc, using advances in otolith microchemistry; such an approach, when combined with current tagging and recapture studies should be expanded to provide a more comprehensive and accurate image of juvenile survival patterns prior to, during, and after their Delta migration.

2. Sacramento River inflow targets and Delta outflow targets can be achieved without compromising the ability of the reservoirs to meet existing upstream temperature and flow requirements

New Information Summary:

Water temperature plays a critical role in the life history of native fishes, particularly salmonids. Water temperature requirements vary substantially by life stage and actual water temperatures vary significantly both temporally and spatially. Furthermore, temperature requirements for individual life stages can vary depending on habitat quality, nutrition, and antecedent conditions. Healthy fish with a variety of habitat options are more likely to survive stressful temperatures than unhealthy fish.

The State Water Board's 2010 Report notes that additional analysis and modeling will be needed to determine how best to apply the percentage of unimpaired to allow Sacramento inflow requirements to be met while ensuring cold water temperature protections for fish in upstream tributaries at key times of the year. The 2010 Delta Flows Report also recognizes that inflow requirements should be proportionally allocated among the mainstem Sacramento and San Joaquin Rivers and their key tributaries. A proportional allocation of releases to meet downstream criteria among all source streams is necessary to ensure the flow-related connectivity between the upstream and Delta that is necessary for migratory species to complete their life cycles. A disproportionate allocation can lead to adverse flow and temperature conditions below facilities that are disproportionately responsible for meeting the criteria.

Increasing Delta outflow need not come at the expense of upstream reservoir storage, as recent modeling has demonstrated. We strongly recommend that that State Water Board build on the CALSIM modeling done in development of BDCP Alternative 8 to ensure adequate upstream cold water pool protections. As the State Water Board is well aware, one of the significant limitations of the CALSIM model is that it is difficult to model reservoir carryover requirements in the model and the model is driven to maximize CVP/SWP exports within available constraints. As discussed at the September 6, 2012 workshop, recent modeling that purports to show that increasing delta outflow will necessarily reduce upstream storage does not incorporate existing reservoir storage criteria, and it may assume continued levels of diversions that drive reservoir storage lower. CALSIM modeling of Alternative 8 in the BDCP process, which seeks to increase Delta outflow per the SWRCB's request, has demonstrated that increased Delta outflow can be accomplished without impairing upstream reservoir storage. The approach to modeling Alternative 8 in CALSIM should be further refined, in consultation with the fish and wildlife agencies, to take account of minimum releases needed to meet downstream temperature compliance points in the spring and summer months, and this revised modeling analysis should be applied to a broader range of alternative outflow objectives in this proceeding.

> [National Marine Fisheries Service. 2009. Biological Opinion on proposed long term operations of the Central valley Project and State Water Project. Available at: http://www.swr.noaa.gov/ocap/NMFS_Biological_and_Conference_Opinion_on_the_Long-Term_Operations_of_the_CVP_and_SWP.pdf]

The 2009 NMFS biological opinion (pp. 592-603) imposes reservoir carryover storage and release requirements on Shasta Reservoir for the protection of winter and spring run Chinook salmon. This biological opinion establishes performance measures that require a minimum of 2.2 million acre feet (MAF) of storage in Shasta Reservoir at the end of September in 87% of years, with end of April storage of 3.8 MAF in 82% of years, and end of September storage of 3.2 MAF in 40% of years. (NMFS 2009: 592) In years when end of September storage falls below these targets, the biological opinion establishes decision-making processes to establish reservoir release schedules for fall, spring and summer months. (NMFS 2009: 592-603)

The amount of cold water storage at the end of September limits the geographic extent of suitable spawning habitat for salmon in the Sacramento River (known as the temperature compliance point), and 2.2 MAF of storage at the end of September is generally necessary to provide sufficient cold water to establish the temperature compliance point at Balls Ferry of the following year in 80% of years.[6] (NMFS 2009: 593) The biological opinion establishes the following performance standards relating to the temperature compliance point:

- Meet Clear Creek Compliance point 95 percent of time
- Meet Balls Ferry Compliance point 85 percent of time
- Meet Jelly's Ferry Compliance point 40 percent of time
- Meet Bend Bridge Compliance point 15 percent of time

(NMFS 2009: 592)[7]

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[6] Balls Ferry is located approximately 23 miles upstream from the Red Bluff Diversion Dam. In Water Rights Order 90-5, the Board required the Bureau to maintain water temperatures below 56° F in the Sacramento River at Red Bluff Diversion Dam, except when factors beyond the control of the Bureau prevented meeting this temperature requirement. In recent years the temperature compliance point has been established at Balls Ferry or further upstream. (NMFS 2009 at 263)

[7] In its written summary submission to the State Water Board during the 2010 proceeding, NMFS provided a brief summary of storage objectives for Shasta Reservoir to protect listed salmon. Available online at: http://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/deltaflow/docs/exhibits/nmfs/nmfs_summary.pdf

The 2010 Public Trust Report briefly mentioned these requirements of the 2009 biological opinion and acknowledged that these reservoir storage requirements were (1) the minimum necessary to avoid jeopardy and were (2) constrained by water deliveries to senior water rights holders:

> *It is important to note that the flow protections described in the project description and RPA are the minimum flows necessary to avoid jeopardy. In addition, NMFS considered provision of water to senior water rights holders to be non-discretionary for purposes of the ESA as it applies to Section 7 consultation with the USBR, which constrained development of RPA Shasta storage actions and flow schedules.*

(SWRCB 2010: 23-24) (internal citations omitted)

The 2009 NMFS biological opinion also establishes minimum flow schedules and the following minimum temperature requirements:

River	Requirements	Reference
Clear Creek	60°F or lower at Igo gauge from June 1 to Sept 15 56°F or lower at Igo gauge from Sept 15 to Oct 31	Page 589
American River	65°F or lower at Watt Avenue Bridge from May 15 through October 31	Page 614
Stanislaus River	56°F or lower at Orange Blossom Bridge from 10/1 – 12/31 52°F or lower at Knights Landing and 56°F or lower at Orange Blossom Bridge from 1/1 – 5/31 55°F or lower at Orange Blossom Bridge from 1/1-5/31 65°F or lower at Orange Blossom Bridge from 6/1-9/30	Page 621

In addition, the biological opinion notes that non-flow measures can contribute to meeting these downstream water temperature requirements, including temperature control devices, temperature curtains, and other structural and operational modifications. (*See, e.g.*, NMFS 2009: 615-16)

However, it should be noted that these protections are principally designed to protect endangered and threatened runs; while these performance measures provide some protection for fall run Chinook salmon (which is not listed under the ESA), additional reservoir storage and downstream temperature requirements later in the year (October) should be considered to adequately protect fall run Chinook salmon in light of their different spawning and migration timing.

3. Relationship of increased flows to salmonid survival and migration

New Information Summary:

Several factors associated with increased flows influence salmonid migration rate and survival. In recent studies, migration rates of juvenile salmon were found to be fastest in the upper river region and slowest in the Delta. Additionally, survival of salmonid smolts migrating through the Sacramento River and through the Delta is extremely low, and a substantial number of the losses in the Delta can be attributed to the effects of the CVP and SWP operations.

> [Michel, C.J., A.J. Ammann, E.D. Chapman, P.T. Sandstrom, H.E. Fish, M.J. Thomas, G.P. Singer, S.T. Lindley, A.P. Klimley and R.B. MacFarlane. 2012. The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*). Environmental Biology of Fishes. DOI: 10.1007/s10641-012-9990-8]

Michel et al (2012) examined the migration patterns of acoustically tagged late fall run Chinook salmon yearling smolts during their outmigration through California's Sacramento River and San Francisco Estuary in 2007–2009. Migration rates (14.3 km·day^{-1} (± 1.3 S.E.) to 23.5 km·day^{-1} (± 3.6 S.E.)) were similar to rates published for other West Coast yearling Chinook salmon smolt emigrations. Migration rates were fastest through the upper river regions, and slowest in the Delta. Additionally, the study modeled the influence of different reach specific and environmental factors on movement rate and population spreading. Results suggested that several factors associated with increased flows positively influenced migration rate including (in order of importance), river width to depth ratio, river flow, water turbidity, river flow to mean river flow ratio, and water velocity. Water temperature did not improve model fit, suggesting, among other things, the specific significance of flow as opposed to temperature in fish distribution and migration.

> [Michel, C. River and Estuarine Survival and Migration of Yearling Sacramento River Chinook Salmon (*Oncorhynchus Tshawytscha*) Smolts and the Influence of Environment. A thesis submitted in partial satisfaction of the requirements for the degree of Master of Arts in Ecology and Evolutionary Biology. December 2010.]

In this thesis, Michel summarized the results of three years of acoustic tagging results on salmon survival and migration rates. Michel (2010) concluded that the average survival rate for late fall run Chinook salmon released in 2007-2007 with acoustic tags was only 3.9% for the migration from Battle Creek / upper Sacramento River release site to the ocean and that survival from the release site to the Delta was below 40% in all three years and was below 20% in 2007. (Michel 2010 at 8 and Fig. 4). As the author notes, these three years were generally dry years with lower flows, so results may be different in higher flow years.

> [del Rosario, R. B., Y. J. Redler, and P. Brandes. 2010. Residence of Winter-Run Chinook Salmon in the Sacramento-San Joaquin Delta: The role of Sacramento River hydrology in driving juvenile abundance and migration patterns in the Delta. Abstract submitted to the CalNeva conference (manuscript in preparation). Available at: http://www.waterboards.ca.gov/waterrights/water_issues/programs/bay_delta/deltaflow/docs/exhibits/nmfs/nmfs_exh7.pdf]

This study found that Sacramento River flow at Freeport was a statistically significant predictor of the abundance of winter run Chinook salmon caught at Chipps Island, with higher flow during the migration period corresponding to higher abundance. Abundance of juveniles in the Chipps Island trawl was not found to be correlated with prior year's adult escapement in a statistically significant way:

> *The hydrology of the Sacramento River drives winter-run smolt abundance and emigration patterns in the Delta. The annual cumulative winter run smolt abundance is highly dependent on the amount of flows in the Sacramento River, such that higher volume of water flowing in the river during the winter run emigration period results in greater abundance of winter run smolts both entering the Delta at Knights Landing (multiple regression, R2=0.76, F=12.6, p=0.003), and subsequently exiting the Delta at Chipps Island (multiple regression, R2=0.93, F=53.7, p<0.0001; Figure 1). This positive correlation between smolt abundance, expressed as annual cumulative CPUE at either sampling location, is not significantly correlated with annual spawner abundance (p>0.25).*

(del Rosario et al 2010: 4) Thus increased Sacramento River inflow resulted in higher survival rates for winter run salmon.

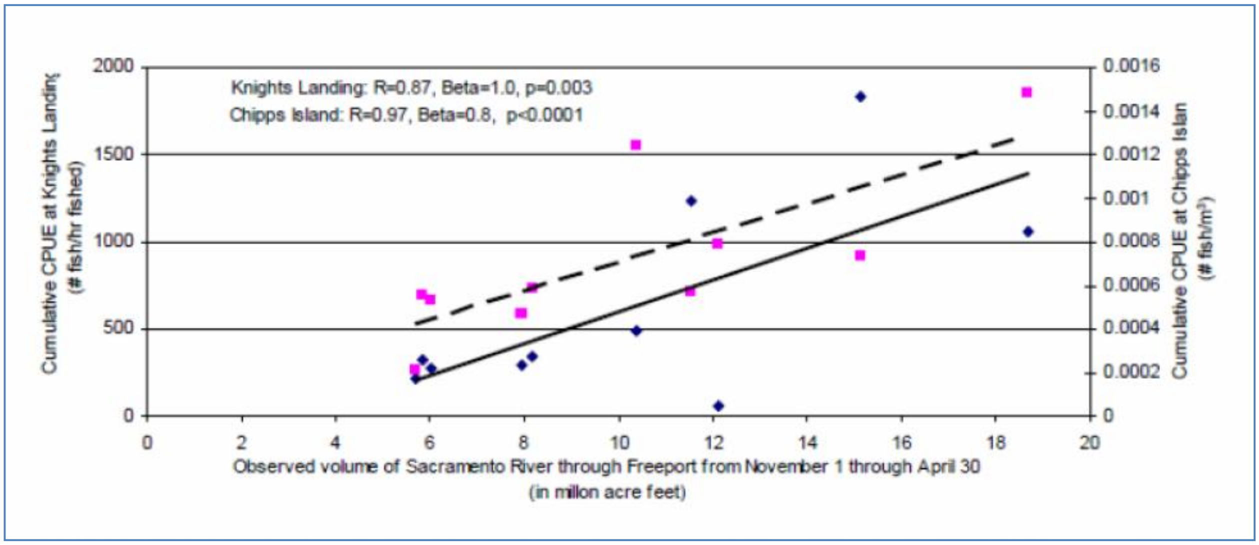

Fig. 8 Higher volume of flows during the winter run migration period results in greater abundance of winter run smolts entering the Delta at Knights Landing (diamonds, solid line) and subsequently exiting at Chipps Island (squares, dashed line), 1999-2008. (Reprinted from del Rosario et al 2010)

4. Importance of Inflow to Floodplains

Flood flows are essential for maintaining complex channel and floodplain features and, by inundating floodplains, provide essential spawning and rearing habitat for native fish. Pulse flows flush nutrients from inundated floodplains and create turbid habitat in the Delta improving growth and survival for native Delta species.

It is well established that juvenile Chinook salmon have faster growth rates on floodplains than in main-stem river channels (Sommer et al., 2001; Jeffres et al., 2008). Juvenile Chinook can enter and rear on floodplains during their downstream migration. Faster growth rates result in juveniles that are larger and have a higher likelihood of survival to adulthood. Although floodplain inundation provides important ecological benefits for salmon and the Delta generally, floodplain flows are relatively rare events along the Sacramento River due to levees and hydrologic alteration by dam. Loss of floodplain habitat has facilitated a less dynamic environment and one that is conducive to alien species that compete with juvenile salmon for prey in the limited habitat they do have or predate upon them. Due to the fact that many of these alien species are not capable of capitalizing on ephemeral floodplain inundation, the creation of additional floodplain habitat will serve the dual role of leveraging the evolutionary adaptations of central valley salmon to take advantage of the productivity of the flood pulse and reduce the concentration of predators and competitors in the existing habitat.

New Information Summary:

Information developed since 2010 reinforces the diverse benefits to salmonids of increased flows coupled with increased floodplain inundation and habitat availability. Specifically, new information emphasizes that juvenile salmon experience enhanced growth rates while utilizing floodplain habitat. Enhanced juvenile growth rates are correlated with higher juvenile survival rates. In addition, new information stresses the importance of floodplain habitat to combat the effects of climate change. (*See* climate change analysis below).

> [J. Katz. 2012. The Knaggs Ranch Experimental Agricultural Floodplain Pilot Study 2011-2012, Year One Overview. Available at http://baydeltaconservationplan.com/Libraries/Dynamic_Document_Library/YBFE_Planning_Team_%E2%80%93_Knaggs_Ranch_Pilot_Project_Year_One_Overview_6-13-12.sflb.ashx]

The Knaggs Ranch is a cooperative project between U.C. Davis and the Department of Water Resources (and supported by various other agencies, landowners and organizations) that proposes to incrementally develop a flood-neutral management approach in the Yolo Bypass that will benefit agriculture, fish, and waterfowl. The Pilot Study was initiated to evaluate growth of juvenile Chinook salmon in flooded agricultural fields. The main result of the study, high juvenile salmon growth rates while utilizing floodplain habitat, reinforces existing literature that indicates juveniles experience faster growth rates on floodplains. The report states:

> "*The remarkable growth rates and condition of juvenile Chinook reared on the Knaggs experimental agricultural floodplain illustrate the potential for managing seasonally inundated habitat for Chinook salmon. Managed agricultural floodplain habitat appears to produce bio-energetically favorable rearing conditions, when compared to conditions in the Sacramento River. Our initial results provide strong evidence that juvenile Chinook permitted to access seasonally inundated floodplain on Yolo By-pass experience 1) more rapid growth, 2) substantially improved body condition, 3) delayed out-migration timing, and 4) a superior out-migration route. These floodplain benefits will results in higher quality out-migrants and likely improved rates of return. It is our conclusion that gaining access to floodplain rearing for millions of naturally produced fish is the first step in re-establishing self-sustaining stocks of Chinook salmon in the Central Valley.*" (p.10)

> [Nislow, K. H. and J. D. Armstrong. 2011. Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. Fisheries Management and Ecology. DOI: 10.1111/j.1365-2400.2011.00810.x]

See Nislow 2011 summary above finding that there is need for a management approach that integrates flow management in the upper and lower watershed as well as other factors promoting increased growth, survival and access to productive floodplain habitat.

5. Importance of Inflow to Maintain Flow Corridors

As noted above, anadromous fish utilize the Delta for a number of critical functions including migrating (both upstream as adults and downstream as juveniles). Therefore, Delta inflow requirements must be sufficient to provide contiguous habitat between the upstream tributaries and the Delta. The State Water Board should consider whether its flow requirements will protect upmigrating adults coming into the Bay Delta Estuary in addition to helping juveniles migrate from their natal streams through the Estuary to the ocean. The State Water Board's 2010 Report identified the absence of a migratory corridor for returning adult salmon as an issue requiring attention.

New Information Summary:

Flow measures should be considered that both assist juveniles in route through the estuary and adults upmigrating through the Delta. Recent information notes that regulatory processes to date have not considered measures specific to assisting adult upmigration.

> [Environmental Protection Agency. August 2012. Water Quality Challenges in the San Francisco Bay/Sacramento-San Joaquin Delta Estuary, EPA's Action Plan. Available at: http://www.epa.gov/sfbay-delta/pdfs/EPA-bayareaactionplan.]

> [Environmental Protection Agency. February 2011. Water Quality Challenges in the San Francisco Bay/Sacramento-San Joaquin Delta Estuary, Unabridged Advance Notice of Proposed Rulemaking. Available at: http://www.epa.gov/sfbay-delta/pdfs/BayDeltaANPR-fr_unabridged.pdf]

In August 2012, after releasing its advanced notice of proposed rulemaking (ANPR) in February 2011, the United States Environmental Protection Agency (EPA) released its "Action Plan" for the Delta after assessing the effectiveness of current regulatory mechanisms in place to protect water quality in the Delta. Generally, EPA concludes that "…*Clean Water Act (CWA) programs currently are not adequately protecting aquatic resources of the Bay Delta Estuary*." The Action Plan proceeds to recommend various actions to address water quality concerns in the Delta.

Appendix 1 of the Action Plan specifically identifies the issue of fragmented fish migration corridors in the Delta. The Plan notes:

> *"Migratory fish rely on diverse habitats during different life stages and they require appropriate cues and connections to guide them to those habitats. Juvenile salmon use flow as the primary cue to maneuver from their spawning grounds through the rivers to the estuary. Salinity gradients and tidal action can then guide them to the ocean. Adult fish follow the unique chemical signature of their natal stream, although straying is common. Along these migratory paths, contaminants, high temperatures, low dissolved oxygen, physical barriers, and predators may interfere with migratory success. Thus, salmon management requires a watershed approach to ensure a connected and unblocked migratory corridor."* (EPA 2012: 26)

The EPA Plan notes that regulatory response to date has focused on helping juveniles make it through the estuary and to the ocean. Little attention has been paid to measures that may aid adults upmigrating through the Delta to their natal streams. The EPA notes:

> *"Migratory passage along the San Joaquin River is a beneficial use that may not be adequately protected. Outmigrating juveniles have some protection; adults migrating back to their natal streams have little protection. The absence of migratory cues for returning adult San Joaquin fish has not been comprehensively addressed in a regulatory framework.*
>
> *Although critical, the remediation of temperature and dissolved oxygen alone is unlikely to restore depleted salmon stocks unless water from the San Joaquin River and its tributaries supports a migratory corridor to and from the Estuary during both the season of adult upmigration and young outmigration."* (p.27)

Similarly, in the February 2011 ANPR, EPA found that,

> *Retrospective analysis of earlier sonic tagging data found significant impairment of adult salmon migration to San Joaquin tributaries when total state and federal exports exceeded three times the volume of water entering from the San Joaquin River at Vernalis."* (p. 58) (internal footnotes omitted)

The EPA analysis focuses on the San Joaquin River but clearly states that the problem is one that is central to the comprehensive Delta plan proceedings.

> "*EPA supports the work of the SWRCB to establish objectives for the San Joaquin River and the Delta that result in conditions which establish a migratory corridor for both juvenile and adult salmon*." (p.28**)**

The EPA urges the State Water Board to be mindful of the evolving science related to migratory corridors in the Delta such as sonic tagging studies.

In its BDCP Red Flag comments cited above, DFG echoed concerns about San Joaquin flows and Delta hydrodynamics during the adult migratory period:

> *The continuation of zero and [negative] SJR flows at Antioch is not protective of San Joaquin Basin fish. While the PP_ELT and PP_LLT [modeling of effects of the proposed project in the early and late long term periods] show an increase in OMR and SJR flows due to a reduction in south Delta exports, the continuation of low flows in August and September followed by 0 cfs in October and November and [negative] 2000 cfs in December is not protective. Positive SJR flows during this time are important and necessary to cue upstream adult migration, reduce straying, and to help address water quality concerns (e.g., DO and temperature).* (p.4)

C. DELTA HYDRODYNAMICS & SALMON SURVIVAL

New Information Summary:

Substantial research is underway to examine the effects of CVP/SWP exports, river flows, DCC gate operations, and other factors on the survival of salmon and steelhead through the Delta (and in upstream reaches). While data from 2006-2010 have been analyzed and published, results of studies and monitoring associated with operations in 2011 (a wet year with positive OMR for part of the spring) and 2012 (a below normal year with the Head of Old River Barrier (HORB) installed) are not yet available. However, recent studies continue to show very low survival rates through the Delta and show that current protections in D-1641 are inadequate to protect migrating salmonids.

> [Perry, R. W., P. L. Brandes, J. R. Burau, A. P. Klimley, B. MacFarlane, C. Michel, and J. R. Skalski. 2012. *Sensitivity of survival to migration routes used by juvenile Chinook salmon to negotiate the Sacramento-San Joaquin River Delta*. Environ. Biol. Fish. DOI 10.1007/s10641-012-9984-6]

In order to evaluate the relative benefit of management approaches that alter survival rates versus diverting fish away from low-survival routes and towards high-survival routes, Perry et al 2012 examine a 3-year data set of route-specific survival and movement of juvenile Chinook salmon in the Sacramento-San Joaquin Delta to quantify the sensitivity of survival to changes in migration routing at two major river junctions in the Sacramento River. Their results indicate that management actions that influence only migration routing were less effective at creating increased survival than actions that altered both migration routing and route-specific survival. They observed significant variation in survival rates among fish released between 2006 and 2009, with survival rates of less than 50% in every year except for the January 2007 release:

> *Although rankings of route-specific survival vary somewhat across release groups, one pattern remained consistent: survival probabilities for the Sacramento River were always greater than survival for migration routes through the interior Delta (via Georgiana Slough and the Delta Cross Channel; Fig. 3). (Perry et al 2012:7)*

The authors concluded that because overall survival rates are low in all routes, increasing survival through the Delta "*would require management actions that affect not only migration* *routing, but also survival within migration routes*." (p. 9) The authors also noted several limitations of this study. For instance, their analysis assumed that management actions only alter migration routing but not route-specific survival; however, as they note, changes in flow has been observed to change route-specific survival, and changes in the abundance of salmon in each route may change survival from predation. (p. 11) As a result, the authors cautioned that, "*absolute changes in survival should be interpreted with caution*," but relative changes in survival between routes should provide stronger information for managers. (p. 11) Finally, because physical barriers change flow levels as well as migration routing, and nonphysical barriers only change migration routing, the authors caution that,

> *under the assumption of constant route-specific survival, non-physical barriers would realize only a fraction of the maximum possible increase in population survival. With respect to route-specific survival, physical barriers may yield a larger change in survival than non-physical barriers because physical barriers alter discharge and hydrodynamics of each migration route.*

(Perry et al 2012:11-12)

> [Singer, G., A. R. Hearn, E. D. Chapman, M. L. Peterson, P. E. LaCivita, W. N. Brostoff, A. Bremner, and A. P. Klimley. 2012. *Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (Oncorhynchus tshawytscha) and steelhead trout (Oncorhynchus mykiss).* Environ Biol Fish DOI 10.1007/s10641-012-0037-y]

This paper presents results from studies of migratory survival of salmon and steelhead that were released in 2009 and 2010 with acoustic tags. The DCC gates remained closed during the releases in both years, and the study did not evaluate the effects of flow or exports on survival. The authors calculated route specific survival rates and the proportion of fish using each route, in order to estimate the proportion of fish surviving the migration through the Delta using each route. The authors observed that, "*Although overall migratory success to the Golden Gate was similar between 2009 and 2010, reach specific success was very different between years*." (p. 9) Overall survival from Elkhorn Landing (near Sacramento) to the Golden Gate Bridge was estimated as follows for each year and species:

	2009	2010
Salmon	19.2%	23.6%
Steelhead	14.6%	13.8%

(p. 9) However, as compared to 2009, in 2010 survival was lower through the Delta but higher through San Francisco Bay. (pp. 9-10) With respect to survival through the Delta, the authors noted that,

> *Success for both species in the Delta was above 60 % in 2009, yet dropped to below 45 % in 2010. Conversely, successful migration through San Francisco Bay was only around 50 % in 2009, yet increased to over 75 % in 2010. This apparent reversal in the relative success rates (which might be assumed to reflect mortality) may be counterintuitive, given that flows were higher in 2010, and*

> *increased flows are often associated with increased survival (Sims and Ossiander 1981). Survival of salmonid smolts in the Delta is positively correlated (r=0.95) with volume of flow and that the survival rate changed greatly as the flow changed. The survival was nearly 100 % when the flows were above 708 m3 s−1 (25 000 cfs), but less than 20 % when the flows were near 283 m3 s−1 (10 000 cfs) (Fischer et al. 1991). The paradox we observed may have resulted from indirect effects of climate and flow– the 2010 releases occurred in March, 1 month later than in 2009.*

(pp. 10-11) Consistent with Perry et al 2010, the authors concluded that survival rates through the East Delta were lower than other routes, even with the DCC closed:

> *It has been suggested that fish entrained in the East Delta have lower survival rates than other routes (Perry et al. 2010), although it is important to note that Perry defined "survival" as migration to Chipps Island. This was consistent with our results - throughout the duration of our study, fish migrating through the East Delta had lower overall survival than fish choosing either the West Delta or the mainstem Sacramento River, with the exception of West Delta steelhead in 2009 (Fig. 6).*

(p. 15) Although their study did not directly examine why survival was lower in the East Delta routes, the authors note that migratory survival is generally inversely related to migratory distance, and note that fish entrained into the East Delta have a longer route to the ocean and potentially encounter the CVP and SWP pumps, and they also noted that,

> *Additionally, the Operations Criteria and Plan (OCAP) Biological Assessment (BA) (USBR 2008) contains regressions of monthly steelhead salvage at the Central Valley Project and State Water Project pumping facilities, which shows a significant relationship between number of steelhead salvaged and the amount of water exported during the months of January through May, the same time that our tagged fish where in the Sacramento River Watershed. Our study suggests that entrainment in the east delta was negatively correlated with success to the ocean.*

(p. 15)

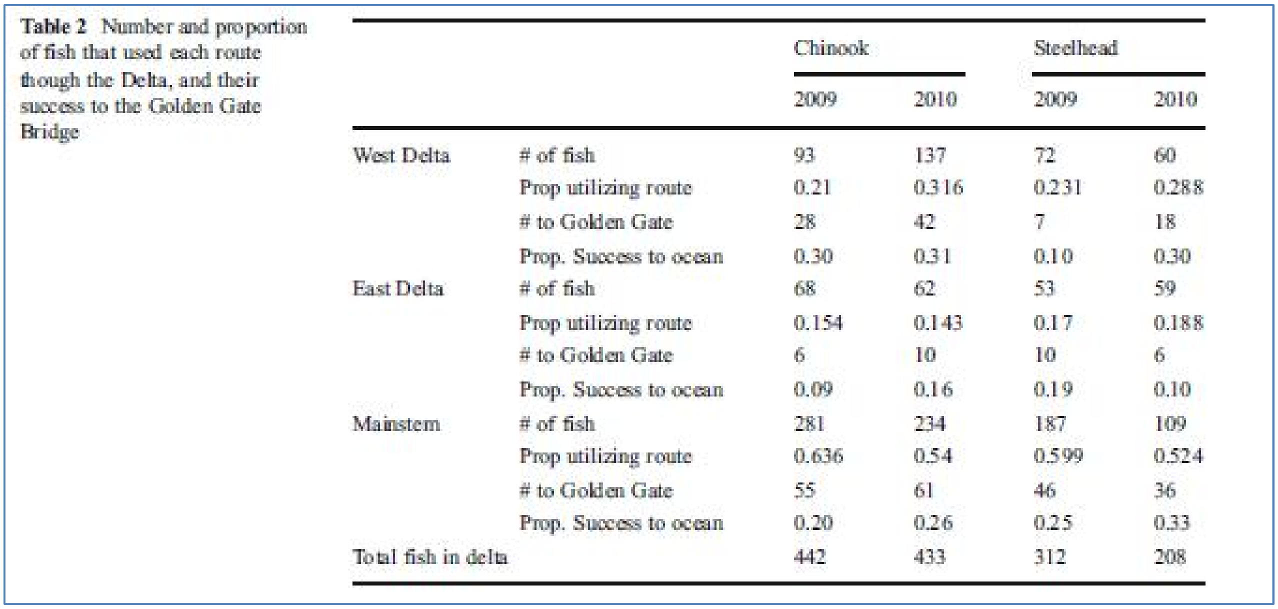

Table 2 Number and proportion of fish that used each route though the Delta, and their success to the Golden Gate Bridge

		Chinook		Steelhead	
		2009	2010	2009	2010
West Delta	# of fish	93	137	72	60
	Prop utilizing route	0.21	0.316	0.231	0.288
	# to Golden Gate	28	42	7	18
	Prop. Success to ocean	0.30	0.31	0.10	0.30
East Delta	# of fish	68	62	53	59
	Prop utilizing route	0.154	0.143	0.17	0.188
	# to Golden Gate	6	10	10	6
	Prop. Success to ocean	0.09	0.16	0.19	0.10
Mainstem	# of fish	281	234	187	109
	Prop utilizing route	0.636	0.54	0.599	0.524
	# to Golden Gate	55	61	46	36
	Prop. Success to ocean	0.20	0.26	0.25	0.33
Total fish in delta		442	433	312	208

Fig. 9 (Reprinted from Singer et al 2012)

> [Perry, R. W., J. R. Skalski, P. L. Brandes, P. T. Sandstrom, A.P. Klimley, A. Ammann, and B. MacFarlane. 2010. *Estimating Survival and Migration Route Probabilities of Juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta*. North American Journal of Fisheries Management 30:142–156. DOI: 10.1577/M08-200.1]

This study reports results of acoustic tag survival studies for salmon released in migration years 2007-2009. The overall survival through the Delta (the fraction surviving through all routes) averaged less than 33% for migration years 2007–2009. Survival was substantially lower for fish that were entrained into the interior Delta, including fish entrained through the Delta Cross Channel Gates; salmon migrating along the Sacramento River were between 1.5 and 6.6 times more likely to reach Chipps Island. The study showed that low flows in the Sacramento River (as well as opening the Delta Cross Channel gates) increase the chances of fish being entrained into the interior Delta, with lower survival rates.

> [National Research Council. 2012. Sustainable water and environmental management in the California Bay-Delta. National Research Council. The National Academies Press, Washington, DC. Available at: https://download.nap.edu/catalog.php?record_id=13394]

In their 2012 report, the National Academy of Sciences concluded that, "*The committee accepts the conclusion that pump operations pose a risk to juvenile salmonids. The survival of salmonid smolts migrating through the Delta is low. Several studies make this point.*" (p. 81) For instance, the NAS report reviewed Michel 2010 and found it supported the conclusion that survival to the Bay was, "*an order of magnitude less than that typically reported for yearling Chinook smolts migrating past eight dams in the Snake Columbia River system*," and that 20-30% of smolts died in the Delta and that, "*[t]hese losses are substantive and are at least in part attributable to pump operations that alter current patterns into and through the channel complex, drawing smolts into* *the interior waterways and toward the pumps*." (p. 81) The committee also acknowledged that salmon survival from the San Joaquin River in recent years has been estimated to be between 5 and 8 percent. (p. 81) But the committee warned that "*delta-specific management actions may not yield the large survival benefits as some might expect. Migrating smolts incur substantial levels of mortality outside of passage through the Delta including mortality directly and indirectly associated with SWP and CVP pump operations*." (p. 81)

> [Cavallo, B., J. Merz, and J. Setka. 2012. Effects of predator and flow manipulation on Chinook salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary. Environ. Biol. Fish. DOI 10.1007/s10641-012-9993-5]

Cavallo et al (2012) examined the effects of predator control and increased flow (resulting from opening the Delta Cross Channel gates) on survival rates for juvenile salmon migrating through the Delta from the Mokelume River. Their evaluation of removal of non-native, piscivorous fish found that migratory salmon survival after predator reduction improved in half of the treatments (there were significant improvements in survival after the first predator reduction treatment (from <0.80 to >0.99) but there was no apparent improvement in survival as a result of the second predator reduction treatment (survival decreased to pre-impact levels)). The authors suggested that daily (rather than weekly) predator removals, or removals across a broader geographic area, may be necessary to see any benefits for salmon survival. They also acknowledged that, "*we cannot rule out that observed changes in impact reach salmon survival occurred for reasons other than reduced predation pressure*." (p. 9) Increased flow and decreased tidal effect, however, resulted in decreased emigration time and increased survival in juvenile salmon. These results demonstrate that habitat manipulation through increased flow in the Delta tidal transition zone can be an effective approach to enhance salmon survival.

D. RECENT SALMONID LIFE CYCLE MODELS

New Information Summary

NMFS is developing a new life cycle model for Central Valley salmon runs. The 2011 independent peer review panel found that no existing life cycle models (including the IOS model) were adequate for evaluating the effects of the RPAs, and instead recommended that NMFS develop its own model. New life cycle models should help inform future management actions to restore listed salmon and steelhead runs.

> [Rose, K., J. Anderson, M. McClure, and G. Ruggerone. June 14, 2011. *Salmonid Integrated Life Cycle Models Workshop: Report of the Independent Workshop Panel. Delta Science Program*. Available at: http://deltacouncil.ca.gov/sites/default/files/documents/files/Salmonid_ILCM_workshop_final_report.pdf]

This report summarized an independent panel review of existing salmon life cycle models, including the SALMOD, Shiraz, IOS, Delta Passage submodel, and OBAN models. The panel recommended that instead of using any of these existing models, NMFS should develop its own life cycle model, stating that:

> *The Panel recommends that NMFS develop a model (or models) from the beginning. NMFS should use the existing models as guidance and the foundation, but should not try to modify one of the existing models to use for evaluating water management and the RPA actions. None of the models reviewed was completely appropriate alone for the needed life cycle model. Furthermore, none of the codes from the existing models, including SLAM, which is a general model, should be used for the NMFS model.*

(Rose 2011:8; see pp. 12-13, 9, 18). In addition, the panel identified concerns with using several of the models:

> *Several of the models presented at the workshop (IOS, Shiraz, SALMOD, and OBAN) use the same approach of representing life stage survivals as Beverton-Holt (or Ricker) like functions (density-dependence). Environmental covariates (e.g., water temperature, flow) are then added to these functions based on correlation analyses. The Panel had several cautions about using this approach for a model designed to address water management and RPA actions.*

(Rose 2011: 13-14). The panel also suggested that NMFS' life cycle model should explicitly consider the impacts of degraded freshwater habitat and competition with hatchery fish as a source of density dependence, even at low abundances (p. 16), and emphasized that the life cycle model should be developed to include life history variation and spatial distribution elements of the Viable Salmonid Population frameworks, instead of only modeling abundance (p. 16-17).

> [Zeug, S., P. S. Bergman, B. J. Cavallo, and K. S. Jones. 2012. *Application of a Life Cycle Simulation Model to Evaluate Impacts of Water Management and Conservation Actions on an Endangered Population of Chinook Salmon*. Environ. Model Assess. DOI 10.1007/s10666-012-9306-6]

This paper describes sensitivity analysis of the IOS life cycle model for winter run Chinook salmon. The paper reports that, "Delta survival, water year, and egg mortality were significant drivers of variability in age 3 escapement" (p. 10) and that "harvest may have a profound effect on salmon population dynamics" (p. 10). The model predicted that escapement was very sensitive to increases in water temperature, with a 10% increase in temperature producing a 95.7% reduction in escapement, with escapement less sensitive to changes in flow and not sensitive to changes in exports or ocean conditions. (p. 11) However, the authors also acknowledged some of the limitations of the model, for instance stating that:

> *several of the relationships in the IOS model are based on limited data that influence the estimate of input parameters and the form of uncertainty distributions associated with those estimates. For example, river migration survival has been hypothesized to be influenced by flow,* ***yet survival during the river migration stage is not influenced by flow in our model because the values we used to inform the relationship were***

> ***taken from a field study conducted over three low-flow years.*** (p. 11) (footnotes omitted) (emphasis added).

They also acknowledged that, "*The lack of significant changes in escapement with a 10% change in flow, exports and ocean conditions may reflect the type of data used to parameterize these relationships*." (p. 11) The model used uniform random variables for ocean conditions and smolt to age 2 survival, which the authors indicated could significantly affect model output.

E. CLIMATE CHANGE CONSIDERATIONS

The State Water Board's 2010 Flow Report did not specifically analyze the projected impacts of climate change on native species or their habitat. The report does suggest that the current criteria may not be appropriate in the future given the uncertainty associated with climate change effects.

> "*The numeric criteria are all short term criteria that are only appropriate for the current physical system and climate. There is uncertainty in these criteria even for the current physical system and climate, and therefore for the short term. Long term numeric criteria, beyond five years, for example, and assuming a modified physical system, are highly speculative. Only the underlying principles for the proposed numeric criteria and the other measures are advanced as long term determinations*." (p.128)

The 2010 Flow Report appears to anticipate that climate change will be considered in the context of an adaptive management program.

New Information Summary:

Recent literature finds that many native California fish, including salmonids, are vulnerable to extirpation in the near future. Climate change effects enhance that vulnerability. The effects of climate change can be ameliorated by restoring floodplain connectivity and stream flow regimes, re-aggrading incised channels and developing regional management plans that focus on restoring native fish.

> [Beechie, T., H. Imaki, J. Greene, A. Wade, H. Wu, G. Pess, P. Roni, J. Kimball, J. Stanford, P. Kiffney and N. Mantua. 2012. Restoring salmon habitat for a changing climate. River Research and Applications. DOI: 10.1002/rra.2590]

Beechie et al (2012) developed a decision support process for adapting salmon recovery plans that incorporates (1) local habitat factors limiting salmon recovery, (2) scenarios of climate change effects on stream flow and temperature, (3) the ability of restoration actions to ameliorate climate change effects, and (4) the ability of restoration actions to increase habitat diversity and salmon population resilience. Through the application of this process to systems in the pacific northwest, their findings indicated that restoring floodplain connectivity, restoring stream flow regimes, and re-aggrading incised channels were the restoration actions most likely most likely to ameliorate stream flow and temperature changes and increase habitat diversity and population resilience. Additionally, the potential benefits associated with this suite of actions stood in contrast with in-stream rehabilitation actions, which they found were unlikely to ameliorate climate change effects.

> [United States Environmental Protection Agency. August 2012. Water Quality Challenges in the San Francisco Bay/Sacramento-San Joaquin Delta Estuary, EPA's Action Plan. Available at: http://www.epa.gov/sfbay-delta/pdfs/EPA-bayareaactionplan.]

As noted above, in August 2012, the EPA released its "Action Plan" for the Delta after assessing the effectiveness of current regulatory mechanisms in place to protect water quality in the Delta. Generally, EPA concludes that "…Clean Water Act (CWA) programs currently are not adequately protecting aquatic resources of the Bay Delta Estuary." (p.2) The Action Plan notes that adverse effects from the loss of functional floodplain habitat in the Delta are likely to be exacerbated by climate change.

> *"Beginning in the 1850s, settlers diked, drained, and converted the floodplains, riparian corridors, and wetlands of the Bay Delta watershed into farms, cities and suburbs. (See Figure 3) A diversity of unique natural communities were destroyed and displaced, along with the fish and wildlife they supported. The losses include approximately 313,000 acres of wetlands in the Delta, 637,000 acres of riparian forest along the Sacramento River, and 329,000 acres of riparian forest along the San Joaquin River. Throughout the watershed, levees were built near creeks and rivers, thereby disconnecting them from their historical floodplains. Consequently, the floodplains that once provided valuable rearing and foraging habitat for fishes when seasonally inundated were converted to other uses. In addition, the loss of wetlands, floodplains, and riparian corridors greatly diminished the ability of these areas to accommodate flooding and recharge groundwater aquifers. Anticipated effects of climate change – including rising sea levels and more intense rainfall events – may exacerbate the ecological and flood control problems associated with the conversion of these aquatic habitats."*(p.100)

This excerpt highlights the importance of floodplain habitat in the Delta to ameliorate the effects of climate change.

> [BDCP "Red Flag" Documents [California Department of Fish and Game; US Fish and Wildlife Service; and National Marine Fisheries Service. April 2012 BDCP EA (Ch. 5) Staff "Red Flag" Review Comprehensive List. Available at: http://baydeltaconservationplan.com/Libraries/Dynamic_Document_Library/Effects_Analysis__Fish_Agency_Red_Flag_Comments_and_Responses_4-25-12.sflb.ashx]

In their review of the February 2012 BDCP draft effects analysis, the state and federal fish and wildlife agencies observed significant adverse effects from the combination of CVP/SWP operations under BDCP and climate change, which could lead to the extinction of several salmon runs. For instance, the National Marine Fisheries Service wrote that,

> *The analysis indicates that the cumulative effects of climate change along with the impacts of the PP may result in the extirpation of mainstem Sacramento River populations of spring-run and winter-run Chinook salmon over the term of the permit.*

(p.28) Similarly, DFG found that:

> *Winter-run redd dewatering and lower weighted usable spawning habitat in the Sacramento River under the preliminary proposal is not acceptable. This would lead to a significant decline in the population (as estimated by the JPE).*
>
> *Spring-run egg mortality in the mainstem of the Sacramento River is near 100 percent during dry and critical dry years. This type of egg mortality could lead to the extirpation of spring-run Chinook salmon from the mainstem of the Sacramento River during one drought cycle.*

(p. 3-4) Because of these concerns, NMFS recommended that operational criteria be developed that would ensure the protection of suitable habitat in the upper Sacramento River.

> [Moyle, P.B., R.M. Quinones, J. Kiernan. 2012. Effects of Climate Change on Inland Fishes of California: With Emphasis on the San Francisco Estuary Region. California Energy Commission White Paper. Available at: http://uc-ciee.org/downloads/Effects%20of%20Climate%20Change%20on%20the%20Inland%20Fishes%20of%20California.pd]

In 2003, the California Energy Commission created its Climate Change Center to document climate change research relevant to the state. The Center commissioned a report to analyze the effects of climate change on inland fishes in California. The report notes that anadromous fish will be especially affected by climate change:

> *"California's native inland fish fauna is in steep decline, a pattern which is reflected in the status of fishes native to streams flowing into the San Francisco Estuary and in the estuary itself. Climate change will further reduce the distribution and abundance of these mostly endemic fishes and expand the distribution and abundance of alien fish species. The decline and likely extinction of many native fishes reflects dramatic shifts in the state's aquatic ecosystems; shifts which are being accelerated by climate change. Fishes requiring cold water, such as salmon and trout, will especially suffer from climate change impacts of warmer water and reduced summer flows. Additionally, desirable species living in the San Francisco Estuary and the lower reaches of its streams will have to contend with the effects of rising sea level along with changes in flows and temperature."* (p.5)

The report includes both dams and alien species among the top factors negatively affecting native species. The report notes that many native aquatic species will disappear in the future without regional management strategies in place that incorporate measures for, among other things, obtaining and preserving habitat that can act as a climate change refugia and managing coldwater pools in reservoirs to favor native fish.

II. RECOMMENDED CHANGES TO THE BAY-DELTA WATER QUALITY CONTROL PLAN AND PROGRAM OF IMPLEMENTATION

A. Recommendations for New and Revised Objectives in the Bay Delta Water Quality Control Plan

We recommend that the State Water Board consider the following measures in its update of the water quality control plan, consistent with the potential objectives identified in the 2009 staff report:

1. Sacramento River Inflow and Delta Outflow Objectives: Increase winter/spring inflow and outflow objectives to improve migratory survival of juvenile salmonids into and through the Delta sufficient to achieve the SWRCB's narrative salmon doubling objective and other specific targets to restore and maintain natural, self-sustaining, and ecologically and commercially viable anadromous fish populations (see below). Releases from upstream sources should be made proportionally to each stream and watershed as a fraction of unimpaired flow to preserve ecological connectivity between the Delta and upstream watersheds and to avoid concentrating impacts on a subset of source areas.

2. Floodplain Habitat Flow Objectives: Establish Sacramento River inflow and structural modifications objectives such that flows from the Sacramento River inundate floodplains for 15-120 days between December and May every year or twice in every three years.

3. Reverse Flow Objectives/Export:Inflow Objectives: Establish objectives limiting reverse flows in Old and Middle River (OMR) and/or other restrictions on hydrodynamics and exports (e.g., I:E ratios) that reduce juvenile entrainment and improve migratory survival in the winter and spring months in order to achieve specific survival and other targets (see below). In addition, establish objectives that provide adequate migratory corridors through the Delta for both juveniles and adults, including pulse flow releases and restrictions on exports during fall months to allow for successful upmigration of adults, particularly those coming into the San Joaquin River.

4. Maintain Adequate Upstream Temperature Conditions: Build on the CALSIM modeling done for BDCP Alternative 8 to ensure that upstream reservoirs maintain adequate end of April and end of September storage (cold water pools) and release sufficient flows to maintain temperature compliance points downstream from these reservoirs while meeting Delta flow objectives.

B. Recommendations for the Program of Implementation to Address Climate Change and Changed Circumstances

We provide the following recommendations to account for climate change and changed circumstances:

(1) Develop and implement a robust adaptive management program tied to clearly defined biological outcome metrics that clearly define success.
(2) Develop and implement protective flow objectives that will enhance species' natural resiliency to habitat disturbances (e.g., through increased spatial distribution of populations) and increase diversity of life history stages.

We recommend that the State Water Board develop a robust adaptive management program that establishes targets and defines desired outcomes for public trust values and beneficial uses of the Bay Delta system that are specific, measureable, achievable and relevant to the particular goals that characterize the plan's overarching purpose (protecting the public trust values and beneficial uses of the Delta ecosystem) and timebound (S.M.A.R.T.), and evaluates the performance of the WQCP objectives over time toward achieving these targets. The State Water Board should establish quantitative targets when possible, such as survival, abundance, and spatial distribution metrics, as opposed to narrative outcomes. For instance, outcomes for Chinook salmon should include metrics identifying quantifiable improvements in the survival of outmigrating juveniles and metrics identifying increased abundance targets sufficient to meet the State Water Board's narrative salmon doubling objectives and other targets for restoring and maintaining natural, self-sustaining, and ecologically and commercially viable anadromous fish populations. For a more detailed description of this process, please see the TBI et al August 17, 2012 submission for Workshop 1. The flow objectives and adaptive management program should be sufficient to achieve greater diversity of life history strategies for salmonid populations and enhance the resiliency of those populations. In other words, the State Water Board should identify objectives that will increase and sustain salmonid life history diversity to ensure a more resilient population that is better able to respond to future climatic disturbances.

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RIVER RESEARCH AND APPLICATIONS

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RESTORING SALMON HABITAT FOR A CHANGING CLIMATE

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ABSTRACT

An important question for salmon restoration efforts in the western USA is ‘How should habitat restoration plans be altered to accommodate climate change effects on stream flow and temperature?’ We developed a decision support process for adapting salmon recovery plans that incorporates (1) local habitat factors limiting salmon recovery, (2) scenarios of climate change effects on stream flow and temperature, (3) the ability of restoration actions to ameliorate climate change effects, and (4) the ability of restoration actions to increase habitat diversity and salmon population resilience. To facilitate the use of this decision support framework, we mapped scenarios of future stream flow and temperature in the Pacific Northwest region and reviewed literature on habitat restoration actions to determine whether they ameliorate a climate change effect or increase life history diversity and salmon resilience. Under the climate change scenarios considered here, summer low flows decrease by 35–75% west of the Cascade Mountains, maximum monthly flows increase by 10–60% across most of the region, and stream temperatures increase between 2 and 6°C by 2070–2099. On the basis of our literature review, we found that restoring floodplain connectivity, restoring stream flow regimes, and re-aggrading incised channels are most likely to ameliorate stream flow and temperature changes and increase habitat diversity and population resilience. By contrast, most restoration actions focused on in-stream rehabilitation are unlikely to ameliorate climate change effects. Finally, we illustrate how the decision support process can be used to evaluate whether climate change should alter the types or priority of restoration actions in a salmon habitat restoration plan. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS: restoration; climate change; decision support; adaptation; salmon habitat; stream flow; stream temperature

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INTRODUCTION

Climate change is predicted to have significant effects on Pacific salmon and their ecosystems in western North America, and several reports suggest that restoring habitats for salmon in some places may be pointless because climate change will make their habitats inhospitable (Lackey, 2003; Nelitz *et al.*, 2007). By contrast, recent modelling of the combined effects of climate change and habitat restoration indicates restoration actions are likely to result in a net benefit to salmon populations despite future shifts in temperature and hydrology (Battin *et al.*, 2007). This lack of consensus on how climate change will affect salmon populations inhibits the development of clear guidance on how to modify habitat restoration efforts in response to climate change. With millions of dollars spent each year to restore habitats for threatened and endangered salmon in the western USA, there is increasing concern that climate change effects on freshwater habitats may limit the future effectiveness of certain salmon recovery efforts (Lackey *et al.*, 2006; Battin *et al.*, 2007; Mantua *et al.*, 2010) and that the priority or design of specific restoration actions should be altered to accommodate future climate change (Mote *et al.*, 2003).

Making the decision to adapt a restoration plan for climate change is not straightforward, as predicted climate change effects vary widely throughout the Pacific salmon range, and some species have life histories that will likely allow them to persist throughout most of their range despite shifts in temperature and precipitation (Waples *et al.*, 2009). Stream temperatures are expected to increase in most rivers, and the threat to salmon recovery is high where temperatures are near lethal or sub-lethal thresholds for salmon, but low in many rivers with current temperatures well below those thresholds. Furthermore, some rivers are expected to see large increases in peak flows, whereas other rivers are expected to experience decreased low flows (Arnell, 1999, Mantua *et al.*, 2010). However, past land uses and water abstraction have often degraded habitats to a greater degree than that predicted from climate change, presenting substantial

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opportunities to improve salmon habitats more than enough to compensate for expected climate change effects over the next several decades (Battin *et al*., 2007). For salmonids, variation in life history strategies and habitat requirements—along with their demonstrated capacity to adapt to new environments—further complicates the development of general guidance for modifying restoration strategies to accommodate climate change (Quinn, 2005; Beechie *et al*., 2006; Bryant, 2009). This complex interplay of climate effects, restoration opportunities, and potential salmon responses poses a considerable challenge for effectively restoring salmon populations in a changing climate.

In this paper, we present a simple logic framework and data sets to assist managers in adapting salmon habitat restoration efforts to climate change in the Pacific Northwest, USA (PNW). Our approach consists of four components: (1) a set of guiding questions that serve as a starting point for evaluating the potential effects of climate change on freshwater habitat restoration effectiveness; (2) maps showing future stream flow and temperature scenarios; (3) a review of the ability of specific river restoration actions to ameliorate future effects of climate change or to increase salmon resilience; and (4) a simple decision support structure that integrates these three components to help managers evaluate whether salmon restoration actions should be reprioritized or redesigned for a climate-altered future. Together, these components guide decisions on whether and how to adapt or reprioritize actions in light of expected climate-induced habitat changes.

STUDY AREA

The study area encompasses the Columbia River basin and coastal drainages of Oregon and Washington (Figure 1), with climatic and ecological conditions ranging from wet forests in the Cascade Mountains to semi-arid and desert regions in the central plateaus (Omernik and Bailey, 1997). The study area is bordered by the Rocky Mountains to the east, and the Cascade Mountains separate coastal drainages from the interior Columbia basin. Mean annual precipitation ranges from <200 mm/year in the central deserts to 3550 mm/year in the Cascade Range (Daly *et al*., 2002), and elevations range from sea level to over 3700 m in the Rocky Mountains and over 4200 m in the Cascade Mountains. Five anadromous salmon species (*Oncorhynchus* spp.) and steelhead (*O. mykiss*) are found in the study area, along with bull trout (*Salvelinus confluentus*), Dolly Varden char (*S. malma*), and rainbow and

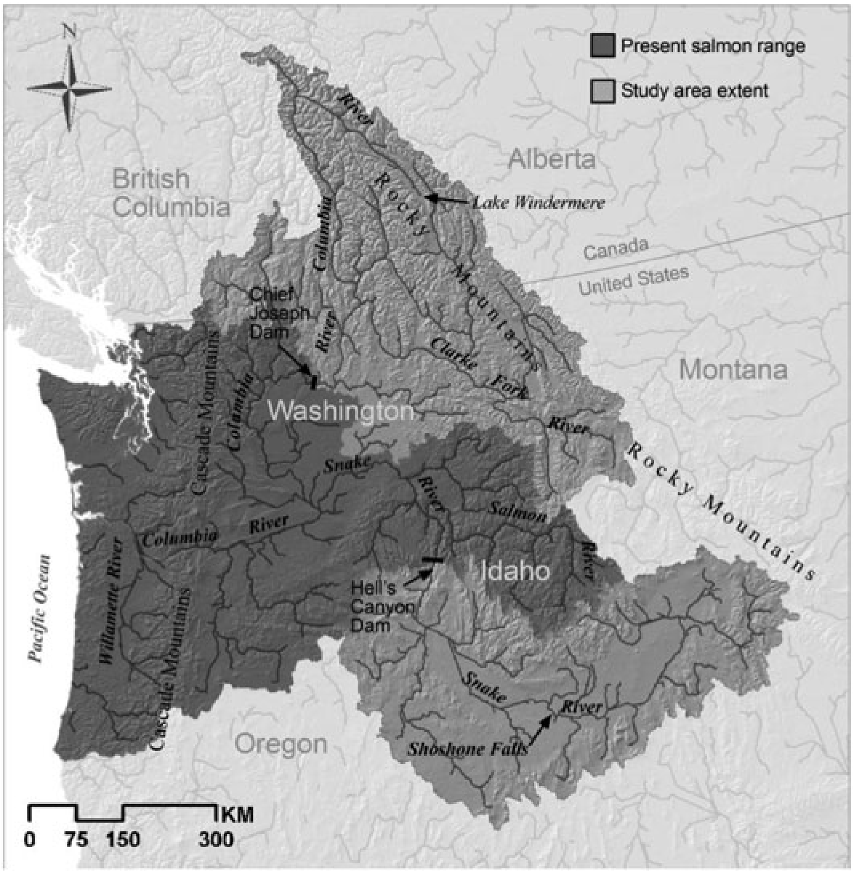

Figure 1. Map of the study area indicating major rivers, mountain ranges, and current and historical ranges of salmon

cutthroat trout (*O. mykiss, O. clarkii*). Current ranges of salmon and steelhead are limited to coastal rivers, the Columbia River basin downstream of Chief Joseph dam and the Snake River basin downstream of Hells Canyon Dam. Historical ranges extended into the upper reaches of the Columbia River (Lake Windermere) and into the Snake River basin up to Shoshone Falls. Resident trout species (rainbow, cutthroat, and bull trout) occupy streams throughout the region, with bull trout generally restricted to colder streams at higher elevations.

FRAMEWORK AND GUIDING QUESTIONS

Determining how a specific change in stream flow or temperature will impact a salmon population depends in part upon species-specific tolerances and life history requirements, and in part upon the expected change in stream flow and temperature relative to those tolerances. The timing of important salmon life history events varies both within and among species (e.g. Groot and Margolis, 1991; Quinn, 2005; Figure 2). For example, salmonids with ocean-type life histories (e.g. pink, chum, and some Chinook) tend to spawn in the fall and winter, do not rear in freshwater during summer, and migrate to sea in the winter or early spring. Salmonids with stream-type life histories (e.g. coho salmon, steelhead, and some Chinook salmon) spawn between fall and late spring, rear in freshwater for 1 or 2 years, and usually migrate to sea in spring or early summer. Hence, each species and life history strategy will encounter a different suite of stream flow and temperature effects because they occupy different habitats and vary in timing of life history events. Climate change effects will also vary among rivers (e.g. Mote *et al*., 2003; Beechie *et al*., 2006; Rieman *et al*., 2007; Crozier *et al*., 2008), adding additional complexity to understanding how climate change will affect salmonid populations.

Because there are many possible combinations of climate change effects and life history responses to evaluate across the study region, we do not attempt a comprehensive review of all possible effects, nor do we use detailed population models to estimate climate change effects on restoration actions (e.g. Battin *et al*., 2007), mainly because many types of restoration actions cannot be modelled with any certainty and evaluation of hundreds of salmon populations is not feasible (Bartz *et al*., 2006; Scheuerell *et al*., 2006). Rather, we summarize key temperature thresholds by species and life history stage, summarize climate change scenarios for stream temperature and flow, and allow local practitioners to relate local climate change scenarios to locally relevant salmonid tolerances. We also review the likely effectiveness of various restoration techniques in a climate-altered future.

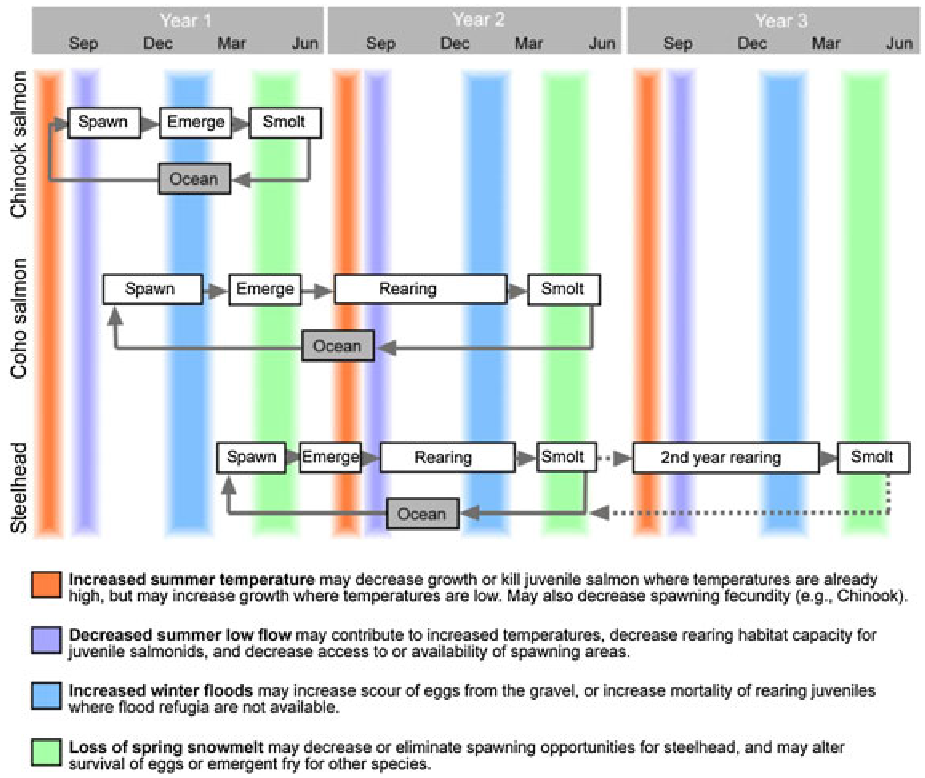

Figure 2. Timing of climate change effects on stream flow and temperature by life history stages of ocean type Chinook salmon, coho salmon, and steelhead

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For example, actions that create new summer rearing habitats in an area expected to exceed upper lethal temperature limits will not likely improve salmonid populations over the long term. By contrast, actions that significantly reduce stream temperature or create thermal refugia for the same species are more likely to retain their effectiveness in a future with increasing temperatures. Therefore, we reviewed recent literature to evaluate whether specific restoration action types will likely ameliorate climate change effects on flood flows, low flows, or stream temperature.

We also developed four guiding questions to evaluate the potential impacts of climate change on project prioritization and design:

(1) What habitat restoration actions are necessary for recovery of local salmon populations?
(2) Do future stream flow and temperature scenarios alter the types of habitat restoration actions that are necessary for recovery?
(3) Does the restoration plan or action ameliorate a predicted climate change effect on stream flow or temperature?
(4) Will the restoration plan or action increase habitat diversity and salmon population resilience?

Systematic consideration of these questions will help determine whether restoration objectives or priorities should be altered to accommodate future climate change. Answering the first question requires local information about restoration plans and objectives, which restoration planners and practitioners can acquire from salmon recovery plans developed under the Endangered Species Act. However, information required to answer the last three questions is rarely readily available to restoration groups. Therefore, in the following sections, we summarize information needed to address questions 2–4 for salmon restoration actions in the PNW.

SCENARIOS FOR CLIMATE CHANGE EFFECTS ON STREAM FLOW AND TEMPERATURE IN THE PACIFIC NORTHWEST

Recent climate change scenarios modelled for the PNW suggest a clear warming trend, but the magnitude of estimated temperature increase varies with choice of climate model and emissions scenario (Elsner *et al*., 2010). By contrast, even the sign of future precipitation changes is not consistent among different scenarios, with some predicting precipitation increases and others predicting decreases (e.g. Elsner *et al*., 2010). A multi-model averaged climate change scenario under A1B emissions indicates an average temperature increase in the PNW of 3.5°C by 2080, with wetter winters, drier summers, and an increase in average annual precipitation of 5% (Elsner *et al*., 2010; Mote and Salathé, 2010). Because all the future climate scenarios evaluated by Elsner *et al*. (2010) predict warming trends, the models predict that more precipitation will fall as rain and less as snow and that this effect will be most pronounced in mid-elevation areas (Hamlet and Lettenmaier, 1999). In this paper, we use this multi-model average from Elsner *et al*. (2010) to drive a coupled stream flow and temperature model (Whited *et al*., in press) to produce scenarios of stream temperature and flow regimes that may have significant impacts on salmon populations and food webs that support them.

Although the A1B multi-model average is commonly considered to be an informative future climate scenario (i.e. it is closest to most model estimates and the weighting scheme discounts extreme values; Mote and Salathé, 2010), there remains considerable uncertainty around any estimate of future precipitation or air temperature. Uncertainties around future temperature and precipitation predictions have three main sources: (1) the factors that force climate change (including future greenhouse gas and aerosol emissions), (2) global climate model (GCM) errors, and (3) 'natural' variability in the climate system (Deser *et al*., 2010; Hawkins and Sutton, 2011). In general, the variation in temperature or precipitation predictions among different emissions scenarios is smaller than the variation among different GCMs (Mote and Salathé, 2010). For example, the multi-model average predictions of PNW climate for three emissions scenarios in the 2040s indicate a temperature increase of 1.7–2.4°C and a precipitation increase of 1–2% (Figure 3); the 2080s simulations indicate a 2.7–4.7°C increase in temperature and 3–6% increase in precipitation. However, the variation among GCMs for the 2040s is roughly 2°C for each emissions scenario (compared with a range of <1°C among emission scenarios) and as high as 3.5°C among GCMs in the 2080s (compared with ~2°C among emissions scenarios). Variation among GCMs is even greater for precipitation predictions, with a range as high as −8% to +23% for precipitation by the 2080s (compared with 3–6% between emissions scenarios). The combined emissions scenario, model uncertainties, and natural variability for air temperature in the PNW suggest an increase of 1–3°C by the 2040s and 2–6°C by the 2080s (multi-model averages of 2°C and 3.5°C, respectively). The combined uncertainties for precipitation suggest a −6% to +14% change in precipitation by the 2040s and a −8% to +23% change by the 2080s (multi-model averages of +2% and +5%, respectively). Finally, both air temperature and precipitation are expected to continue increasing through the end of the 21st century regardless of the GCM used, and our use of climate scenarios for the 2080s is not intended to suggest a stable future climate.

Stream flow and temperature methods

Changes in stream flow and temperature were simulated using a two-step modelling process that (1) predicted daily

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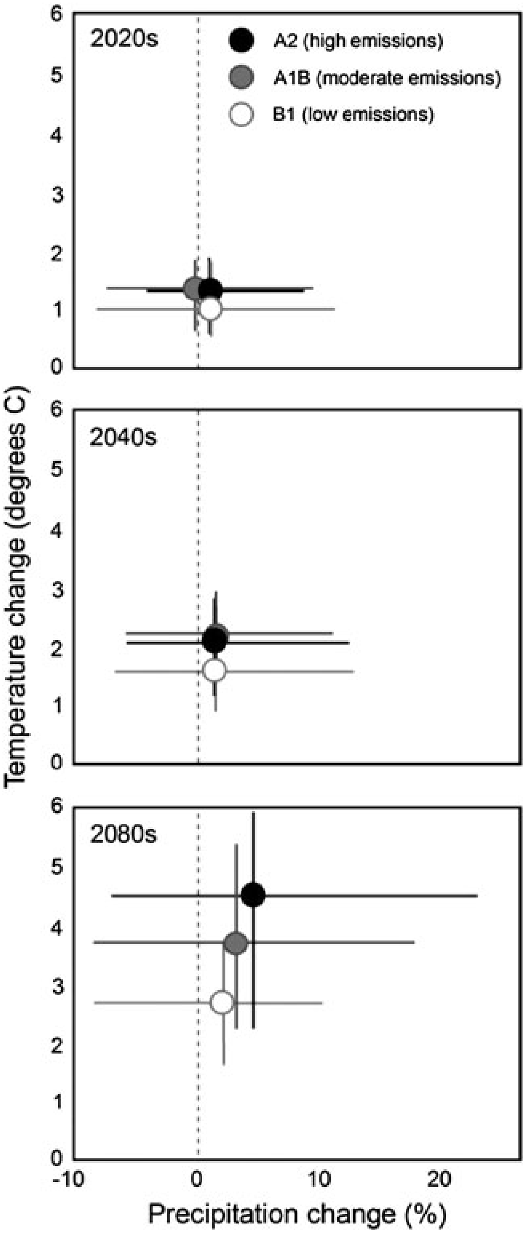

Figure 3. Variation in global climate model (GCM) predictions of precipitation change (%) and temperature increase (°C) in the Pacific Northwest. Circles indicate ensemble model averages for each of three emissions scenarios, and lines indicate range of predictions from 20 different GCMs for each emissions scenario. Based on data from Mote and Salathé (2010)

runoff using the macroscale variable infiltration capacity (VIC) model and (2) dynamic runoff routing, stream flow and stream temperature simulations based on VIC that estimate water balance, energy balance, and runoff outputs. The VIC model produces daily runoff and soil moisture, as well as associated forcing variables including incoming shortwave and long wave radiation that are used later in the stream temperature model. The coupled stream flow and temperature model was based on a hierarchical dominant river tracing algorithm that defines the underlying hydrography for stream flow and temperature calculations (Wu *et al*., 2011). The coupled model, called the dominant river tracing-based stream flow and temperature model, produces gridded daily stream flow and stream temperature data on the basis of water and heat transport in river networks, thermal dynamics of stream water and the surrounding environment, and the coupling of hydrologic routing processes and associated thermal dynamics (Whited *et al*., in press). Stream flow and temperature scenarios were based on the multi-model average future climate scenario described previously that provided daily gridded precipitation and air temperature data at one-sixteenth degree resolution (Elsner *et al*., 2010). Only cells with flow accumulation areas greater than six upstream cells (equivalent to a drainage area of approximately 200 km^2) were included in the regional mapping because smaller drainage areas were not considered reliable for future scenarios (Wu and Kimball, unpublished data).

Stream flow and temperature were calibrated to measured stream flow and temperatures at seven US Geological Survey sites in the Columbia River basin and then validated against an independent 10-year record of daily stream flows at 12 gauges and a 7-year record of daily stream temperatures at 11 gauges. Model validation indicated strong correlation between measured and simulated stream flow and temperature at the majority of gauges (Figure 4). Although there was no consistent positive or negative bias in either stream flow or temperature, some deviations between modelled and measured stream flow or temperature are likely due to differences between the way VIC models runoff, groundwater, and stream flow compared with local physical processes. For example, in the Willamette basin, groundwater discharge

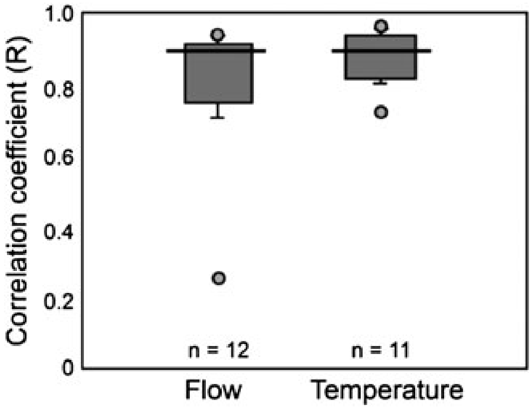

Figure 4. Summary of dominant river tracing-based stream flow and temperature model validation results, illustrating distribution of correlation coefficients (*R*) for modelled versus measured stream flow and temperature. Heavy horizontal line indicates median *R*, box indicates 25th and 75th percentiles, lines indicate 10th and 90th percentiles, and circles indicate range of values. (Wu and Kimball, unpublished data)

from the fractured basalts of the Cascade Mountains leads to higher summer stream flow and lower summer temperature than predicted by the dominant river tracing-based stream flow and temperature model, primarily because the VIC model does not effectively model deep groundwater storage and its influence on flow. Therefore, the VIC model underestimates summer stream flow, which in turn leads to an overestimate of summer stream temperature. Other studies have found regional biases in mean annual runoff associated with arid regions or snowmelt systems and showed overall underestimation of mean annual stream flow in the PNW from VIC modelling (Gangopadhyay and Pruitt, 2011). However, validation of stream flows for this study did not suggest a clear spatial pattern of positive or negative biases.

We focused our flow analysis on mean monthly flows for four periods: 1970–1999, 2000–2029, 2030–2069, and 2070–2099. We calculated change in magnitude of the maximum and minimum monthly flows between periods for each stream cell, as well as the change in timing of maximum and minimum monthly flows between periods. We focused on predicted *change* in flow relative to the modelled historical baseline rather than absolute stream flows to minimize impacts of errors in the flow model on our results. That is, we assume that biases in the stream flow model will be in the same direction for all periods within a grid cell and that using the change in flow as our primary metric will reduce the impact of those biases on our analysis. Finally, we used cluster analysis to map three flow regimes (rainfall-dominated, snowmelt-dominated, and transitional) during each period (Beechie *et al*., 2006).

We chose to map temperature predictions directly to allow the greatest flexibility in biological interpretations. That is, we avoided selection of specific thermal limits because thermal tolerances vary considerably among species for each life stage. To aid in biological interpretation of these temperature maps, we provide both species-specific and generalized salmonid thermal limits (Table I), as well as published temperature criteria that are recommended for protection of Pacific salmon from negative temperature effects (Table II). Most upper lethal limits are between 20 and 24°C and recommended temperature thresholds for the 7-day average daily maximum range from 13 to 18°C. In the absence of local data on thermal tolerances of salmonids (which vary among species and environments), these data can be used to gauge the likelihood that stream temperature changes will be significant for local species.

Results: stream flow change scenario

Areas of the PNW with a snowmelt-dominated hydrologic regime (in which the maximum monthly flows are during the spring snowmelt) shrink considerably under the ensemble climate change scenario as snow level rises across the region (Figure 5). By 2070–2099, the snowmelt hydrologic regime no longer exists in the north Cascades and upper Snake River basin, and the only remaining snowmelt-dominated area is in the Canadian Rockies. The transitional regime, which has

Table I. Temperature thresholds (°C) for critical parts of the salmonid life cycle, including general and species specific information

Life stage	Chinook (*O. tshawytscha*)	Chum (*O. keta*)	Coho (*O. kisutch*)	Pink (*O. gorbuscha*)	Sockeye (*O. nerka*)	Steelhead (*O. mykiss*)
Adult migration						
Optimal threshold			15.6			
Lethal threshold	22	21	21			
Thermal blockage						22
Adult holding and spawning						
Optimal threshold	14.5	12.8	15.6			12.8
Detrimental to internally held gametes			20			
Incubation and early fry development						
Upper threshold	14.5	10	12	12	12.5	12
Juvenile rearing						
Optimal threshold	14.8[a]	15	17			19
Lethal threshold		21	23		20	
UZNG[b]	24	19.8	23.4	21		24
Smoltification						
Impairment threshold	12–17		15			13

Temperatures cited are for constant exposure, unless otherwise noted. Data compiled from Bjornn and Reiser (1991), Eaton and Scheller (1996), McCullough *et al*. (2001), and Richter and Kolmes (2005).

[a] Natural rations level

[b] Upper zero net growth (UZNG) temperature: maximum weekly temperature at which fish can live for several days but at which they do not ingest enough food to gain weight

Table II. Recommended temperature criteria (upper thresholds; °C) for Pacific salmon and steelhead

	Life stage						Reference
	Adult migration	Spawning	Incubation	Juvenile rearing	Smoltification (non-steelhead)	Steelhead smoltification	
7-DADM	18	13	13	16	16	14	Richter and Kolmes, 2005; US EPA, 2003
Weekly mean	16	10	10	15	15	12	Richter and Kolmes, 2005

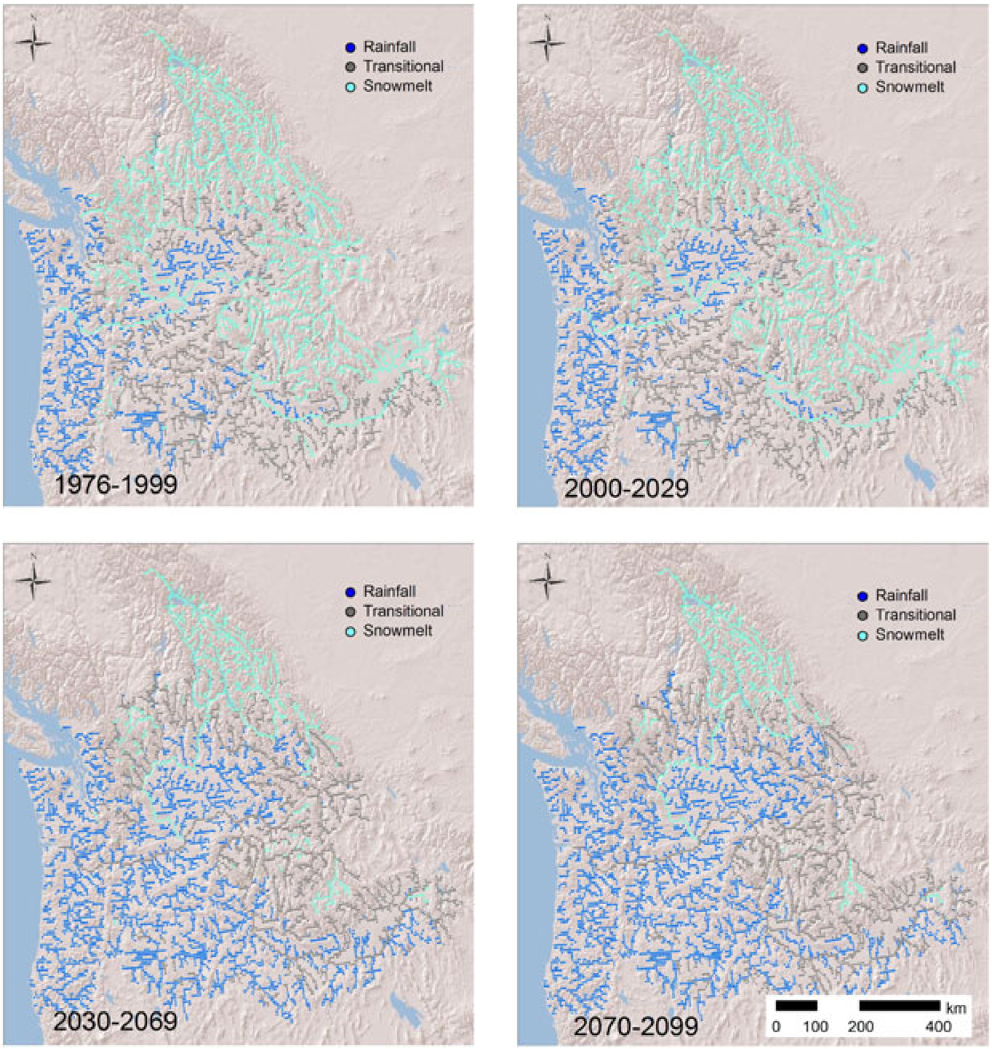

Figure 5. Modelled hydrologic regime through time, based on cluster analyses of mean monthly flows for each period

both spring snowmelt and fall–winter high flows, shifts inland and northwards, leaving only small areas of the transitional regime in the north Cascades and the Rocky Mountains. The rainfall-dominated regime, which has the highest flows during fall–winter floods, has historically been limited to the maritime climate west of the Cascades and small low-elevation portion of the interior Columbia basin. By 2070–2099 however, the rainfall-dominated regime expands to nearly the entire interior Columbia basin in this climate change scenario.

The ensemble climate scenario suggests the largest decreases in summer low flows will be west of the Cascade Mountains, where minimum monthly flows decrease by 10–70% over the course of the 21st century (Figure 6). The largest changes are in basins that currently have a transitional hydrologic regime (with both a fall/winter storm peak and a late spring snowmelt peak), and large decreases in minimum monthly flows result from a nearly complete loss of the spring snowmelt peak and a concomitant decline in late summer flows. More modest decreases in low flow (10–35%) are predicted in the Rocky Mountains south of the US–Canada border and in the Blue Mountains of northeastern Oregon. In these areas, the hydrologic regime shifts from snowmelt to transitional, and the decline in snowpack results in earlier spring melt and a decrease in late summer stream flows (Figure 6). Minimum monthly flows in the Canadian Rockies increase by 10% or more, largely as a result of a predicted increase in precipitation and snowpack. Increased minimum flows are also predicted in the upper Snake River basin, caused by a shift in minimum monthly flows from the cold January–February period to minimum flows in summer following spring snowmelt. In this region, there is little predicted change in summer low flows, but the minimum winter flows increase significantly.

Simulated maximum monthly flows increase by 10–50% across most of the region as a result of an increasing fraction of precipitation falling as rain rather than snow (Figure 7). The few areas where maximum monthly flows are expected to increase by more than 50% are located in the Cascade Mountains and in the middle and lower Snake River basin. The large increases in the Cascade Mountains are predominantly a result of a shift from transitional to rainfall-dominated hydrographs, with future flood flows in the fall and winter being considerably larger than at present. Large predicted increases in the monthly average peak stream flow in the Snake River tributaries result mainly from large increases in spring precipitation. Overall, the ensemble scenario suggests increasing volume of winter runoff and increased flooding in transitional basins and increasing spring flows in snow-dominant basins. Reductions in summer low flows are projected to be largest in the transitional basins in the Cascade and Olympic Mountain ranges.

Results: stream temperature change scenario

Increased air temperatures will lead to increased water temperatures on both the west and east sides of the Cascade Mountains, and the scenario indicates a 1–4°C increase in stream temperatures (maximum weekly mean temperature) across the region by the 2030–2069 period and a 2–6°C increase by the 2070–2099 period (Figure 8). Highest mean weekly water temperatures vary significantly across the region in all periods, with highest temperatures in reaches of the Snake and Willamette River basins (Figure 9). Because these areas are close to or exceed published thermal tolerances of most salmon species even during the historical period (1970–1999), they are most likely to shift to stressful or lethal thermal conditions in the future. Notably, many rivers within the current salmon range have modelled temperatures above published lethal or protective thresholds (Tables I and II), yet salmon currently occupy the majority of these rivers. Stream temperatures in the northern part of the Columbia basin are currently within thermal tolerances of most rearing juvenile salmonids, and under this climate change scenario, projected temperature increases remain the lowest in the region and within thermal tolerances. This area is outside the current salmon range because of blocked migration by dams, but within their historical range. Most coastal river systems and rivers originating on the west slope of the Cascade Mountains are likely to remain within published thermal tolerances even in the 2070–2099 period. These river systems have the smallest projected temperature increases, whereas the largest increases are expected in the main stem Columbia River and tributaries in the middle and lower Columbia basin.

REVIEW OF RESTORATION ACTIONS AND CLIMATE CHANGE

We grouped restoration actions on the basis of the watershed processes or functions they attempt to restore (Beechie *et al.*, 2010) and then classified them as either likely or not likely to ameliorate a climate change effect on high stream flows, low stream flows, and stream temperatures (Table III). We classified actions on the basis of a literature review of restoration action effectiveness and watershed processes to develop a comprehensive summary of each action's likelihood of ameliorating climate change effects. Our basic rules were to (1) classify an action as likely to ameliorate an effect if we could find literature support for that response and (2) avoid including effects that were theoretically possible but not supported by data. In a few cases, the literature was sparse and suggested mixed effects depending on the context. In those cases, we classified the action as having a context-dependent effect on stream flow or temperature to indicate that the ability of the action to ameliorate a climate effect depends on the situation in which the action is employed. Although these rules may omit a few effects, we felt that it was more important to provide clear guidance on the dominant effects and avoid including actions that only rarely would ameliorate the climate change effect. Nevertheless, this review is not intended to imply that less robust actions should be avoided in all circumstances. For instance, where summer rearing habitats constrain population recovery and summer stream flow and temperature are not expected to change significantly, any action that addresses causal factors for habitat and population declines should be implemented even if it does not ameliorate a climate change effect. Only in cases where

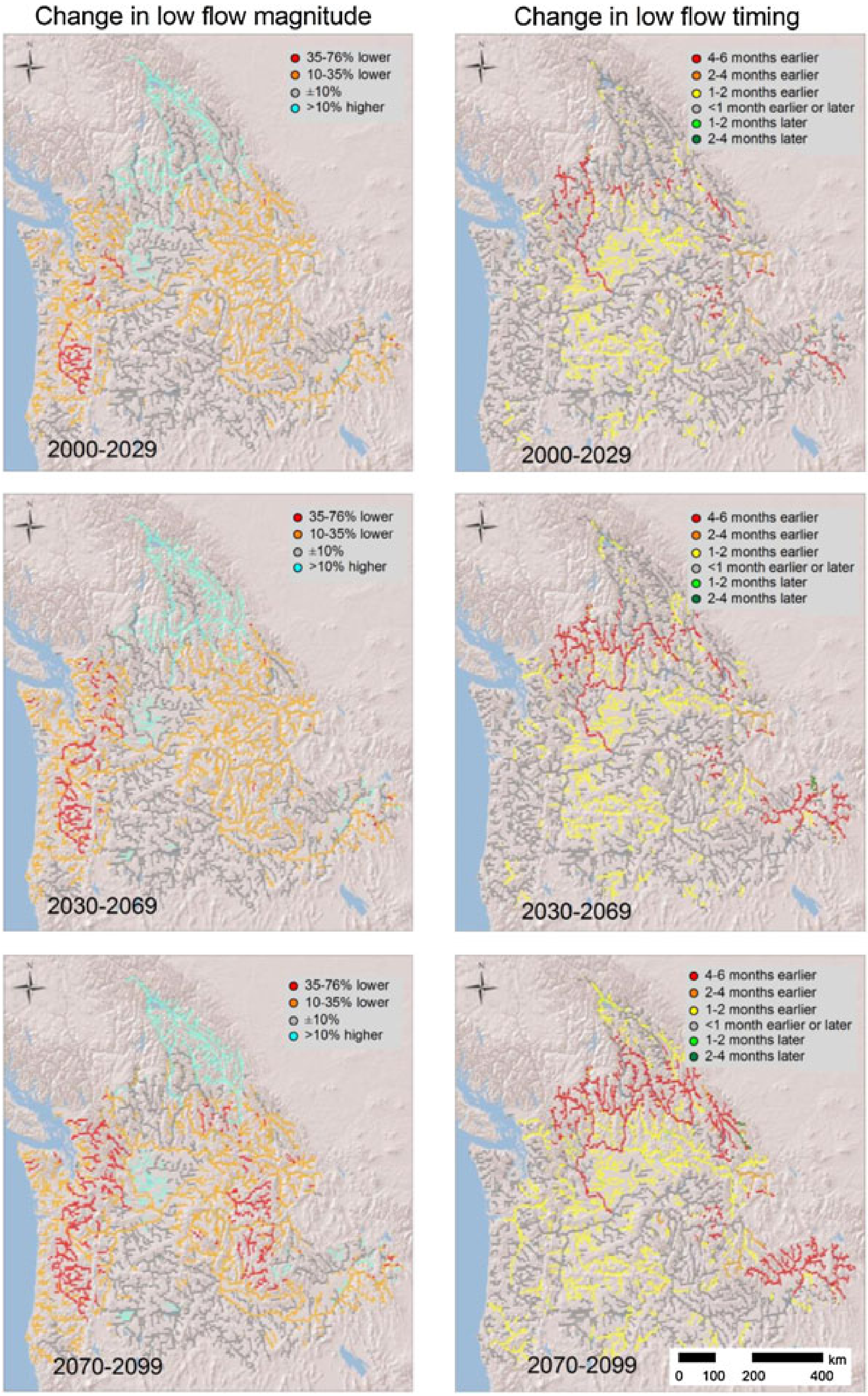

Figure 6. Modelled change in the minimum mean monthly flow and shift in timing of minimum mean monthly flow. Ratio is minimum mean monthly flow from the future period divided by the minimum mean monthly flow from the period 1970–1999. For shift in low flow timing, areas mapped in red indicate a shift from minimum flow in winter (usually February) to minimum flow in August. Areas in yellow predominantly indicate a shift from minimum monthly flow in September to August

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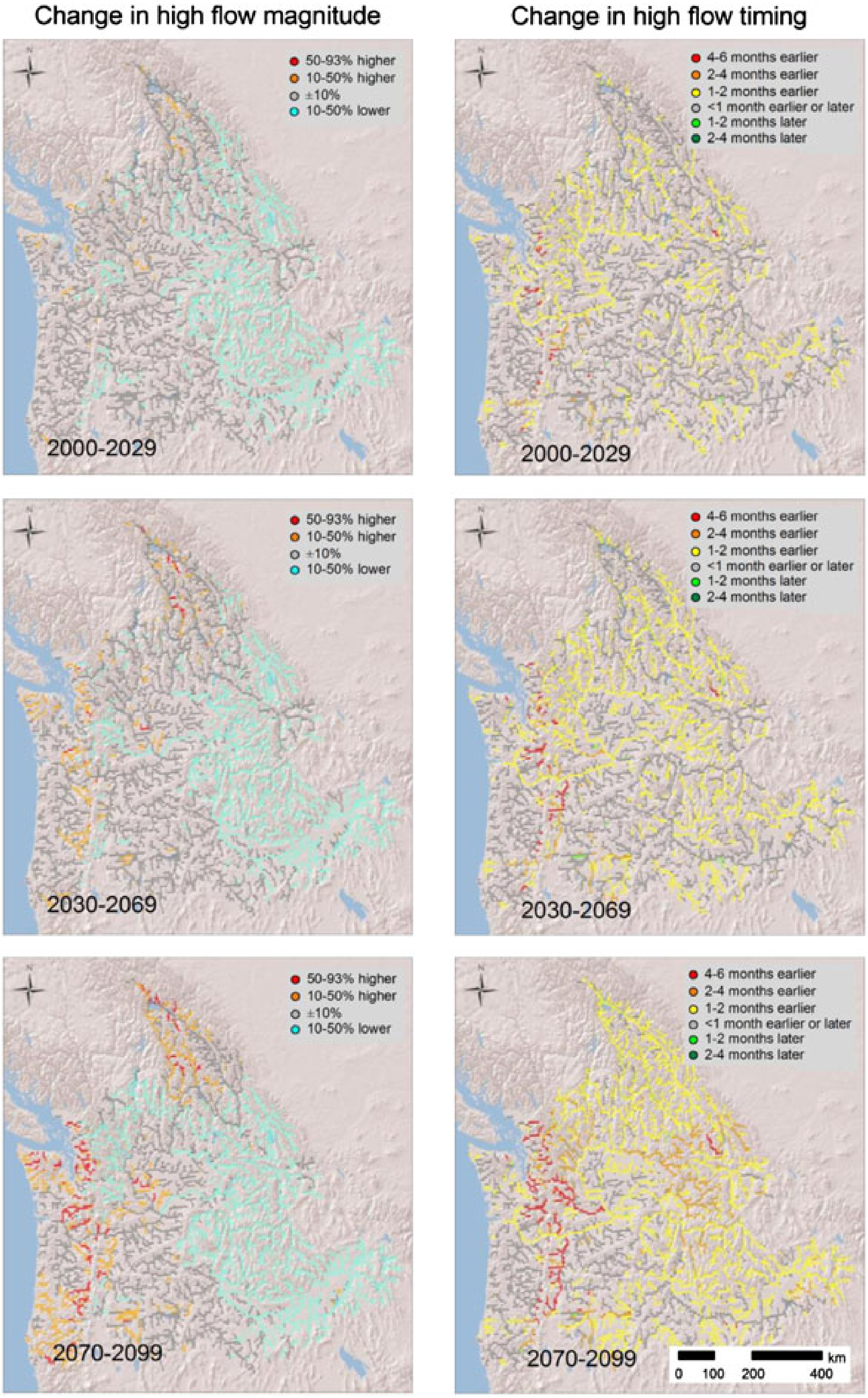

Figure 7. Modelled change in the maximum mean monthly flow and shift in timing of maximum monthly flows. Ratio is maximum mean monthly flow from the future period 2070–2099 divided by the maximum mean monthly flow from the period 1970–1999. For timing of maximum monthly flows, areas mapped in red indicate a shift from maximum monthly flow during spring snowmelt (usually April or May) to maximum flows during December and January winter storms. Areas in yellow indicate areas with maximum monthly flow remaining in late winter or spring, but shifted 1–2 months earlier (generally April–May to February–March)

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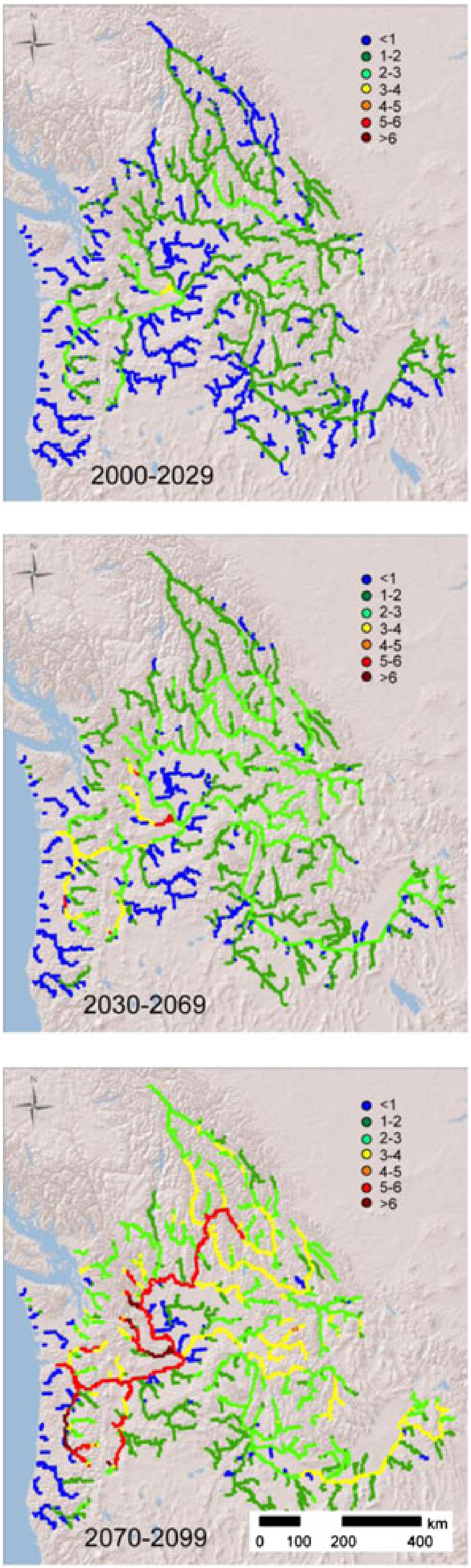

Figure 8. Modelled increase in maximum average weekly temperature through time in the Columbia River basin

climate effects are expected to impact a project's or plan's effectiveness within a few decades do we suggest adjustments to project priorities or designs.

We also review restoration actions in the context of their ability to maintain or increase resilience of river ecosystems and salmon populations (Waples *et al*., 2009). We define resilience as the ability of a system to absorb change and still maintain its basic ecosystem functions and relationships, even though the balance of habitat types or species may shift slowly through time (Holling, 1973; Waples *et al*., 2009). Pacific salmon are adapted to wide array of natural disturbance regimes by virtue of their life history diversity, and restoration actions designed to reduce constraints on life history diversity allow Pacific salmon a broader range of options by which to respond to climate change (Waples *et al*., 2008, 2009)—conferring resilience to both populations and meta-populations (Greene *et al*., 2010; Schindler *et al*., 2010). That is, restoration actions that increase habitat diversity to the point that salmon have the ability to express alternative life history strategies are considered to potentially increase population resilience. For example, restoring diverse floodplain habitats or reconnecting cold-water tributaries to main stem habitats by barrier removals offers salmon a variety of physical and thermal conditions, allowing multiple species to persist and to express varied life history strategies within species (Poole *et al*., 2008; Waples *et al*., 2009). In contrast, creation of pools by adding wood to a small stream generates a small increase in habitat diversity but does not offer an array of habitats that allow expression of alternative life histories. Hence, we consider the former action to potentially increase resilience but not the latter.

Restoring connectivity

Restoring connectivity (longitudinal, lateral, and vertical) typically improves both physical and biological functions of river systems. Restoring longitudinal connectivity for salmon is primarily intended to reestablish salmon migration to diverse habitats that have been lost through construction of artificial barriers such as dams or culverts, but it often also restores downstream transport of essential flows, sediment, and wood or organic matter. Restoring lateral connectivity generally refers to reconnection of rivers to their floodplains by removal of levees or bank armouring. These actions restore the ability of the river system to create and sustain diverse habitats and to allow migration of salmon into those habitats. Actions that aim to restore vertical connectivity seek to aggrade incised or scoured channels, which increases the connection between surface and subsurface flows and increases floodplain connectivity over time.

Longitudinal connectivity (barrier removal). The primary aims of restoring longitudinal connectivity by removal of dams or other blocking structures are to (1) reestablish upstream and

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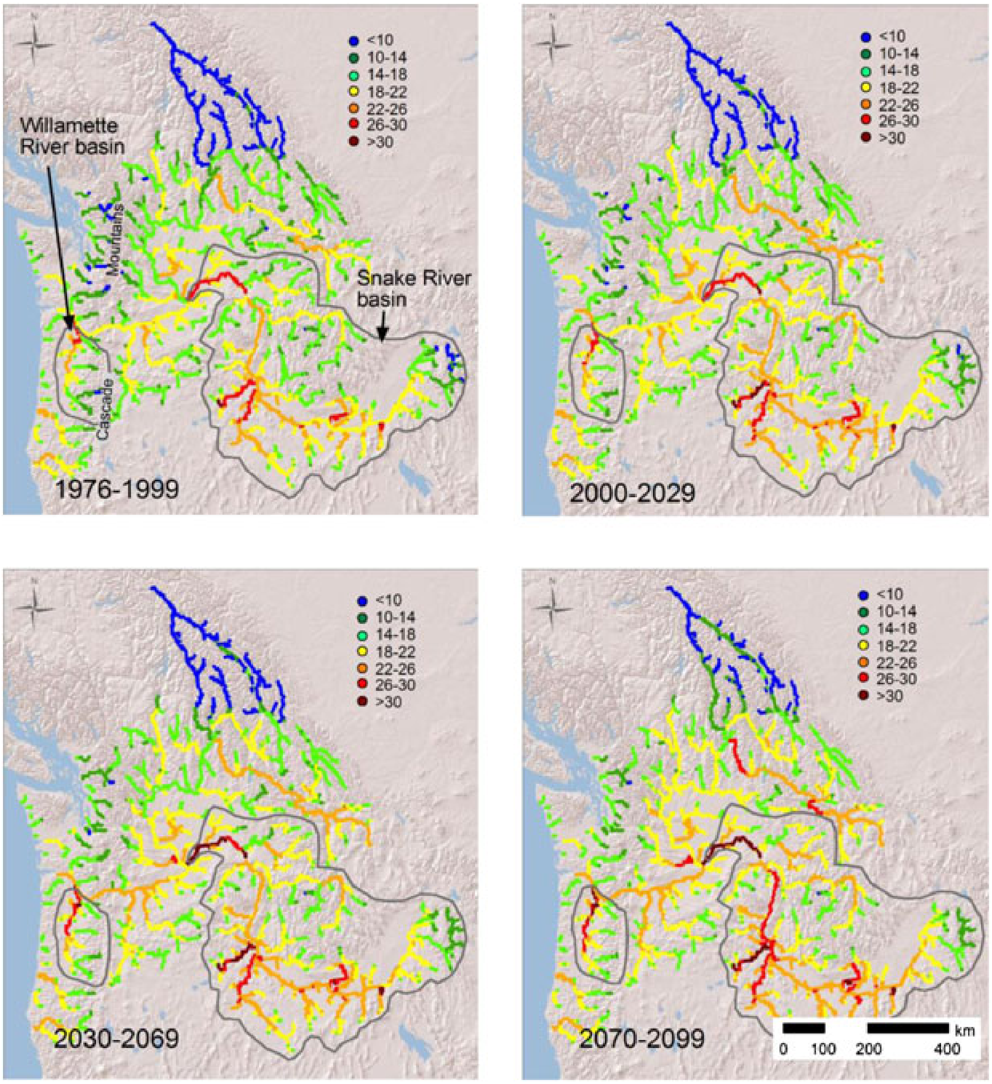

Figure 9. Modelled maximum weekly temperature through time in the Columbia River basin

downstream fish migration pathways and (2) restore natural stream flow, sediment, and organic matter transport (Pess *et al*., 2005). Removal of dams or providing fish passage on dams that cannot be removed will allow fish to access important upstream cool water habitats when downstream areas become too warm (McClure *et al*., 2008; Pess *et al*., 2008), thereby increasing habitat and life history diversity at the population and meta-population scales (Beechie *et al*., 2006; Waples *et al*., 2009). Where dams or other structures contribute to reduced low flows or increased stream temperature, dam removal can also ameliorate low base flow and high temperature problems by restoring downstream movement of sediment and water (Burroughs *et al*., 2009).

Lateral connectivity (floodplain reconnection). The aims of re-establishing lateral connectivity between river channels and floodplains are often twofold: to restore river floodplain dynamics that create diverse habitats and to restore fish access to floodplain habitats (Pess *et al*., 2005; Waples *et al*., 2009). These actions, which typically include reconnection or creation of side channels and sloughs, removal or set back of levees and dikes, and re-meandering of dredged or straightened channels, can ameliorate peak flow increases by storing flood water and reducing flood peaks (Sparks *et al*., 1998; McAlister *et al*., 2000) or by increasing the availability of velocity and thermal refugia (Sommer *et al*., 2001; Morley *et al*., 2005; Jeffres *et al*., 2008; Poole *et al*., 2008). Similarly, removing levees or re-meandering channels can ameliorate temperature increases by increasing length of hyporheic flow paths beneath the floodplain, which can cool water during the summer (Arrigoni *et al*., 2008; Konrad *et al*., 2008; Poole *et al*., 2008; Opperman *et al*.,

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Table III. Summary of restoration action types and their ability to ameliorate climate change effects on peak flow, low flow, stream temperature, or to increase salmon population resilience

Category	Common techniques	Ameliorates temperature increase	Ameliorates base flow decrease	Ameliorates peak flow increase	Increases salmon resilience
Longitudinal connectivity (barrier removal)					
	Removal or breaching of dam	●	●	○	●
	Barrier or culvert replacement/removal	○	○	○	●
Lateral connectivity (floodplain reconnection)					
	Levee removal	●	○	●	●
	Reconnection of floodplain features (e.g. channels, ponds)	●	○	●	●
	Creation of new floodplain habitats	●	○	●	●
Vertical connectivity (incised channel restoration)					
	Reintroduce beaver (dams increase sediment storage)	●	●	●	●
	Remove cattle (restored vegetation stores sediment)	●	●	●	○
	Install grade controls	●	●	●	○
Stream flow regimes					
	Restoration of natural flood regime	●	●	○	◒
	Reduce water withdrawals, restore summer baseflow	●	●	○	○
	Reduce upland grazing	○	◒	◒	○
	Disconnect road drainage from streams	○	○	●	○
	Natural drainage systems, retention ponds, other urban stormwater techniques	○	◒	●	○
Erosion and sediment delivery					
	Road resurfacing	○	○	○	○
	Landslide hazard reduction (sidecast removal, fill removal)	○	○	○	○
	Reduced cropland erosion (e.g. no-till seeding)	○	○	○	○
	Reduced grazing (e.g. fencing livestock away from streams)	◒	○	○	○
Riparian functions					
	Grazing removal, fencing, controlled grazing	●	○	○	○
	Planting (trees, other vegetation)	●	○	○	○
	Thinning or removal of understory	○	○	○	○
	Remove non-native plants	◒	◒	○	○
Instream rehabilitation					
	Re-meandering of straightened stream, channel realignment	◒	○	○	◒
	Addition of log structures, log jams	◒	○	○	○
	Boulder weirs and boulders	◒			
	Brush bundles, cover structures	○	○	○	○
	Gravel addition	○	○	○	○
Nutrient enrichment					
	Addition of organic and inorganic nutrients	○	○	○	○

Actions are grouped by major processes or functions they attempt to restore: connectivity (longitudinal, lateral and vertical), watershed-scale processes (stream flow and erosion regimes), riparian processes, instream rehabilitation, and nutrient enrichment. Filled circles indicate positive effect, empty circles indicate no effect, and partially filled circles indicate context-dependent effects. See text for supporting citations.

2010). Increasing habitat diversity by restoring lateral connectivity generally allows for increased life history diversity within a population (Waples *et al*., 2009), which has been linked to increased population resilience (Greene *et al*., 2010; Schindler *et al*., 2010). Floodplain reconnection actions generally do not ameliorate base flow decreases.

Vertical connectivity (restoring incised channels). Channel incision (or downcutting) has degraded stream and riparian habitats in many rivers of the PNW by lowering water tables, reducing exchange between surface and subsurface flows, and decreasing late summer stream flows. Associated losses in riparian vegetation lead to reduced shading

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and organic matter inputs to streams and increased stream temperatures (Elmore and Beschta, 1987; Poole and Berman, 2001). Moreover, incised streams rarely access their floodplains, high flows are concentrated within the incised channel, and fish have no access to slow-water refugia during floods (Harvey and Watson, 1986; Elmore and Beschta, 1987; Shields *et al*., 1995). Efforts to restore incised streams by increasing sediment storage and aggrading the channel aim to restore floodplain aquifer storage, increase summer base flow and decrease summer stream temperature, and increase availability of flood refugia (Pollock *et al*., 2007; Beechie *et al*., 2008b). Some restoration techniques, such as use of beaver dams to increase sediment storage, have the added effects of increasing summer base flows, locally decreasing or buffering stream temperature and increasing habitat diversity and productivity (Ponce and Lindquist, 1990; McRae and Edwards, 1994; Pollock *et al*., 2003; Pollock *et al*., 2007). Hence, restoration of incised channels has the potential to ameliorate climate-induced increases in stream temperature, effects on peak flows and low flows, and also to increase life history diversity through creation of off-channel and pond habitats. We emphasize that ameliorating climate change effects through aggradation techniques is specific to incised channels and that the same techniques may have different responses in other settings. For example, water may be warmer in a beaver pond within an otherwise closed canopy system, although stream cooling may still occur downstream of the pond (Robison *et al*., 1999).

Restoring stream flow regimes

Flood flows are increased to a moderate degree by logging and forest roads (Jones and Grant, 1996), grazing effects (Belsky *et al*., 1999), and to a much greater degree by impervious surfaces in urban areas (Booth *et al*., 2002). The primary mechanism by which logging roads increase peak flows is interception of subsurface flow through soils (which moves relatively slowly) and rapid routing of water to streams through ditches (Furniss *et al*., 1991; Jones and Grant, 1996). Road rehabilitation actions to decrease peak flow effects generally focus on addition of cross-drains to reduce routing of water directly from road ditches to the stream (Furniss *et al*., 1991). In an urban environment, the primary focus is to reduce the impacts of impervious surfaces by creating additional stormwater retention structures or modifying impervious surface areas so that rapid runoff is routed into groundwater storage rather than storm drains (e.g. Booth and Leavitt, 1999). In many cases, increased runoff and flood flows cause summer baseflows to decrease due to loss of infiltration and water storage in soils (e.g. Belsky *et al*., 1999). Hence, reductions of grazing or logging effects on flood flows may also increase low flows in summer.

Low stream flows are often reduced by withdrawal of water from streams for irrigation or consumptive uses (Poff *et al*., 1997; Myers *et al*., 1998), and both peak and low flows may be dramatically reduced by water storage behind dams (Stanford *et al*., 1996; Poff *et al*., 1997). Restoring some or all of abstracted water to streams through purchase of water rights or increased irrigation efficiency can dramatically increase low flows to streams (Poff *et al*., 2010) and directly ameliorate climate-induced decreases in low stream flow or increased stream temperature. In some cases, flow regulation has decreased peak flows to the point that many geomorphological and ecological functions of streams are lost (Olden and Poff, 2004). Moreover, low flows may be reduced in summer, which can also lead to increased stream temperature. In such cases, restoring 'environmental flow regimes' can ameliorate not only low stream flows, but can also increase habitat diversity by restoring channel-forming flows that maintain habitat diversity and other ecological functions (Stanford *et al*., 1996; Poff *et al*., 2010). Hence, where water storage or withdrawal has decreased low flows, purchase of water rights or use of water conservation measures that leave more water in the stream can ameliorate predicted decreases in low flows. Some dams can release cool water from deep in the reservoir, allowing dam operations to ameliorate stream temperature increases. Where water storage has decreased peak flows, restoration of channel forming flows can increase habitat diversity through restoration of physical functions that create diverse habitat features in streams and across the floodplain and also maintain riparian functions (Poff *et al*., 1997)—thereby increasing resilience of river ecosystems to climate change.

Reducing erosion and sediment delivery

In forested environments of the PNW, sediment supply to stream channels is typically increased through surface erosion on unpaved roads or by increased landsliding from roads or clearcuts (Reid and Dunne, 1984; Sidle *et al*., 1985). Therefore, sediment reduction efforts in forest environments commonly focus on road rehabilitation to decrease landslide hazards and surface erosion (Beechie *et al*., 2005; Roni *et al*., 2008). Landslide hazard reduction is typically achieved by removing or abandoning roads, or rebuilding stream crossings to avoid fill failures when culverts become blocked (Madej, 2001; McCaffery *et al*., 2007). Despite these efforts, future increases in storm intensity and a shift from snow to rainfall may drive more frequent mass wasting in forest environments, especially where road management has not yet achieved reductions in landslide hazard. Effects of increased surface erosion on roads can be abated by resurfacing the road or adding cross drains or water bars to prevent delivery of eroded sediments to streams (Furniss *et al*., 1991).

DOI: 10.1002/rra

In croplands, surface erosion is often increased by erosion of exposed soil in fallow fields (Wendt and Burwell, 1985; Ebbert and Roe, 1998). An increasingly common strategy to manage surface erosion in agricultural lands is no-till seeding, which preserves vegetative cover on croplands and dramatically reduces erosion and sediment delivery to streams (Wendt and Burwell, 1985; Ebbert and Roe, 1998). Grazing effects on sediment supply include removal of hillslope vegetation and erosion of exposed soils, as well as trampling of banks and increased bank erosion (Medina *et al*., 2005). Grazing impacts can be controlled either by removal of livestock from key areas (especially stream banks and riparian areas) or by grazing rotations that retain sufficient vegetative cover to reduce surface erosion (Medina *et al*., 2005). Although each of these actions can improve stream habitat by decreasing fines in the stream bed, increasing pool depth, or narrowing widened channels—none of these actions ameliorate decreased low flows, increased flood magnitude, or increased stream temperature (although increased pool depth may create thermal refugia in rare cases). Moreover, these actions do little to increase habitat or life history diversity except in cases where extremely high sediment supply has filled pools and reduced the diversity of habitat types (see Beechie *et al*., 2005 for examples).

Restoring riparian functions

Riparian rehabilitation actions aim to restore riparian functions such as stream shading, root reinforcement of banks, supply of large wood and organic matter, and trapping sediment or filtering nutrients (Kauffman *et al*., 1997; Pollock *et al*., 2005). In forested environments, restoration of riparian functions commonly focuses on thinning or replanting of riparian forests to restore wood recruitment and shade functions and, secondarily, to restore other functions (Beechie *et al*., 2000; Welty *et al*., 2002; Meleason *et al*., 2003). Restored riparian functions do not directly ameliorate the stream flow changes predicted by climate change models, but may mitigate stream temperature increases via increased shading (Johnson, 2004), or via increased wood recruitment and sediment storage in headwater channels that have been scoured to bedrock (Pollock *et al*., 2009). However, removal of certain non-native species that use more water than native species and provide less shade can ameliorate increased stream temperatures or decreased flows. In non-forest environments, replanting of denuded or managed riparian zones and removal or reduction of livestock grazing typically results in regrowth of riparian vegetation and should also ameliorate increases in stream temperatures through increased shade, bank stability, and narrowing of stream channels (Medina *et al*., 2005). Riparian restoration can lead to modest increases in habitat diversity over the long term via formation of pools or hiding cover (Beechie *et al*., 2000), whereas actions that seek to thin riparian zones are unlikely to affect either stream flow or temperature (Pollock *et al*., 2009). Finally, restoration of normative flow regimes on regulated rivers should help recovery of riparian areas on larger rivers, as seedling establishment for key riparian species is often dependent on flood magnitudes and duration (Stanford *et al*., 1996; Mahoney and Rood, 1998). Riparian restoration can be expected to increase ecosystem resilience in the sense that rivers with intact riparian buffers can buffer ecological functions against changes in stream flow, but it is unlikely to increase life history diversity and salmon resilience beyond the buffering of temperature effects.

Instream rehabilitation

Instream rehabilitation includes restoration actions that seek to improve habitat conditions by actively altering channel habitat structure (e.g. adding wood debris, spawning gravel), reconstructing channel characteristics (re-meandering), or by providing cover for fish (Roni *et al*., 2008). Such fixed structures are susceptible to failure or require maintenance, especially in the face of increased magnitude and frequency of peak flow events as predicted by climate change models. Although instream rehabilitation actions such as wood and boulder placement have been documented to provide quick improvements in both physical habitat and fish production (Cederholm *et al*., 1997; Solazzi *et al*., 2000; Roni and Quinn, 2001), they do not restore the underlying disrupted process (typically large wood delivery) and are unlikely to last more than one or two decades without additional intervention or maintenance (Roni *et al*., 2002). Moreover, instream rehabilitation actions generally do not ameliorate changes in temperature, base flow, or peak flows. For example, some studies have shown that creation of pool-riffle sequences can lead to increased hyporheic exchange and increased temperature variability, but none has shown a significant net decrease in stream temperature (Crispell and Endreny, 2009; Hester *et al*., 2009). This is most likely because the subsurface flow path is too short to significantly affect stream temperature (Poole *et al*., 2008). By contrast, restoring sediment storage to channels that are incised to bedrock may reduce stream temperatures if the loss of sediment has completely eliminated hyporheic exchange and increased stream temperature (Pollock *et al*., 2009). In such cases, use of wood or boulder structures to store sediment may decrease stream temperature. Finally, instream habitat actions can increase local habitat complexity (particularly if a large portion of the stream is treated), but such actions are unlikely to increase life history diversity or resilience of salmon populations.

DOI: 10.1002/rra

Nutrient enrichment

The purpose of nutrient enrichment is to compensate for lack of marine-derived nutrients from reduced salmon returns by adding nutrients and carbon to boost stream or lake productivity, and ultimately fish production (Bilby *et al.*, 1998; Gresh *et al.*, 2000; Kiffney *et al.*, 2005). These exogenous sources of nutrients are important to the productivity of naturally oligotrophic rivers of the PNW where many salmonid populations are food-limited (e.g. Boss and Richardson, 2002). As with instream rehabilitation actions, nutrient additions do not address the ultimate cause of low nutrient levels as a result of reduced salmon runs and, in the absence of increased salmon returns, are dependent on continually adding nutrients to maintain any benefits (Roni *et al.*, 2008). Nutrient additions do not ameliorate climate change effects on stream flow, stream temperature, or habitat diversity. However, an important secondary effect of increased stream temperature is increased metabolism in juvenile fishes, which increases food requirements to maintain positive growth (McCullough *et al.*, 2001; Boughton *et al.*, 2007). Where reduced nutrients and food resources have already compromised growth of juvenile salmonids, rehabilitation actions to increase nutrient supply—thereby increasing invertebrate abundance and prey availability for juvenile salmonids—may indirectly ameliorate temperature effects on salmonid growth rates (Wipfli and Baxter, 2010). However, this would require a consistent, long-term nutrient supplementation programme and would not lead to self-sustaining nutrient levels without continual intervention.

DECISION SUPPORT STRUCTURE TO EVALUATE CLIMATE CHANGE EFFECTS ON SALMON RESTORATION

We proposed four guiding questions to help determine whether restoration plans or actions should be altered to accommodate climate change (first column of Figure 10). We have also provided key maps and information to answer these questions (Figures 3–7, Tables 1–3). However, translation of this information into adaptation of restoration plans or actions can be ambiguous, so we offer two simple decision support tools to assist in evaluating restoration plans or actions in the context of climate change. Both are simple flow charts that illustrate how answers to the guiding questions might lead to logical adaptations of restoration plans or actions. We do not intend these to be rigid protocols with predefined outcomes because there are many possible combinations of future climates, restoration strategies, and species responses, and it is difficult to arrive at a set of rules that will apply to all possible cases. Rather, we intend these tools to illustrate how answers to the guiding questions can be integrated to arrive at management decisions in the context of local goals and objectives, as well as in the context of local climate change scenarios.

Evaluating a salmon recovery plan

In most cases, the first of the guiding questions has been answered in the process of developing local salmon recovery plans (e.g. Shared Strategy Development Committee, 2007). That is, an important component of salmon recovery plans is the identification of habitat impairments that constrain salmon population growth, and which, if addressed, will increase abundance or productivity (population growth rate) of the population (McElhany *et al.*, 2000; Beechie *et al.*, 2003). From this analysis, a list of important habitat recovery actions can be developed and prioritized (Beechie *et al.*, 2008a). However, these lists are commonly developed without consideration of future climate change effects on habitats and therefore have not considered how climate change might alter the suite of restoration actions identified as necessary to achieve salmon recovery.

Evaluating whether potential climate change effects on stream flow or temperature will change the list of restoration actions necessary for salmon recovery (question 2) begins a decision tree that helps restoration planners determine whether a salmon recovery plan should be revised to accommodate future climate change effects (Figure 10). Answering this question requires examination of potential climate change effects on stream flow and temperature (Figures 3–6) and a qualitative assessment of whether future stream flows or temperatures are likely to alter conclusions about which habitat restoration actions are necessary for salmon recovery. If climate change effects on stream flow or temperature are not expected to change the types or priority of restoration actions, then restoration actions may proceed according to the current plan. An important caution is that any assessment using mapped scenarios of flow or temperature changes should recognize that the resolution of the maps is quite low (in our analysis, the smallest grid cell representing a stream is 6 × 6 km) and that there is considerable variation in predicted stream flow and temperature changes among emissions scenarios and GCMs (Elsner *et al.*, 2010). Therefore, any evaluation of these stream flow and temperature scenarios should acknowledge that uncertainty in the climate scenarios is high.

If the evaluation of climate change scenarios indicates a change in the types of actions needed for recovery, then planned actions should be evaluated to determine whether they ameliorate the local climate change effects (question 3). For example, a coho salmon population may currently be constrained by winter rearing habitat availability, but potential increases in summer stream temperatures and decreases in summer stream flows (Figure 9) may reduce summer rearing habitat availability to the point that it

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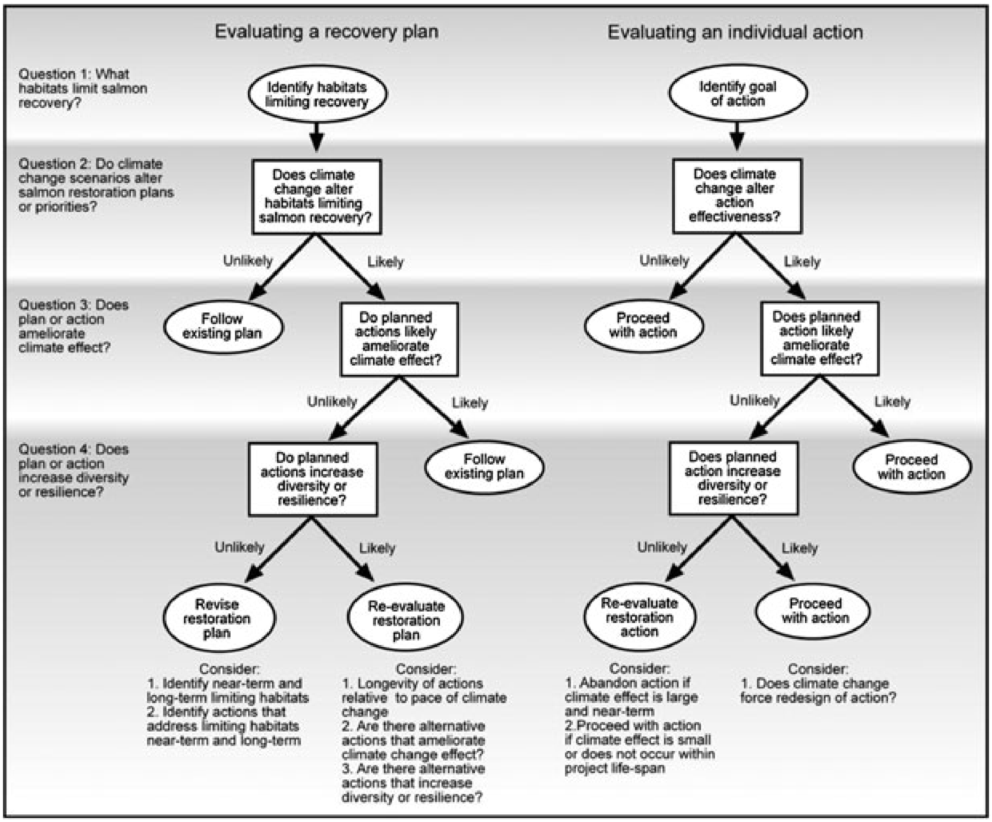

Figure 10. Schematic diagram of the decision-making process for adapting salmon recovery plans or individual restoration actions to climate change, and relationship to the four guiding questions

becomes the primary constraint on a population's recovery. If the planned restoration actions are likely to ameliorate climate change effects on stream flow or temperature (from Table III) and preserve the anticipated effectiveness of the restoration plan, then restoration can also proceed without modification. However, if actions will not ameliorate the climate change effects, revisions to the restoration plan should be considered. We acknowledge that determining whether the plan will ameliorate a temperature effect enough to prevent stream temperatures from exceeding critical thresholds is extremely difficult. In most cases, available data and models are not sufficient to answer this question quantitatively and with confidence. However, most restoration actions are not expected to reduce stream temperatures by more than 1–2°C (e.g. Medina *et al*., 2005; Arrigoni *et al*., 2008), so we suggest as a rule of thumb that restoration actions in areas that are less than 1–2°C below a critical threshold be considered unlikely to ameliorate a climate change effect. Nevertheless, it is possible that some combinations of actions might reduce stream temperature by more than 2°C, and local experience with restoration actions and changes in stream flow or temperature should be considered in management decisions. Moreover, salmon are often adapted to higher temperatures than are typically reported in the literature, and data on local thermal tolerances of salmon should be considered.

When revision of a plan is warranted, the degree to which the plan should be revised depends on whether the proposed actions contribute to increasing resilience of the population (question 4). Where the main habitat restoration actions in a plan contribute significantly to increasing resilience of populations (e.g. by increasing habitat diversity; Waples *et al*., 2009), the plan may be followed with the understanding that climate change may reduce effectiveness of the habitat restoration plan over the long term. There will always be considerable uncertainty about whether the actions can increase resilience enough to allow population recovery. But in any case, restoring diverse habitats will increase resilience of the riverine ecosystem—thereby increasing the likelihood that a salmon population can recover under a warming climate. Where the main habitat restoration actions do not contribute significantly to increasing habitat diversity or resilience of a population, then the restoration plan should be revised to increase the likelihood that actions either ameliorate climate change effects or increase habitat diversity and ecosystem resilience. The re-evaluation should focus on identifying actions that will help the population recover under both existing and future

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limiting habitats, so that climate change effects on habitat conditions and population performance do not hinder recovery of the population. Restoration of key physical and biological processes will allow a river ecosystem to adjust naturally to changes in key ecosystem drivers such as stream flow and temperature and will be more robust to variation in future climate patterns than actions that attempt to control river behaviour or build specific habitat features (Waples *et al*., 2009; Beechie *et al*., 2010). We stress that even where detailed models are used to assess how climate change will affect habitats that limit population recovery (e.g. Battin *et al*., 2007), there will always be considerable uncertainty in both model structure and climate change scenarios. Therefore, we encourage adjustments to recovery plans that broaden the portfolio of actions to accommodate a wide range of potential future climate scenarios.

Although we did not model future stream flow and temperature for multiple emissions scenarios and climate models, previous studies give us some indication of the range of potential outcomes for air temperature and precipitation (e.g. Elsner *et al*., 2010, Mote and Salathé, 2010). On the basis of those studies, it seems prudent to consider a range of potential stream temperature increases at least 2°C higher than those predicted from our A1B ensemble climate scenario (although we recognize that there is not always a strong correlation between air temperature and stream temperature). We cannot suggest a similar range of values for stream flows because no studies have modelled variation in stream flow among GCMs in the PNW (although Elsner *et al*., 2010 modelled stream flow differences among two emissions scenarios). Nevertheless, uncertainty in precipitation predictions is very high, suggesting that a conservative approach might anticipate that changes in stream flow (either high or low) might be considerably larger than our map illustrates.

Finally, population status may also influence management choices. Populations at very low abundance may require an emphasis on near-term habitat recovery actions to stabilize abundance (i.e. longevity of actions may be only 10–20 years), whereas more stable populations may benefit more from restoration of processes that persist for much longer periods. For near-term actions, climate change will likely produce relatively small effects on habitat conditions, and plans that emphasize near-term actions may need little revision regardless of climate change threats. However, this is a relatively rare case (most populations are threatened rather than endangered), and emphasizing restoration of habitat-forming processes is more likely to succeed over the long term (Beechie *et al*., 2010).

Evaluating an individual habitat restoration action

Individual restoration actions are perhaps simpler to evaluate because their future effectiveness is primarily a function of their intended purpose, which can be very narrowly defined. Answering the four guiding questions leads to one of three potential decisions: proceed with the action as planned, redesign the project to accommodate climate change, or abandon the project in favour of other projects that maintain their effectiveness in the face of climate change. The first outcome—proceeding with the action as planned—is appropriate when climate change does not alter effectiveness or longevity of the action, or when the action ameliorates the climate change effect sufficiently to maintain project effectiveness in the future (Figure 10). Redesigning a project to accommodate climate change is most appropriate where the action effectiveness is not reduced but longevity may be reduced as a function of a climate change effect (e.g. if peak flows will increase then the project should be designed to accommodate larger peak flows than observed at present). Finally, it is prudent to consider abandoning a specific project if climate change will likely negate its intended purpose, the action does not ameliorate the effect, and the action does not increase diversity and resilience. In these cases, the action may be abandoned in favour of other actions that will maintain their effectiveness in the face of climate change.

In evaluating the potential effects of climate change on individual restoration projects, it is first necessary to know which species and life stage the restoration action targets in order to evaluate whether climate change alters the effectiveness of the action. For example, if an action is intended to restore a winter rearing habitat, then changes to winter stream flows will be an important evaluation criterion whereas summer stream temperatures may not. Once the purpose of an action is identified, one can ask whether climate change will alter action effectiveness. If the effectiveness is not altered, then the action can proceed pending evaluation of climate change effects on project longevity (Figure 10). If the effectiveness is likely to be reduced, then one should consider whether the action type significantly ameliorates climate-related changes in stream flow and temperature. Evaluating the ecological impacts of different temperature change scenarios is relatively straightforward, as each species and life stage has a relatively specific range of thermal tolerances (Tables I and II), and temperature change magnitudes (Figures 2 and 3) can be compared with those tolerances to judge whether climate change will likely reduce project effectiveness. Finally, it is also important to consider how long the restoration action will last when determining whether it will ameliorate the impacts of climate change. Actions such as restoring floodplain connectivity or removing migration barriers restore underlying watershed processes, can last many decades, and will likely be the most effective long-term strategies for climate change because they both ameliorate climate change effects and increase habitat diversity and resilience. Other actions that may last only two or three decades without continued intervention will only provide

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short-term amelioration for climate change impacts and are unlikely to appreciably increase resilience over the long term.

SUMMARY AND CONCLUSIONS

We developed a set of guiding questions and data to inform adaptation of habitat restoration plans for salmonids in northwestern USA. These same questions are applicable to any salmon restoration effort, and—moreover—generally applicable to restoration of many species or ecosystems. Key elements of adapting any restoration strategy to climate change include (1) understanding the current recovery needs, (2) evaluating whether climate change effects will likely alter those needs, (3) determining whether restoration actions can ameliorate climate change effects, and (4) determining whether restoration actions can increase ecosystem resilience. These components are not specific to salmon, nor are they specific to aquatic species. These same questions can be used for any ecosystem in which restoration actions might need to be adapted to accommodate environmental effects of climate change. The key questions that must be answered for any adaptation strategy are as follows: Does climate change alter restoration needs in the future? And can restoration actions increase ecosystem resilience by reducing climate change effects or increasing habitat diversity? When these questions are applied to other species or environments, data needs include an understanding of current restoration plans, an assessment of how climate change might alter restoration needs, data on likely environmental effects of climate change, and a review of potential restoration actions to evaluate their likely effectiveness under future climate scenarios.

Although habitat restoration can contribute to increasing resilience of salmon populations to climate change, restoration of freshwater habitats alone may not be enough for their recovery. Climate change effects are imposed on top of a long history of insults, including harvest and hatchery effects on population status, a broad array of habitat losses that have dramatically reduced salmon abundance in the western USA, and continuing changes in ocean conditions that are at least partly a result of climate change. These combined constraints have reduced wild salmon populations to the point that many have been listed under the US Endangered Species Act. Hence, recovery of these populations may also require adjustments to hatchery production and harvest levels that impact wild populations, which we did not address here. In combination, such actions will likely increase abundance and diversity in wild populations, allowing them to adapt to a changing climate.

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Effects of predator and flow manipulation on Chinook salmon (*Oncorhynchus tshawytscha*) survival in an imperiled estuary

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Abstract We evaluated the effects of non-native, piscivorous fish removal and artificial flow manipulation on survival and migration speed of juvenile Chinook salmon, *Oncorhynchus tshawytscha,* emigrating through the eastern Sacramento-San Joaquin Delta of California (Delta) using a Before-After-Control-Impact study design. Acoustically-tagged salmon survival increased significantly after the first predator reduction in the impact reach. However, survival estimates returned to pre-impact levels after the second predator removal. When an upstream control gate opened (increasing flow and decreasing tidal effect) juvenile salmon emigration time decreased and survival increased significantly through the impact reach. Though a short-term, single season experiment, our results demonstrate that predator control and habitat manipulation in the Delta tidal transition zone can be effective management strategies to enhance salmon survival in this highly altered system.

Keywords Predation · Telemetry · Tidal · Flows · Sacramento—San Joaquin Delta

Introduction

The San Francisco Estuary is the largest of its kind on the west coast of North America and among the most altered ecosystems in the United States (Cohen and Carlton 1998). Diversions from the Sacramento-San Joaquin Delta (Delta), the upper extent of tidal estuary, provide water for 25 million people and support a $32 billion agricultural industry (CDFA 2006). Juvenile Chinook salmon (*Oncorhynchus tschawytscha*), including two endangered stocks, suffer high mortality rates as they migrate through the industrialized Delta (Perry et al. 2010), and predation by striped bass (*Morone saxatilis*) and other non-native fish is thought to be one of several major contributing factors although to what extent has not been established (Nobriga and Feyrer 2007; NMFS 2009). Flow, turbidity, habitat quality, and predator density are thought to influence predation (Anderson et al. 2005), but no Delta experiments have evaluated the relative influence of these factors (although see Lindley and Mohr 2003 for a paper modeling striped bass predation on winter-run Chinook salmon). As a consequence, the

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efficacy of predator removal as a potential management action is also unclear.

The need to aide in the recovery of salmon populations, identified as endangered or threatened under federal and state regulations (Lindley et al. 2004), while also allowing for continued use of water for societal purposes (e.g. hydropower, flood control, municipal and agricultural diversions) has led to increased interest among resource managers for the potential implementation of predator control measures throughout major salmonid systems of the Pacific United States (Beamesderfer et al. 1996; Zimmerman and Ward 1999). However, there is considerable uncertainty regarding whether such actions might be effective in the Delta. The failures of predator control programs implemented elsewhere have been attributed to a number of factors, including: 1) prey populations were not limited by predation, 2) removal efforts did not impact a sufficiently large fraction of the predatory population, 3) strong evidence was lacking for the benefits of predator removal, 4) poor understanding of non-native predator life history traits, or 5) large removals triggered a compensatory response in the predator populations (Hubbs 1940; Jacobsen 1945; Meachum and Clark 1979; Otis 1988; EIFAC 1991; Goeman and Spencer 1992; Moyle and Marchetti 2006).

Nevertheless, there have been a number of successes in controlling predaceous fishes. Examples include sea lamprey (*Petromyzon marinus*) in the Great Lakes (Smith and Tibbles 1980; Koonce et al. 1993), reduced predation on sockeye salmon (*Oncorhynchus nerka*) following arctic char (*Salvelinus alpinus*) reduction in Alaska's Wood River system (Meachum and Clark 1979), and the increased production of sockeye salmon following an eradication program of northern pikeminnow (*Ptychocheilus oregonensis*) in Cultus Lake, British Columbia (Foerster and Ricker 1941). Beamesderfer et al. (1996) evaluated the effectiveness of northern pikeminnow removal in the Columbia and Snake rivers. Their results indicated that the number of large piscivorous northern pikeminnow could be significantly reduced by exploitation rates of only 10–20 %. Moreover, they concluded that salmonid survival in the Columbia River would benefit greatly from a low rate of northern pikeminnow exploitation as long as it did not stimulate a compensatory response among other predator populations.

Within the highly engineered Delta system, flow manipulation via artificial pulse and control structure operations has also gained interest in affecting survival of emigrating Chinook salmon (Perry et al. 2010). Analysis of coded-wire tagging releases between 1989 and 2006 in the southern Delta have shown river flows can positively influence juvenile salmon survival, but have also shown considerable variability between and within years. These experiments to-date have been unable to untangle complicated interactions between hydrologic conditions (where river inflow is only one factor) and biological factors such as predation (Hankin et al. 2010).

Though some aspects of Delta salmon ecology are well-studied (Sommer et al. 2001; McLain and Castillo 2009; Perry 2010), no experimental investigations have been conducted to directly estimate short-term, reach-specific changes in salmon survival associated with: 1) intensive predator reduction, and 2) large magnitude flow change (caused by opening of the Delta Cross Channel [DCC]). In this study we examined the relative effects of experimental reductions of potential predators and a flow pulse on the survival of emigrating juvenile Chinook salmon in the Delta.

Material and methods

The study was conducted on the North Fork Mokelumne River between 15 and 30 May 2010, within the migration period of fall-run Chinook salmon and when the DCC operation may change (Fig. 1). The experiment area is approximately 5.6 km of the North Fork Mokelumne River and includes one 1.6 km predator-removal reach (impact) and one 2.0 km control reach. These sites were chosen because they were similar in size, depth and general habitat structure and previous fish sampling in the area demonstrated similar fish species (unpublished data). We utilized a paired Before-After Control-Impact (BACI) design (Stewart-Oaten et al. 1986), where acoustically-tagged fish were released in 8 paired groups (16 subgroups each with 25 to 42 fish; average 32) both before and after predator removal and before and after a change in river flows (DCC opening). Five acoustic receivers were deployed at entrances to all potential study area pathways to detect experimental fish as they emigrated from the study reaches (Fig. 1). Acoustic receivers were retrieved and the final data was downloaded at the study's completion on 29 June 2010.

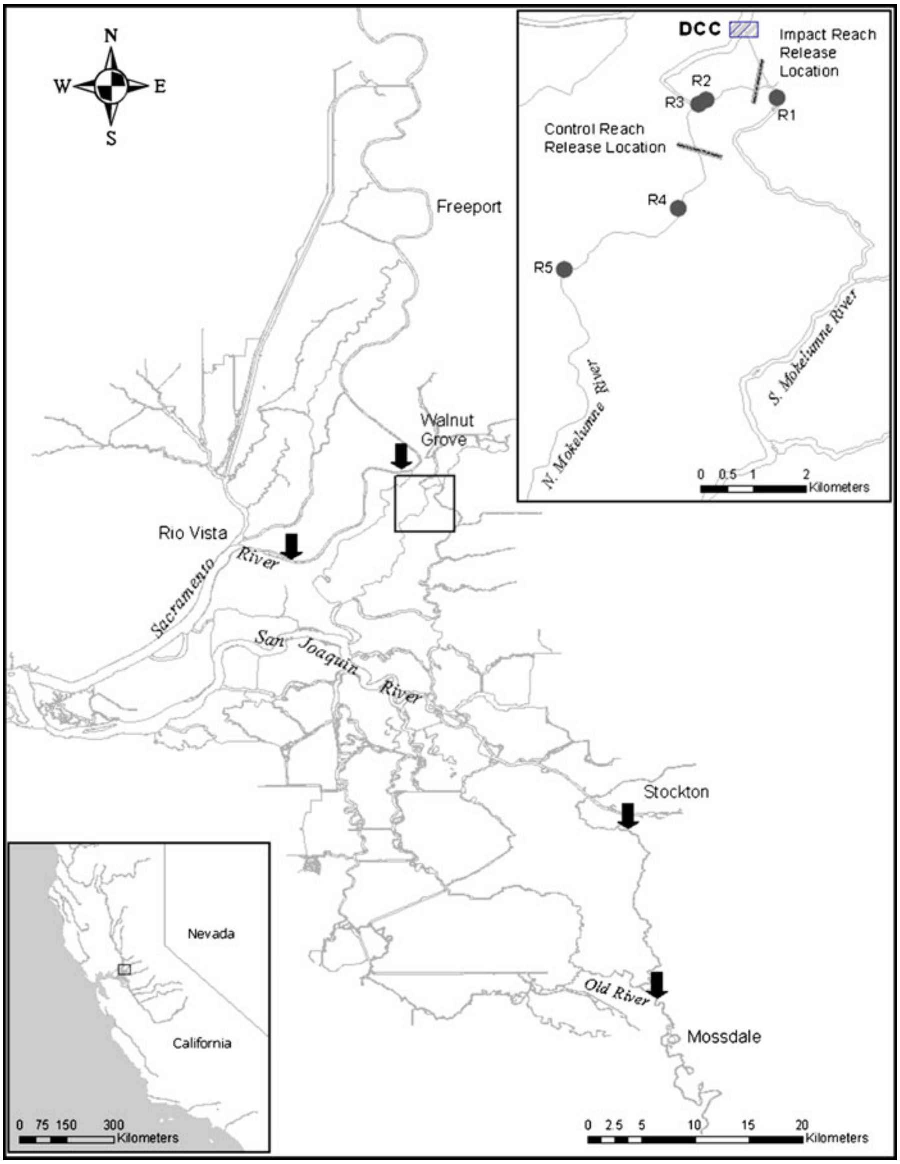


Fig. 1 Sacramento-San Joaquin Delta. Upper right corner inset shows North Fork Mokelumne River study area including release locations for acoustically tagged fish and acoustic receivers (R1 to R5). Study area was approximately 2.7 km downstream of the Delta Cross Channel (DCC). In the impact reach, survival was estimated from the release point to R2 (1.6 km). In the control reach, survival was estimated form the release point to R4 (2.0 km). Solid arrows bracket the channel length within which riverine conditions (*unidirectional flows*) rapidly change to tidal conditions (*bidirectional flow*). Downstream most arrows indicating transition point at high river flows, upstream most arrows indication transition point at low river inflows. See Fig. 6 for further information

Our study utilized Juvenile Salmon Acoustic Telemetry System (JSATS) acoustic tags which have been used extensively in rivers of the Pacific Northwest (McMichael et al. 2010), but which are new to the Delta. JSATS acoustic transmitters are small (0.433 g in air; 5.21 mm W × 12.00 mm L × 3.77 mm H; volume 0.14 ml) and have been designed specifically for use in juvenile salmonids. JSAT tags used in this study were set to a programmable pulse rate (PRI) of 5 s. The ability to tag smaller Chinook salmon is critical because the vast majority of juveniles passing through the Delta are less than 100 mm (Brandes and McLain 2001; McLain and Castillo 2009; Miller et al. 2010).

Tagging procedure

Juvenile fall-run Chinook salmon were obtained from the Mokelumne River Hatchery. Experimental fish averaged 102 mm (86–121±6.9 SD) in fork length (FL), with an average weight of 11.4 g (± 0.8 SD). Only healthy, uninjured, and unstressed fish were used for this study; fish were transferred from the holding area by a dip net with a water sanctuary to an anesthetic tank containing a 100 mg/l buffered tricaine methanesulfonate (MS-222) solution. Once anesthetized, fish were reassessed for health (e.g., infections, abrasions, hemorrhaging, gill coloration). Fish with obvious injuries, deformations, >20 % scale loss or other health issues were rejected. Fish too small for tag burden (i.e., tag weight >4 % body weight; Zale et al. 2005) or unduly stressed were also rejected. In a surgery cradle, fish were placed ventral-side up and anesthetic solution was pumped into their mouths via a tube attached to a pipette. The anesthetic was flushed over gills in order to keep the fish fully anesthetized throughout the procedure. An incision ~10 mm in length was made parallel to the ventral midline (~3 mm to the side of the ventral midline and 3 mm anterior to the pelvic girdle). A sterilized ultrasonic tag was then inserted into the peritoneal cavity of the fish, placed just under the incision. The incision was then closed with two interrupted sutures (using Suprmid Extra Nylon Cable Sutures). Once finished, fish were placed in live tanks and allowed to recover from surgery and anesthesia for at least 18 h (Moser et al. 1990; Stuehrenberg et al. 1990).

Experimental release

Experimental fish were released at the peak ebb tide available during daylight hours. On days when tagged fish were released, one paired group was released near-simultaneously into both the control and impact reaches. No more than one paired group was released per day. On consecutive days, two paired groups (G_1 and G_2) were released at the beginning of the study (before), 2 paired groups were released on consecutive days after the first predator removal (G_3 and G_4), 2 paired groups were released on consecutive days after the second predator removal (G_5 and G_6) and the final 2 paired groups were released on consecutive days 1 week after the second predator removal (G_7 and G_8). Prior to the release of the last two paired fish groups, the DCC, located upstream, was opened and flow conditions in the experimental area (affecting both the impact and control reaches) changed from tidal influence (9 to 18 m^3 sec^{-1} average daily flow) to river discharge influence (150 m^3 sec^{-1}; Fig. 2).

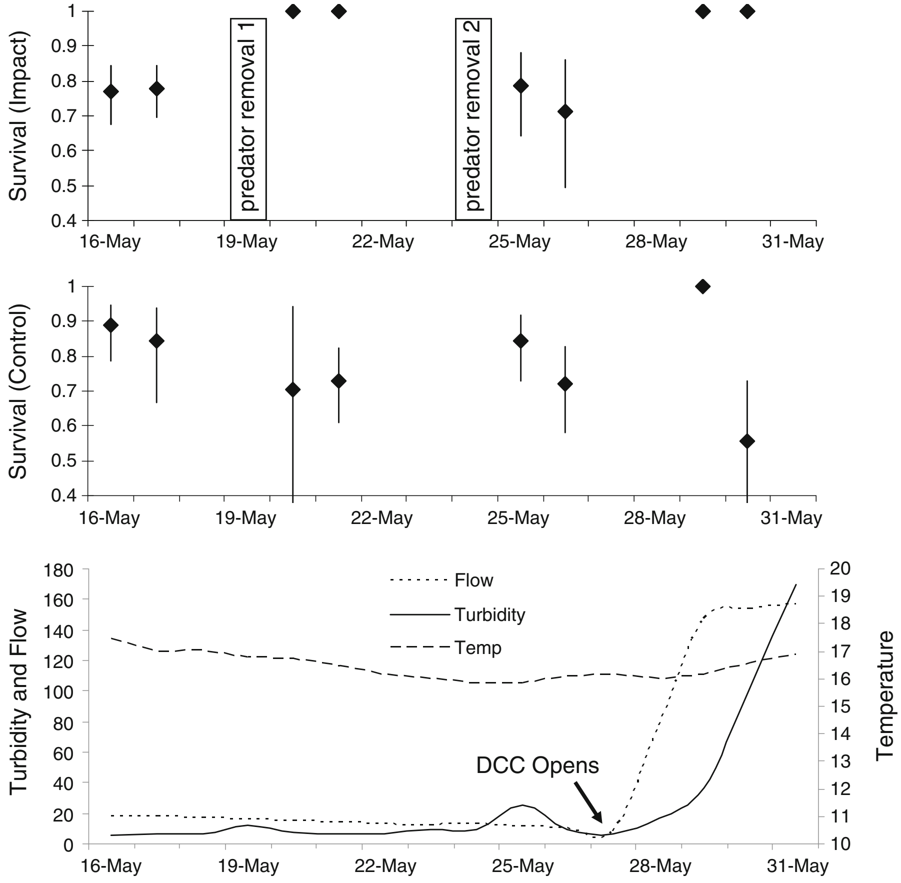


Fig. 2 Model averaging-based estimates of mean survival (±95 % confidence intervals) for salmon in the impact reach (*top graph*) and control reach (*middle graph*). Daily average flows (m^3 sec^{-1}), turbidity (NTU), and water temperature (°C) for the study area (*bottom graph*)

Predator removal

Boat electrofishing was conducted by a four-person crew using a shallow-draft, 5.3 m aluminum boat (Smith-Root, Electro-fishing model SR-16H; outboard motor with power trim) to perform a three-pass depletion sampling to remove and estimate numbers of potential predators in the impact reach (Raleigh and Short 1981; Meador et al. 1993). A single pass of electrofishing required ~5 s of electrofishing effort per meter of shoreline sampled. The combination of boat design, highly experienced operators, and slow shoreline water velocities allowed fine control of anode position and very thorough coverage of the immediate shoreline area relative to typical boat electrofishing operations. The reach was not blocked by nets because populations within discrete sites can be treated as effectively closed for the 24 h period associated with sampling (Korman et al. 2009). Captured fish were held in a live well with running water until each sampling pass was completed and then transported to holding pens at the bottom of the study site. Individual fish were measured and species was noted. Fish species identified in the literature as potentially predatory (Moyle 2002) were placed in the holding pens until the end of the study and then released to the impact reach (e.g. Fritts and Pearsons 2004; Sanderson et al. 2009). Non-predators were returned to the impact reach after identification and measurement.

Data analysis

We determined predator population density by least squares linear regression of predator catch per effort (CPE; electrofishing pass; y-axis) against cumulative catch (x-axis), lagged for one unit of effort (previous cumulative catch) because each electrofishing removal effort remained constant (Maceina et al. 1995).

We used the Cormack-Jolly-Seber mark-recapture model to estimate survival probabilities for both the control and impact reaches; estimation methods were analogous to those described by LaCroix (2008) and Skalski et al. (2001). For both the impact and control reaches, the full model estimated detection probability and survival for each subgroup. Reduced models for the control reach included modeling survival as constant among subgroups, and modeling survival as a covariate of flows. In the impact reach, our paired BACI experimental design made it possible to fit a reduced model whereby survival was estimated as a covariate of survival estimates for the control reach, and also as a covariate of predator removal treatments and flows. Specifically our covariate constrained model for estimating survival in the impact reach was:

$$\mathrm{logit}(\Phi_{\mathrm{IGi}}) = \beta_0 + \beta_1(\Phi_{\mathrm{CGi}}) + \beta_2(\mathrm{I}_1) + \beta_3(\mathrm{Flow}) \tag{1}$$

where Φ_{IGi} is the estimated survival in the impact reach for subgroup of paired group i (linked to beta slope parameters by the logit function to constrain parameters to the interval between 0 and 1); Φ_{CGi} is estimated survival in the control reach for subgroup of paired group i; I_1 is a dummy variable coding for the first predator removal; flow is a dummy variable coding for the change in flow conditions.

We assessed goodness-of-fit (GOF) for the full models using a parametric bootstrapping technique. Reduced candidate models were evaluated for their fit to tag detection data using an information theoretic approach (Burnham and Anderson 2002). Akaike's information criterion adjusted for small sample size ($\mathrm{AIC_c}$) was calculated for each model. Model weights ($\mathrm{AIC_c}w$) were then calculated using the difference in $\mathrm{AIC_c}$ values between the "best model" and other candidate models. Model weights range from 0–1 and are interpreted as the probability that the model under consideration is the best given the data. Model averaged survival and unconditional confidence intervals were calculated using model weights.

To assess differences in travel times of tagged fish through the study area we used a general linear mixed model with release group as a random effect and tested for effects of flow and fish size. Flows, turbidity and temperatures in the study area were downloaded from CDEC (California Date Exchange Center; http://cdec.water.ca.gov) for stations DLC (downstream of DCC) and WBR (Woodbridge Dam on the Mokelumne River). However, flows for our specific study reach are not measured directly, and so we estimated study reach flows using CDEC stations DLC and WBR, and "base" DSM2 HYRDO simulations described by Kimmerer and Nobriga (2008). To assess the influence of river inflows on the location of the tidal transition zone experienced by juvenile salmonids, we calculated percentage of time with positive flows by river kilometer (rkm), again using DSM2 HYDRO data from Kimmerer and Nobriga (2008).

General trend analyses were performed in using the JMP linear regression model function, which performs an analysis of variance (ANOVA; Sall et al. 2001). AIC, Akaike weights, Bootstrap analyses and mark–recapture estimates were performed in Program MARK (White and Burnham 1999).

Results

Within the study reach, mean daily flows ranged from 18.1 m^3 sec^{-1} (16 May) to 8.6 m^3 sec^{-1} (27 May) before DCC opening to 156.3 m^3 sec^{-1} (31 May) after DCC opening. Mean daily temperatures ranged from 17.4°C (16 May) to 15.9°C (24 May) before DCC opening to 16.9°C after opening. Mean daily turbidity ranged from 5.4 NTU (16 May) to 25.7 (25 May) before DCC opening to 169.5 (31 May) after opening. A total of 641 potential predators, consisting of 15 different introduced taxonomic groups (including hybrids), were removed during the study (Table 1). Each successive electrofishing pass captured fewer predators, indicating predators were being depleted by removal from the impact reach (Fig. 3). From the depletion relationships depicted in Fig. 3, we estimated 91 % (144 of 158) of predators vulnerable to electrofishing were captured in the first removal (19 May), and 83 % (497 of 601) in the second removal (24 May). The most common predators were *Lepomis* spp. (n=330 fish) and *Micropterus* spp. (n=255 fish). Ten striped bass were also captured in predator removals.

Goodness-of-fit testing indicated full models for control and impact reaches fit the data well (P=0.7 and P=0.2, respectively) and $\hat{c}$ was estimated near 1 for both; thus, no evidence of overdispersion in tag detection data. In the control reach, the model estimating survival for each release group (i.e. the full model) provided the best fit with an AIC_c weight>0.99. For the impact reach, the model including paired survival estimates from the control reach as covariates and which included the first predator removal and flow effects was the "best fit" with an AIC_c weight=0.72. The next best model was the same as the "best fit", but also included the second predator removal effect (AIC_c weight=0.28).

Survival estimates and unconditional 95 % confidence intervals varied considerably among release groups, with mean values ranging from 1 (100 %

Table 1 Potential predatory fish captured in the Impact reach of the North Fork Mokelumne River, 19 and 24 May 2010

Common name	Scientific name	Removal period		Fork Lenth (mm)
		19-May	24-May	Mean±SD
American shad	*Alosa sapidissima*	0	3	365±46.1
Black crappie	*Pomoxis nigromaculatus*	0	1	195
Blackbass hybrid	*Micropterus spp.*	8	0	114±40.7
Bluegill	*Lepomis macrochirus*	21	91	121±27.5
Brown bullhead	*Ameiurus nebulosus*	0	11	110±64.3
Green sunfish	*Lepomis cyanellus*	2	0	126±5.7
Hybrid sunfish	*Lepomis spp.*	0	21	127±25.0
Largemouth bass	*Micropterus salmoides*	50	81	175±79.2
Redear sunfish	*Lepomis microlophus*	44	171	126±28.0
Redeye bass	*Micropterus coosae*	0	74	111±34.0
Smallmouth bass	*Micropterus dolomieu*	5	0	228±99.9
Spotted bass	*Micropterus punctulatus*	6	39	143±64.8
Striped bass	*Morone saxatilis*	7	3	265±62.5
Warmouth	*Lepomis gulosus*	0	1	132
White catfish	*Ameiurus catus*	1	1	270±24.0
	Totals	144+497=641		

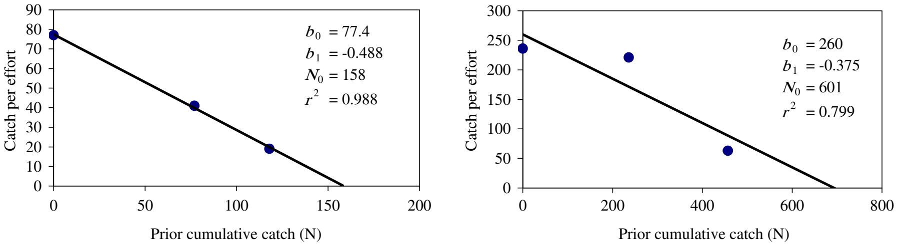
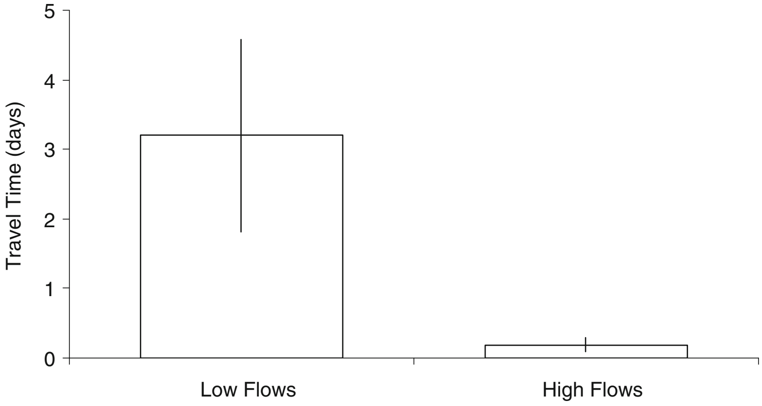


Fig. 3 Plots and regressions for numerical catch per effort versus cumulative catch (*N*) for the predator removal reach on the North Fork Mokelumne River (see Fig. 1). Three consecutive passes were made in the impact reach on 5/19/2010 (*left*) and 5/24/2010 (*right*). Dashed lines indicate least-square regression lines. Regressions intercepts (b_0), regression slopes (b_1), and coefficients of determination (r^2) are given; N_0 represents estimated numbers of predators inhabiting the study reach

survival through the study reach) to 0.55 (Fig. 2). Survival in the control reach varied among the eight release groups, and was not explained by the flow covariate. Impact reach survival also varied among groups, but model selection indicated that a significant proportion of the changes were associated with predator removal and flow effects. Survival improved significantly after the first predator reduction treatment (from <0.80 to >0.99), but estimated survival decreased to pre-impact levels after the second predator reduction treatment (Fig. 2). Flows and turbidity in the study area changed when the DCC gates opened on 27 May 2010. Flow (and turbidity) changes did not clearly influence survival in the control reach; both the highest and lowest survival rates observed occurred on consecutive days in the control reach after DCC gates opened (Fig. 2). However, in the impact reach, estimated salmon survival increased when the DCC gates opened. Opening of the DCC gates was also associated with a significant reduction (P=0.027) in travel time through the study area, from an average of 3.19 ±1.38 days to an average of 0.19 ±0.09 days (Fig. 4). In addition to changes in daily average flows (Fig. 3), analysis of 15-minute increment flow data showed opening of the DCC gates stopped tidal reverse flows and caused daily tidal flux to decrease from 250 m^3 sec^{-1} to less than 150 m^3 sec^{-1} (Fig. 5).

The influence of river inflows on the location of tidal transition zones differs among Delta locations. For the Sacramento River, 43 km of riverine habitat (with 100 % positive or unidirectional flow) is added as river flows increase from 292 m^3 sec^{-1} to 837 m^3 sec^{-1} and the tidal transition zone is displaced downstream by approximately 16 rkm (Fig. 6a). With DCC open, the Mokelumne River experienced mostly positive flows, more so with inflows at 18 m^3 sec^1 (relative to inflows at 8 m^3 sec^{-1}). With DCC closed, the Mokelumne River was entirely tidal and insensitive to the three levels of inflow assessed (Fig. 6b). As San Joaquin River inflows increased from 40 m^3 sec^{-1} to 162 m^3 sec^{-1}, the tidal transition zone moved approximately 21 rkm downstream (Fig. 6c).

Fig. 4 Average travel time in days (±SE) through the study area for release groups G1 to G6 (*Low Flows*) and for release groups G7 and G8 (*High Flows*). General linear mixed model analysis indicated a significant effect of flow (P=0.027), but no significant effect associated with fish size (P=0.878)



Discussion

Observational studies using acoustically tagged salmon in the Delta have allowed estimation of survival and migrations rates (e.g. Perry et al. 2010) and are greatly enhancing our understanding of salmon migration behavior. Our telemetric study of juvenile Chinook salmon is novel because it is the first instance of Delta survival and migration rates being estimated for Chinook smolts less than <135 mm, and also because this study marks the first use of acoustic tags as part of an experimental manipulation of predators and flows, two factors thought to influence emigrating salmon in the Delta and elsewhere (Lindley and Mohr 2003). Our results suggest intensive, site-specific predator removals can improve juvenile salmon survival immediately following the first predator removal. However, effectiveness with repeated treatments is unclear. Similar to some previous studies (Goeman and Spencer 1992), we observed an apparent response from the predator removal whereby predator densities increased and salmon survival decreased (to pre-impact levels) following the second predator removal. While mechanisms are unclear, removal of a stable predator community accomplished in the first treatment was apparently undone within one week by an influx of new predators. If site-specific predator removals are to benefit juvenile salmon survival, sustained effort over time (with daily rather than weekly removals) may be necessary. Alternatively, predator removals over a larger geographic area might be effective in reducing the pool of predatory fish available to re-colonize. On the Snake and Columbia rivers, the apparent success of northern pikeminnow bounty harvest (Beamesderfer et al. 1996) may be attributable to the relatively aggressive and geographically broad scope of predator reductions.

Delta studies have shown increased river flows may be associated with enhanced salmon survival (reviewed by Hankin et al. 2010), but no studies have elucidated the scale at which these benefits may occur. Though the spatial and temporal scope of our study was limited to an intensive investigation over a short time period, juvenile salmon survival changed in apparent response to experimental manipulation of predators and flows. While a significant response to the second predator removal was not apparent, we observed significantly improved survival after the first predator removal in the impact reach and significantly decreased travel times throughout the study area after the DCC gates opened and flow conditions rapidly shifted from tidal (bidirectional) to riverine (unidirectional). Perry et al. (2010) observed slower migration rates and increased mortality for juvenile Chinook salmon entering the tidally-influenced portion of the Sacramento River. Our study is consistent with the analysis by Perry et al. (2010) and supports a mechanism where river flows may affect salmon survival by altering the location of the tidal transition zone. If the tidal transition zone occurs where habitat conditions

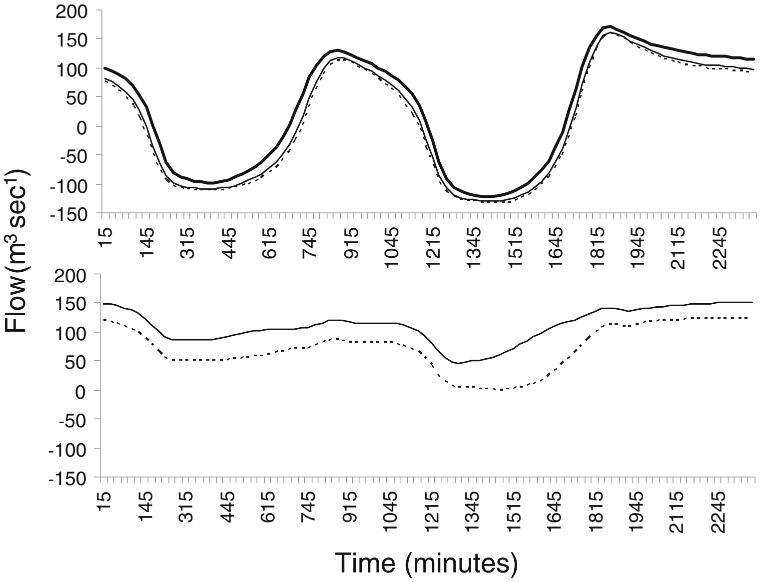


Fig. 5 15-min DSM2 HYDRO simulated flows with DCC closed (top) and DCC open (bottom) and NF Mokelumne River inflows at 8 m^3 sec^{-1} (*dashed line*), 18 m^3 sec^{-1} (*solid line*), 47 m^3 sec^{-1} (*heavy line*). Simulations for DCC open conditions are limited because DCC gates close for flood control when Sacramento River flows exceed approximately 700 m^3 sec^{-1}

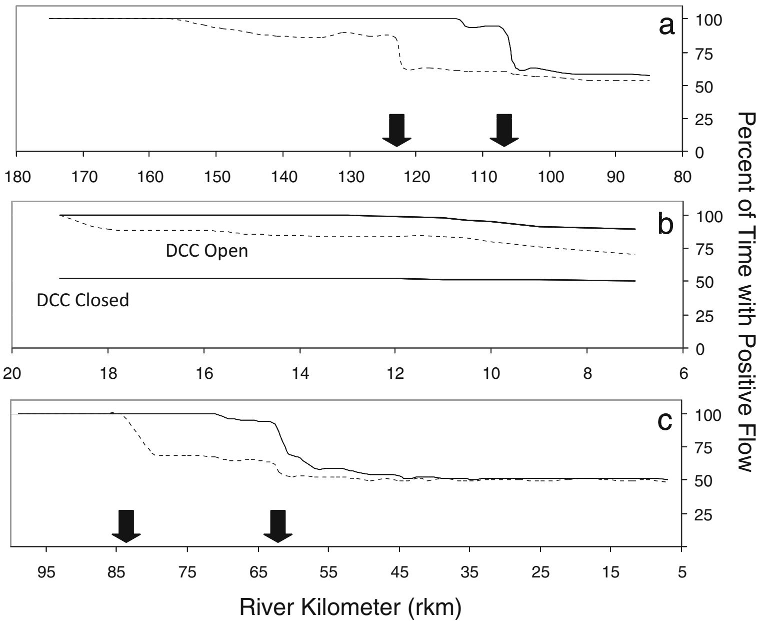


Fig. 6 Transition, by river kilometer, from riverine conditions (*unidirectional flow*) to tidal conditions (*bi-directional flow*). Sacramento River **a** inflow at 837 m^3 sec^{-1} (*solid line*) and at 292 m^3 sec^{-1} (dashed line). NF Mokelumne River **b** inflow at 18 m^3 sec^{-1} (*solid line*), and at 8 m^3 sec^{-1} (*dashed line*) with DCC closed and open. San Joaquin River **c** inflow at 162 m^3 sec^{-1}(*solid line*) and at 40 m^3 sec^{-1} (*dashed line*). Moving from upstream to downstream for each inflow level, solid arrows indicate the point of rapid transition from riverine conditions (*unidirectional flow*) to tidal conditions (*bidirectional flow*). Arrows correspond to those depicted in Fig. 1

are poor, or where predator densities are high, juvenile salmon are likely to experience greater predation mortality, and perhaps impaired growth. This should be studied more fully.

Electrofishing depletion data (Table 1) illustrates that the community of potential predators was effectively altered in our experiment. However, we cannot rule out that observed changes in impact reach salmon survival occurred for reasons other than reduced predation pressure. For example, reduced interspecific interactions (e.g. interference competition for shoreline rearing habitat) is also a plausible mechanism for improved salmon survival (Case and Gilpin 1974). Changes in biotic or abiotic conditions unmeasured in our study could have also caused or contributed to observed changes in juvenile salmon survival. Additional replicated experiments and different experimental designs would be necessary to identify and resolve these uncertainties.

Management implications

Resource managers seeking to improve salmon survival might target habitat enhancement actions or predator removals to channel segments where tidal transition typically occurs. Our analysis of flow data identifies these channel segments on the mainstem Sacramento and San Joaquin rivers. As an alternative to modifying habitat or predator abundance, managers could alter flow regime to increase the linear distance of river habitat with unidirectional flow. These small-scale habitat perturbations could provide a short, temporal expansion of complexity, which has been for the most part eliminated within the central Delta (Moyle et al. 2010). While DCC gate operations provide an outstanding setting for heuristic experimentation, the drastic flow change which occurs when the DCC gates open is not typical or representative for Delta water operations on the Sacramento River. For example, to produce an equivalent event on the adjacent Sacramento River would require flows to increase from 292 to 4,380 m^3 sec^{-1} (a 15x increase); a magnitude of flow change which occurs only during flood events. As illustrated by conditions with DCC gates closed (Fig. 5), Mokelumne River inflows within the range of typical operations (8 to 47 m^3 sec^{-1}) cannot appreciably influence or displace the tidal transition zone. While closing the DCC gates may be beneficial to Sacramento River emigrants, our study suggests it is likely detrimental to juvenile salmonids originating from the Mokelumne River.

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Impending extinction of salmon, steelhead, and trout (Salmonidae) in California

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Abstract California contains the southernmost native populations of most Pacific Coast salmon and trout, many of which appear to be rapidly headed toward extinction. A quantitative protocol was developed to determine conservation status of all salmonids native to the state. Results indicate that if present trends continue, 25 (78%) of the 32 taxa native to California will likely be extinct or extirpated within the next century, following the bull trout (*Salvelinus confluentus*), which was extirpated in the 1970s. California's salmonids are adapted to living in a topographically diverse region with a Mediterranean climate, characterized by extreme seasonal and inter-annual variability in streamflow. Consequently, California salmonids have evolved extraordinary life history diversity to persist in the face of stressful conditions that often approach physiological limits. The spatial distributions of California salmonids vary from wide-ranging anadromous forms to endemic inland forms persisting in only a few kilometers of stream. Eighty-one percent of anadromous taxa are threatened with extinction and 73% inland taxa are either threatened or already extinct. Although specific drivers of decline differ across species, major causes of decline are related to increasing competition with humans for water, human degradation of watersheds, and adverse effects of hatchery propagation. Climate change, interacting with the other causes of decline, is increasing the trajectory towards extinction for most populations. Bringing all of California's salmonid fishes back from the brink of extinction may not be possible. If there are bold changes to management policy, however, self-sustaining populations of many species may be possible due to their inherent ability to adapt to changing conditions.

Keywords Status assessment · Aquatic conservation · Climate · Hatchery · Mediterranean

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Introduction

> "…political compromise can't halt the forces that lead to extinction. Political compromises resolve human contests, but they seem to exert little or no influence over complex ecosystems. Without drastic action, the relentless ticking of the extinction clock continues."
>
> Paul VanDevelder, High Country News, March 4, 2011

Salmon, trout, and their relatives (Salmonidae) are iconic fishes of the Northern Hemisphere. They have adapted to cold productive oceans, rushing streams, and deep cold lakes, supporting fisheries wherever they occur. Salmonids have evolved diverse life history strategies in response to living in landscapes shaped by glaciers, volcanoes, earthquakes, and climatic extremes (Waples et al. 2008). Many undertake long oceanic and freshwater migrations while others evolved in isolation under extreme local conditions (Moyle 2002). Mobility coupled with natal homing and remarkable behavioral plasticity has resulted in a handful of species producing hundreds of genetically distinct runs, regional populations, and subspecies, representing distinctive color patterns, behaviors, and ecological attributes, tuned to local environmental conditions (Allendorf and Waples 1996; Behnke 2002). Many are top predators in the ocean and freshwater systems they inhabit. Their adaptability has also made some species extremely abundant, resulting in valuable fisheries throughout the northern hemisphere and, through introductions, the southern hemisphere as well (Montgomery 2003).

Despite their ecological, cultural, aesthetic, and economic importance, salmonid fishes are in severe decline in many, if not most, of their native habitats. Many populations have been extirpated, especially in heavily industrialized areas (Montgomery 2003). Perhaps nowhere in the world is the diversity of salmonids and their problems more evident than in California where a highly endemic fish fauna is interacting with intense human population pressure (Lackey et al. 2006; Moyle et al. 2008). The state's dynamic geology and climate have resulted in evolution of many distinctive forms, all characterized by distinctive zoogeographic, genetic, and life history patterns, such as three subspecies of golden trout in the Sierra Nevada and eight distinct types of Chinook salmon (Table 1). The diversity of salmonids is also the result of California's large size (411 000 km^2), varied topography, and long coast line (spanning 10° of latitude) which is adjacent to the California current region of the Pacific Ocean (Moyle 2002), one of the most productive oceanic ecosystems in the world (Carr 2001). Based on genetic and ecological distinctiveness we recognize 32 salmonid taxa native to California (21 of them anadromous, 11 of them non-anadromous), although just eight are considered "full species" (Table 1). Twenty-five of these taxa support or once supported major commercial and sport fisheries, while the rest historically supported at least small recreational fisheries. Today, most of these fisheries are either shut down or severely limited. In addition, the anadromous forms represent the southernmost native populations of the full species to which they belong.

The thirty-two taxa in this paper fit the definition of species under the federal Endangered Species Act of 1973, as 'full' species, subspecies, Evolutionary Significant Units (ESUs) or Distinct Population Segments (DPSs) although four are not yet officially recognized as such. Fifteen (47%) of them are already listed under state and federal Endangered Species Acts (Table 1) and one, the bull trout, last observed in the state in 1974, is extirpated. Even with half the native salmonids officially imperiled, no overview of salmonid status exists for California. In this paper, such an overview is presented based on standardized status assessments made independently of assessments of state and federal agencies. Because the decline of California's native salmonids may foreshadow similar declines to the north, our study can be viewed as a foundation for understanding synergistic impacts of human population growth and climate change on salmonid-bearing aquatic systems. As such, we discuss vulnerability of California salmonids to climate change and other significant anthropogenic threats, especially hatchery propagation.

Our appraisal of the conservation status of the salmonid fishes of California was designed to answer the following questions:

1. What is the conservation status of all California salmonids, both individually and in aggregate?
2. How does this status assessment compare to official Endangered Species Act assessments?
3. What are the major factors affecting status?

Table 1 List of all native salmonid fishes known to breed in California, ranked by level of extinction threat. Conservation status is for California only and approximates the IUCN classification system. For definitions of status scores and categories see Table 4

Species	Distribution	Status score	Conservation status
Bull trout, *Salvelinus confluentus*	Pacific Northwest	0.0	Extirpated in CA
Central coast coho salmon, *Oncorhynchus kisutch*[b]	California[d]	1.1	Endangered[a]
Pink salmon, *O. gorbuscha*	Pacific Coast[d]	1.3	Endangered
Upper Klamath-Trinity spring Chinook salmon, *O. tshawytscha*[b]	California[d]	1.6	Endangered
Southern Oregon Northern California coast coho salmon, *O. kisutch*[b]	California & Oregon[d]	1.6	Endangered[a]
Chum salmon, *O. keta*	Pacific Coast[d]	1.6	Endangered
Central Valley late fall Chinook salmon, *O. tshawytscha*[b]	California[d]	1.7	Endangered
Klamath Mountains Province summer steelhead, *O. mykiss*[c]	California[d]	1.7	Endangered
Southern California steelhead, *O. mykiss*[c]	California[d]	1.7	Endangered[a]
Paiute cutthroat trout, *O. c. seleneris*	California	1.7	Endangered[a]
Northern California coast summer steelhead, *O. mykiss*[c]	California[d]	1.9	Endangered[a]
McCloud River redband trout, *O. m. stonei*	California	1.9	Endangered
Kern River rainbow trout, *O. m. gilberti*	California	1.9	Endangered
Central Valley winter Chinook salmon, *O. tshawytscha*[b]	California[d]	2.0	Vulnerable[a]
Central Valley spring Chinook salmon, *O. tshawytscha*[b]	California[d]	2.0	Vulnerable[a]
Central Valley fall Chinook salmon, *O. tshawytscha*[b]	California[d]	2.0	Vulnerable
California golden trout, *O. m. aguabonita*	California	2.0	Vulnerable
Little Kern golden trout, *O. m. whitei*	California	2.0	Vulnerable[a]
Eagle Lake rainbow trout, *O. m. aquilarum*	California	2.1	Vulnerable
Lahontan cutthroat trout, *O. c. henshawi*	Western USA	2.1	Vulnerable[a]
Upper Klamath-Trinity fall Chinook salmon, *O. tshawytscha*[b]	California[d]	2.4	Vulnerable
California Coast fall Chinook salmon, *O. tshawytscha*[b]	California[d]	2.4	Vulnerable[a]
Central Valley steelhead, *O. mykiss*[c]	California[d]	2.4	Vulnerable[a]
South Central California coast steelhead, *O. mykiss*[c]	California[d]	2.4	Vulnerable[a]
Central California coast winter steelhead, *O. mykiss*[c]	California[d]	2.7	Vulnerable[a]
Northern California coast winter steelhead, *O. mykiss*[c]	California[d]	3.3	Near Threatened[a]
Goose Lake redband trout, *O. m. subsp.*	California	3.3	Near Threatened
Coastal cutthroat trout, *O. clarki clarki*	Pacific Coast	3.4	Near Threatened
Southern Oregon Northern California coast fall Chinook salmon, *O. tshawytscha*[b]	California & Oregon[d]	3.7	Near Threatened
Mountain whitefish, *Prosopium williamsoni*	Pacific Northwest	3.9	Near Threatened
Klamath Mountains Province winter steelhead, *O. mykiss*[c]	California & Oregon[d]	3.9	Near Threatened
Coastal rainbow trout, *O. m. irideus*	Pacific Coast	4.7	Least Concern

[a] Taxon listed by federal and/or state Endangered Species Acts

[b] Taxon is an evolutionary significant unit (ESU)

[c] Taxon is a distinct population segment (DPS)

[d] Taxon is anadromous

4. How do factors causing declines differ for anadromous and resident taxa?
5. What conservation strategies are likely to be most effective in maintaining salmonid populations in California?

Materials and methods

Evaluation of status In order to answer the above questions we compiled existing information for each salmonid taxon in California (including peer-reviewed literature, agency reports, gray literature, and observations of the professional biologists). For listed species, we also reviewed the official listing and status reports as important sources of information. All sources were condensed into comprehensive species accounts with standard format, found in Moyle et al. (2011, in press). For the majority of California taxa these accounts represent the most complete and exhaustive review of biological and management data assembled to date. Status assessments were produced using information contained in each species account using a standardized protocol designed to quantify extinction risk for California salmonids (Tables 2, 3, 4, 5).

The status scores were the numeric average of seven extinction threat metrics: 1) area occupied, 2) estimated adult abundance, 3) intervention dependence, 4) tolerance, 5) genetic risk, 6) climate change, and 7) anthropogenic effects (Table 2). Each of these metrics was rated on a 1–5 scale, where a score of ‘1’ indicated a highly negative effect on species viability and ‘5’ indicated a neutral or positive effect, and ‘2’ through ‘4’ were intermediate (Table 2). Collectively, the metrics were designed to analyze major factors affecting salmonid viability in California with minimal redundancy among them. The results of the seven metrics were then averaged to produce an overall numeric threat score for each species ranging from 1 to 5, one being at highest risk of extinction and five being reasonably secure at this time.

Anthropogenic threats analysis Scoring the anthropogenic threats metric required a secondary analysis of 15 anthropogenic factors associated with salmonid decline in California (Tables 3, 4; full descriptions of categories can be found in Appendix A). The 15 anthropogenic threats addressed include: 1) major dams, 2) agriculture, 3) grazing, 4) rural residential development, 5) urbanization, 6) instream mining, 7) mining, 8) transportation, 9) logging, 10) fire, 11) estuary alteration, 12) recreation, 13) harvest, 14) hatcheries, 15) alien species.

Each of these human-caused limiting factors was rated on a five-level ordinal scale rated “critical,” “high,” “medium,” “low,” or “no” threat level (Table 3). Each taxon’s anthropogenic threat score was then assigned a 1–5 value via the scoring rubric (Table 2, metric 7).

Table 2 Scoring rubric used to assess status of native salmonid fishes in California. Each metric scored 1 through 5. Final status score is the average of all seven metrics scores. Note that there are separate “area occupied” metrics (1A and 1B) for resident vs. anadromous species. All metrics as of December 31, 2010

1A. Area occupied: resident salmonids
  1. One watershed/stream system in California only, based on watershed designations in Moyle and Marchetti (2006)
  2. 2–3 watersheds/stream systems without fluvial connection
  3. 3–5 watersheds/stream systems with or without fluvial connection
  4. 6–10 watersheds/stream systems
  5. More than 10 watersheds/stream systems

1B. Area occupied: anadromous salmonids
  1. 0–1 apparent self-sustaining populations
  2. 2–4 apparent self-sustaining populations
  3. 5–7 apparent self-sustaining populations
  4. 8–10 apparent self-sustaining populations
  5. More than 10 apparent self-sustaining populations

2. Estimated average adult abundance
  1. ≤500
  2. 501–5000
  3. 5001–50,000
  4. 50,001–500,000
  5. 500,000 +

3. Dependence on human intervention for persistence
  1. Captive broodstock program or similar intensive measures required to prevent extinction
  2. Continuous active management of habitats (e.g., water addition to streams, establishment of refuge populations, or similar measures) required
  3. Frequent (usually annual) management actions needed (e.g., management of barriers, special flows, removal of alien species)
  4. Long-term habitat protection or improvements (e.g., habitat restoration) needed but no immediate threats need to be dealt with
  5. Species has self-sustaining populations that require minimal intervention

4. Environmental tolerance under natural conditions
  1. Extremely narrow physiological tolerance (thermal maxima or minima, sensitivity to dissolved oxygen levels, swimming ability, etc.) in all habitats
  2. Narrow physiological tolerance to conditions in all existing habitats or broad physiological limits but species may exist at extreme edge of tolerances
  3. Moderate physiological tolerance in all existing habitats
  4. Broad physiological tolerance under most conditions likely to be encountered
  5. Physiological tolerance rarely an issue for persistence

In order to facilitate broader understanding of our status ratings, we calibrated our numeric scoring rubric so that our ratings would approximate the five

Table 2 (continued)

5. Genetic risks
   1. Fragmentation, genetic drift, and isolation by distance, owing to very low levels of migration, and/or frequent hybridization with related fish are major forces reducing genetic viability
   2. As above, but limited gene flow among populations, although hybridization can be a threat
   3. Moderately diverse genetically, some gene flow among populations; hybridization risks low but present
   4. Genetically diverse but limited gene flow to other populations, often due to recent reductions in connectivity
   5. Genetically diverse with gene flow to other populations (good metapopulation structure)
6. Vulnerability to climate change
   1. Vulnerable to extinction in all watersheds inhabited
   2. Vulnerable in most watersheds inhabited (possible refuges present)
   3. Vulnerable in portions of watersheds inhabited (e.g., headwaters, lowermost reaches of coastal streams)
   4. Low vulnerability due to location, cold water sources and/or active management
   5. Not vulnerable, most habitats will remain within tolerance ranges
7. Anthropogenic threats analysis
   1. One or more threats rated *critical* or 3 or more threats rated *high* – indicating species could be pushed to extinction by one or more threats in the immediate future (within 10 years or 3 generations)
   2. 1 or 2 threats rated *high* – species could be pushed to extinction in the foreseeable future (within 50 years or 10 generations)
   3. No *high* threats but 5 or more threats rated *medium* – no single threat likely to cause extinction but all threats in aggregate could push species to extinction in the next century
   4. 2–4 threats rated *medium* – no immediate extinction risk but taken in aggregate threats reduce population viability
   5. 1 threat rated *medium* all others *low* – known threats do not imperil the species

status categories used by the International Union for the Conservation of Nature (IUCN) (Table 4). The scores only apply to salmonids in California, so species with wide distribution outside the state (e.g., chum or pink salmon) could receive low scores within the state, reflecting California's geographic position at the edge of their range. Examples of the conservation status assessment and anthropogenic threats analysis can be found as Appendix C.

Information quality Because the quality and quantity of information varied among species, each species account was rated, on a 1–4 scale, for certainty of status determination. A score of "1" relied solely on professional judgment while a score of "4" indicated that information was based primarily on published literature (Tables 5).

Results

Of the 32 salmonid taxa native to California, only bull trout have been extirpated, although 12 (38%) taxa are in danger of extinction in the near future if present trends continue (endangered, scores of 1.0–1.9). Another 12 (38%) species are sufficiently threatened to be on a trajectory towards extinction (vulnerable, scores of 2.0–2.9), while six (19%) are in long-term decline or have small isolated populations but currently do not face extinction (near-threatened, scores of 3.0–3.9). A single (3%) taxon, coastal rainbow trout, was found to be of least concern (≥4.0; Fig. 1). The average status score of all extant taxa was 2.3. The certainty ratings of status evaluations averaged 3.1 out of 4.0 (SD 0.8), with 78% of accounts based on extensive peer-reviewed and/or agency literature and only 3% based mainly on our professional judgment.

Of the 15 salmonids listed by the state and/or federal Endangered Species Acts (ESA), our analysis found one to have been extirpated, five to be endangered, eight to be vulnerable and one to be near-threatened (Table 1). Conversely, of the 12 fishes that we rated as endangered 5 (38%) were already formally listed under the ESA, as were 8 (67%) of the 12 fishes we rated vulnerable and 1 (17%) of the 6 we rated near threatened.

All seven status metrics were positively correlated with one another ($P<.05$) indicating that declines of most species were caused by multiple factors. Similarly, a Principal Components Analysis (JMP 9 2011) showed that all seven eigenvectors for the first component weighted approximately equally (Appendix B). Each species, however, had its own distinctive combination of metrics contributing to its score. The metrics contributing most often to a taxon's endangered or vulnerable status were climate change (74% of species received scores of 1 or 2), genetic risk (71%) and anthropogenic threats (71%). Only the coastal

Table 3 Criteria for ordinal ranks assigned to anthropogenic threat factors with expected timelines for decline

Factor threat level	Criteria	Temporal impact
Critical	Could push species to extinction	3 generations *or* 10 years, whichever is less
High	Could push species to extinction	10 generations *or* 11–50 years, whichever is less
Medium	Unlikely to drive a species to extinction by itself but contributes to increased extinction risk	Next 100 years
Low	May reduce populations but extinction unlikely as a result	Indefinite
No	No known impact to the taxon under consideration	–

rainbow trout was rated as least concern (score ≥4.0) because of its large populations, wide distribution, high tolerance of environmental change and genetically diverse populations.

Of the 15 causes of decline included in scoring of the anthropogenic threats the ones most often rated "critical" or "high" were hatcheries (45%), major dams (29%), estuary alteration (29%), harvest (26%), logging (23%) and alien species (23%). Thirteen species (42%) had at least one "critical" rating, indicating the factor had a high likelihood of causing extinction in the near future, while 19 species (61%) received at least one "high" rating. The largest number of "high" ratings awarded to a single species was six. All species had different combinations of causes of decline by kind and severity (Table 6).

Discussion

1. *What is the conservation status of California salmonids, both individually and in aggregate?*

The majority of salmonid species are declining rapidly and, if present trends continue, 78% (25 of 32 extant forms) are likely to be extirpated from the state in coming decades. Over three-quarters of these taxa are regional endemic species, so their loss would likely represent global extinction (Moyle et al. 2008). This pattern reflects the decline of the inland fishes in general (Moyle et al. 2011) but is much more severe and involves species that once supported large fisheries. Timelines of extinction trajectories depend on human activities, but the rapid decline of two ESUs of coho salmon (Fig. 2) provides documentation of the speed with which once-abundant fish taxa can diminish to near extinction. Coho salmon numbered in the hundreds of thousands only 50–60 years ago and were significant members of the state's coastal stream and ocean ecosystems (Brown et al. 1994); today they number in the hundreds (National Marine Fisheries Service 2010) making the recently completed recovery plan for California coho salmon (NMFS 2010) a strategy to prevent imminent extinction.

Likewise, the combined abundance of Chinook salmon ESUs in the Central Valley once averaged around 2 million fish annually (Yoshiyama et al. 1998); today three of the runs (spring, winter, late-fall) average only a few thousand fish each. The fall-run has recently been experiencing extreme annual

Table 4 Conversion of numeric status scores to verbal status category definitions. To facilitate understanding the conservation implications of the ratings, the scoring rubric was calibrated to correspond to IUCN status categories at each integer break. 'ESA' is federal Endangered Species Act of 1973 and/or the California Endangered Species Act

Status category	Definition	Scores
Extinct	Globally extinct or extirpated from inland waters of California	0
Endangered	High risk of extinction in the wild, in short-term (<10 generations). Qualify for listing as endangered under ESA	1.0–1.9
Vulnerable	High risk of endangerment in the wild, but less so than endangered species. Most qualify for threatened listing under ESA	2.0–2.9
Near-threatened	Declining, fragmented and or small populations that can be subject to rapid or unexpected status change. Qualify as Species of Special Concern in California	3.0–3.9
Least Concern	California populations do not appear to be in overall decline; abundant and widespread	4.0–5.0

Table 5 Certainty of status assessment, rated from low (1) to high (4)

1. Status is based on professional judgment, with little or no published information
2. Status is based on professional judgment augmented by moderate amounts of published or gray literature
3. Status is based on reports found mainly in the in gray literature with some information in peer-reviewed sources but where data gaps exist in some important areas
4. Status is based on highly reliable information, with numerous accounts in the peer-reviewed and agency literature

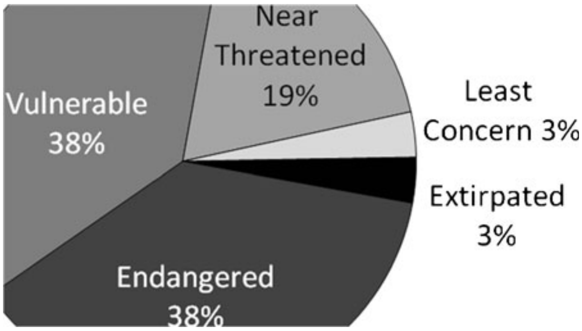

Fig. 1 2011 Conservation status of native salmonid fishes of California (N=32). See Table 5 for category definitions

fluctuations in abundance, reaching an all-time low of 66000 in 2008 (Anadromous Fish Restoration Program website) and appears to be heavily influenced by hatchery production (Williamson and May 2005; Williams 2006; Lindley et al. 2009).

Depending on the rate at which climate change and human impacts continue to alter California's aquatic environments, it is possible that a majority of California's endemic salmon, trout and steelhead could follow coho salmon to extinction within 50 to 100 years. Two of the species with high likelihood of being extirpated from the state are pink salmon and chum salmon (Table 1), species that have never been particularly common in California although they were a recognized part of fish fauna in the 19th and 20th centuries and contributed to salmon harvest (Moyle et al. 2008).

Table 6 Proportion of the 31 extant California salmonid taxa affected by 15 categories of anthropogenic causes of decline. See text and Table 2 for descriptions of causes and definitions of critical, high, medium, and low rating levels

	Threat level (% taxa)				
Cause of decline	Critical	High	Medium	Low	No effect
Major dams	6	23	42	13	16
Agriculture	0	16	55	10	19
Grazing	0	6	68	26	0
Rural residential	0	0	32	55	13
Urbanization	0	3	35	39	23
Instream mining	0	6	52	19	23
Mining	0	6	10	81	3
Transportation	0	6	52	39	3
Logging	6	16	52	26	3
Fire	0	10	58	32	0
Estuary alteration	3	26	39	0	32
Recreation	0	0	26	74	0
Harvest	3	23	39	35	0
Hatcheries	10	35	23	19	13
Alien species	13	10	39	39	0

2. *How does this status assessment compare to official Endangered Species Act assessments?*

For ESA-listed salmonid species we relied on the same information used by state and federal agencies for status assessment, but we applied a standardized protocol to all species. This approach allowed direct comparison of the status of both listed and unlisted species. With several notable exceptions, our results largely supported ESA listings of species that face high levels of extinction threat. However, our results also suggest that less than half of California salmonids that face similar high levels of extinction threat are listed. Thus, of the 12 most endangered salmonids in our analysis, only five are listed under the state or federal ESAs (Table 1). The incongruity between official lists and our assessment likely stem from differences in methods and scope but may also reflect the peculiarities of the ESA listing processes, as well

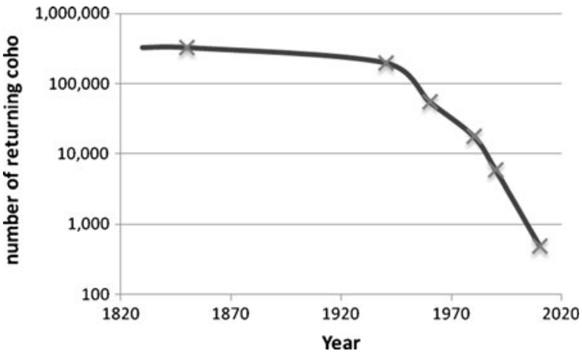

Fig. 2 Annual abundance estimates of adult coho salmon returning to California rivers to spawn. Data from NOAA (2010) and Brown et al. (1994)

differing evaluations of what constitutes an ESU or DPS. Regardless of cause, our status assessment suggests that state and federal ESAs are not sufficiently protecting California's salmonid fishes against extinction.

3. *What are the major factors affecting status?*

Although causes of decline are multiple and interacting, climate change and hatchery propagation appear to be the two most pressing extinction threats to California's salmonids. In California, 150 years of water capture and diversion have fundamentally changed the nature of aquatic ecosystems, especially in the state's Central Valley. Historically, aquatic habitats were complex and spatially heterogeneous with streamflow that varied both seasonally and interannually. The legacy of land use and water development has both simplified and stabilized California's waterways. Not only has recent anthropogenic action radically altered quality, extent and spatial patterns of fish habitat, but selection regimes under which the state's native fishes evolved have also been irrevocably altered. Species can track this change via phenotypic plasticity or by populations adapting to changing local conditions (Waples et al. 2008), both of which are ultimately dependent on genetic diversity. In light of the wholesale changes to California's aquatic habitats and the dependency of salmonid fishes on cold, clean and abundant water it is remarkable that we have lost only one salmonid taxon to extinction. This is particularly true when the long history of dependence on hatchery production to mitigate for habitat loss is considered in light of recent insights into the deleterious genetic effects of hatchery propagation on wild stocks (Goodman 2005; Akari et al. 2008; Chilcote et al. 2011). The capacity for hatchery introgression to genetically interrupt local adaptation in naturally reproducing populations is particularly troubling because it likely reduces the capacity of "wild" stocks to track changes to physical habitats. Our analysis suggests a lag effect, whereby the cumulative impact of past actions are now pushing salmonids towards extinction at a rate amplified by changing climatic conditions.

Increasing human population pressure, coupled with naturally stressful environments at the southern limit of the family's distribution, make California's salmonid fauna particularly vulnerable to climate change. The multiple stressors documented here are likely to be amplified by ongoing increases in temperature, changes in precipitation patterns, and decreases in snowpack (Mote et al. 2003). Accordingly, vulnerability to climate change was the metric with the largest negative effect on salmonid status. Put simply, all California populations are being adversely impacted by the shrinking availability of coldwater habitats.

Summer and fall are expected to be warmer and drier in the next century (Scavia et al. 2002), conditions associated with low salmonid survival (Lehodey et al. 2006; Wells et al. 2008). Anadromous salmonids can tolerate water temperatures from 0 to 25° C; however, survival and reproduction for most species are impaired at temperatures higher than 18°C (Brett 1971; Richter and Kolmes 2005). At the southern edge of their range, salmonids in California often already experience environmental conditions near the limit of their tolerance (Moyle et al. 2008). For instance, summer temperatures in many California rivers already exceed 22°C (McCullough 1999; California Data Exchange Center 2009). Thus, small thermal increases in summer water temperatures can result in suboptimal or lethal conditions and consequent reductions in salmonid distribution and abundance (Ebersole et al. 2001; Roessig et al. 2004).

Changes in how, when, and where precipitation falls in California also significantly alter salmonid habitats. During summer and fall, rising water temperatures are being exacerbated due to lower base flows resulting from reduced snowpack (Stewart et al. 2004; Hamlet et al. 2005; Stewart et al. 2005). Snowpack losses are expected to be increasingly significant at lower elevations, with elevations below 3000 m suffering reductions of as much as 80% (Hayhoe et al. 2004). Consequently, in the long run, changes in stream flow and temperature are expected to be most significant in streams fed by the relatively lower Cascades and northern Sierra Nevada, while the southern Sierra Nevada with its much higher elevations is predicted to retain a higher proportion of its snowpack (Mote et al. 2005).

Connectivity among habitats is becoming increasingly important as temperatures climb. In particular, seasonal access to cold water areas, especially smaller streams at higher elevations, is becoming more important to salmonids seeking coldwater refuges (Crozier et al. 2008). Under these conditions, mainstem rivers such as the Klamath River will be available primarily as seasonal migration corridors (Quiñones and Moyle in press). Habitat connectivity becomes as important as habitat quantity and quality when populations decrease and habitat is fragmented (Isaak et al. 2007). Consequently, removing physical (e.g., dams, shallow water) and physiological (e.g., warm water temperatures) barriers to upstream migration and behavioral thermoregulation will become an increasingly important conservation strategy.

The amount of habitat for warm water species, such as alien bass (*Micropterus* spp.) and sunfishes (*Lepomis* spp.) of the family Centrarchidae, will increase concurrently with decreases in coldwater habitat (Mohseni et al. 2003). Consequently, local declines in salmonid abundance will likely be coupled with increases in abundance of nonnative fishes, many of them predators on salmonids (Marchetti et al. 2001, 2004).

Climate-driven changes to estuarine and ocean systems also have potential to significantly impact anadromous populations (Quiñones and Moyle in press). A combination of melting ice sheets and glaciers, and thermal expansion of oceans contributed to a global sea level rise of 17 cm from 1961 to 2003 and changed the size and characteristics of estuaries (Intergovernmental Panel for Climate Change 2007). In California a roughly 20 cm increase in sea level during the 20th century has been intensified by land subsidence (Knowles and Cayan 2002; Cayan et al. 2008) and has reduced the amount and quality of tidal habitat through physical inundation, associated erosion, and increases in salinity (Scavia et al. 2002). With sea level changes associated with a 2°C temperature increase, Humboldt Bay and San Francisco Bay will likely lose 29–55% of their tidal flats and salt marshes (Galbraith et al. 2002), although increased pressure on levees may result in the sea reclaiming urbanized edge areas or large diked freshwater marshlands such as Suisun Marsh (Lund et al. 2007).

Although the effect of changing climatic conditions on marine salmon production will be patchy and hard to predict (Coronado and Hilborn 1998), some regional trends appear likely. For instance, marine survival rates in California salmon have been closely linked to several cyclical patterns of regional sea surface temperature such as the Pacific Decadal Oscillation, El Niño Southern Oscillation (Beamish 1993; Hare and Francis 1995; Mantua et al. 1997; Mueter et al. 2002), and the North Pacific Gyre Oscillation (Di Lorenzo et al. 2008). With increasing temperatures, concentrations of zooplankton, the primary prey of juvenile salmonids entering the ocean, may decrease, resulting in lower salmon survival (McGowan et al. 1998; Hays et al. 2005). Smolt-to-adult survival is also strongly correlated with upwelling driven by strong winds during the spring and fall (Scheuerell and Williams 2005). In addition to causing increases in surface temperatures similar to El Niño events (Schwing et al. 2010; Wang et al. 2010), climate change is predicted to alter wind patterns, negatively affecting upwelling. Increased acidity (Hauri et al. 2009) also may reduce ocean productivity in California's coastal waters. In response, salmonid distributions in the northern Pacific Ocean are predicted to shift poleward (Pierce 2004).

The southernmost steelhead populations are characterized by a relatively high genetic diversity compared to populations farther north (McCusker et al. 2000). It is likely that southern salmonid gene pools reflect a history of resilience as well as adaptations to watersheds characterized by aridity and extreme seasonal variation (Nielsen et al. 1999). Extinction of these highly endangered southern populations will likely result in loss of traits adapted to the very environmental characters that embody predicted climatic changes to watersheds further north.

Hatchery propagation of fish species is generally designed to increase overall abundance, mostly to support commercial and sport fisheries, although hatcheries have also been created as mitigation for human actions that have negative effects on salmonid populations. Consequently, while hatchery propagation of salmonids in California began in the 1870s, it was during the period of 1940 to 1960, coincident with the creation of the major dams, that hatchery construction boomed (Moyle 2002; Williams 2006). As a result, Many Central Valley streams with significant natural spawning runs also have a production hatchery on or near them (Yoshiyama et al. 2000). While hatcheries produce large numbers of fish, this production has often masked continued declines of wild stocks (Chilcote et al. 2011). The negative effects of hatchery production on wild stocks can be divided into ecological and genetic impacts, although the two interact considerably. Ecological effects include competition, predation, and disease transfer from hatchery stocks to wild populations (Allendorf and Ryman 1987; Krkosek et al. 2005). Competition between hatchery and wild fish can reduce abundance (Pearsons and Temple 2010) and survival of wild juveniles in river, estuarine and marine habitats

(Nickelson et al. 1986; Levin et al. 2001; Levin and Williams 2002; Nickelson 2003). Hatchery supplementation may even exceed the carrying capacity of the marine habitats, particularly in times of low ocean productivity (Beamish et al. 1997; Levin et al. 2001), resulting in high ocean mortality rates and consequently, lower adult returns (Beamish et al. 1997; Heard 1998; Kaeriyama et al. 2004). Augmentation of populations to support fisheries can increase harvest rates of wild fish to unsustainable levels while saturating the environment with hatchery fish (Naish and Hard 2008).

The natural ability of salmonids to adapt to changing conditions has made them relatively easy to culture. Not surprisingly, propagation also leads to rapid behavioral and morphologic changes in response to selection in the hatchery environment "with attendant deterioration of performance under natural conditions" (Goodman 2005 pg 374). For half a century there has been evidence of decreased performance of hatchery-derived populations of resident trout when compared to analogous wild populations under natural conditions (Greene 1952; Flick andWebster 1964; Moyle 1969) but domestication selection issues are not confined to resident salmonids (Ford 2002). Both genetic models and empirical studies have shown that after just a few generations, domestication yields individual fish with lower reproductive success which can reduce fitness of proximate wild populations (Chilcote et al. 1986; Unwin and Glova 1997; Bisson et al. 2002; Goodman 2005), presumably resulting in unsustainable natural populations (Lynch and Healy 2001). Continuous introgressive hybridization between fish of hatchery ancestry and naturally produced individuals will progressively diminish productivity of naturally spawning populations (Reisenbichler and Rubin 1999; Goodman 2005), presumably resulting in unsustainable natural populations (Lynch and Healy 2001). Recent multi-generational genetic studies (Akari et al. 2007a, b, 2008, 2009) and meta-analysis (Chilcote et al. 2011) have corroborated earlier findings that when fish with hatchery ancestry spawn in the river they produce substantially fewer successfully reproducing offspring than do wild fish from the same genetic stock.

Because hatchery stocks are not dependent on natural reproduction, fitness under natural conditions (or lack thereof) has little effect on the annual production of hatchery smolts. Currently more than 30 million Chinook smolts are produced annually in the Central Valley irrespective of the return rate of hatchery fish. Hatchery juveniles compete directly with naturally reproduced fish in both the river and marine environments. Meanwhile, hatchery genetics continue to penetrate the "wild" genepool as hatchery adults stray and spawn in river, decreasing the fitness and reducing the reproductive capacity of the naturally produced population. In California's Central Valley, fall-run Chinook salmon which spawn in-river are genetically indistinguishable from hatchery stocks (Williamson and May 2005; Lindley et al. 2009). Otolith microchemistry (J. Hobbs, UC Davis, unpubl. data), and recent fractional marking studies (California Department of Fish and Game, unpublished data) also suggest that in-river-spawning fall-run Chinook salmon are predominantly hatchery fish or of recent hatchery origin.

4. *How do factors causing declines differ between anadromous and resident taxa?*

Seventeen (81%) of the anadromous salmonids are in serious decline (scoring <2.9), while 8 (73%) of inland salmonids had similarly low scores. However, different combinations of threat factors drive decline in the two groups. Many resident taxa are endemic to single watersheds in very small areas, such as the golden trouts of the Upper Kern River Basin (Moyle et al. 2008). For such fish localized factors, such as a single introduction of an alien trout species, can have major negative effects. Accordingly, alien species were rated as a major threat (scored 1 or 2) for 64% of resident taxa but not for a single anadromous taxon. In contrast, major dams (43%), estuary alteration (43%), harvest (38%) and agriculture (24%) were rated critical or high for anadromous taxa but not for any resident fishes. Hatchery propagation, on the other hand, has major negative impacts on both groups, although in somewhat different ways. Genetic impact of hybridization with hatchery fish is a major threat for both groups but in anadromous fishes the primary threat comes from intra-taxon hybridization (e.g., interbreeding of hatchery Chinook salmon with naturally reproducing fish) while in most resident taxa the danger is from inter-taxa hybridization,usually rainbow trout interbreeding with golden or cutthroat trout (Moyle et al. 2008). Ecological impacts such as competition, predation and disease transfer between hatchery and wild stocks also have negative effects on both groups although direct competition may be a greater threat overall threat to resident species, such as competition with stocked nonnative trout in Sierra Nevada golden and cutthroat populations (Dunham et al. 2004). The Eagle Lake rainbow trout is a curious mix of these impacts, having been largely maintained by hatchery production for over 60 years (Carmona-Catot et al. 2011), a situation exacerbated by the fact that alien brook trout dominate their principal spawning and rearing stream.

5. *What conservation strategies are likely to be most effective in maintaining salmonid populations in California?*

A species' ability to respond to changing environmental conditions is closely correlated to the magnitude of its genetic variability and consequently life history variation (Reusch et al. 2005; Schindler et al. 2008). Because diverse habitats are necessary for expression of life history variation, decreases in habitat diversity can lead to reductions in life history diversity and to diminished resilience of salmon populations (Waples et al. 2009). Therefore, restoration and protection of physical habitat diversity is essential to maintaining genetic diversity and fostering resilience to both climate change and human population pressure in salmonid stocks (Hilborn et al. 2003; Rogers and Schindler 2008; Schindler et al. 2008; Carlson et al. 2011).

Because habitat diversity is essential to maintaining life history diversity, conservation strategies that restore and improve physical habitat quality, extent, and connectivity are essential tools in improving the odds of salmonid persistence (Greene et al. 2010). This general action must go hand in hand with changing hatchery operations, that reduce the adaptive potential of wild populations via introgression with domesticated hatchery genomes. The following conservation actions address both physical and biological processes and if implemented will increase the likelihood of salmonid recovery and persistence in California in the face of climate change.

General conservation actions

- Develop and implement individualized conservation strategies for all 31 extant taxa with the goal of maintaining self-sustaining populations throughout their range. The strategies must take into account climate change (Quiñones and Moyle in press) as well as increasing water demand, changing land use and recent insight into the negative impacts of hatcheries. An initial management step in the strategy would be to evaluate all species that scored between 1.0 and 2.9 in this report for formal listing as threatened or endangered species under the ESA. For an example, see Carmona-Catot et al. (2011).
- Enforce and strengthen existing laws and regulations, tied to the Clean Water Act, the Endangered Species Act, State Forestry Practice Rules, the Fish and Game Code, and similar measures, to increase protection for salmonids and their rivers.

Hatcheries

- Reform statewide hatchery policy so that the overarching goal of hatcheries is protection of wild populations of fish, rather than enhancing fisheries.
- End gene flow between hatchery strays and naturally reproducing spawning groups. This is essential for recovery of naturally reproducing stocks. Segregation of hatchery and naturally reproducing gene pools may be achieved in two ways: 1) physical segregation via active sorting at weirs or dams whereby only non-hatchery fish are passed upstream above the barrier, 2) use of hatchery brood stocks that are divergent from local genomes so that when hybridization between naturally produced individuals and hatchery strays inevitably occurs the hybrid progeny inherit a genome unfit for local conditions, experience high mortality in the wild and are rapidly culled from the naturally produced gene pool.
- Mark all hatchery fish with external marks so targeted management is possible.
- Relocate salmon and steelhead production hatcheries closer to river mouths in order to reduce mixing of wild and hatchery stocks.
- Relocate at least some harvest from the ocean to rivers and estuaries to allow targeting populations best able to sustain fishing pressure, especially hatchery stocks, while protecting imperiled naturally reproduced anadromous runs from overfishing.
- Close hatcheries where adverse impacts outweigh benefits.

Habitat

- Provide immediate additional protection to 'salmon strongholds' where salmonid diversity is high and habitat conditions are still reasonably good, such as the Smith River and the Blue Creek watershed of the Klamath Basin. This means reducing the human footprint on stronghold watersheds as much as possible by managing the watersheds first and foremost for native fish.
- Restore connectivity between river channels and seasonal habitat such as oxbows, riparian terraces, and floodplains wherever possible.
- Protect and restore cold water habitats, especially streams with groundwater inputs, the mouths of tributaries where hyporheic flows may provide thermal refuges, and watersheds that lie within the coastal fog belt. In regulated streams, reserve as much cold water in reservoirs as possible for providing suitable flows for native salmonids.
- Remove artificial migration barriers (including small and large dams, low flow and warm water barriers) to provide salmonids access to a wider range of habitats, comparable to historic ranges.
- Protect and restore riparian buffers alongside lower order streams (1st–3rd) where riparian vegetation can provide significant protection from solar radiation and maintain cooler water temperatures, as well as reduce sediment input.
- Reduce fine sediment delivery to streams to prevent streams from becoming shallower and thus more likely to become warmer, by improved watershed management (e.g., reducing effects from high road density, logging, and mining).

In summary, the salmonid fauna of California is on the verge of losing much of its diversity, among both anadromous and resident forms. These taxa have distinctive adaptations to stresses imposed by an arid Mediterranean climate. As the human population grows and the climate becomes harsher, conserving salmonids *in situ* as wild self-sustaining populations will require a level of commitment to aquatic conservation so far not seen in this state, including major shifts in water policy (Hanak et al. 2011). In order to prevent a wave of extinctions, new conservation strategies must address the most pressing drivers of salmonid decline in California. To that end, we have presented a partial list of conservation strategies tailored to alleviate the most egregious causes of decline identified by our analysis, climate change and genetic risks posed by hatchery propagation. We feel that this approach can be effective in maintaining salmonid populations in California for the near term. However, as Lackey et al. (2006) pointed out, maintaining self-sustaining runs of each anadromous species for future generations will take nothing short of a fundamental re-evaluation and radical restructuring of California's society.

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Appendix A

Descriptions of factors causing decline used in Anthropogenic Threats Analysis

Major dams Dams were recorded as having a high impact on a species if they cut off a species from a large amount of its range, if they caused major changes to habitat, or if they significantly changed water quality and quantity downstream of the dam. The effects of the reservoirs created by dams were also evaluated. Dams were regarded as having a low impact if they were present within the range of the species but their effects were either very small or poorly known.

Agriculture The effects of agriculture were regarded as being high if agricultural return water or farm effluent heavily polluted streams, if diversions severely reduced flow, if large amounts of silt flowed into streams from farmland, if pesticides had significant impacts or were suspected of having them, and if other factors directly affected the streams in which a species lived. Agriculture was regarded as having a low impact if it was not pervasive in the watersheds in which the species lived or was not causing significant changes to aquatic environments.

Grazing Livestock grazing was separated from other forms of agriculture because its effects are widespread on range and forest lands throughout California, especially the effects of cattle. Impacts are high where stream banks are trampled and riparian vegetation removed, resulting in streams becoming incised and the drying of adjacent wetlands. Removal of vegetation can also result in large amounts of silt being washed into streams, increased summer temperatures, and decreased summer flows. Impacts are low where grazing occurs in watersheds but changes described above are minimal.

Rural residential As California's human population grows, people spread across the landscape, often settling in diffuse patterns along or near streams. This results in water removal, streambed alteration (to protect houses, create swimming holes, construct road crossings, etc.), and pollution (especially from septic tanks). Where such housing is abundant and unregulated, it causes major changes to streams and their fishes and is rated as a high impact. Where such housing is present but scarce, the effects are usually low.

Urbanization When humans concentrate in towns and cities, they alter the streams that flow through them to reduce flooding and acquire the water. Pollution is rampant, both through sewage discharges and through less obvious means such as storm drains. Generally, the bigger the city, the bigger its effects on local streams and fish populations.

Instream mining The most severe instream mining took place during the 19th and early 20th century when miners excavated and dredged river beds for gold, turning them over multiple times. These severe legacy effects are still with us in many rivers. Nearly as severe, at least locally, have been instream gravel mining operations, in which large pits were dug into streambeds and banks altered. Such mining is largely banned (in favor of mining off-channel areas) but also has legacy effects. This was usually rated intermediate when present, although severe legacy affects resulted in high ratings for some species. The impacts of contemporary recreational and professional suction dredge mining for gold can also result in a high rating.

Mining This refers to hard rock mining, in which tailings can be dumped into streams and pollutants result from mine drainage, mostly of abandoned mines. The effects of mercury, used in processing gold in placer and dredge mining is also included here. High ratings come from situation where mines, even if abandoned, form a major threat because their wastes are poised on the edges of rivers (e.g. Iron Mountain Mine near Redding). Low ratings for species usually come from situations where old mines are present but their effects on nearby streams are not known or not obvious.

Transportation Historically, river banks were favorite places to construct roads and railroads, so many rivers and creeks have roads and railroads running along one or both sides, often confining the stream channel and subjecting the streams to pollution from vehicle emissions, waste disposal, and accidents. Also culverts and other drainage modifications associated with roads often block fish migration or restrict fish movements. Dirt roads can become hydrologically connected to streams, increasing siltation and changing local flow regimes and seriously impacting aquatic habitat. The ratings were made based on how pervasive roadside streams are in the areas occupied by the species

Logging Timber harvest has always been one of the major uses of forested watersheds in California. These same watersheds support the most species and highest abundances of fish, including anadromous salmon and steelhead. Logging was relatively unregulated until the mid-20th century, resulting in major degradation of streams through removal of trees as cover and landscape stabilizers. Legacy effects include incised streams with little large wood providing structure and many silt-bottomed reaches. Logging is still a pervasive activity in forested watersheds and is better regulated today than previously, but its effects can still result in siltation of streams, reduced complexity of habitat, and other alterations. High ratings were given when a species occupied streams degraded by either the legacy or contemporary effects of logging. Low ratings were awarded to species that used forested watersheds but where the effects of logging were either mitigated or of small significance.

Fire Forest, range, and scrub fires are part of California's natural landscape but human activities have made them more severe (Gresswell 1999; Noss et al. 2006; Sugihara et al. 2006). Transition from relatively frequent understory fires to less frequent but catastrophic crown fires has been shown to be a major driver in the extinction risk of Gila trout (*Oncorhynchus gilae*) in New Mexico (Brown et al. 2001). There is little reason to think that similar factors are not pervasive in California. A fish species rated high for fire is one in which most of its streams are affected by fire, through increased erosion, increases in temperature, spills of fire-fighting chemicals, and effects of ash and other materials. Low ratings generally applied to fish that lived in areas where fires occur but for various reasons have minimal impact on streams.

Estuary alteration Many California fishes depend on estuaries for at least part of their life cycle. All estuaries in the state are highly altered by human activity, from siltation to pollution, to diking and draining, to removal of sandbars between the estuary and ocean. Thus the more estuarine dependant a fish species is, the more likely it was to get a high rating for this factor.

Recreation Human use of streams as playgrounds has greatly increased along with the human population but the effects are usually minor, although concentrated at periods of time when stream flows are low. Recreation is likely to be rated high as a factor when there is, for example, heavy off-road vehicle use in limited habitat, ski resorts that increase sedimentation (from cleared areas for ski runs), or rafters and swimmers disturbing spawning or holding fish (salmon and steelhead).

Harvest Harvest of fishes is both legal and illegal. Both can have severe impacts on fish populations, especially of large fishes or ones that are isolated and therefore easy to catch (e.g. summer steelhead).

Hatcheries Most fishes do not have populations supported in part by fish hatcheries but for those that do, hatcheries often have negative effects on wild populations through competition for space and food, direct predation, and loss of fitness and genetic diversity (Kostow 2009; Chilcote et al. 2011). The severity of these effects was rated based in part on hatchery dependence and/or the threat of interbreeding between wild and hatchery populations.

Alien species Non-native species are present in every California watershed and their impacts on native species through hybridization, predation, competition, and disease are often severe (Moyle and Marchetti 2006). Fish species were rated high in this category if there were studies demonstrating major direct or indirect impacts of alien invaders. They were rated low if contact with aliens was frequent but not negative.

Appendix B

Table 7 Principal component analysis (JMP 9) revealed relatively equal weighting of all seven metrics on the final status scores of 31 extant taxa. Standard deviation for eigenvectors for principal component one was .051

	Prin1	Prin2	Prin3
Area occupied	0.39254	0.26367	−0.3819
Adult population	0.39413	0.17271	0.34441
Intervention dependence	0.3584	0.40222	0.25614
Tolerance	0.304	0.60252	0.59553
Genetic risk	0.43836	0.01002	0.27654
Climate change	0.3152	0.56583	0.43763
Anthro threats	0.42213	0.23574	0.21744

Appendix C

Table 8 Example of Anthropogenic Threats Analysis to determine viability of California golden trout

Threat	Rating	Explanation
Major dams	Low	Isabella Reservoir effects water quality in the South Fork Kern River
Agriculture	No	No known impact
Grazing	High	Pervasive in the area, although less severe than in the past
Rural residential	No	No known impact
Urbanization	No	No known impact
Instream mining	No	No known impact
Mining	Low	Relatively few effects of mining
Transportation	Low	Trails and off-road vehicle routes can be a source of sediment for streams
Logging	Low	This is an important land use in the region but probably has little direct effect on golden trout streams
Fire	Low	Because of fire suppression, headwater areas contain greater fuel loads than historically, although hot fires are unlikely given the sparse plant communities
Estuary alteration	No	No estuaries in range
Recreation	Medium	Human use of meadows is a constant threat, but more in past than present
Harvest	Low	Potentially a problem; most fishing is catch and release
Hatcheries	Low	Constant genetic and demographic threats from hatchery fish to support fishery
Alien species	Critical	Hybridization with rainbow trout is primary extinction threat and a major cause of limited distribution

Table 9 Example of a conservation status assessment summary table for California golden trout

Metric	Score	Justification
Area occupied	1	Unhybridized trout are confined to a few small tributaries in one watershed
Estimated adult abundance	3	Tributary populations show signs of genetic bottlenecking but probably still contain 100–1000 adults
Intervention dependence	3	Persistence requires maintenance of upstream migration barriers and continued monitoring and nonnative removal
Tolerance	2	Require conditions present in relatively undisturbed small alpine meadow streams
Genetic risk	1	Hybridization with rainbow trout is a constant high risk
Climate change	3	High southern Sierra Nevada will likely retain significant snowpack, effects of climate change may be partially mitigated by improved management
Anthropogenic threats	1	See Table 4
Average	2.0	14/7
Status Category		Vulnerable
Certainty (1–4)	4	Well documented in scientific and agency literature

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The effects of environmental factors on the migratory movement patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract Understanding smolt migration dynamics is a critical step in the preservation and conservation of imperiled salmonids in California's Sacramento River system. Late-fall run Chinook salmon yearling smolts were acoustically tagged and tracked during their outmigration through California's Sacramento River and San Francisco Estuary during 2007–2009. Migration rates were 14.3 km·day^{-1} (± 1.3 S.E.) to 23.5 km day^{-1} (± 3.6 S.E.), similar to rates published for other West Coast yearling Chinook salmon smolt emigrations. Region-specific movement rates were fastest through the upper river regions, and slowest in the Sacramento/San Joaquin River Delta. River travel times were recorded for smolts travelling through a series of ten monitor-delimited reaches. Using these, a smolt travel time model determined by two parameters (movement rate and rate of population spreading) was then used to determine the influence of different factors on the model's fit, using model selection with Akaike's Information Criterion. The model that allowed for both year and reach to be expressed additively for both travel time and population spreading rate estimates, while accounting for a "release" effect, was the best supported model. Finally, several models incorporated environmental data as a linear predictor of movement rates. The addition of the environmental variables, in order of importance, river width to depth ratio, river flow, water turbidity, river flow to mean river flow ratio, and water velocity all resulted in improved model fit. Water temperature did not improve model fit. These environmental associations are discussed and potential improvements on the travel time model are suggested.

Keywords Environmental factors · Migration · Acoustic telemetry · Smolt · Chinook salmon · Sacramento River · Biotelemetry

Introduction

The migration of juvenile Chinook salmon (*Oncorhynchus tshawytscha)* from their riverine origin to the food-rich ocean is considered one of the most

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vulnerable periods in a Chinook salmon's life (Healey 1991). During this life stage, juvenile salmon undergo many morphological, physiological, and behavioral changes (known as smoltification) to prepare for the ocean phase of their life cycle. For the Sacramento River's Chinook salmon populations, this freshwater journey may be as long as 600 km, transiting many different habitats, all with varying natural conditions. Additionally, anthropogenic stressors such as water diversions, dams and introduced predators are present throughout the watershed and have contributed to the decline of these populations, to the point of their listing on the Endangered Species Act (ESA). It is therefore essential to the effective management of these stocks to understand the movement patterns and environmental relationships of this outmigration.

Studies have been investigating the timing and patterns of juvenile salmonid migrations on a large-scale focus for decades. Thorpe and Morgan (1978) tracked juvenile Atlantic salmon (*Salmo salar*) fry periodicity during outmigration in Scottish Rivers. Raymond (1968) calculated migration rates by marking and recapturing yearling Chinook salmon smolts traveling through the Snake and Columbia Rivers and their reservoirs. However, to best comprehend the challenges and intricacies of the migration, one must gain knowledge at a finer spatial-temporal scale. Advances in biotelemetry have allowed such resolution (Cooke et al. 2004); specifically the miniaturization of fish tracking tags has allowed the exploration of small-scale movement during smolt migration. These technologies have already yielded migration data on steelhead (*Oncorhynchus mykiss*) smolts in the Cheakamus River in British Columbia, Canada (Melnychuk et al. 2007) and on sockeye salmon (*Oncorhynchus nerka*) smolts in the Fraser River in British Columbia, Canada (Welch et al. 2009) at spatial resolutions that were previously unavailable. More relevantly, Perry et al. (2010) tagged and tracked outmigrating Central Valley late-fall run Chinook salmon smolts through the Sacramento-San Joaquin River Delta (a complex system of sloughs and channels) to determine movement rates and survival depending on the pathway chosen. Once small-scale movement information is available, our knowledge of salmon migrations can begin to delve into what might be governing variability in movement patterns.

A few studies have taken the next logical step and explored how environmental conditions might be influencing these migration dynamics. This step may be the crux of juvenile salmon management and conservation since the majority of the salmon rivers throughout the world have been faced with major anthropogenic influences, which can alter many environmental factors in a river. While these relationships have been studied in several rivers, one could argue that no river has been studied in this aspect as much as the heavily impounded Columbia River watershed. In this system, where environmental variables can be controlled to some extent (and have therefore been studied more), one study concluded that neither of the environmental predictor variables assessed (river discharge volume and water temperature) were found to correlate with migration rates (Giorgi et al. 1997), while another found a strong and consistent relationship between river flow and travel time (Smith et al. 2002), while yet another found strong evidence for a relationship between travel time and river flow on a seasonal basis (Zabel et al. 1998), in all cases with yearling outmigrating Chinook salmon smolts. However, these studies and others have assessed the influence of the environment on migration at large spatial and temporal scales, typically only using river flow and temperature as factors. These relationships are therefore usually limited to inter-annual and inter-population comparisons, thereby only uncovering the strongest and most persistent of patterns. Variations in movement are initiated at short intervals, and environmental factors there may exert significant influences, which may have higher order population consequences.

The study presented here aims to capitalize on one of the largest networks of acoustic receivers in the world, developed by the California Fish Tracking Consortium, and a collaboration between the National Oceanic and Atmospheric Administration (NOAA) and the University of California, Davis (UCD), to provide the first in-depth analysis of the spatial and temporal variation of Chinook salmon movement and migration in the Sacramento River and San Francisco Estuary. Using this information, we first determine total movement rate through the entire watershed during the outmigration. We then use a model of smolt travel time described in Zabel and Anderson (1997) to assess how the incorporation of year, release site, reach, and different environmental variables improve the models fit. Finally, we will discuss how migration and movement dynamics might be influencing smolt survival during this life stage.

Methods

Study area

The Sacramento River is the longest and largest (measured by flow discharge) river to be fully contained within the state of California and is the third largest river that flows in to the Pacific Ocean in the contiguous United States. The headwaters are located south of Mount Shasta in the lower Cascade Range, and the river enters the ocean through the San Francisco Estuary at the Golden Gate Bridge (Fig. 1). The total catchment area spans approximately 70 000 km^2, and the annual mean daily discharge for the Sacramento River from 1956 to 2008 was 668 m^3 s^{-1} (California Department of Water Resources DAYFLOW database).

The study area included approximately 92 % of the current outmigration corridor of late-fall run Chinook salmon, from release to ocean entry. Specifically, the study area's furthest upstream release site at Battle Creek (534 km upstream from the Golden Gate) is only 47 km downstream from Keswick Dam (the first impassable barrier to anadromy) at its confluence with the Sacramento River (Table 1).

Central Valley late-fall run Chinook salmon

The late-fall run is one of the four Chinook salmon runs found in the Sacramento River drainage and is the only run that migrates to sea predominately as yearlings (Moyle 2002). Coupled with the fall run, the pair form an evolutionary significant unit (ESU) deemed a "species of concern" by the Endangered Species Act as of April 15, 2004. Juveniles exhibit a river residency of 7 to 13 months, after which the smolts enter the ocean at 90 to 170 mm fork length (Fisher 1994; Snider and Titus 2000a, b). Potentially due to water diversions and increased predation in bank-altered areas, outmigrating late-fall run juveniles accrue substantial mortality (Moyle et al. 1995).

Acoustic telemetry

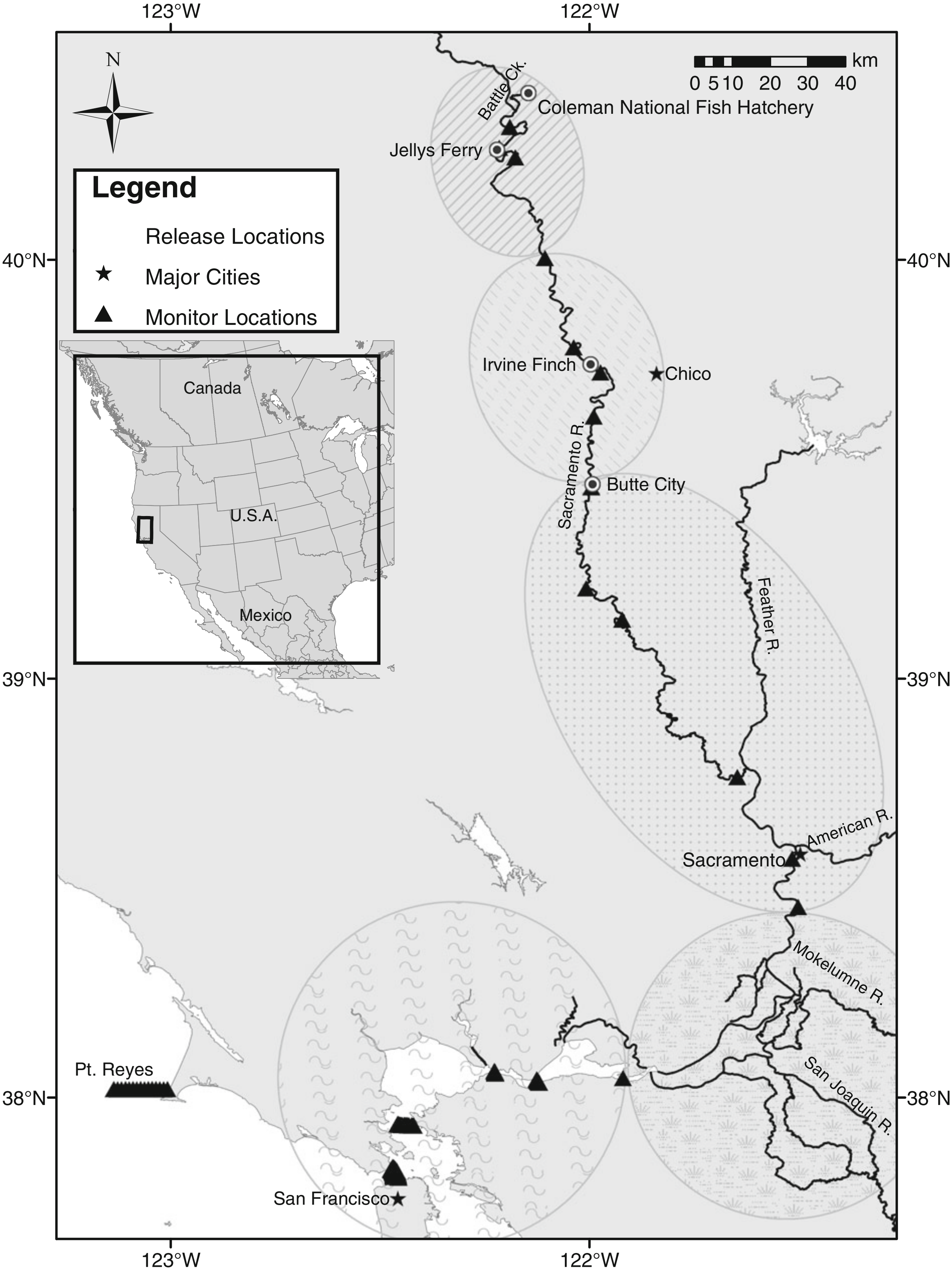
We used Vemco V7-2 L acoustic tags (1.58 g±0.03 S.D.; Amirix Systems, Inc. Halifax, Nova Scotia, Canada) and Vemco VR2/VR2W submergible receivers to track tagged fish. The receiver array spanned 550 km of the Sacramento River watershed from Keswick Dam to the ocean (Golden Gate) (Fig. 1; Table 1). This array of approximately 300 receivers at 210 receiver locations was maintained by the California Fish Tracking Consortium (a group of academic, federal and state institutions, and private consulting firms; http://californiafishtracking.ucdavis.edu/).

The acoustic receivers automatically process all detection data and drop false detections or incomplete codes from the detection file. All detection files were additionally subjected to standardized quality control procedures to minimize the number of false detections. Specifically, we considered for removal detections flagged by an automated script that searched the detection records of each individual smolt to determine if they fulfilled any one of the three following independent conditions: (1) The detection occurred before release date-time of that tag. (2) A single detection that occurred at a location was not between valid upstream and downstream detections (a valid detection is defined as less than 10 d or 50 rkm to prior or next detection). (3) Multiple consecutive detections of a tag at one location were greater than 216 min apart (10 % less than the minimum observed time between consecutive known false detections of the same tag).

Tagging and releases

For three consecutive winters, from January 2007 to January 2009 (henceforth referred to as 2007, 2008 and 2009 seasons, based on the year during which January tagging occurred), 200 to 304 late-fall run Chinook salmon smolts were tagged and released into the Sacramento River watershed. The size of tagged smolts (Table 2) was consistent with the observed size distribution for this Chinook salmon run, albeit larger than other life-history type Chinook salmon smolts (Fisher 1994).

Hatchery origin yearling late-fall run Chinook salmon smolts, obtained from the United States Fish and Wildlife Service's (USFWS) Coleman National Fish Hatchery (Anderson, CA), were used in this study. Acoustic tags were surgically implanted into the peritoneal cavity of anesthetized smolts as described by Ammann et al. (2011, this issue). To minimize potential effects on survival, growth, and behavior, smolts were size selected resulting in an average tag weight to total body weight ratio of 3.6 %, and individual ratios rarely exceeded 5 %.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Coleman National Fish Hatchery
Jellys Ferry
Irvine Finch
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Butte City
Feather R.
American R.
Sacramento
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San Joaquin R.
Pt. Reyes
San Francisco

◀ **Fig. 1** Map of the study area, including the Sacramento River, Sacramento—San Joaquin River Delta, San Francisco Estuary, and Pacific Ocean. Bull's-eye icons signify release locations, stars symbolizes major cities, and black dots symbolizes receiver locations. Shaded regions delimit (from north to south) the upper river, middle river, lower river, delta, and estuary

Lab experiments run concurrently with this study indicated that growth and survival were not significantly affected by the tag burden (Ammann et al. 2011, this issue).

Post-surgery, the smolts were held before release for 7 d in 2007 and 24 h in 2008 and 2009 to ensure proper recovery from surgery. In the 2007 season, a portion of the tagged smolts were released each weekday for three consecutive weeks in January. In the two following seasons, half the smolts were released in December and half in January, both on a single day. All releases occurred at dusk to minimize predation as the smolts became habituated to the riverine environment.

In the first year this study (2007), all 200 smolts were released at the Coleman National Fish Hatchery into Battle Creek, a tributary to the Sacramento River. In the latter 2 years, 300 smolts a year were tagged and simultaneously released from three release sites in the upper 150 rkm of the mainstem Sacramento River (Table 1), allowing the lower release groups a greater likelihood of reaching the lower river and estuary in large numbers (to improve statistical confidence intervals).

Data analysis

Smolt outmigration

Detection probabilities for each receiver location were calculated using the Cormack-Jolly-Seber (CJS) model for live recaptures (Cormack 1964; Jolly 1965; Seber 1965) within Program MARK (created by Gary White, Colorado State University (White and Burnham 1999)). A subset of the receiver locations that had consistently high tag detection probabilities and that were strategically located were chosen to delimit the river reaches that were used in the spatial movement analysis. A total of 14 receiver locations were chosen, from just below the most upstream release site to the Golden Gate (Table 1).

Two metrics for smolt movement were utilized, the former describing total migration movement, and the latter describing small-scale movements during migration. Smolt movement rates from release site to the Golden Gate was calculated for each smolt that survived to the Golden Gate (3–13 % of all smolts, depending on release group and year (C. Michel unpubl. data)) and averaged by release group (by year and release site), representing the mean successful migration movement rate (MSMMR; Table 3). Migration time from release point to the entry of the Sacramento/San Joaquin Delta, as well as migration time from the entry of the Sacramento/San Joaquin Delta to

Table 1 Locations of acoustic receivers and tagged smolt release locations

Location	River km	Description
Battle Creek	534	Release site 2007
Jelly's Ferry	518	Monitor location & release site 2008/09
Bend Bridge	504	Monitor location
China Rapids	492	Monitor location
Above Thomes	456	Monitor location
Below GCID	421	Monitor location
Irvine Finch	412	Monitor location & release site 2008/09
Above Ord	389	Monitor location
Butte City Bridge	363	Monitor location & release site 2008/09
Above Colusa Bridge	325	Monitor location
Meridian Bridge	309	Monitor location
Above Feather River	226	Monitor location
Freeport	169	Monitor location, delta entry
Chipps Island	70	Monitor location, estuary entry
Golden Gate	2	Monitor location, ocean entry

Table 2 Means and standard errors for weight and fork length of acoustically-tagged smolts by year and for all years combined

Year	Weight±SE (g)	Fork length±SE (mm)	Sample size
ALL	46.0±0.4	161.5±0.5	804
2007	46.6±0.7[a]	164.6±0.8[a]	200
2008	52.6±0.8[b]	168.7±0.8[b]	304
2009	38.9±0.5[c]	152.1±0.5[c]	300

[a,b,c] Size distributions with different superscripts are significantly different ($P<0.05$)

the entry into the Pacific Ocean, were also calculated and averaged by release group.

Reach-specific movement

Smolt-specific movement rates were then calculated per major geographic region using the last detection time from the upstream receiver locations and the first detection time from the downstream receiver locations for that region. The regions selected consisted of the upper river (river km (rkm) 518 to 456), the middle river (rkm 456 to 363), the lower river (rkm 363 to 169), the Sacramento/San Joaquin Delta (rkm 169 to 70), and finally the San Francisco Estuary (rkm 70 to 2). Distances between receiver locations were calculated in kilometers using the geographic information system software program ArcGIS 9 (ESRI) and NHDPlus 1:100 K hydrography, giving a movement metric of km·day^{-1}. These movement rates were then represented graphically with boxplots for each region by year interaction (Fig. 2).

To explore the small-scale movements of the smolts tagged in this study, we used an *advection–diffusion* smolt travel time model, explained in detail with regard to the riverine movement of salmonids in Zabel and Anderson (1997) and subsequent publications by those authors (Zabel et al. 1998; Zabel 2002; Zabel et al. 2008). The advection–diffusion model allows a probability density function (p.d.f) for the distribution of travel times in a given reach. Specifically, the model incorporates an advection term (including the parameter r describing the mean rate of downstream movement), and a diffusion term (including the parameter σ describing the rate of population spreading). One key element of the model used is an absorbing boundary for movement rate r at the value of zero; this assumption is acceptable in the case of outmigrating Chinook salmon smolts because it is rare to see upstream movement once migration has commenced. The distribution of smolt travel times under these assumptions are described by the inverse Gaussian distribution, with the following probability density function:

$$g(t) = \frac{L}{\sqrt{2\pi\sigma^2 t^3}} \exp\left(\frac{-(L-rt)^2}{2\sigma^2 t}\right) \tag{1}$$

(Zabel and Anderson 1997). L represents the reach length (in kilometers) and t represents travel time. The inverse Gaussian p.d.f. is unimodal and right skewed which captures the occurrence of most smolts

Table 3 Mean travel time in days from release point to Sacramento—San Joaquin River Delta entry, mean travel time in days from Delta entry to Pacific Ocean entry, and mean successful migration movement rate (MSMMR) for all years and all release groups

Year	Release (rkm)[a]	# released	Release to Delta entry travel time (days)±SE	Delta entry to Ocean entry travel time (days)±SE	Total MSMMR (km·day^{-1})±SE
2007	534	200	13.7±1.6	8.5±2.4	23.5±3.6
2008	517	102	14.2±1.2	14.5±1.0	18.9±1.9
	413	101	10.8±1.2	16.7±3.1	18.1±3.3
	363	101	9.7±0.9	13.8±2.0	15.6±1.8
2009	517	100	14.6±0.5	12.1±4.0	22.7±3.1
	413	100	13.0±0.8	12.6±1.3	18.1±1.3
	363	100	11.0±0.6	14.1±1.9	14.3±1.3

[a] distance (river km (rkm)) from Golden Gate

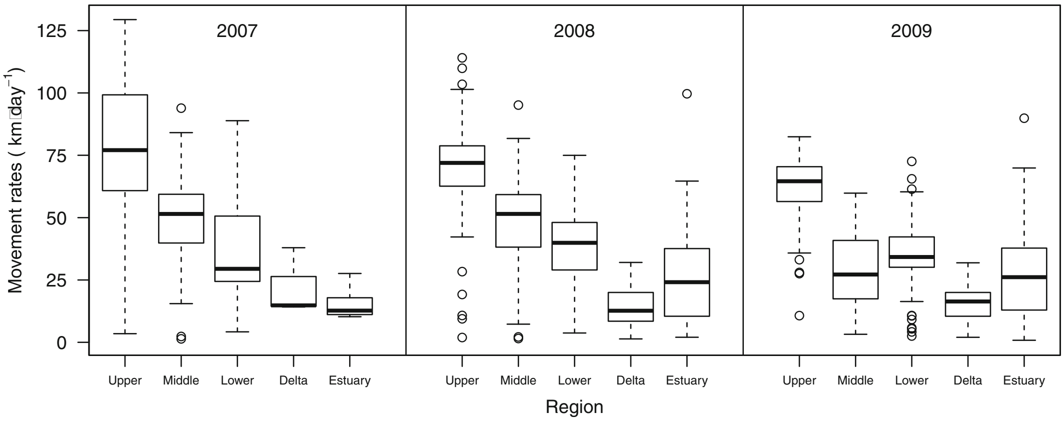

Fig. 2 Yearling late-fall run Chinook salmon migration movement rate distributions by region and year. The bold horizontal lines that dissect the boxes represents the median values, while the upper and lower edges of the boxes represent the 75th and 25th percentiles of the movement data, respectively. The upper and lower ends of the vertical lines represent the maximum and minimum values of the movement data, unless outliers are present. Outliers are data points that are above the 75th percentile or below the 25th percentile by more than 1.5 times the inter-quartile range (the range from the 25th to 75th percentile) of each specific boxplot

travelling at a very similar rate, with a small minority of individuals taking longer to complete the passage of the reach.

We then optimized function (1) using the Nelder-Mead algorithm, given the observed travel times t, to find the most likely estimation for r and σ (i.e. maximum likelihood estimation, MLE). By substituting in more complex parameter structures for r and σ, we explored potentially more accurate models, *e.g.* allowing for reach-specific variability or influence of environmental factors such as flow in estimates. Several models were therefore constructed based on *a priori* understanding of the target population, in an attempt to determine the different sources of variability in the data (Table 4). We used Akaike's Information Criterion to evaluate the strength of evidence for these different models.

The observed travel time data that was used to estimate r and σ included the ten river reaches that are upstream of the influence of tidal fluctuations. The first model we constructed was one that only allowed one movement and spreading rate parameter (r and σ), thereby essentially reducing the entire system to one reach. This model will be referred to hereafter as the *null* model. We also constructed a model allowing movement rate to vary per reach (10 parameters estimated) while spreading rate was again held constant (1 parameter). A third model was constructed in which both movement and spreading rates were allowed to vary per reach (20 parameters total). A fourth and fifth model were built to allow and test for a "release" effect, in other words, allowing smolts that were released from the two downstream sites (Irvine Finch and Butte City) to have a different r estimates (and in the fifth model, σ estimates as well) from the smolts passing through from a more upstream origin, for the one reach downstream of the release site (models referred to as "reach+release"). A sixth model allowed for reach-specific r and σ estimates to also vary by year, while still accounting for a release effect ("reach +release+year"). Finally a series of six more models were constructed to allow six different environmental variables to act as linear predictors for r and σ, as seen in Zabel et al. (1998). These models therefore included an environmental parameter beta coefficient (β), allowing determination of the direction and slope of the relationship. Additionally, by standardizing the environmental variables (subtracting the mean value from each raw data point, then dividing by the standard deviation, essentially giving all standardized variable datasets a mean of zero and a standard deviation of one), standardized beta coefficients were calculated, allowing for the comparison of the strengths of beta coefficients for different models. For a change in one standard deviation unit of the environmental variable, travel time will change by the amount specified by that

Table 4 Model statistics for all smolt travel time models run, with parameter listed first (either movement rate r or spreading rate σ), followed by resolution allowed by parameter structure in parentheses (a "1" represents no spatial or temporal variability). AICc represents Akaike's Information Criterion (corrected for small sample sizes). Models have been sorted from best (at top) to worse fit, in order of increasing AIC values

Model	Parameters	AICc	Standardized β Coefficient
r(reach+release+year) σ(reach+release+year)	28	2,193.4	
r(reach+WDR+flow) σ(reach)	22	2,297.7	−0.1; 0.1
r(reach+release) σ(reach)	22	2,310.4	
r(reach+release) σ(reach+release)	24	2,314.0	
r(reach) σ(reach)	20	2,322.4	
r(reach) σ(1)	11	2,398.4	
r(WDR) σ(1)	3	2,643.0	−3.2
r(flow) σ(1)	3	2,652.0	2.2
r(turbidity) σ(1)	3	2,658.9	1.7
r(FMFR) σ(1)	3	2,659.6	2.5
r(velocity) σ(1)	3	2,666.5	−1.5
r(1) σ(1) *Null model*	2	2,674.3	
r(temperature) σ(1)	3	2,675.8	−0.4

model's standardized beta coefficient. Once the environmental models were ranked based on their AIC, a final model was constructed using a combination of two or more of the best ranked environmental variables. The purpose of this final model is to attempt to construct the best possible model using environmental variables alone. In total we therefore used thirteen different models, and using model selection methods, we should not only be able to determine the best model, but also test for the effect of certain factors.

Once the best model was determined, the parametric estimates of movement rates ($\hat{r}$; km·day^{-1}) and population spreading rates ($\hat{\sigma}$; km·day$^{-½}$) were reported at the resolution offered by the model (Table 5).

Influence of the environment

Spatial-temporal environmental data were collected for this study for the majority of the river reaches, from the release points to the upper limit of tidal influence on the river (rkm 189; Table 6). All variables were chosen a priori based on salmon migration literature and data availability for the watershed.

Table 5 Parametric estimates for movement rate $\hat{r}$ (km·day^{-1}) and population spreading rate (km·day$^{-½}$) for all ten non-tidally influenced river reaches, from the "r(reach+release+year) σ(reach+release+year)" model. For reaches six and eight, estimates for both "run-of-river" (ROR) and downstream released (REL) smolts have been included for 2008 and 2009 (only one release site in 2007)

Reach	Rkm from Golden Gate	Total N	$\hat{r}$ 2007	$\hat{\sigma}$2007	$\hat{r}$2008	$\hat{\sigma}$2008	$\hat{r}$2009	$\hat{\sigma}$2009
1	518–504	293	33.0	25.7	36.8	21.5	34.4	15.1
2	504–492	278	61.3	23.6	65.1	19.4	62.7	13.0
3	492–456	194	27.2	26.3	31.0	22.1	28.6	15.7
4	456–421	147	13.9	31.1	17.7	27.0	15.3	20.5
5	421–412	145	13.0	27.3	16.8	23.2	14.4	16.8
6 ROR	412–389	105	10.6	25.5	14.4	21.3	12.0	14.9
6 REL	412–389	161	–	–	21.3	21.9	18.9	15.5
7	389–363	212	11.1	32.3	15.0	28.1	12.5	21.7
8 ROR	363–325	97	22.2	29.3	26.0	25.1	23.6	18.7
8 REL	363–325	88	–	–	24.1	23.8	21.7	17.4
9	325–309	135	25.6	31.0	29.4	26.8	27.0	20.4
10	309–226	163	25.4	43.0	29.2	38.9	26.8	32.5

The variables included water temperature (°C), river flow ($m^3 \cdot s^{-1}$), water turbidity (ntu), channel water velocity ($m \cdot s^{-1}$), a ratio of river surface width (m) to maximum river depth (m) (WDR), and a ratio of daily river flow to mean river flow over the migration season of the year in question (FMFR). The WDR will increase as the river becomes shallower and wider. If the FMFR value is above one, this means the daily flow was above average for that particular migration season, and if the value is below one, the daily flow was below average for that particular migration season. Variables such as temperature, turbidity and flow were recorded directly from gauge stations on the river (Table 6). Measurements such as water velocity and WDR were simulated using actual flow recordings, high-resolution bathymetric cross-sections, and gradient information in the riverine hydraulics modeling software program HEC-RAS (US Army Corps of Hydraulic Engineers). All reach-specific environmental variables were then averaged by reach and by day. All reach-specific spatial-temporal environmental variables were then associated with their respective reach-specific movement rates in a relational database (Microsoft SQL Server 2005, Microsoft Corporation).

Results

Smolt outmigration

The mean successful migration movement rate (MSMMR) per release group varied by release site and by year (Table 3). Mean total movement rates decreased the further downstream the release group was released. Movement rates varied from 14.3 $km \cdot day^{-1}$ (S.E. =± 1.3 $km \cdot day^{-1}$) for the 2009 Butte City release group (rkm 363) to 23.5 $km \cdot day^{-1}$ (± 3.6 S.E.) for the 2007 Battle Creek release group (rkm 534). An ad hoc analysis of variance confirmed this pattern: release location had a significant effect on MSMMR ($P < 0.05$), while year did not ($P = 0.2$).

Reach-specific movement

Movement rates decreased as smolts moved from upstream regions downstream toward ocean entry, with the fastest movement rates found in the upper river region, followed by a decreasing trend up until the slowest region: the Sacramento-San Joaquin River Delta (Fig. 2). The interaction between region and year suggested a similar trend in all years of generally decreasing movement rates the further downstream the region, but in 2009 movement rates were generally slower and more uniform among regions.

The different smolt travel time models were constructed, and ordered in terms of their AICc value (Table 4). The "r(reach) σ(1)" was found to be much better supported (AICc difference larger than seven) than the null model, suggesting that there is heterogeneity in reach specific movement rates. Additionally, the "r (reach) σ(reach)" model was also much better supported than the "r(reach) σ(1)" model, suggesting that the population spreading rate is also heterogeneous on a reach-specific basis.

Table 6 Sources of environmental data for this study

Environmental variables	Data source[a]	Data Location
Water temperature (°C)	UCD, BOR, DWR, USGS, USFWS	http://cdec.water.ca.gov/
Water turbidity (NTU)	BOR, DWR, USGS	http://cdec.water.ca.gov/
River flow ($m^3 \cdot sec^{-1}$)	BOR, DWR, USGS	http://cdec.water.ca.gov/
Channel water velocity ($m \cdot sec^{-1}$)	HEC-RAS simulations using DWR bathymetry	Ricky Doung, Todd Hillaire *pers. comm.*[b]
Maximum river depth (m)	HEC-RAS simulations using DWR bathymetry	Ricky Doung, Todd Hillaire *pers. comm.*[b]
River surface width (m)	HEC-RAS simulations using DWR bathymetry	Ricky Doung, Todd Hillaire *pers. comm.*[b]

[a] Agency Acronyms: *UCD* University of California—Davis, *BOR* United States Bureau of Reclamation, *DWR* California Department of Water Resources, *USGS* United States Geological Survey, *USFWS* United States Fish and Wildlife Service, *USACE* United States Army Corps of Engineers

[b] Ricky Doung (rdoung@water.ca.gov); Todd Hillaire (hillaire@water.ca.gov)

Parameters allowing for newly released smolts to have a different movement rate from the "run-of-river" smolts (ROR; smolts that are migrating through the reach in question, i.e. smolts that were not recently released) were incorporated into the "r(reach+release) σ(reach)" model, and this substantially improved the models support over the "r(reach) σ(reach)" model (which served as the framework for the new model). Additionally, this model was marginally better supported than the "r(reach+release) σ(reach+release)" model, suggesting that spreading rates were not substantially different between newly released smolts and ROR smolts. The maximum likelihood estimate (MLE) for movement rate for the Irvine Finch group (middle release site) in the first reach after release was 22.3 km·day^{-1} versus 13.4 km·day^{-1} for the ROR smolts in that reach. As for the Butte City release group (furthest downstream release site), their MLEs for movement rate in the first reach after release was 22.3 km·day^{-1} versus 24.0 km·day^{-1} for the ROR smolts.

Parameters allowing for an additive effect of year of release were also incorporated into the smolt travel time model. Given that a release effect had been found, and that 2007 did not have any downstream released fish, the year model had to account for the release effect. Therefore the model "r(reach+release+year) σ(reach+release+year)" was constructed, and was found to have substantially better support than the "r(reach+release) σ(reach+release)" base model. This implies that year had an influence of reach-specific movement and spreading rates in an additive way. The movement rate β coefficients for the 2008 and 2009 years (2007 was the intercept) are both positive, with 2008 having the larger value. This indicates that in general, 2008 had the fastest movement rates, followed by 2009, then 2007. The spreading β coefficients for 2008 and 2009 were both negative, with 2008 having the larger value. This means that 2007 had the largest spreading rates, followed by 2008, and finally 2009 had the smallest spreading rates. This year model was the best supported model of all the models run, and therefore the MLEs for each parameter are shown in Table 5.

Influence of the environment

The influence of different environmental variables was also assessed using the smolt travel time model. Each of these models can be compared to the null model for an indication of fit; the environmental models are based off the null model, and therefore, any improvement in fit is purely due to movement rate variability explained by variability in the environmental factor in question. The environmental model to perform the best was the river width-to-depth ratio model (WDR) (Table 4). WDR had a negative relationship with movement rates, indicating that the deeper and narrower reaches (low WDR) will have faster movement rates. The WDR model also had the strongest standardized β coefficient. The next best supported smolt travel time model was the river flow model, with a positive relationship between flow rates and movement rates. The turbidity and FMFR models were the next best supported models, again with positive relationships with smolt movement rates. The velocity model was also well supported, albeit much less than some of the previously mentioned models, and with one of the weakest standardized β coefficients. The relationship between velocity and smolt movement was negative. Finally, the temperature model was the only environmental model that was not found to be better supported than the null model.

Using the two environmental variables that had the best fitting models, WDR and river flow, we then constructed a new model incorporating both into the "r(reach) σ(reach)" model. This model far outperformed all other environmental models, and was second only to the "r(reach+release+year) σ(reach+release+year)" model.

Discussion

Migration rates from the Battle Creek release site to the ocean in 2007 (23.5 km·day^{-1}), were similar to a mean migration rate of late-fall run Chinook salmon smolts released at the same site and recaptured at the beginning of the San Francisco Estuary using a mid-water trawl (30.25 km·day^{-1}, USFWS Stockton FWO data 1994–2010, [http://www.fws.gov/stockton/jfmp/datamanagement.asp]). The mean migration rate for yearling Chinook salmon smolts on the Columbia River, another large West Coast river, was 21.5 km·day^{-1} (Giorgi et al. 1997). Although migration rates of yearling Chinook salmon on the

Fraser River (a large undammed West Coast river that runs through British Columbia) are not available in the literature, similarly sized sockeye salmon (Oncorhynchus nerka) smolts navigated the watershed at a rate of 15 to 30 km·day^{-1} (Welch et al. 2009). The results for late-fall Chinook salmon smolts presented here in combination with those of yearlings from other studies strongly suggest that like-sized smolts exhibit very similar migration rates regardless of the large river system.

Smolt movement rates varied substantially throughout the watershed. The fastest movement rates were seen in the river regions, with the Upper Sacramento River having the fastest rates of the three, potentially due to the faster water velocities seen there, allowing for faster passive transport of an actively migrating smolt. The slowest movement rates were seen in the Sacramento-San Joaquin River Delta, a highly modified and complex system of sloughs and channels. Water diversions in the southern delta remove nearly 40 % of the historic flows through the delta, resulting in substantial modifications in flow dynamics and directions (Nichols et al. 1986). This creates a region in which smolts have a high susceptibility of entering the interior delta, predisposing them to longer routes, higher predation, and the risk of entrainment into water pumps, inevitably leading to higher mortality rates (Perry et al. 2010).

The use of the smolt travel time model was an effective tool for exploring movement in this system, as well as determining longitudinal patterns of activity interacting with different environmental variables. As we uncover characteristics specific to movement dynamics in this system, we will be able to further improve the conceptual model to explain more of the variability in the observed data. As such, the careful discussion of model fit and parameter estimates should provide insight into more complex models worth exploring.

Movement and population spreading rates were seen to vary on a reach basis, as suggested by different smolt movement model comparisons. This heterogeneity in movement rates was expected, especially when considering the changing river habitats throughout the reaches. This variability demonstrates the need for delving into what environmental variables may be governing these reach specific differences. The changing population spreading rate appears to be in large part due to varying reach length, with the longest reaches having the largest spreading rates. This could be due to the fact that one of the models underlying assumptions is a lack of any diel migratory behavior. In the case of this study, smolts would mostly travel at night (Chapman et al. 2012, this issue), and in the case of the largest reaches (since they could not be traversed in one single night) the smolts would have had to experience diurnal time periods within that reach, thereby slowing the migration for some and effectively increasing the population spreading. We suggest that an improved smolt travel time model be created that allows for diel migration behavior as this is a staple in many smolt populations.

The smolt travel time model that allowed for reach and year variability, while accounting for a “release” effect, was the best supported model of the models tested. This suggests that movement rates varied by year, with 2008 having the fastest movement rates, followed by 2009 then 2007. The rate of population spreading did not follow the same pattern, with a general decrease from 2007 through to 2009. However, all 3 years of the study were all similarly dry years resulting in low river flows (DWR 2009. WSIHIST Water Year Hydrologic Classification Indices, [http://cdec.water.ca.gov/cgi-progs/iodir/wsihist]). This could indicate that movement and population spreading rates may be more similar in these years than when compared to “wet” years. In addition, it is important to note that movement rates and environmental associations found in this study may only be indicative of dry year dynamics.

Given that several release sites were used in this study, there was a need to test for potential release effects on movement rates. The reach-specific smolt travel time model that allowed for a release effect on movement rates was indeed better supported than the similar model without a release effect. Specifically, movement rates for smolts released at Irvine Finch (the middle release site) were substantially faster than movement rates of “run-of-river” (ROR) smolts in the first reach after Irvine Finch, while the relationship between the further downstream Butte City released smolts and their ROR counterparts was both weaker and the opposite. One potential reason for this was that smolts from Irvine Finch were released at dusk, while ROR smolts entered reaches at all times of the day. Given the predisposition for nocturnal migration in this population, there is a strong possibility newly-released smolts moved faster since they all experienced night conditions immediately after release, as opposed to the ROR smolts that did not all experience such an advantage. As for the Butte City smolts, a potential explanation for the lack of a similarly strong pattern could be due to the attenuation of the nocturnal migration behavior in this further downstream reach (Chapman et al. 2012, this issue). Interestingly, although Irvine Finch smolts appear to move faster than ROR smolts immediately after release, the smolts released furthest upstream have the fastest mean successful migration movement rate (MSMMR). This inconsistency brings to light an important distinction to make: travel times used in this modeling exercise are from all smolts in the study, while migration rates provided above are only for the small fraction of the study individuals that successfully outmigrated to the ocean. We determine that there is an appreciable release effect on movement rates in this system, meriting consideration of this occurrence into the construction of smolt travel time models when using several release sites.

River width-to-depth ratio (WDR) was found to have a strong negative relationship with movement rates, meaning that smolts moved slower through wider, shallower reaches. In that the upper river had the fastest smolt movement rates, and was intermittently wide and shallow, this relationship may seem counter-intuitive. However, the upper river region did not have the highest mean WDR, and was composed of deeper river sections interspersed with wider, shallow runs and riffles, suggesting that the movement rates in this region may be associated more with complex differential travel behavior incorporating a range of WDR habitats.

Flow has often been suggested to influence movement rates of yearling Chinook salmon (Zabel et al. 1998; Smith et al. 2002). In this study, flow was found to be positively related with movement rates. Flow generally increases in the downstream direction, in large part due to the progressive additions of water from the numerous tributaries in this system. However, the mean flows experienced by smolts in this study were very similar across regions. One possible interpretation of the relationship between flow and movement could be that it is the temporal (and not the spatial) variability in flow that drives this relationship. Salmonid smolts are known to initiate their downstream migration during storm events (McCormick et al. 1998), analogous with high flows. This was the motivation in creating the model using flow to mean flow ratio (FMFR) as a linear predictor. This relationship was also positive, further supporting our hypothesis. There was indeed some evidence of increased watershed-wide smolt movements during particularly strong storm events. We therefore conclude that the relationship between flow and movement rate may be strong past a certain flow threshold and a more complex model should be explored that may capture the occurrence.

The model using both aforementioned environmental variables was found to be the second best supported model tested. While the beta coefficients for both WDR and river flow were relatively small, they were in agreement with coefficients from their respective individual models. The purpose of taking the two best environmental variables and using them both in one model was an exercise to determine if we could find a well-supported model that resource managers could use in predicting future smolt migration travel times based on environmental variables alone, and in some instances, exercise their control over dam releases to meet salmon management goals. Building such a model is especially important in light of the fact that the best supported model incorporated both reach and year variability; while this does provide meaningful information, the year factor prevents us from making future predictions with it, and it is therefore less useful to resource managers.

Turbidity was seen to have a strong positive relationship with movement rates in this study. From associated work, we know that increases in turbidity correlate strongly with increases in survival (C. Michel, unpubl. data), perhaps because turbidity dramatically decreases predator efficiency (as seen with various predators on salmon smolts in the Fraser River (Gregory and Levings 1998) and with smallmouth bass (*Micropterus dolomieu*) in a laboratory setting (Sweka and Hartman 2003)). Survival rates were low in the upper reaches of the Sacramento River (C. Michel, unpubl. data), coinciding with the location of the primarily nocturnal migration, while higher survival in the lower river coincided with the more even migration through the day seen in the lower river reaches (Chapman et al. 2012, this issue). These results suggest that the relatively clear waters of the upper and middle river regions have much higher predation rates, which may have driven the evolution of a nocturnal migration strategy. However, the lower region has more turbid water and therefore may be more cryptic and beneficial for smolt survival. Perhaps this is what allowed the easement of the nocturnal strategy in the lower river, as also seen by Moore et al. (1998) and Ibbotson et al. (2006) with Atlantic salmon smolts. This then may have allowed migration at all hours which in turn provided smolts with the opportunity to travel larger distances per day, potentially explaining the positive relationship between movement rates and turbidity. Alternatively, or perhaps acting in concert, the relationship between turbidity and movement rates could spawn from the fact that turbidity tends to increase during high river flows during storm events, during which smolts usually initiate migration.

Water velocity was found to be the fifth strongest relationship, and somewhat counter intuitively, was found to be negatively correlated with movement rates. Water velocity can help a smolt move downstream at faster rates by increasing passive transport. This relationship was believed to be the most important environmental factor a priori, however, the direction of the correlation was the opposite of what was expected. One potential explanation is that only travel events during which the smolt was recorded at the upstream and downstream receiver station were used in this correlation analysis. This created a problem in that during high flow events (with fast water velocities), detection probability decreased due to increased noise, increased monitor tilt, and increased turbidity, and therefore fewer movement recordings were available during high flows. This potential shortcoming may have further reaching consequences in this analysis; it could be that other environmental variables tested did not have many associated travel events near their extremes during high flow events due to low detection probabilities.

Temperature was the only environmental variable to show no indication of influencing movement rates. Much work has been done on the effect of increases in temperature on smolt migration initiation, suggesting that temperature should indeed be tightly linked to movement rates. However, the negative results seen in this study are not the uncommon in the literature. Two other studies have found no significant relationship between temperature and migration rate in yearling Chinook salmon smolts (Giorgi et al. 1997; Smith et al. 2002). One potential reason for the lack of effect could be that the smolts were released all at once, during two releases each season, and therefore experience a narrow range of temperatures. This is in contrast with many studies that do find a relationship between temperature and migration rate; data used are frequently from random sampling of the outmigrating smolt population using continuous trapping methods over a long field season. This problem could be further exacerbated by the fact that the Upper Sacramento River displays relatively constant water temperatures because Shasta Dam releases cold water from the bottom of Lake Shasta year round (which offers the question of how well can smolts time their outmigration to enter the ocean at the optimal time for feeding and growth if a potentially critical temperature cue is subdued?). Finally, since the study occurred during three similarly dry years (low rainfall and snowpack) in northern California, there is good evidence that there may not have been enough variability in temperatures to obtain a measurable effect.

The patterns and rates elucidated in this paper can provide valuable insight into the migration dynamics of Chinook salmon smolts of other runs, sizes, and stages of development, but caution should be employed in this extrapolation. The smolts used in this study were relatively large yearling Chinook salmon, and were force released into the river system, and therefore could be expressing patterns different from natural and other hatchery populations.

The imperiled Central Valley Chinook salmon stocks will require sound fisheries and resource managing for any hope of an eventual recovery, and this cannot be achieved without understanding the movement and migration dynamics and causal mechanisms of emigrating smolts, arguably the most vulnerable life stage. This study provides new insights on temporal and spatial movement dynamics through the entire watershed, and suggests some environmental factors that shape the emigration. We also present a conceptual model for smolt travel times than can be applied to the Sacramento River Chinook salmon populations. Future directions for this model should include the construction of more complex models to capture certain intricacies that we have presented. Furthermore, due to unavailability of sufficient environmental data, we applied the model to the river section only, but future work should attempt to include the delta and estuary sections of the watershed. A more accurate conceptual model for smolt travel time in the Sacramento River will allow resource managers to fully consider the consequences of anthropogenic activities that may have detrimental effects on salmon populations, and also to best predict migration dynamics of future cohorts facing environmental changes.

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UNIVERSITY OF CALIFORNIA

SANTA CRUZ

RIVER AND ESTUARINE SURVIVAL AND MIGRATION OF YEARLING SACRAMENTO RIVER CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) SMOLTS AND THE INFLUENCE OF ENVIRONMENT

A thesis submitted in partial satisfaction
of the requirements for the degree of

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in

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by

Cyril J. Michel

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TABLE OF CONTENTS

LIST OF FIGURES

Chapter 1

Chapter 2

LIST OF TABLES

Chapter 1

Chapter 2

ABSTRACT

RIVER AND ESTUARINE SURVIVAL AND MIGRATION OF YEARLING SACRAMENTO RIVER CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) SMOLTS AND THE INFLUENCE OF ENVIRONMENT

by

CYRIL J. MICHEL

Identifying where sources of enhanced mortality of outmigrating Chinook salmon (smolts) occur, and the movement patterns associated with this life stage, are critical steps in the preservation and conservation of imperiled salmonids in California’s Sacramento River system. To that end, 200-300 late-fall run Chinook salmon yearling smolts were acoustically tagged per year and tracked during their outmigration in California’s Sacramento River during 2007-2009. Total outmigration survival to the ocean environment varied from 3.1% (± 1.5 S.E.) to 5.5% (±1.2 S.E.), depending on the release year, with an all year total outmigration survival of 3.9% (± 0.6 S.E.), substantially lower than published survival of other West Coast yearling Chinook salmon smolt emigrations. The migration rates of the smolts that successfully reached the ocean varied significantly based on release location, from an average of 14.32 km·day^{-1} (± 1.32 S.E.) to 23.53 km·day^{-1} (± 3.64 S.E.). The high spatial resolution of survival estimates of Chinook salmon (*Oncorhynchus tshawytscha*) revealed that smolts exhibited relatively low survival (92-97% survival·10km^{-1}) in the upper reaches of the Sacramento River, as well as in the

Sacramento River Delta and San Francisco Estuary (67-94% survival·$10km^{-1}$). No significant inter-annual variation in survival, total river migration rates, or smaller scale movement rates were found, potentially due to similar hydrographic conditions among the three years. Survival did fluctuate significantly depending on month of release and river reach. Several natural and anthropogenic factors that are known to affect smolt survival rates were assessed; variables associated with river channelization, turbidity and sinuosity were all found to have positive relationships with survival within the river, suggesting increases in these variables may increase survival (likely by means of reducing predation). Smolts exhibited strong nocturnal movements while in the less turbid and channelized upper regions of the river which dissipated to temporally uniform movements in the more turbid and channelized lower regions of the river, suggesting that eased predatory action may have caused smolts to discontinue the nocturnal strategy. Survival data suggests a refocusing of fisheries and resource managers' efforts, specifically with regards to hatchery release strategies and the current concentration of mitigation efforts in the delta.

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INTRODUCTION

In California's Central Valley (comprised of the Sacramento and San Joaquin Rivers, as well as their tributaries), freshwater salmon ecology has become inextricably associated with human interests. In a watershed where 47% of historical salmon spawning, migration and rearing habitats are inaccessible due to dams (Yoshiyama et al. 2001), an estimated 40% of the historical, pre-colonization river discharge is lost to water exports (Nichols et al. 1986). Finally, where approximately 90% of historical Central Valley wetlands, which are important for salmonid rearing, have disappeared to allow for agriculture and flood control (Frayer et al. 1989), one must think of this watershed as, at best, an altered ecosystem. As a result of these modifications and others, the four distinct Central Valley Chinook salmon (*Oncorhynchus tshawytscha*) populations are either endangered, threatened, or a "species of concern" according to the U.S. Endangered Species Act (ESA). Moreover, the commercial importance of water resources and a $255 million salmon fishing industry (Office of the Governor of California 2008) makes habitat and population recovery to pre-colonization levels impossible. It is therefore imperative that we understand the influence of the environment on Chinook salmon survival and behavior, both to assess the impact of current habitat modifications, but also to provide recommendations into how to improve management of this watershed with respects to one of its most valuable resources.

The outmigration of juvenile Chinook salmon (smolts) is among the most vulnerable life stages during which habitat modification can have strong influences.

During this relatively short life stage, a smolt will sometimes travel hundreds of kilometers and transit several different habitats with varying degrees of anthropogenic modification. Human activities can directly influence smolt survival, but also indirectly through the intermediary of changed environmental conditions. Thus, the focus of my first chapter is on survival patterns of a population of outmigrating Central Valley Chinook salmon smolts, on the environmental factors that correlate with them, and finally, an assessment of the influence of watershed modification.

Salmonids employ numerous life-history strategies to maximize fitness and survival. Specifically, movement patterns during migration contribute to survivability, and different migration strategies can vary in their effectiveness (Stearns 1976). For example, Chinook salmon have two distinct early life history strategies to maximize survival and growth: "ocean-type" juveniles that leave the river and travel to the ocean weeks after hatching and "stream-type" juveniles that feed in the river for up to one year and outmigrate to the ocean at a much larger size (Gilbert 1912). Depending on the river and ocean conditions for each year, one of these life history strategies may result in better survival than the other. In this investigation, I have therefore quantified movement during the outmigration of "stream-type" juveniles, highlighted potential movement strategies and associations with the environment, and discussed the sources of mortality that may have shaped them in the second chapter of this thesis.

The fisheries and resource management applications of the information collected in this study are invaluable in many regards. This study has provided high spatial and temporal resolution survival estimates, illuminating regions of particularly high and low survival. These estimates, coupled with environmental data, will allow resource managers to concentrate mitigation efforts on specific mortality hot-spots while benefiting from evidence for potential causality for both low and high survival. This study also provides managers with a detailed description of the outmigration of the smolts in question, and the correlations with environmental variables, allowing them to better predict the consequences of anthropogenic activities that occur along the migratory corridor, or predict migration dynamics of future cohorts facing environmental changes. Finally, and perhaps most importantly, this study has discerned survival and movement dynamics that may be shared by the ESA. listed Chinook salmon runs in the Central Valley, adding to a knowledge base that will be fundamental to conservation actions.

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Chapter 1

River and estuarine survival of yearling Sacramento River Chinook salmon (*Oncorhynchus tshawytscha*) smolts and the influence of environment

INTRODUCTION

Chinook salmon (*Oncorhynchus tshawytscha*) are a cultural and economic resource to the western United States and Canada, including the state of California. Of the California salmon rivers, the Sacramento River supports the largest, most diverse, and until recently, healthiest salmon stocks. However, since 2007, the largest of the Sacramento River populations, the fall run Chinook salmon, has crashed, and adult returns to the basin have been as low as 25% of the long-term 30-year average (in 2009; Azat 2010). Emergency action has been taken by the Pacific Fisheries Management Council, including a moratorium on commercial and recreational fisheries for coastal and inland waters of the entire state for the 2008-2009 seasons, causing an estimated loss of $255 million and 2,263 jobs (Office of the Governor of California, 2008). This precipitous decline is thought to have been driven by poor ocean conditions (Lindley et al. 2009), but it is clear that it is a combination of many stressors that have brought Sacramento River salmon to such a delicate state (Yoshiyama et al. 1998).

One of the most vulnerable stages in a Chinook salmon's life is the downstream migration of juveniles heading to the ocean from their riverine origins

(Healey 1991). During this life stage, the juvenile salmon undergoes many physiological and behavioral changes (known as smoltification) to prepare for the ocean phase of their life cycle. For the Sacramento River's Chinook salmon populations, this freshwater journey may be as long as 600 kilometers, transiting many different habitats. Additionally, anthropogenic stressors such as water diversions, dams and introduced predators are present throughout the watershed.

Environmental factors can influence smolt survival directly or indirectly by influencing the distribution and foraging of the smolt predators. For example, Smith et al. (2002) found that survival decreased as river flow decreased for subyearling fall run Chinook salmon in the Snake River; Gregory and Levings found that increased turbidity resulted in increased survival for juvenile Chinook salmon in the Fraser River (1998), and Baker et al. (1995) found that temperature explained a substantial portion of the variation in survival rates for subyearling fall run Chinook salmon in the Sacramento – San Joaquin River Delta, especially as temperatures neared lethally high levels.

Understanding the magnitude and potential variation in smolt mortality is a logistically and quantitatively difficult problem. Cormack (1964), Jolly (1965), and Seber (1965) developed methods for determining temporally explicit survival estimates in rivers via mark-multiple recapture models. Burnham (1987) then developed a spatially explicit approach adapted for estimating survival of migrating fish in rivers, which, for example, was used for survival estimates on a river-reach scale for Columbia River salmon (Muir et al. 2001, Skalski et al. 2001). These quantitative mark-recapture techniques can be expanded to assess what environmental conditions correlate with variations in survival.

In this study, I quantify the spatial and temporal patterns of Chinook salmon survival in the Sacramento River system. I capitalized on one of the largest networks of acoustic monitors in the world developed by the California Fish Tracking Consortium (http://californiafishtracking.ucdavis.edu/), and a collaboration between the National Oceanic and Atmospheric Administration (NOAA) and the University of California, Davis (UCD), to utilize these aforementioned techniques on the late-fall run Chinook salmon population in California's Central Valley. Previous investigations of Chinook salmon in the Sacramento River only allowed for low-resolution estimates of survival (Snider 2000 a, b). Additionally, most work had focused on only the Sacramento-San Joaquin River Delta (Baker and Morhardt 2001, Brandes and McLain 2001), a small portion of the smolt migration corridor.

I will address the two following hypotheses:

(1) Total and reach-specific outmigrating late-fall run Chinook salmon smolt survival rates vary spatially and temporally in the Sacramento River, Sacramento-San Joaquin Delta and San Francisco Estuary.

(2) Environmental variables that vary in space and time can explain a substantial portion of variation in reach-specific survival rates.

This represents the first high-resolution analysis of the magnitude and spatial-temporal variation in survival of outmigrating Chinook salmon smolts in the Sacramento River and San Francisco Estuary and the potential natural and anthropogenic drivers of mortality. This represents a leap forward in our understanding of the environmental factors that may influence survival rates of outmigrating Chinook salmon smolts. This knowledge is critical to efforts to mitigate the sources of mortality or predict survival rates of future cohorts facing environmental changes. Finally, assessing what environmental conditions influence variation in late-fall run Chinook salmon survival will help give us insight into factors affecting the survival dynamics of other valued salmon runs in California such as the winter and spring run, listed under the United States Endangered Species Act as endangered and threatened, respectively (Moyle et al. 1995).

METHODS

Study area

The Sacramento River is the longest and largest (measured by flow discharge) river that is fully contained within the state of California, and is the third largest river that flows into the Pacific Ocean in the contiguous United States (Fig. 1). The headwaters are located just south of Mount Shasta in the lower Cascade Range and the river enters the ocean through San Francisco Estuary at the Golden Gate. The total catchment area spans approximately 70,000 km^{-2}. The Sacramento River and its tributaries have been heavily dammed, and it is estimated that approximately 47% of the historic area that was used for spawning, migration and/or rearing of Chinook salmon is no longer accessible (Yoshiyama et al. 2001). The Sacramento River watershed includes diverse habitats, from a pristine run-riffle river, to a heavily channelized and impacted waterway further south, to an expansive tidally-influenced freshwater delta at its confluence with the San Joaquin River, and finally to the San Francisco Estuary, the largest and most modified estuary on the west coast of the United States (Nichols et al. 1986). The annual mean daily discharge for the Sacramento River from 1956 to 2008 was 668 m^3s^{-1} (Interagency Ecological Program, 2004). However, this water does not continue downstream unimpounded, it is estimated that current water discharge of the Sacramento and San Joaquin Rivers combined amounts to approximately 40% of the historical, pre-colonization discharge (Nichols et al. 1986). The damming and water diversions of the Sacramento River and its tributaries have also homogenized river flows throughout the year, notably reducing the historical winter high flows and flooding (Buer et al. 1989).

The study area included approximately 92% of the current outmigration corridor of late-fall run Chinook salmon, from release to ocean entry. Specifically, the study area's furthest upstream release site at Jelly's Ferry (518 km upstream from the Golden Gate Bridge) is only 47 km downstream from Keswick Dam, the first impassable barrier to anadromy.

Central Valley late-fall run Chinook salmon

The California Central Valley (includes the Sacramento and San Joaquin Rivers, as well as their tributaries) has four distinct Chinook salmon populations (runs) that all migrate at different times of the year. Additionally, these populations demonstrate one of two early life history strategies: "ocean-type" and "stream-type" (Gilbert 1912). Ocean-type Chinook salmon are born in the lower reaches of large rivers and spend very little time (days to weeks) in the river before migrating to the ocean. Stream-type juveniles are born in the headwaters of large rivers and spend up to a year in the river (“yearling”), migrating to the ocean at a relatively large size. Among the different runs and early life history strategies, it becomes clear that different populations have found different migration strategies to maximize survival (Taylor 1990).

The late-fall run is one of the four runs found in the Sacramento River drainage, and is the only to exhibit a predominately stream-type life history (Moyle 2002). It is considered to be a “species of concern” by the Endangered Species Act as of April 15, 2004. Juveniles exhibit a river residency of 7 to 13 months, after which smolts will enter the ocean at a size of approximately 160 mm (Fisher 1994). Potentially due to water diversions and increased predation in bank-altered areas, outmigrating late-fall run juveniles accrue substantial mortality (Moyle et al. 1995).

The historical distribution of the late-fall run Chinook salmon is hard to estimate, due to the paucity of historical data. Late-fall run Chinook salmon were not distinguished from fall run fish until 1966, when counts were initiated after the construction of the Red Bluff Diversion Dam (RBDD) in the mid 1960s (Yoshiyama et al. 1998). However, we know that ideal late-fall run Chinook salmon spawning habitat consists of year-round cold water allowing the rearing of yearlings, and that their current spawning range is from Red Bluff (480 river km (rkm) upstream from the Golden Gate Bridge) to the first barrier to anadromy, Keswick Dam (rkm 565) (Fisher 1994, Moyle et al. 1995, Yoshiyama et al. 2001). We assume that this run historically used the cold waters upstream of Keswick Dam, specifically the Upper

Sacramento, McCloud and Pit Rivers for spawning (Yoshiyama et al. 1998). Since these rivers are no longer accessible, the large majority of late-fall run Chinook salmon spawning grounds disappeared with the construction of Keswick and Shasta Dams.

Acoustic Telemetry

Acoustic tagging technology was used to acquire high-resolution movement and survival estimates. I used Vemco V7-2L acoustic tags (1.58g ± 0.03 S.D.; Amirix Systems, Inc., Halifax, Nova Scotia, Canada) and Vemco VR2/VR2W submergible monitors to track tagged fish. The monitor array spanned 550 km of the Sacramento River watershed from Keswick Dam to the ocean (Golden Gate). This array of approximately 300 monitors was maintained by the California Fish Tracking Consortium, and positioned to maximize detection probability at key sites along the outmigration corridor.

The acoustic monitors automatically process all detection data and drop false detections or incomplete codes from the detection file. All detection files were additionally subject to standardized quality control procedures to minimize the number of false detections. For example, detections that occurred before the release date-time of each tag, or detections that did not share a tag identification number (tagID) with any of the released fish, were excluded from analysis.

Tagging and Releases

For three consecutive winters, from January 2007 to January 2009 (henceforth referred to as 2007, 2008 and 2009 seasons, based on the year during which January tagging occurred), 200 to 300 late-fall run Chinook salmon smolts were tagged and released into the Sacramento River watershed. The size of tagged fish (Table 1) was consistent with observed size frequency for this run, albeit larger than other life-history type Chinook salmon smolts (Fisher 1994).

Hatchery-origin yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) smolts, obtained from the United States Fish and Wildlife Service's (USFWS) Coleman National Fish Hatchery (Anderson, CA), were used in this study. Approximately 85-90% of the hatchery smolts are the progeny of hatchery-origin adults trapped in Battle Creek (tributary to the Sacramento River); parents of the remaining hatchery smolts' are natural-origin adults trapped on the mainstem Sacramento River just below Keswick Dam (K. Niemela, USFWS, Red Bluff, CA 96080, unpubl. report).

Acoustic tags were surgically implanted into the peritoneal cavity of anesthetized fish as described by two studies (Adams et al. 1998a, Martinelli et al. 1998). Tag weight did not exceed 5% of the total body weight to minimize potential affects on survival, growth, and behavior. This cutoff point was conservative, considering much of the literature shows tag-to-body ratios can be up to 6% and not affect growth (Moore et al. 1990, Adams et al. 1998a, Martinelli et al. 1998), and up to 8 % and not affect swimming performance (Brown et al. 1999, Anglea et al. 2004, Lacroix et al. 2004).

Tagged fish were kept in captivity for a minimum of 24 hr after surgery to ensure proper recovery. In the 2007 season, a portion of the tagged fish was released each weekday for three consecutive weeks in January. In the two following seasons, half the smolts were released in December and half in January, both on a single day. All releases occurred at dusk to minimize predation as the smolts became habituated to the riverine environment.

In the first year (2007), all 200 fish were released at the Coleman National Fish Hatchery into Battle Creek, a tributary to the Sacramento River. In the latter two years, approximately 300 fish were tagged each year and simultaneously released from three release sites in the upper 150 rkm of the mainstem Sacramento River, allowing the lower release groups to reach the lower river and estuary in larger numbers. Fish were transported at low densities (~ 10 $g \bullet l^{-1}$) via coolers with aerators to the release sites. In years of multiple release sites, transport times were extended for closer sites to keep potential transport stress equal among all release groups.

Data Analysis

Juvenile Chinook salmon express obligate anadromy, meaning that they will travel toward the ocean once the emigration has begun, with scarce exceptions (Healey 1991). Therefore, in a linear system such as the Sacramento River, if a fish is detected at one monitor site, but is never detected thereafter, we assume that the fish has died somewhere in the reach between the monitor where it was last detected and the next downstream monitor location.

Calculating mortality using fish absence as a proxy works if we assume detection efficiency is perfect. Unfortunately, detection efficiency is not 100% given current tagging technology. Therefore, to accurately calculate the mortality rates of the emigrating Chinook salmon while accounting for detection probability, I used the Cormack-Jolly-Seber (CJS) model for live recaptures within Program MARK (created by Gary White, Colorado State University(White and Burnham 1999). The CJS model was originally conceived to calculate survival of tagged animals over time, by re-sampling (recapturing individuals) an area and calculating survival and recapture probabilities using maximum likelihood models. For species that express an obligate migratory behavior, a spatial form of the CJS model can be used, in which recaptures (i.e., detected acoustically more than once) are structured spatially along a migratory corridor (Burnham 1987). The model determines if fish not seen at certain monitors were ever seen at any monitor downstream of that specific monitor, thus enabling calculation of maximum-likelihood estimates for detection efficiency of all monitor locations (p), all survival estimates (Φ), and 95% confidence intervals for both (Lebreton et al. 1992).

Detection efficiencies are calculated by assessing the number of tags missed by a monitor location. This can be done if a missed tag is seen at a downstream location and therefore assumed to have passed the upstream location. In addition, as sample size decreases further downstream, detection efficiencies have increasingly large errors until the final monitor location, where survival and detection efficiency at that station are not identifiable. Because accurate estimates of survival at ocean entry were important, parallel monitor lines were installed at the Golden Gate about 1 km apart to calculate both detection efficiency and survival at the inner Golden Gate line. Additionally, in the latter two tagging seasons, I benefitted from the installation of a monitor line at Point Reyes, seaward from the Golden Gate approximately 60 km to the north. This acoustic monitor curtain allowed an estimate of detection efficiency for the outer Golden Gate line, thereby further reducing error in the estimation of survival and detection efficiency to the inner Golden Gate line.

After the three-year study was completed, monitor locations were assessed for their detection probability and functional reliability over the three-year period, and their location within the watershed. Those that were consistently efficient monitor locations were chosen to delimit the river reaches that were used in spatially comparing mortality. A total of 19 monitor locations were chosen, spanning from just below the most upstream release site to the Golden Gate (Fig. 1; Table 2). Between them, I delineated 17 reaches in which mortality can be accurately estimated (the detection efficiency and survival of the 18th and last reach cannot be distinguished).

The acoustic monitors automatically process all detection data and drop false detections or incomplete codes. Unfortunately, the downloadable detection files are not completely accurate, and occasionally, in areas with high densities of pinging tags or other acoustic noises, false detections are deemed correct by the monitor and saved in the detection files. Detection data was thus stored in a relational database (Microsoft SQL Server 2005, Microsoft Corporation) and analyzed for quality control. Detections that occurred before release date-time of each tag were then deleted. Next, single detections at locations that are not between valid upstream and downstream detections (a valid detection is defined as less than 10 days OR 50 rkm to prior or next detection) were deleted. Finally, if multiple consecutive detections of a tag at one location are greater than 216 minutes apart (10% less than the minimum observed time between consecutive known false detections of the same tag) the detections were considered for removal. These different conditions removed false detections to the best of my ability.

Hypothesis 1

Overall survival was first assessed from the release site to the Golden Gate for each release group. Using the 19 monitor locations, survival for 17 reaches was calculated, using the survival and detection probability linear model (in logit space) allowing for each reach to have a parameter ("full model"). This model, and all other models, allowed for full parameters for the estimation of detection efficiencies (i.e., allowing detection efficiencies to vary per monitor location). I calculated reach-specific survival for each release group separately. By multiplying these survival rates together, the cumulative survival per release group is estimated. Multiplying the cumulative survival rate by the release size produces an estimate of total fish per release group that reached the ocean. Standard error for the cumulative survival estimates were calculated using the delta method.

The influences of study design factors on survival rates were then assessed with Program MARK. To do this, a separate survival model was created for each factor. The influence of these factors was assessed by allowing each group (e.g., 3 groups for the release year model: 2007, 2008 and 2009) within each model to have its own set of survival parameters. Each survival model was added to some form of a base model (often representing a null hypothesis) one by one and then compared to the base model using model selection. The model selection criterion used was Akaike's Information Criterion (AIC), an excellent tool for model comparing and selection because it balances precision and accuracy by penalizing a model for the total amount of parameters it has. Therefore, we are effectively comparing model parsimony and not simply model goodness-of-fit. As suggested by Burnham and Anderson (2002), AIC values were corrected for small sample sizes (AICc), and corrected for over-dispersion (QAICc). If a test model improved the parsimony (lower QAICc) in relation to the base model by a difference of more than seven (Burnham and Anderson 2002), the test model was deemed substantially more parsimonious, and therefore supported over the base model.

The effects of reach (n=17), release year (n=3), release month (n=2), and release site (n=3) were tested. This was done by comparing the parsimony of each model to the parsimony of a "null model". The null model only allowed one parameter for survival (representing the null hypothesis: constant survival through space and time). To allow for these factors to express reach-specific variability in survival, each group (e.g., each year with the above example) has its own reach-specific survival estimates within the confines of one model. The most supported models (based on AIC scores) were then interpreted to determine if the tested factor could have a substantial influence on survival by comparing the models to their counterparts that did not include the factor in question.

Finally, the influence of individual covariates (fork length (mm) and weight (g)) on the parsimony of the survival model was assessed. This can be done by adding a parameter to the linear regression model for survival that represents the covariate. Program MARK then utilizes the parameter to include the individual contribution into the likelihood estimation of survival. The model selected *a priori* to add these covariates to is the reach-specific survival model. This model can then be compared to the simple reach-specific survival model without any individual covariates to determine whether parsimony increases.

Considering this study utilized hatchery-origin smolts for these analyses, the ability to suggest these smolts are adequate surrogates for wild (or natural-origin) smolts in terms of determining survival dynamics would be very useful. A pilot tagging project on natural-origin late-fall run Chinook salmon smolts was conducted in 2009 concurrent with hatchery-origin tagging. A total of 18 wild smolts were captured, acoustically tagged, and released in the mainstem Sacramento at Red Bluff (rkm 478) and in tributary Mill Creek (confluence with Sacramento River at rkm 460). Using the same methods as with hatchery-origin smolts, estimates of reach-specific survival were calculated for the natural-origin smolts. A survival model incorporating detection information from both wild-origin smolts and hatchery-origin smolts released in the 2009 season was created. This model allowed both smolt groups to have their own set of survival parameters. This model was compared to a survival model incorporating the same detection data but constructed as a reach-specific survival model, with both groups sharing the same survival parameters. Essentially, the comparison of the two models determined if natural-origin and hatchery-origin had similar or different survival estimates, based on which model was more supported. This permitted an approximate suggestion of how the hatchery-origin smolt survival estimates compare to a limited sample of the wild population.

Hypothesis 2

Data for environmental variables were compiled for the river reaches, from the release points to the upper limit of tidal influence on the river (rkm 189). They were grouped into two types: spatial-temporal natural variables and spatial natural and anthropogenic variables. All variables were chosen *a priori* based on salmon survival literature and data availability for the watershed. To formalize the approach on investigating the influence of the environment on survival, a conceptual model was constructed (Fig. 2). Riparian habitat and river morphology are spatial variables which influence water temperature, turbidity, and water dynamics. These variables likely govern the behavior of the smolts and their predators, and thus the smolts' susceptibility to predation. Due to the inability to directly measure predation, estimated mortality (using the above methods) was considered as a proxy for predation.

The spatial-temporal variables included water temperature (ºC) (Kjelson and Brandes 1989, Baker et al. 1995, Newman and Rice 2002, Smith et al. 2002, Connor et al. 2003), water flow ($m^3 \cdot s^{-1}$), channel water velocity ($m \cdot s^{-1}$) (Kjelson and Brandes 1989, Smith et al. 2002, Connor et al. 2003), water turbidity (Nephelometric Turbidity Units (ntu); Gregory 1993, Gregory and Levings 1998), maximum river depth (m), and the ratio of river width (m) to maximum river depth (m, WDR). The WDR will increase as the river becomes shallower and wider. Spatial-temporal variables such as temperature, turbidity and flow were recorded directly from gauge stations on the river (Table 3). Measurements such as channel water velocity, depth and river width were simulated using actual flow recordings, high resolution bathymetric cross-sections and gradient information in the riverine hydraulics modeling software program HEC-RAS (US Army Corps of Hydraulic Engineers).

The spatial variables included water diversions (diversions$\cdot$km^{-1}) (Kjelson and Brandes 1989, Perry et al. 2010), riparian habitat type (% of riparian zone covered by either agricultural, natural, or urban land) (Gregory et al. 1991, Pusey and Arthington 2003), riprap (% of total shore reinforced with riprap) (Schmetterling et al. 2001), levees (% of total shore reinforced with leveed walls) and sinuosity (actual river length divided by the length of a direct line between the nodes delimiting each reach). All spatial variables were calculated using the geographic information system software program ArcGIS (ESRI, 1999). Spatial and spatial-temporal variables were associated to tag detections in a relational database.

Once data for the environmental variables were collected, they were averaged per appropriate unit. The spatial variables, not changing through time, were simply averaged per reach. The spatial-temporal variables were averaged per year, month of release, release site, and reach. Having the spatial-temporal variables averaged per smallest group denomination allowed for the maximum amount of spatial-temporal resolution associated to the mortality data.

Within Program Mark, riverine survival was modeled as a logit function of two linear predictors (Eqn 1), while detection efficiency was allowed to vary fully per reach (in the style of the full model). The survival model included an intercept (β_0), a parameter for the reach length (km), and a parameter for an environmental variable. This is a novel approach to relating environmental data to smolt survival, although the technique has been employed instead with detection efficiencies (Melnychuk 2009). The environmental parameter will also have an associated beta coefficient (β), allowing determination of the direction and slope of the relationship. Additionally, by standardizing the environmental variables (subtracting the mean value from each raw data point, then dividing by the standard deviation, essentially giving all standardized variable datasets a mean of zero and a standard deviation of one), standardized beta coefficients can be calculated, allowing for comparison of the strengths of beta coefficients for different models. For a change in one standard deviation unit of the environmental variable, survival will change by the amount specified by that model's standardized beta coefficient.

$$\text{Logit}\ (\Phi) = \beta_0 + \beta_1[\mathit{Reach\ Length}] + \beta_2[\mathit{Env.\ Variable}] \tag{1}$$

All environmental models were compared to a base model to test for a significant improvement in parsimony. The purpose of this base model is to include all sources of mortality that should not be attributed to the environment. The base model specified *a priori* included both reach length and initial mortality after release (Olla et al. 1994, Olla et al. 1995). I adopted reach length, needing to control for the large variation in lengths, but did not incorporate initial release mortality. This was determined after I compared survival models allowing for different survival estimates in the first one and two reaches after release in comparison to all other reaches to the "full model" (reach-specific survival model), and the initial release mortality models were not significantly more parsimonious. In essence, this compared survival through the same reaches of smolts released at that point and smolts released further upstream and found no significant evidence of different survival rates. Therefore, the final base model specified constant survival as a function of reach length.

Environmental models were also compared to the full model. The full model is widely used as the CJS model for calculating survival between, and detection probabilities at, each recapture event, and is typically the most parsimonious model. Comparing environmental models to the fully reach-varying model provided a rough estimate of the distance from potentially maximum parsimony.

Spatial and spatial-temporal environmental models cannot be compared to each other for causative and statistical reasons. In terms of causation, the spatial variables often govern the spatial-temporal variables (i.e., % leveed shoreline influences width and depth of river) (Fig. 2). Statistically, strictly spatial variables should not be added to the spatial-temporal varying base model due to the temporal grouping parameters (i.e., year, time) which would unnecessarily penalize the model for the superfluous parameters. Therefore, the different spatial and spatial-temporal environmental models were analyzed separately, and can only be compared to like models.

Once the environmental variables that had the strongest associations with survival estimates were determined, two sample *t-tests* were used to determine if variations existed between treatments that also exhibited significant variations in survival.

RESULTS

Hypothesis 1

Total survival through the entire studied migration corridor (rkm 518 to 2) per year varied from 3.1 to 6.1% (Table 4), with an all year total outmigration survival of 3.9% (± 0.6 S.E.). Release group-specific survival through the entire migration corridor averaged between 3 and 13%. In both 2008 and 2009, when three release sites were used, a consistent pattern emerged, such that the furthest upstream release group exhibited the lowest survival, the furthest downstream release group exhibited relatively moderate survival, and finally the middle release group had the best survival of the three.

Fish weight and fork length varied significantly among years ($P<0.001$), and pairwise hypothesis testing using Bonferroni and Tukey's HSD tests both indicate that fish sizes were statistically different between all years.

Survival on a reach-by-reach basis was quite variable. Through the three years of the study, the upper river reaches (reaches 1 through 8; rkm 518 to 325) had lower survival rates. The lower Sacramento River had relatively higher survival (reaches 9-12; rkm 325-169), whereas the delta and estuary had lower survival (reaches 13-17; rkm 169-2) (Fig. 3, Fig. 4). In the 2007 season, survival of tagged smolts within the Battle Creek tributary (rkm 534-518) was relatively very low, 63% (± 1.0 S.E.) per 10 km. Reach-specific survival rates throughout the three years in the Sacramento River-

San Francisco Estuary ranged from 67% per 10 km reach in the lower estuary reach (Richmond Bridge to Golden Gate; rkm 15-2) to 100% per 10 km reach in the last river reach before the delta (City of Sacramento to Freeport; rkm 189-169) (Table 5; Fig. 4). Detection efficiencies were also estimated grouping all three years of the study and were found to be satisfactory for CJS modeling, ranging from 0.52 to 1.00 (Table 5).

The influence of reach on survival rates was found to be significantly more parsimonious (ΔQAICc >7) than the Null Model (constant survival through space and time; Table 6). All the design structure factors were then added to the survival model including the influence of reach, and then tested for significance against the reach-specific survival and null model. The factors of year, month, release site, and the covariates of fork length and weight were all tested, entertaining every factorial possibility. The only model found to be statistically more parsimonious than the reach-specific model included month as a factor. That is, along with reach, month of release had a substantial effect on reach-specific survival. Specifically, in both 2008 and 2009 (2007 was omitted due to only one release month) smolts released in December had significantly higher survival rates in the upper river than smolts released in January (Fig. 5).

Wild (natural-origin) reach-specific survival rates were estimated and compared to study's hatchery-origin survival rates, and in most reaches, survival per 10 km per reach for both populations were not statistically different (Fig. 6). Furthermore, the parsimony of the survival model allowing for wild and hatchery smolts to have separate survival estimates was significantly less parsimonious (ΔQAICc=12) than the full model, further suggesting that reach-specific survival of wild smolts was not different than hatchery smolts.

Hypothesis 2

Riverine survival rates were then constrained to spatial environmental variables and compared to a base model of constant survival per km per reach. The environmental models found to be significantly more parsimonious were, in order of decreasing significance, % riprap shoreline, % levee shoreline, sinuosity, diversions per km, and finally % natural riparian habitat (Table 7). The fully reach dependent survival model ("full model": constant survival per reach through time) is significantly more parsimonious than all spatial environmental models. The two most significant spatial variables, % riprap shoreline and % levee shoreline (Fig. 7), as well as sinuosity and diversions per km, had positive standardized beta coefficients, indicating that an increase in the variable produced an increase in survival. Natural riparian habitat had the opposite influence on survival rates.

Riverine survival rates were then constrained similarly with spatial-temporal environmental variables, and again compared to a base model of constant survival per km per reach. The models found to be significantly more parsimonious than the base model are, in order of decreasing significance, maximum river depth, turbidity, and WDR (Table 8). The fully reach-dependent survival model ("full model") is indistinguishable from the best fit environmental model (maximum river depth). The standardized beta coefficients for the variable models are all positive with the exception of the WDR. Thus, survival is greater with deeper channels, greater turbidity, and channels that have increasing depth relative to width.

Two-sample *t-tests* were run to test for monthly differences in maximum river depth, turbidity, and WDR for both 2008 and 2009. Both turbidity and WDR were found to be significantly different by month in both years ($P<0.05$; Table 9).

DISCUSSION

Hypothesis 1

Overall survival of smolts to the ocean (3.9%) was low in this study relative to other large rivers along the west coast. Welch et al. (2008) found that yearling Chinook salmon smolts from the Snake River (tributary of the Columbia River) had an overall survival of 27.5% (± 6.9 S.E.) to the ocean (distance traveled 910 km) in 2006. That study also found that overall survival for yearling Chinook salmon smolts from various tributaries of the Fraser River to the ocean (distance traveled 330.8-395.2 km) had an overall survival varying from 2.0% (± 3.6 S.E.) to 32.2% (± 20.7 S.E.), with the majority of the tributary and year-specific survival estimates above 15%. Additionally, Rechisky et al. (2009) found that outmigrating yearling Chinook salmon smolts from the Yakima River (another tributary of the Columbia River) had an overall survival of 28% (± 5 S.E.) to the ocean (distance traveled 655 km). Previous studies in the Sacramento River are limited, but indicate poor survival of Coleman Hatchery-origin late-fall run Chinook salmon smolts, similar to this study (1.3 to 2.3% overall survival to rkm 239 (Snider 2000b, a)), but never before has survival been calculated to ocean entry.

It could be hypothesized that the recent declines of California's Central Valley Chinook salmon populations (Lindley et al. 2009) reflect the low survival seen in this study. To put the overall outmigration survival in perspective of several life stages, I compared this study's outmigration survival to known smolt-to-adult return rates (SAR). SAR represents the percent of outmigrating Chinook salmon smolts that survive to return as adults to the original spawning reaches, and is calculated per cohort. Therefore, SAR incorporates the combination of mortality during the outmigration, mortality and harvest during the ocean phase, and finally pre-spawning ground mortality and harvest in the returning river stage. Smolt-to-adult return rates (SAR) for the Sacramento River, and specifically for Coleman hatchery-origin late-fall run Chinook salmon, are available, but not yet for the same cohorts as in this study. As a proxy, the long-term average SAR (brood years 1992-2005) for Coleman hatchery-origin yearling late-fall run Chinook salmon was 0.53% (± 0.04 S.E.) (Regional Mark Information System, http://www.rmpc.org/). If the cohorts of this study were assumed to have similar SAR as the long-term average, overall outmigration mortality for late-fall run Chinook salmon smolts released (or native) to Battle Creek (and potentially the upper Sacramento River and tributaries) could be responsible for a considerable portion of salmon mortality for such a short life stage (Fig. 8).

Survival in the 2007 season was surprisingly low in the short nine kilometer passage through Battle Creek to the Sacramento River. Poor survival in Battle Creek was likely due to high densities of Sacramento pikeminnow (*Ptychocheilus grandis*) observed there (CJM pers. observation; K. Brown, USFWS - Coleman National Fish Hatchery, Anderson, CA 96007, pers. comm.), potentially caused by hatchery-subsidized prey abundance. Sacramento pikeminnow are one of the main predators of salmonid smolts in the Sacramento River (Brown and Moyle 1981), along with striped bass (*Morone saxatilis*) (Stevens 1966), largemouth bass (*Micropterus salmoides*), and several avian species. Efforts to reduce the seemingly unnatural high densities of predators in Battle Creek could be an effective strategy for maximizing survival of the large number of outmigrating hatchery and wild-origin smolts.

Due to the resulting low numbers of fish reaching lower reaches in 2007, survival estimates had such wide confidence intervals that understanding changes in reach-specific mortality was difficult. The release strategy was therefore changed for the 2008 and 2009 seasons to potentially increase the number of fish reaching downstream sections, thus reducing survival estimate confidence intervals. Additionally, only fish that successfully reached the Sacramento River in 2007 (131 individuals after Battle Creek) were included for comparative survival analysis with the two following years.

In the latter two years of the study, three simultaneous release sites were used, and appeared to have an effect on overall survival to the ocean. The furthest upstream release group had the lowest survival and the middle release group had the highest survival in both years. Although the release site interaction with reach model was less parsimonious than the base model (reach), and the 95% confidence intervals around the cumulative survival estimates at the entrance to the ocean do not indicate significant differences, it is noteworthy that the pattern was consistent through both years. One explanation for this could stem from the fact that late-fall run Chinook salmon smolts take longer to outmigrate the further downstream they are released (Michel unpubl. data). There could consequently be a tradeoff between bypassing the high mortality of the upper river with additional temporal exposure to predation further downstream. Currently, a large portion of hatchery produced Chinook salmon smolts are released downstream of their native nurseries, in an attempt to minimize riverine mortality, but at a cost of increased straying rates of returning adults (Quinn 1993). Considering the lack of evidence suggesting an improvement in survival with this release strategy, the cessation of this practice should be considered by fisheries managers.

The year of release did not have a significant influence on reach-specific survival rates. The study occurred during three dry years (low rainfall and snowpack) in northern California, with 2008 deemed as critically dry (Department of Water Resources 2009). Therefore, the survival dynamics and environmental associations found in this study represent those for years of relatively low freshwater flow and may be different during wet years.

The rates of survival were relatively low in the reaches of the upper river and higher in the reaches of the lower river. Total river survival was 23.5% (± 1.7 S.E.), considerably higher than previous studies on the Sacramento River (Snider 2000a, b). River survival on the Columbia River varied from 26.6% (± 1.5 S.E.) to 61.2 % (± 1.6 S.E.) depending on the year or release group (Welch et al. 2008). Potential reasons for the bipartite survival dynamics in the Sacramento River will be discussed in the environmental influence section.

The rate of survival was relatively low in the Sacramento – San Joaquin River Delta. Survival of outmigrating Sacramento River Chinook salmon smolts has been known to be low in the delta (Baker and Morhardt 2001, Brandes and McLain 2001), reportedly due to low river flow, lethally high water temperatures and entrainment into the predator-rich interior delta by water pumping for agriculture (Kjelson and Brandes 1989). Perry et al. (2010) found delta survival of Coleman hatchery-origin late-fall run Chinook salmon smolts to be 35% (± 10 S.E.) and 54% (± 7 S.E.) in December 2006 and January 2007 respectively. These estimates are similar to this study's estimate of delta survival (93.7% per 10km, corresponding to a total delta survival of 52.6% (± 3 S.E.)).

Salmonid smolt survival rates in the San Francisco Estuary do not exist in the literature (only indices allowing temporal comparisons exist (Brandes and McLain 2001)), an unfortunate information gap considering that this region had the lowest survival rates of the outmigration corridor. Welch et al. (2008) found yearling Chinook salmon smolts to have a survival of 61.8% (± 1.9 S.E.) through the lower river and estuary of the Columbia River while this study found smolt survival through the estuary alone to be 31.4%, considerably lower. Possible reasons for the low survival through the estuary include the physiological stresses of acclimatizing to salt water, the increased presence of some predators such as marine mammals, and the poor condition of the estuary (Nichols et al. 1986).

The significant effect of reach was informative, and in one case, counterintuitive (Fig. 3). Possibly due to the biased management focus on salmon survival in the delta (in large part motivated by concerns of the detrimental effects of water exports for agriculture), many believe that mortality during the river migration is greatest in the delta. Moreover, it is alleged by many that the more anthropogenically modified lower river has lower survival rates than the more natural upper river for outmigrating salmonids. However, this study demonstrated that not only does the upper river have significantly lower survival than the lower river, but the poor survival in the upper river is comparable in magnitude to the poor survival seen in the delta and estuary.

Although the sample size of the tagged wild (natural-origin) population was too small (n=18) for useful confidence intervals, and the tag weight-to-body weight ratio was generally above the 5% threshold, survival for both wild and the study's hatchery populations were not different in most reaches. Survival rates seemed to follow the same pattern of lower upstream survival and higher downstream survival. Moreover, model comparison confirmed that there is no evidence that the 18 natural-origin smolts and the study's hatchery-origin smolts had different survival estimates. Because none of the wild fish were detected below the lower river reaches, survival comparisons for the delta and estuary were not possible. This evidence suggests, though very cautiously, that hatchery-origin late-fall run Chinook salmon smolts may be used as surrogates for studying wild late-fall run Chinook salmon smolt survival in the Sacramento River.

Fish weight and fork length varied significantly among years, however, the survival models including size covariates were not found to be more parsimonious than the base model. Specifically, I did not detect a substantial effect of weight and fork length were not found to influence survival in a significant way. This seems counterintuitive considering gape-limited predators almost certainly have a significant impact on smolt survival and because larger smolts are likely superior at evading predators. However, having a minimum size limit on smolt tagging to enforce the 5% tag weight-to-body weight ratio restricted this study's smolt size range to about 145 mm to 180 mm (10th percentile to 90th percentile). This may have reduced size variability sufficiently to mask any size effects.

The month of release had a significant influence on survival in the two latter years when two release months were implemented. In the 2008 and 2009 tagging season, the December release groups had higher survival than the January release groups, especially in the upper river. This could be evidence for environmental change between months. Perry et al. (2002) found a monthly variation in survival in the Sacramento - San Joaquin Delta in the 2006/2007 winter with Coleman hatchery yearling late-fall run Chinook salmon smolts, except he found higher survival in December rather than January. This variation was thought to be in part due to variation in environmental conditions such as temperature and turbidity.

While creating a base model that would incorporate all sources of mortality that are not attributable to the environment, I found that there seemed to be no initial release mortality effect (i.e., immediately following release) on survival. This suggests that there is no evidence for hatchery "naïveté"-induced or handling stress-induced mortality of smolts soon after release.

In conclusion, hypothesis 1 is supported. There is evidence for both spatial (by reach) and temporal (by month) variation in survival rates for the three years of this study and it is likely that environmental variability is a contributor. Environmental variability is influential on the survival of outmigrating Chinook salmon smolts because they transit a wide range of environmental conditions during their extensive journey, all of which may have different impacts on their survivability.

Hypothesis 2

Of the spatial variables, significant relationships with riverine survival were found with, in order of decreasing significance, % riprap shoreline, % levee shoreline, sinuosity, diversions per km, and finally % natural riparian habitat (Table 7). With the exception of sinuosity, the four other variables are correlated to each other by a Pearson's correlation coefficient of at least 0.64. This is because, in the Sacramento River, riprap often accompanies levees and the river is leveed in the lower, more populated reaches (therefore, less natural habitat) with more need for water diversions. It is difficult to understand which of these correlated variables is having a dominating influence on survival without controlling for the others. However, the overall channelization of the river (entailing both the levee and riprap riverbank factors) seems to have the most influential effect on smolt survival, and the relationships between natural riparian habitat and water diversions with survival may be spurious. Sinuousity is less correlated with the other variables and will be discussed separately.

Traditionally, levees, riprap, and channelization have been considered to be detrimental for salmon populations due to their degradation of spawning grounds (reduced input of gravel) (Buer et al. 1989), lack of prey and cover, and increased predators on juveniles (Chapman and Knudsen 1980, Schmetterling et al. 2001, Garland et al. 2002). However, a positive effect of channelized reaches on smolt survival was found in the present study. This might be because smolts actively migrate through channelized reaches, thus reducing the period of exposure to sources of mortality. In the Sacramento River, channelized reaches often have higher turbidity that acts as cover. Furthermore, the presence of predators may be restricted to only the immediate vicinity of the riprap, lowering the potential detrimental effects of channelization. Channelization of rivers leads to increased depth and uniformity of bathymetry and flows, all of which reduce predator habitat and ambush areas, and ease downstream migration. Similarly, smolt survival in the Columbia River was higher in deep impoundments compared to shallower undammed reaches (Welch et al. 2008). In contrast, if we are to consider the non-channelized upper reaches that exhibit low survival, it could be that the shallow run-riffle structure of the river has created many opportunities for predators to ambush passing smolts.

Sinuosity was negatively correlated with indices for channelization, and positively correlated with natural riparian habitat, suggesting at first that the river is most sinuous in the upper reaches. However, unlike most other variables, sinuosity does not follow a strict downstream gradient. Sinuosity must consequently co-vary with small-scale fluctuations in indices for channelization and natural riparian habitat. Given that sinuosity had a positive beta coefficient, suggesting that the more sinuous the river, the better the survival, sinuosity may be having an influence on survival independent of other measured variables.

As expressed in the conceptual model, spatial variables control spatial-temporal variables that theoretically influence riverine survival rates. Therefore, I have concluded that channelization and sinuosity influence survival, but have not determined the mechanisms. Of the spatial-temporal variables tested, I found significant relationships with riverine survival for maximum river depth, turbidity, and width-to-depth ratio (WDR). The beta coefficients for depth and WDR both suggested similar information: the greater the absolute depth or relative to the width of the reach, the greater the survival. Deep rivers with a low WDR are defining characteristics of channelized reaches of a large river, in agreement with the results in this study that channelized river reaches improved smolt survival.

Turbidity was also found to have a significant influence on survival rates, and the positive beta coefficient indicated that more turbid water improved survival. This theory, explained by decreased predator efficiency in turbid water, has been established in previous research in other large rivers of the west coast, the Fraser and the Columbia (Gregory and Levings 1998, Anderson et al. 2005). In the present study, the concept that smolts use cryptic techniques was corroborated by the finding that smolts exhibited a nocturnal migratory behavior in the clear upper river. As smolts entered the more turbid water of the lower river reaches, the nocturnal pattern became less defined, suggesting that smolts substituted turbidity for nocturnal cover to avoid predation (Michel unpubl. data). In the Sacramento River, water clarity in the lower reaches is reduced in part by tributaries contributing suspended sediment.

Diversions have been known to have an important negative influence on smolt survival, in part due to being physically drawn into the pumps, but also as a location of high predation in response to the aggregation of smolts (Brown and Moyle 1981). However, diversions were not found to have a significant influence on survival rates in this study. In the river reaches used for this analysis, there were a total of 352 water diversions, the majority being found in the lowest river reaches. These same reaches were found to have high survival, and so it seems that the potentially detrimental direct effects of the diversions were not important to outmigrating late-fall run Chinooks salmon smolts within the Sacramento River under the environmental conditions found in 2007-2009. Perhaps the larger size of the late-fall run smolts relative to other salmon populations decreases their susceptibility to entrainment by water diversions. Many diversions are now screened in an attempt to limit the number of smolts that are drawn into the pumps. It should be noted that very large water diversions within the Sacramento – San Joaquin River Delta are thought to have strong influences on smolt survival (Brandes and McLain 2001), a region in which the analysis of the influence of diversions did not extend in the present study.

Although channelization, turbidity, and sinuosity have accounted for a considerable amount of variation in survival rates, other factors also appear to be significant. As an example, the maximum river depth survival model alone was as parsimonious as the fully reach dependent survival model, meaning maximum river depth alone could account for the majority of the spatial-temporal variation in survival in these years. Furthermore, given that month of release significantly affected survival (in 2008 and 2009), two-sample *t-tests* were run and found that both turbidity and WDR were significantly different by month in both years. This is an indication that two of the three important spatial-temporal environmental factors could theoretically be responsible for the monthly variation in survival. In conclusion, attempting to associate environmental variables to survival rates has produced compelling information, reinforcing its merit in understanding survival dynamics in this system, and thus hypothesis 2 is supported.

CONCLUSIONS

This study is one of the first telemetry studies to correlate survival rates with riverine characteristics. Indeed, there were strong associations between environmental variables (such as channel depth) and survival rates. Furthermore, no other salmonid survival study has been able to measure smolt migration survival at such a high spatial resolution. However, some key assumptions and limitations are worth mentioning to promote the continuation and improvement of these studies.

Skalski (1998) determined seven key assumptions related to study design of a single release-multiple recapture study; here I have addressed the three that apply to this study:

Marked individuals are representative of the larger population of interest: This study was limited to hatchery fish due to their increased size and availability over wild fish, and therefore I can theoretically only extrapolate this study's findings to hatchery populations with confidence. However, being that the wild (natural-origin) and hatchery-origin populations share similar individual sizes and migration times, the two populations are likely both encountering the same sources of mortality during their migration. Furthermore, results from the natural-origin late-fall run Chinook salmon smolt pilot study suggest reach-specific survival estimates in the Sacramento River are the same as for the hatchery-origin smolts used in this study.

Survival and detection likelihood are not influenced by tagging or sampling: To address these issues, a series of tagging effects experiments were conducted concurrently with the study on smolts from the same population, late-fall run Chinook salmon smolts from Coleman National Fish Hatchery. Results show that tagging had no effect on survival within the first 34 days (A. Ammann, NMFS-SWFSC, Santa Cruz, CA 95060, unpubl. data), a timeframe allowing for the majority of tagged smolts to migrate completely out of the Sacramento river and estuary (Michel unpubl. data). Additionally, swimming performance tests showed no statistical difference in maximum swimming speeds between tagged and control fish (A. Ammann, NMFS-SWFSC, Santa Cruz, CA 95060, unpubl. data).

All tagged fish are correctly identified as either alive or dead: The first situation that could violate this assumption is if a fish is deemed dead when it is actually alive. This could happen if a fish sheds its tag and is therefore deemed dead. During the above mentioned survival experiments, there was not a single recorded case of tag ejection. The reciprocal is when a fish is deemed alive when in fact it is dead. This could happen when a predator eats a tagged fish and proceeds to migrate while having the tag in its gastric system. With the technology available today, there is no definitive way of knowing if you are tracking the predator instead of your study species (Vogel 2010). For this study, the migration path was plotted over time and space for each individual fish and visually inspected, and all suspicious migratory behaviors (such as a fish moving continuously downstream then suddenly turning around and moving back upstream, sometimes past the original release location) were removed. However, it is likely minor inaccuracies occurred in the survival estimates. Perhaps advances in tag technology will allow for a system for detecting when a tagged smolt has been consumed in the near future.

Due to the limited availability of environmental data in the Sacramento – San Joaquin Delta and San Francisco Estuary, environmental factors were only associated with survival in the regions beyond tidal influence. Nevertheless, while such a study has already been attempted (Kjelson and Brandes 1989), future work should explore these relationships in the delta and estuary using the methodology presented in this paper.

The use of the seaward Golden Gate line to calculate the detection efficiency of the river-ward line has some shortcomings. Tidal currents are notoriously strong at the Golden Gate, and these currents do affect detection probabilities (A. Ammann, NMFS-SWFSC, Santa Cruz, CA 95060, unpubl. data). Due to the close proximity of the two Golden Gate lines (within 2 km), strong tides affect the lines' detection probabilities similarly, which could result in fish being detected by neither line, leading to the under-estimation of survival to ocean entry. Thus, survival estimates for the last reach (reach 17), from Richmond Bridge to the Golden Gate, represent minimum estimates of survival, and true survival could be significantly higher.

One conclusion that could be extrapolated from this study is the apparent need to channelize the entire Sacramento River and artificially raise turbidity. While such modifications may improve survival of outmigrating yearling late-fall run Chinook salmon smolts, many other Chinook salmon life stages would be negatively impacted (Buer et al. 1989), potentially resulting in further declines in already dwindling salmonid populations.

The reach-specific survival estimates provide resource managers with the first high-resolution survival information for the Sacramento River watershed, allowing the identification of high mortality reaches for Chinook salmon smolts and the factors that may cause mortality. For the most part, ongoing efforts to improve Chinook salmon smolt survival have concentrated on anthropologic influences within the delta.

While the findings presented here do not disagree with this emphasis, more attention toward low survival in the upper river and estuary is warranted. This suggests the need to not overlook natural processes in influencing survival of a species.

This study also provides insight into how survival dynamics might be structured for U.S. Endangered Species Act (ESA) listed Sacramento River Chinook salmon populations, which could facilitate conservation measures. Specifically, the Sacramento River winter run Chinook salmon population is considered to be endangered by the ESA, and smolts from this population are known to outmigrate from the Sacramento River over the same time window, at similar sizes (approximately 120 mm), using the same routes. It is likely that the survival dynamics and environmental associations are similar for the late-fall run and winter Chinook salmon populations.

Finally, analytic exploration of possible environmental causes are valuable not only for ecological understanding of the smolt life-history stage, but also to increase capabilities of improving survival and making stock predictions incorporating environmental conditions.

The imperiled Central Valley Chinook salmon stocks will require sound fisheries and resource managing for eventual recovery, and this can not be achieved without understanding the survival dynamics and causal mechanisms of arguably the most vulnerable life stage. This study provides novel information on the small scale temporal and spatial survival dynamics, on the total survival throughout the entire migration, and finally provides suggestions on what environmental factors could be driving these dynamics, and how.

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Table 1. Means and standard errors for weight and fork length of acoustically-tagged smolts by year and for all years combined.

Year	Weight ± SE (g)*	Fork length ± SE (mm)*	Sample size
ALL	46.0 ± 0.4	161.5 ± 0.5	804
2007	46.6 ± 0.7^a	164.6 ± 0.8^a	200
2008	52.6 ± 0.8^b	168.7 ± 0.8^b	304
2009	38.9 ± 0.5^c	152.1 ± 0.5^c	300

*Size distributions with different superscripts are significantly different ($P < 0.05$)

Table 2. Locations of acoustic monitors and tagged fish release locations.

Location	River km	Description
Battle Creek	534	Release site 2007
Jelly's Ferry	518	Monitor location & release site 2008/09
Bend Bridge	504	Monitor location
China Rapids	492	Monitor location
Above Thomes	456	Monitor location
Below GCID	421	Monitor location
Irvine Finch	412	Monitor location & release site 2008/09
Above Ord	389	Monitor location
Butte City Bridge	363	Monitor location & release site 2008/09
Above Colusa Bridge	325	Monitor location
Meridian Bridge	309	Monitor location
Above Feather River	226	Monitor location
I-80/50 Bridge Sacramento	189	Monitor location
Freeport	169	Monitor location
Chipps Island	70	Monitor location
Benicia Bridge	52	Monitor location
Carquinez Bridge	41	Monitor location
Richmond Bridge	15	Monitor location
Golden Gate East Line	2	Monitor location
Golden Gate West Line	1	Monitor location

Table 3. Sources of environmental data for this study.

Environmental variables	Data source*	Data Location
Water temperature (ºC)	UCD, BOR, DWR, USGS, USFWS	http://cdec.water.ca.gov/
Water turbidity (NTU)	BOR, DWR, USGS	http://cdec.water.ca.gov/
River flow (m^3·sec^{-1})	BOR, DWR, USGS	http://cdec.water.ca.gov/
Channel velocity (m·sec^{-1})	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* [†]
Channel depth (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* [†]
River surface width (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* [†]
Water diversions (diversions·km^{-1})	CalFish Passage Assesment Database	http://nrm.dfg.ca.gov/PAD/Default.aspx
Riparian habitat type (% of total)	DWR Land Use Survey	http://www.water.ca.gov/landwateruse/lusrvymain.cfm
Riprap (% of total shore)	DWR, USACE, USFWS Sacramento River Bank Survey	Adam Henderson, James Oliver *pers. comm.* [†]
Levees (% of total shore)	DWR	Alison Groom *pers. comm.* [†]

*Agency Acronyms: UCD= University of California - Davis, BOR= United States Bureau of Reclamation, DWR= California Department of Water Resources, USGS= United States Geological Survey, USFWS= United States Fish and Wildlife Service, USACE= United States Army Corps of Engineers

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Table 4. Survival to ocean entry by release group for each year, including an estimate for survival for all release groups combined for both 2008 and 2009 (representing total survival from rkm 518 to ocean), and a total estimate for a release groups and years combined. The column "# at Golden Gate" represents actual detected smolts, while "% of release ± SE (modeled)" represents the product of reach-specific survival for all reachs using estimates from CJS model (and therefore accounting for detection efficiency). "*ALL*" in release column represents the total studied watershed survival, combining release group survival for each reach. In some cases (2008), comparatively lower survival in lower reaches for 412 and 363 release groups accounted for "*ALL*" survival to ocean being lower than survival for 518 release group over the same distance.

Year	**Release (rkm)***	**# released**	**# at Golden Gate**	**% survival to ocean ± SE (modeled)**
2007	518†	131†	4	3.1 ± 1.5
2008	518	102	6	6.1 ± 2.4
	412	101	9	8.9 ± 2.8
	363	101	7	7.2 ± 2.6
	ALL			3.8 ± 0.9
2009	518	100	4	4.3 ± 2.1
	412	100	12	13.2 ± 3.8
	363	100	8	8.1 ± 2.7
	ALL			5.5 ± 1.2
ALL	*ALL*			3.9 ± 0.6

*distance (kilometers) from Golden Gate

†smolt mortality in Battle Creek not included

Table 5. Survival rates and detection probabilities by reach for all years combined.

Region	Reach #	Rkm from Golden Gate	% Survival·10km^{-1} ± SE	Detection probability ± SE (of downstream station)
Upper Sacramento River	1	518 - 504	96.8 ± 0.8	0.93 ± 0.01
	2	504 - 492	94.7 ± 1.3	1.00 ± 0.00
	3	492 - 456	91.5 ± 0.9	0.90 ± 0.02
	4	456 - 421	93.1 ± 1.0	0.93 ± 0.02
	5	421 - 412	95.2 ± 1.9	0.93 ± 0.02
	6	412 - 389	94.1 ± 0.9	0.87 ± 0.02
	7	389 - 363	92.6 ± 1.1	0.92 ± 0.02
	8	363 - 325	94.2 ± 0.7	0.52 ± 0.03
Lower Sacramento River	9	325 - 309	98.9 ± 1.2	0.58 ± 0.03
	10	309 - 226	99.1 ± 0.3	0.71 ± 0.03
	11	226 - 189	98.1 ± 0.6	0.75 ± 0.03
	12	189 - 169	100 ± 0.0	0.82 ± 0.02
Sacramento/San Joaquin Delta	13	169 - 70	93.7 ± 0.5	0.89 ± 0.03
San Francisco Estuary	14	70 - 52	87.8 ± 2.2	0.86 ± 0.03
	15	52 - 41	88.0 ± 4.2	0.81 ± 0.04
	16	41 - 15	90.2 ± 3.0	0.68 ± 0.07
	17	15 - 2	67.0 ± 5.8	0.85 ± 0.06*

*Calculated using the Pt. Reyes Ocean Monitor Line and Golden Gate West Monitor Line

Table 6. Survival models for different study design factors, ordered from best to worst parsimony. The Δ QAICc statistic represents the QAICc distance from the most parsimonious model. The number of parameters includes the parameters for estimation of detection probabilities (reach-specific).

Survival (Φ) treatment	**Δ AIC**	**# Parameters**
Reach x Month	0.00	53
Reach + Fork length + Weight	21.20	37
Reach + Fork length	22.30	36
Reach x Year	24.30	71
Reach	24.60	35
Reach + Weight	25.40	36
Reach x Month x Year	31.70	107
Reach x Release site	47.10	59
Reach x Release site x Month	60.00	101
Reach x Release site x Year	87.00	119
Reach x Release site x Month x Year	185.70	203
Null model (constant survival)	263.93	19

Table 7. Survival models for spatially varying environmental data, ordered from best to worst parsimony. The Δ QAICc statistic represents the QAICc distance from the most parsimonious model. The number of parameters includes the parameters for estimation of detection probabilities.

Model	QAICc	Δ QAICc	# Parameters	Standardized β coefficient ± SE
Full model	2634.8	0	22	
% Riprap shoreline	2687.6	52.8	14	1.04 ± 0.22
% Levee shoreline	2697.9	63.1	14	0.61 ± 0.13
Sinuosity	2703.1	68.3	14	0.46 ± 0.10
Diversions·km^{-1}	2707.0	72.2	14	0.55 ± 0.15
% Natural riparian habitat	2714.3	79.5	14	-0.45 ± 0.13
% Agriculture riparian habitat	2721.3	86.5	14	
% Urban riparian habitat	2725.4	90.6	14	
Base model (constant survival·km^{-1})	2725.5	90.7	13	

Table 8. Survival models for spatially and temporally varying environmental data, ordered from best to worst parsimony. The Δ QAICc statistic represents the QAICc distance from the most parsimonious model. The number of parameters includes the parameters for estimation of detection probabilities.

Model	QAICc	Δ QAICc	# Parameters	Standardized β coefficient ± SE
Full model	1975.1	0.0	17	
Max channel depth (m)	1978.4	3.3	24	1.91 ± 0.28
Turbidity (ntu)	2001.4	26.3	24	1.52 ± 0.27
Width/Depth (WDR)	2012.2	37.1	24	-0.64 ± 0.12
Flow ($m^3 \cdot sec^{-1}$)	2039.0	63.9	24	
Base model (constant survival·km^{-1})	2039.5	64.4	23	
Channel velocity ($m \cdot s^{-1}$)	2040.2	65.1	24	
Temperature (ºC)	2041.5	66.4	24	

Table 9. Comparisons of spatial-temporal environmental variables by year and month of release that had a significant effect on late-fall run Chinook salmon smolt survival using a two-sample T-test.

2-sample T-test		Depth		Turbidity		WDR	
Year	**Month**	**Mean**	**P**	**Mean**	**P**	**Mean**	**P**
2008	Dec	5.4	0.43	9.0	< 0.01	37.2	0.02
	Jan	5.2		6.7		34.7	
2009	Dec	5.3	0.03	4.4	< 0.01	37.0	< 0.01
	Jan	5.9		6.0		33.0	

Figure Captions

Fig. 1. Study area map including the Sacramento River, Sacramento – San Joaquin River Delta, San Francisco Estuary and Pacific Ocean. Bull's-eye icons signify a release location, star symbolizes a major city, and black dot symbolizes a monitor location.

Fig. 2. Conceptual model of ecosystem influences on late-fall run Chinook salmon smolt survival in the Sacramento River.

Fig. 3. Percent survival per 10 km per reach for all three study years combined. Figure is delimited based on the regions identified on the associated map. Error bars represent 95% confidence intervals.

Fig. 4. Cumulative survival of all smolt release groups by study year. Reach 1 represents the uppermost reach, and reach 17 represents the lowest reach, at the ocean entry at the Golden Gate. Error bars represent 95% confidence intervals.

Fig. 5. Cumulative survival of outmigrating smolts by month of release in (a) 2008 and (b) 2009 study years. Reach 1 represents the upper-most reach, and reach 17 represents the lowest reach, in the San Francisco Bay Estuary. Error bars represent 95% confidence intervals.

Fig. 6. Percent survival per 10 km per reach for the wild and hatchery smolt groups over 15 river reaches (rkm 475-169 (Freeport)). Reach numbering is not the same as employed in remainder of paper, 2009 year allowed for the use of more monitor locations due to increased detection efficiencies. Black square symbols represent wild survival, and gray circle symbols represent hatchery survival. Associated error bars represent 95% confidence intervals.

Fig. 7. Percent survival per 10 km per reach (squares) for all three study years combined for the non-tidally influenced reaches of the Sacramento River (reaches 1-12), plotted with the % of total riverbank per reach that is either riprapped (dotted line) or leveed (dashed line). Survival error bars represent 95% confidence intervals.

Fig. 8. Percent cumulative survival of hatchery released smolts to adult return (to the spawning grounds). This represents a hypothetical example of the contribution of outmigration mortality (value used is all year survival of 3.9%) to the total smolt-to-adult rate (long term average for Coleman hatchery late-fall run Chinook salmon smolts 0.53%). Cumulative months since departure represents the approximate life stage timeline for adult late-fall run Chinook salmon returning as age 3 fish, the most common returning age class (Fisher 1994). The line between

3.9% and 0.53% does not represent true survival rate by month or per life stage, it assumes constant survival.

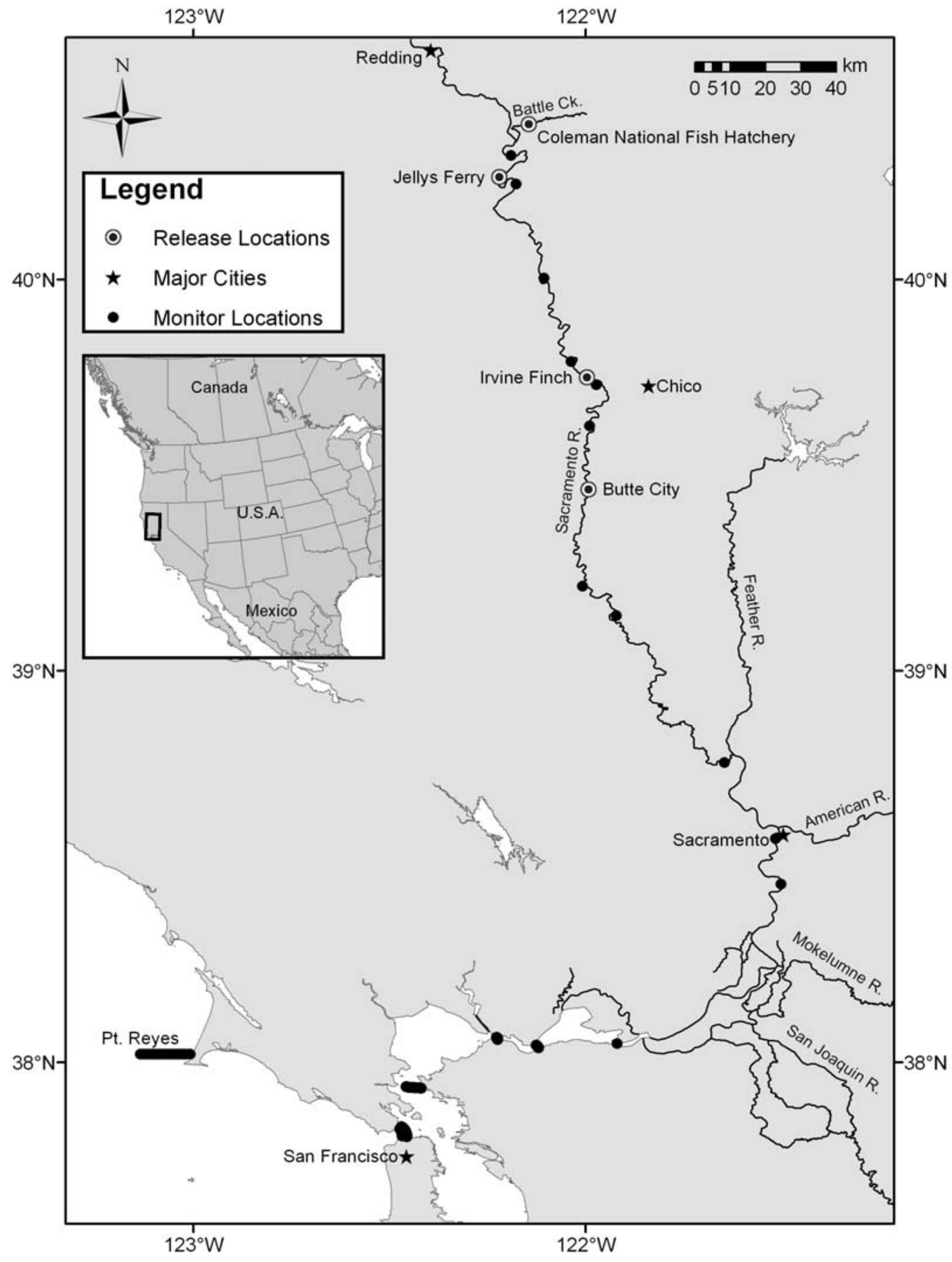
123°W
122°W
N
Redding
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
0 5 10 20 30 40 km
Legend
◉ Release Locations
★ Major Cities
● Monitor Locations
40°N
39°N
38°N
Canada
U.S.A.
Mexico
Irvine Finch
Chico
Sacramento R.
Butte City
Feather R.
American R.
Sacramento
Mokelumne R.
San Joaquin R.
Pt. Reyes
San Francisco

Fig. 1

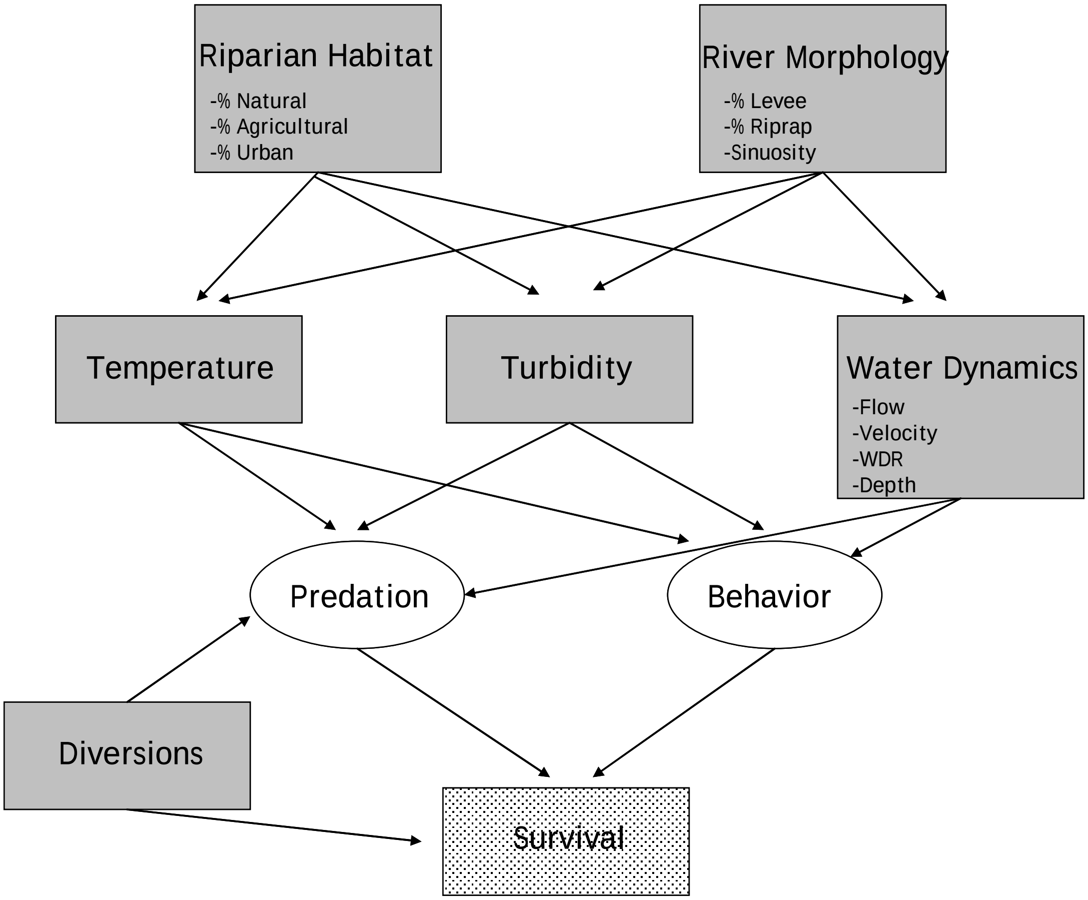
Riparian Habitat
-% Natural
-% Agricultural
-% Urban
River Morphology
-% Levee
-% Riprap
-Sinuosity
Temperature
Turbidity
Water Dynamics
-Flow
-Velocity
-WDR
-Depth
Predation
Behavior
Diversions
Survival

Fig. 2

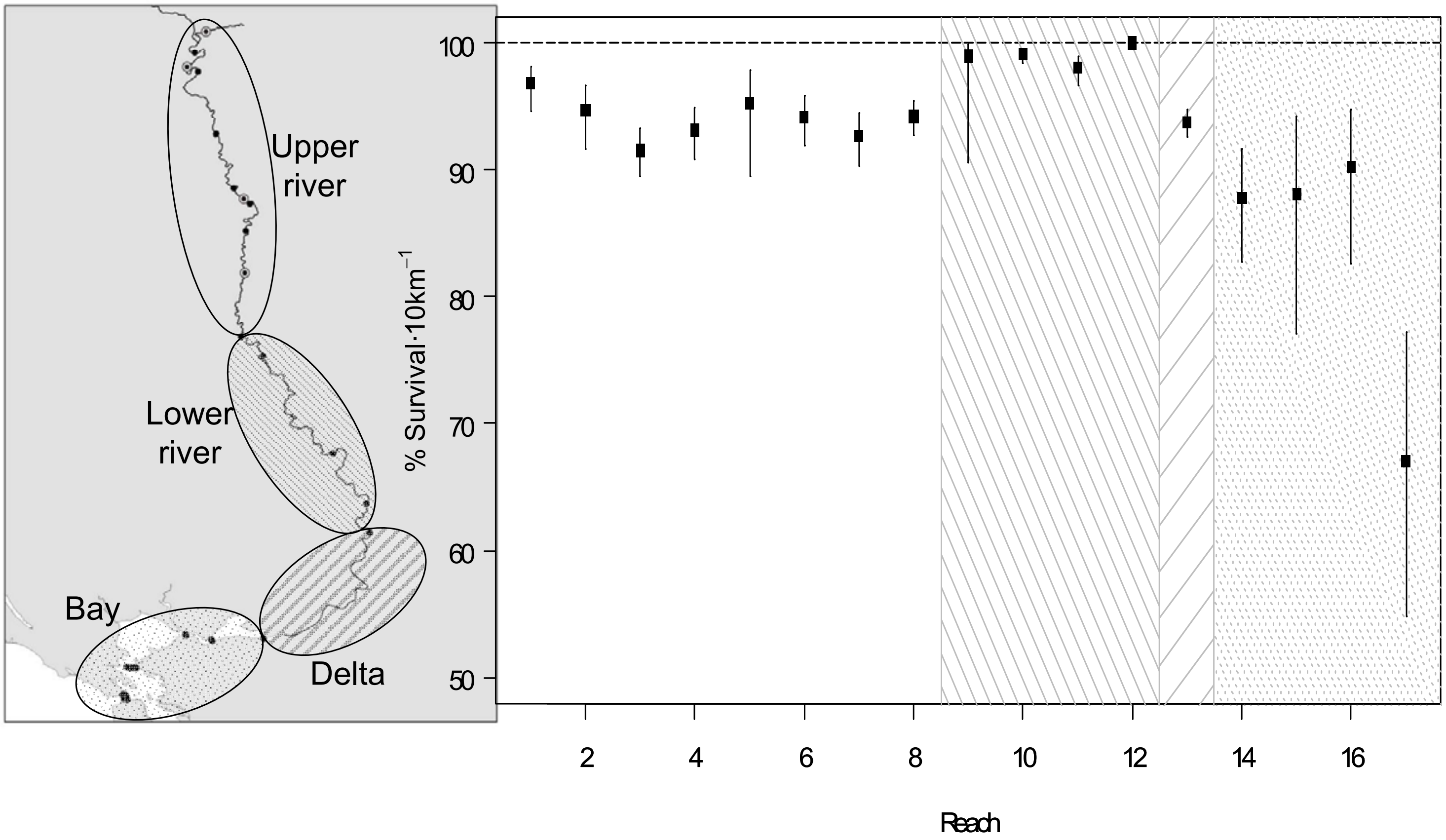
Upper river
Lower river
Bay
Delta
% Survival·10km^{-1}
100
90
80
70
60
50
2
4
6
8
10
12
14
16
Reach

Fig. 3

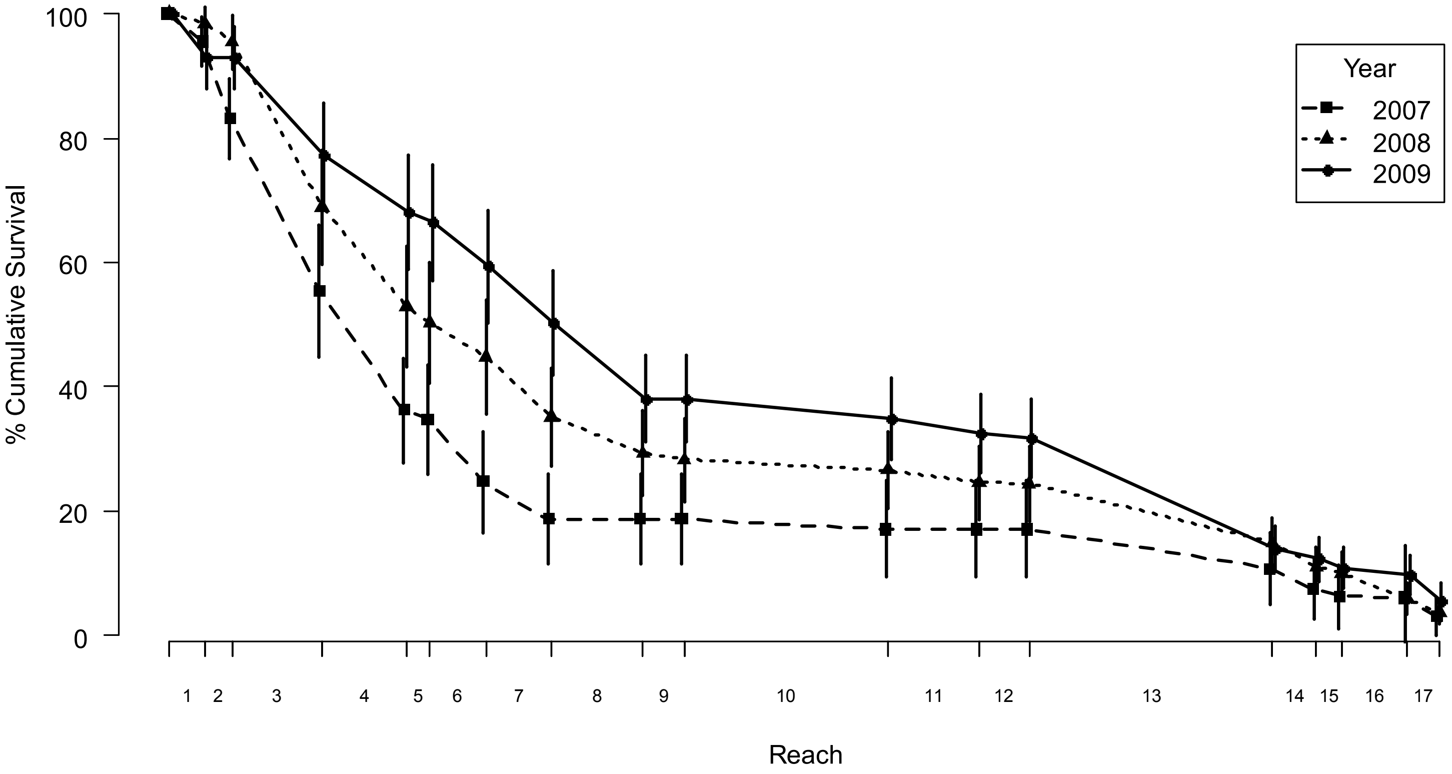
% Cumulative Survival
100
80
60
40
20
0
Reach
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Year
2007
2008
2009

Fig. 4

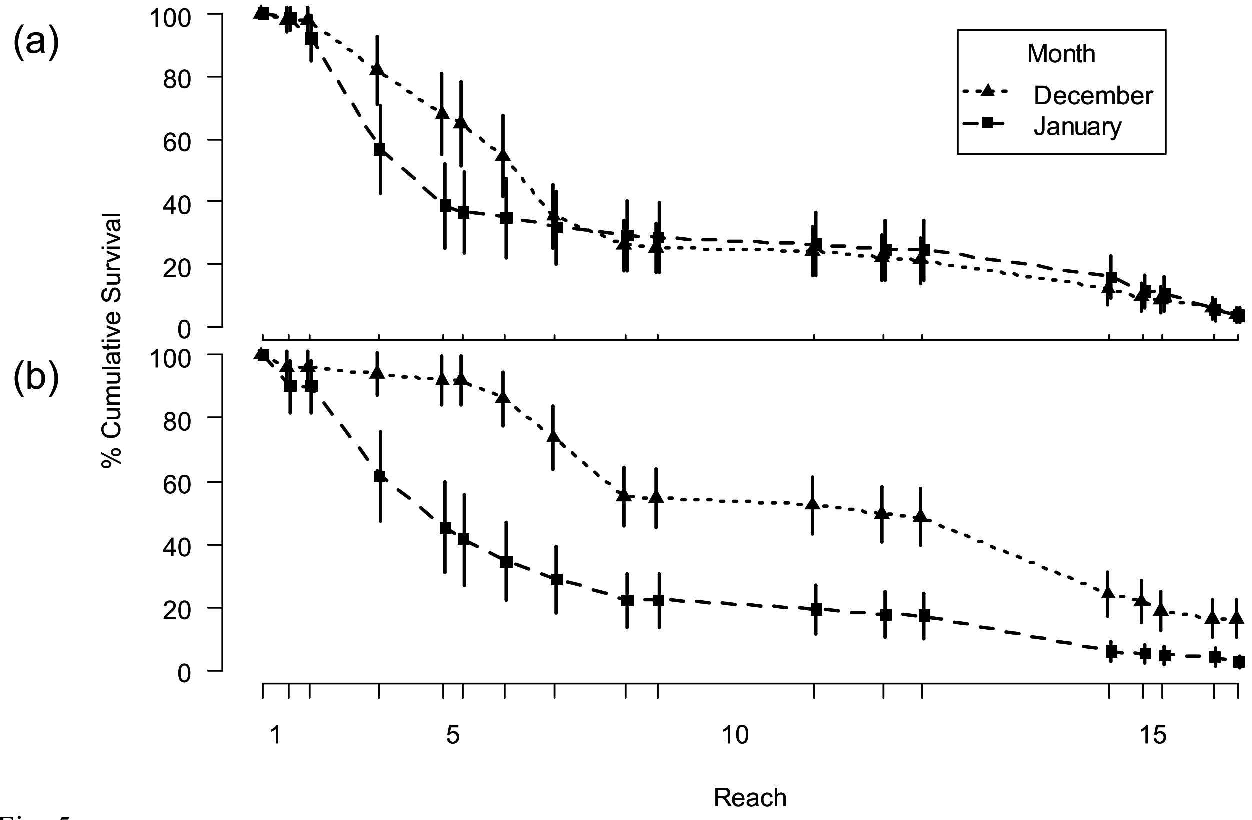
(a)
(b)
% Cumulative Survival
100
80
60
40
20
0
Month
December
January
1
5
10
15
Reach

Fig. 5

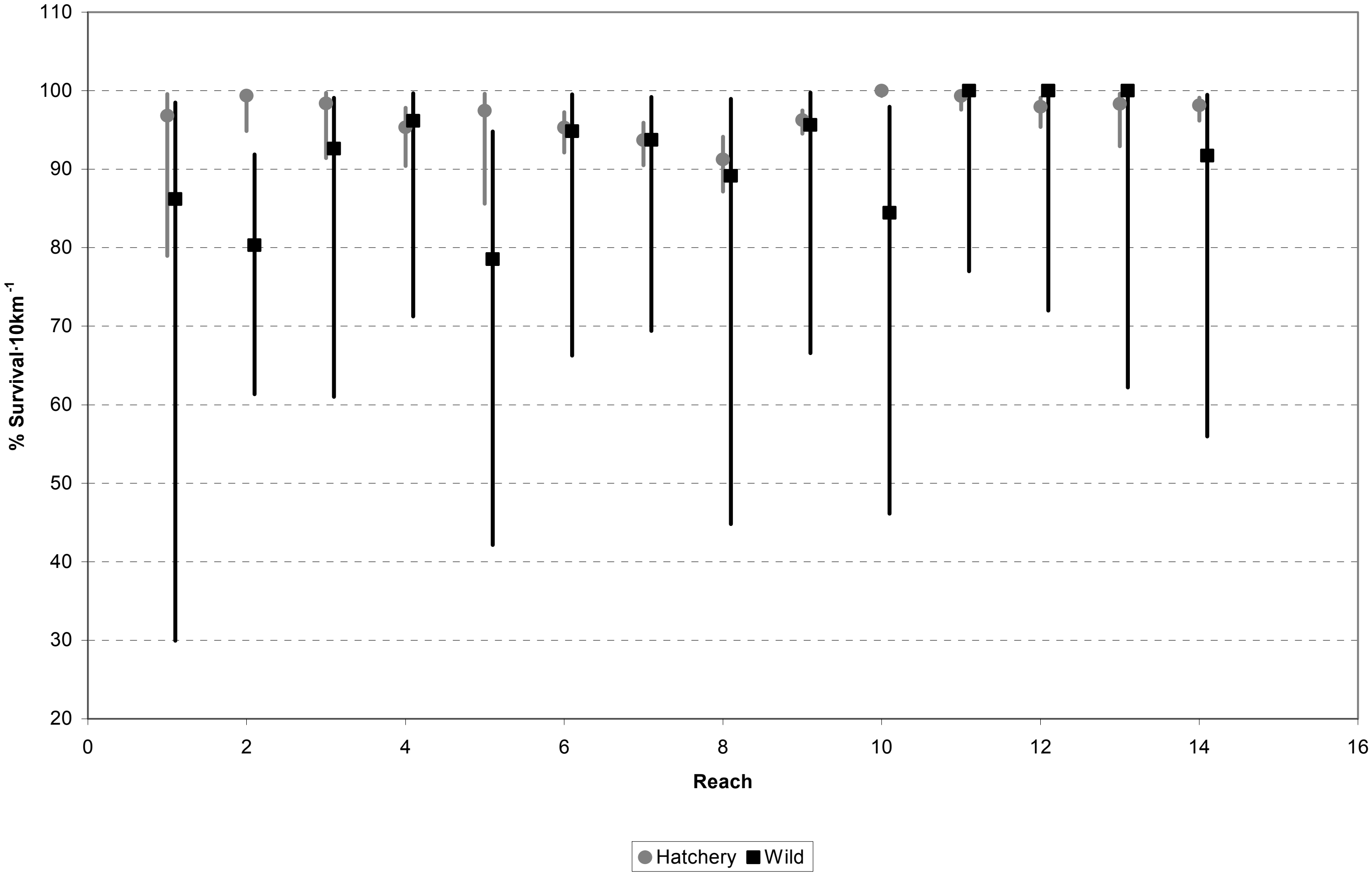
110
100
90
80
70
60
50
40
30
20
% Survival·10km-1
0
2
4
6
8
10
12
14
16
Reach
● Hatchery
■ Wild

Fig. 6

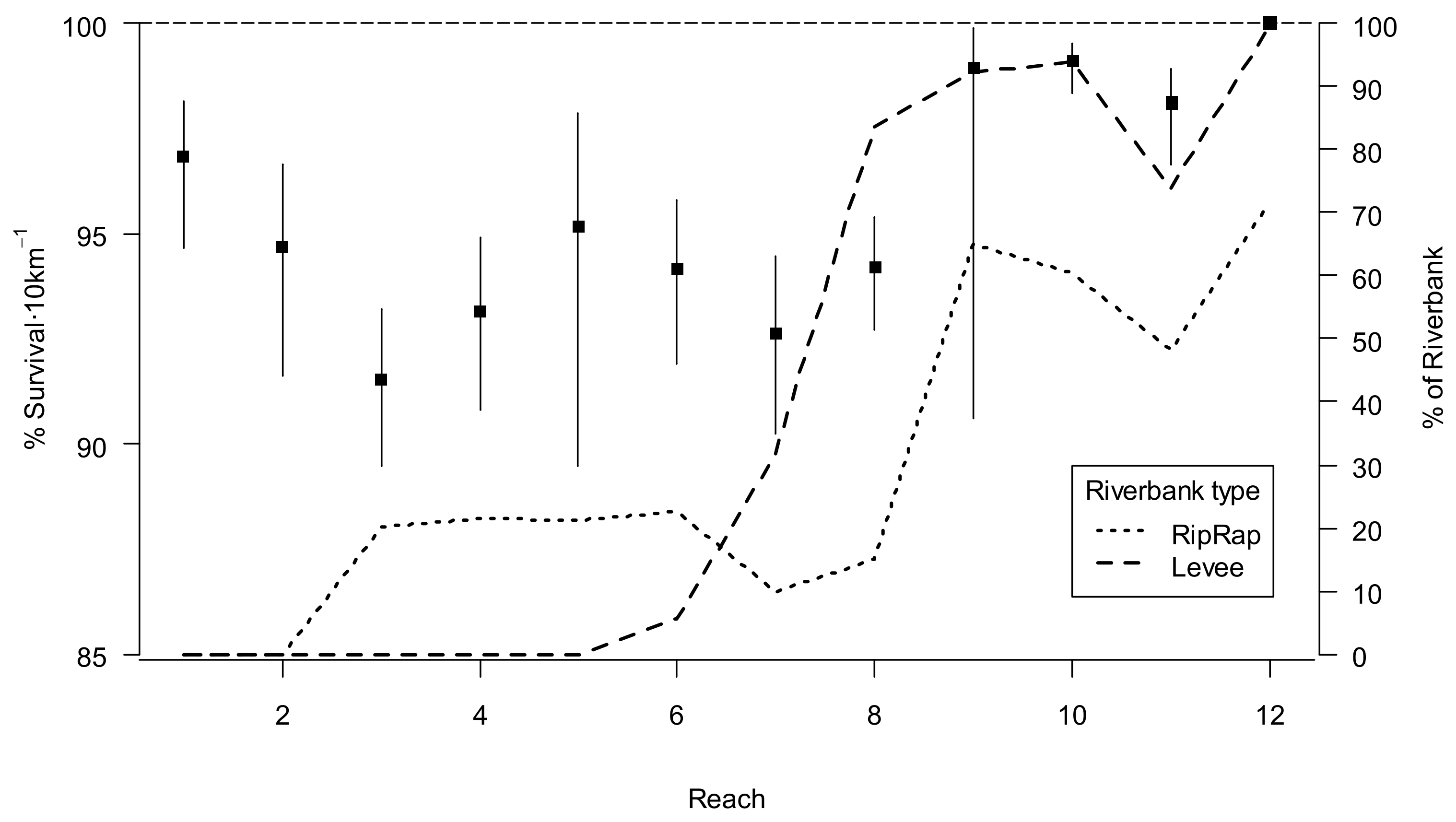
100
95
90
85
% Survival·10km^{-1}
2
4
6
8
10
12
Reach
100
90
80
70
60
50
40
30
20
10
0
% of Riverbank
Riverbank type
RipRap
Levee

Fig. 7

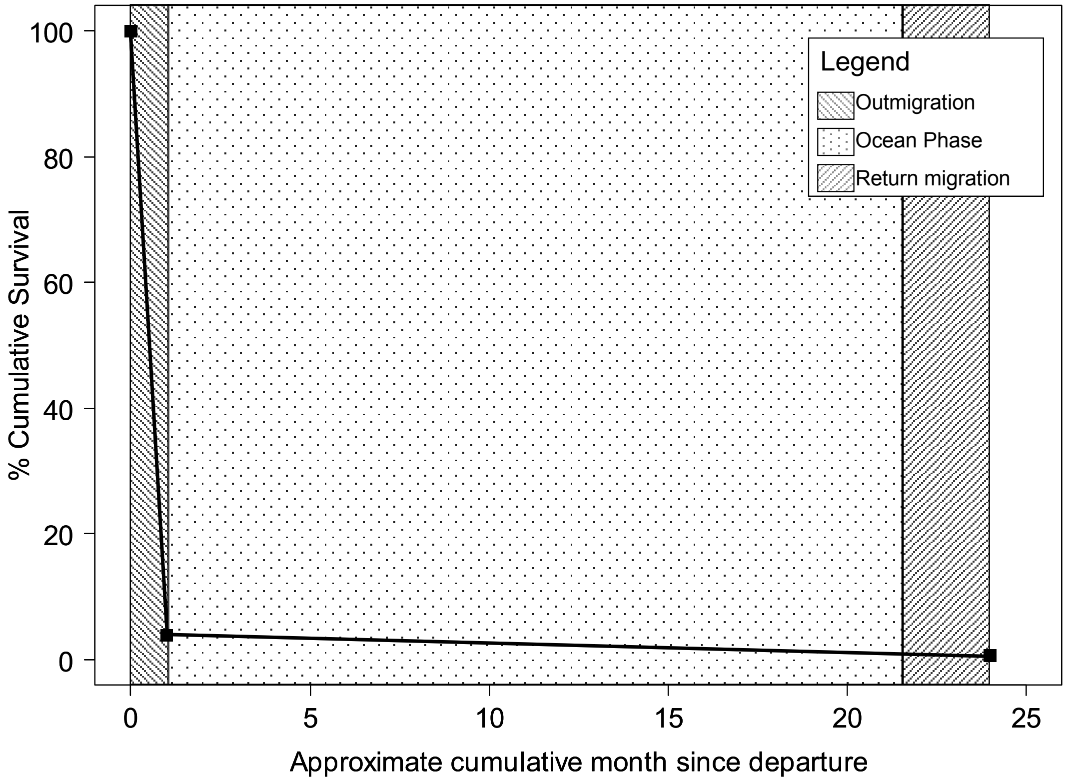
Legend
Outmigration
Ocean Phase
Return migration
% Cumulative Survival
0
20
40
60
80
100
0
5
10
15
20
25
Approximate cumulative month since departure

Fig. 8

Chapter 2

The effects of environmental factors on the migratory patterns of Sacramento River yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*)

INTRODUCTION

Migrations in the animal kingdom have fascinated humans for centuries, and their associated folklore is intrinsically tied to many different cultures and beliefs. Perhaps none are more written about or culturally important than the Pacific salmon migrations. Specifically, the Chinook or “king” salmon have fascinated people for ages due to their sheer size, power and determination.

The term migration can have a multitude of definitions, but with respect to salmonids, perhaps migration is best defined by Dingle and Drake (2007) as “a seasonal to-and-fro movement of populations between regions where conditions are alternately favorable or unfavorable (including one region in which breeding occurs)”. In this paper I attempt to better understand the beginning half of this migration, the migration of juvenile salmon from their riverine nursery to the food-rich ocean, often considered one of the most vulnerable stages in a Chinook salmon’s life (Healey 1991). During this life stage, juvenile salmon undergo many morphological, physiological, and behavioral changes (known as smoltification) to prepare for the ocean phase of their life cycle. For the Sacramento River’s Chinook salmon populations, this freshwater journey may be as long as 600 kilometers, transiting many different habitats, all with varying natural conditions. Additionally, anthropogenic stressors such as water diversions, dams and introduced predators are present throughout the watershed.

Studies have been investigating the timing and patterns of juvenile salmonid migrations on a large-scale focus for decades. Thorpe and Morgan (1978) tracked juvenile Atlantic salmon (*Salmo salar*) fry periodicity during outmigration in Scottish Rivers. Raymond (1968) calculated migration rates by marking and recapturing yearling Chinook salmon smolts traveling through the Snake and Columbia Rivers and their impoundments. However, to best comprehend the intricacies of the migration, one must understand that a migration is determined by the fine scale movements that constitute it. New fish tracking technologies have allowed the exploration of small-scale movement during migration. These technologies have already yielded high-resolution migration data on steelhead (*Oncorhynchus mykiss*) smolts in the Cheakamus River in British Columbia, Canada (Melnychuk et al. 2007), and on sockeye salmon (*Oncorhynchus nerka*) smolts in the Fraser River in British Columbia, Canada (Welch et al. 2009). Once small-scale movement information is attainable, our knowledge of salmon migrations can begin to delve into what might be governing variability in movement patterns.

A few studies have explored how environmental conditions might be influencing migration dynamics (Giorgi et al. 1997, Smith et al. 2002), but at large spatial and temporal scales. These relationships are therefore usually limited to inter-annual and inter-population comparisons, thereby only uncovering the strongest and most persistent of patterns. Smaller-scale, more subtle environmental factors may also exert significant influences on salmonid movement patterns, which may have higher order population consequences. Elucidating these require incorporation of high-resolution movement data.

I have structured this study to answer the two following hypotheses:

(1) Total migration and reach-specific movement rates of outmigrating late-fall run Chinook salmon smolts vary spatially and temporally in the Sacramento River, Sacramento-San Joaquin Delta and San Francisco Estuary.

(2) Environmental variables can explain a substantial portion of variation in reach-specific movement rates.

This study aims to capitalize on one of the largest networks of acoustic monitors in the world developed by the California Fish Tracking Consortium (http://californiafishtracking.ucdavis.edu/), and a collaboration between the National Oceanic and Atmospheric Administration (NOAA) and the University of California, Davis (UCD), to provide the first high-resolution analysis of the spatial and temporal variation of Chinook salmon movement and migration in the Sacramento River and San Francisco Estuary. Using this information, I will provide insight into which environmental variables (natural and anthropogenic) explain variations in movement patterns. Finally, relating migration and movement dynamics to smolt survival will be the important final step in understanding the intricacies of this life stage.

This work is essential for improving both our basic ecological understanding and management of salmon. It represents an advancement in our awareness of the environmental factors that likely influence the out-migration of late-fall run Chinook salmon smolts. Without this type of information, resource managers are unable to consider the consequences of anthropogenic activities that may have detrimental effects on salmon populations, or predict migration dynamics of future cohorts facing environmental changes. Finally, assessing what environmental conditions influence variation in late-fall run Chinook salmon movement will provide guidance into factors affecting the movement dynamics of other valued salmon runs in California.

METHODS

Study area

The Sacramento River is the longest and largest (measured by flow discharge) river to be fully contained within the state of California, and is the third largest river that flows in the Pacific Ocean in the contiguous United States (Fig. 1). The headwaters are located slightly south of Mount Shasta in the lower Cascade Range, and the river enters the ocean through the San Francisco Estuary at the Golden Gate Bridge. The total catchment area spans approximately 70,000 km^2.

The Sacramento River and its tributaries have been heavily dammed, and it is estimated that approximately 47% of the historic area that was used for spawning, migration and/or rearing of Chinook salmon is no longer accessible (Yoshiyama et al. 2001). The Sacramento River watershed includes diverse habitats, from a pristine run-riffle meandering river, to a heavily channelized and impacted waterway further south, to an expansive tidally-influenced freshwater delta at its confluence with the San Joaquin River, and finally to the San Francisco Bay Estuary, the largest and most modified estuary on the West Coast of the United States (Nichols et al. 1986). The annual mean daily discharge for the Sacramento River from 1956 to 2008 was 668 $m^3 \cdot s^{-1}$ (Interagency Ecological Program 2004), however, it is estimated that today, water discharge of the Sacramento and San Joaquin Rivers combined amounts to approximately 40% of the historical, pre-colonization discharge (Nichols et al. 1986). The damming and water diversions of the Sacramento River and its tributaries have also homogenized river flows throughout the year, notably reducing the historical winter high flows and flooding (Buer et al. 1989).

The study area included approximately 92% of the current outmigration corridor of late-fall run Chinook salmon, from release to ocean entry. Specifically, the study area's furthest upstream release site at Battle Creek (534 km upstream from the Golden Gate) is only 47 km downstream from Keswick Dam, the first impassable barrier to anadromy (Table 1).

Central Valley late-fall run Chinook salmon

The California Central Valley, which includes the Sacramento and San Joaquin Rivers and their tributaries, has four distinct Chinook salmon populations (runs) that migrate at different times of the year. Additionally, these populations demonstrate one of two early life history strategies: "ocean-type" and "stream-type" (Gilbert 1912). Ocean-type Chinook salmon are born in the lower reaches of large rivers and spend very little time (days to weeks) in the river before migrating to the ocean. Stream-type juveniles are born in the headwaters of large rivers or tributaries and spend up to a year in the river (yearling) before migrating to the ocean at a relatively large size. Among the different runs and early life history strategies, it becomes clear that different populations have found different migration strategies to maximize survival (Taylor 1990).

The late-fall run is one of the four runs found in the Sacramento River drainage, and is the only run to exhibit a predominately stream-type life history (Moyle 2002). Coupled with the fall run, the pair form an evolutionary significant unit (ESU) deemed a “species of concern” by the Endangered Species Act as of April 15, 2004. Juveniles exhibit a river residency of 7 to 13 months, after which smolts will enter the ocean at a size of approximately 160 mm (Fisher 1994). Potentially due to water diversions and increased predation in bank-altered areas, outmigrating late-fall run juveniles accrue substantial mortality (Moyle et al. 1995).

The historical distribution of the late-fall run Chinook salmon is hard to estimate, due to the paucity of historical data. Late-fall run Chinook salmon were not distinguished from fall run fish until 1966, when counts were initiated after the construction of the Red Bluff Diversion Dam (RBDD) in the mid 1960s (Yoshiyama et al. 1998). However, we know that ideal late-fall run spawning habitat consists of year-round cold water allowing the rearing of yearlings, and that their current spawning range is from Red Bluff (480 river km (rkm) upstream from the Golden Gate) up to the first barrier to anadromy, Keswick Dam (rkm 565) (Fisher 1994, Moyle et al. 1995, Yoshiyama et al. 2001). We assume that this run historically used the cold waters upstream of Keswick Dam, specifically the Upper Sacramento, McCloud and Pit Rivers for spawning (Yoshiyama et al. 1998). Since these rivers are no longer accessible, the large majority of late-fall run Chinook salmon spawning grounds disappeared with the construction of Keswick and Shasta Dams.

Acoustic Telemetry

I used Vemco V7-2L acoustic tags (1.58g ± 0.03 S.D.; Amirix Systems, Inc. Halifax, Nova Scotia, Canada) and Vemco VR2/VR2W submergible monitors to track tagged fish. The monitor array spanned 550 km of the Sacramento River watershed from Keswick Dam to the ocean (Golden Gate) (Fig. 1). This array of approximately 300 monitors was maintained by the California Fish Tracking Consortium (a group of academic, federal and state resources agencies, and private consulting firms) and positioned to maximize detection probability at key sites along the outmigration corridor.

The acoustic monitors automatically process all detection data and drop false detections or incomplete codes from the detection file. All detection files were additionally subjected to standardized quality control procedures to minimize the number of false detections. For example, detections that occurred before the release date-time of each tag or detections that did not share a tag identification number with any of the released fish were excluded from analysis.

Tagging and Releases

For three consecutive winters, from January 2007 to January 2009 (henceforth referred to as 2007, 2008 and 2009 seasons, based on the year during which January tagging occurred), 200 to 300 late-fall run Chinook salmon smolts were tagged and released into the Sacramento River watershed. The size of tagged fish (Table 2) was consistent with the observed size frequency for this Chinook salmon run, albeit larger than other life-history type Chinook salmon smolts (Fisher 1994).

Hatchery origin yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) smolts, obtained from the United States Fish and Wildlife Service's (USFWS) Coleman National Fish Hatchery (Anderson, CA), were used in this study. Approximately 85-90% of the hatchery smolts are the progeny of hatchery-origin adults trapped in Battle Creek (tributary to the Sacramento River); the remaining hatchery smolts' parents are natural-origin adults trapped on the mainstem Sacramento River just below Keswick Dam (K. Niemela, USFWS, Red Bluff, CA 96080, unpubl. report).

Acoustic tags were surgically implanted into the peritoneal cavity of anesthetized fish as described by two studies (Adams et al. 1998a, Martinelli et al. 1998). To minimize potential effects on survival, growth and behavior, tag weight did not exceed 5% of the total body weight. This cutoff point was conservative, considering much of the literature shows tag-to-body ratios can be up to 6% and not effect growth (Moore et al. 1990, Adams et al. 1998a, Martinelli et al. 1998), and up to 8% and not affect swimming performance (Moore et al. 1990, Adams et al. 1998b, Brown et al. 1999, Anglea et al. 2004, Lacroix et al. 2004).

Post-surgery, the fish were kept in captivity for a minimum of 24 hours to ensure proper recovery from surgery. In the 2007 season, a portion of the tagged fish were released each weekday for three consecutive weeks in January. In the two following seasons, half the smolts were released in December and half in January, both on a single day. All releases occurred at dusk to minimize predation as the smolts became habituated to the riverine environment.

Fish were transported at low densities (~ 10 $g \bullet l^{-1}$) via coolers with aerators to the release sites. In years of multiple release sites, transport times were extended for closer sites to keep potential transport stress equal among all release groups. In the first year of the tagging effort (2007), all 200 fish were released at the Coleman National Fish Hatchery into Battle Creek, a tributary to the Sacramento River. In the latter two years, 300 fish a year were tagged and released simultaneously from three release sites in the upper 150 rkm of the mainstem Sacramento River, allowing the lower release groups a greater likelihood of reaching the lower river and estuary in large numbers (to improve statistical confidence intervals).

Data Analysis

After the three-year study was completed, monitor locations were assessed for their tag detection probability and functional reliability over the three-year period (Michel unpubl. data) and their location within the watershed. Detection efficiencies are calculated by assessing the number of tags missed by a monitor location. This can be done if a missed tag is seen at a downstream location and therefore we can assume it had to pass the upstream location. Detection probabilities were calculated using the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) within Program MARK (created by Gary White, Colorado State University (White and Burnham 1999)). Those monitor locations that had consistently high tag detection probabilities and that were strategically located were chosen to delimit the river reaches that were used in spatially comparing movement. A total of 19 monitor locations were chosen, from just below the most upstream release site to the Golden Gate (Table 1).

Hypothesis 1

Total elapsed time from release site to the Golden Gate was calculated for each smolt that survived to the Golden Gate (3-13% of all smolts, depending on release group and year (Michel unpubl. data)) and averaged per release group (by year and release site), representing mean total outmigration time. Respective fish movement rates ($km \cdot day^{-1}$) from release site to ocean entrance at the Golden Gate monitoring location were also calculated and averaged per release group, representing the mean successful migration movement rate (MSMMR). A two-factor (year and release site) analysis of variance (ANOVA) was performed to determine the influence of year and release site on total movement rate. Reach-specific and smolt-specific movement rates were then calculated using the last detection time from the upstream monitor locations and the first detection time from the downstream monitor locations. Distances between monitor locations were calculated in kilometers using the geographic information system software program ArcGIS (ESRI, 1999), giving a movement metric of kilometers per day over ground. Reach-by-reach movement rates were also averaged among all detected smolts, and then associated to the detection probabilities of each reach's upstream and downstream node. The product of the two detection probabilities equals the proportion of individual movement rates sampled out of all the individual smolts that are estimated to have traversed each reach.

Once movement rates were calculated, I tested for the influence of the study design factors. The outmigration corridor was then delimited into 5 different regions for the ensuing ANOVA. The regions were the run-riffle upper Sacramento River, the deeper and more uniform middle Sacramento River, the deep and channelized lower Sacramento River, the tidally influenced Sacramento-San Joaquin River Delta, and finally the San Francisco Estuary. I averaged reach-specific and smolt-specific movement rates per region. I then tested for the assumption of homogeneity of variance and of normal distributions among the groups of observations. If these assumptions were true, I then used a mixed-effect ANOVA, which allows for both fixed factors (such as year and region) and random factors (in this case individual fish) to test for the effect of year, month, release site, and region. Including region as a factor can be a source of non-independence of measurements. An individual will travel through different regions, and could theoretically express individual variation in movement rates. The mixed-effect ANOVA can statistically test for fixed factor effects while controlling for individual variation.

As fish were only released from one location during one month in the first year (three locations and two months in the other two years), the preliminary linear mixed-effect ANOVA did not test for the influence of release location on movement rates. Therefore, the analysis tested for year, region, the interaction of the two, and for the random factor.

To determine the influence of release location and month on movement rates, a second mixed-effect ANOVA was then performed excluding data from the 2007 season. This ANOVA included the factors of year, region, release site, release month, all interaction terms, and the random factor.

While these analyses will test for large-scale variation in movement rates (by year and by month), small-scale variation in movement was also calculated. An hourly reach-specific metric of movement was calculated, consisting of the frequency of novel smolt arrivals per hour of the day for each monitor location. Novel reach arrivals per hour were then summed for each region, giving a frequency distribution of hourly fish movement per region.

A contingency table was then constructed to test if any discernable hourly arrival pattern varies across regions. This was used to determine if there is contingency (non-independence) between the two factors, region and hour of arrival (or a binning of these). For this, Pearson's chi-squared test of independence was used (tests the null hypothesis that the two factors are not related).

Hypothesis 2

Environmental data were collected for this study for the majority of the river reaches, from the release points to the upper limit of tidal influence on the river (river km (rkm) 189; Table 3). Environmental variables collected can be grouped into two types: several spatial-temporal variables and one purely spatial variable. All variables were chosen *a priori* based on salmon migration literature and data availability for the watershed.

The single spatial variable was river sinuosity (actual river length divided by the length of a direct line between the nodes delimiting each reach). The temporally varying spatial variables included water temperature (ºC), river flow ($m^3 \cdot s^{-1}$), water turbidity (Nephelometric Turbidity Units (ntu); McCormick et al. 1998), channel water velocity ($m \cdot s^{-1}$), and a ratio of river surface width (m) to maximum river depth (m) (WDR; Tiffan et al. 2009). The WDR will increase as the river becomes shallower and wider. Spatial-temporal variables such as temperature, turbidity and flow were recorded directly from gauge stations on the river (Table 3). Measurements such as water velocity and WDR were simulated incorporating actual flow recordings, high resolution bathymetric cross-sections and gradient information in the riverine hydraulics modeling software program HEC-RAS (US Army Corps of Hydraulic Engineers 1995). All spatial variables were calculated using the program ArcGIS.

All reach-specific spatial-temporal environmental variables were then averaged by reach and by day. Spatial variables were averaged per reach. All reach-specific spatial and spatial-temporal environmental variables were then associated with their respective reach-specific movement rates in a relational database (Microsoft SQL Server 2005, Microsoft Corporation). When a specific smolt movement spanned several days, weighted averages of the appropriate daily spatial-temporal environmental variables were used. A Pearson's correlation test was then performed to calculate correlation coefficients for each environmental variable, similar to Smith et al. (2002). Additionally, the statistical significance of each environmental correlation coefficient on movement was calculated.

Different environmental variables are frequently correlated with one another, and caution must be employed to minimize spurious conclusions. I therefore calculated all Pearson's correlation coefficients between variables that had strong influences on movement rates. When there was a significant relationship between two environmental variables ($r^2 > 0.7$ and $P < 0.05$ (Giorgi et al. 1997)), the lesser of the two movement-correlated variables was dropped from further analysis.

Once the more influential environmental variables were determined, their means and standard errors were calculated to the resolution of each significant study design factor (e.g. if year was significant, mean and standard error were calculated for each year). Using this information, I suggest hypotheses for how the environmental variables may have influenced spatial and temporal variability in movement rates.

RESULTS

Hypothesis 1

The mean successful migration movement rate (MSMMR) and total outmigration time per release group varied by release site and by year (Table 4). Mean total movement rates decreased the further downstream the release group was released. Movement rates varied from 14.32 $km \cdot day^{-1}$ (± 1.32 S.E.) for the 2009 Butte City release group (rkm 363) to 23.53 $km \cdot day^{-1}$ (± 3.64 S.E.) for the 2007 Battle Creek release group (rkm 534). Total outmigration time increased the further downstream the release group was released, varying from approximately 39 days for the 2008 Butte City release group to approximately 24 days for the 2007 Battle Creek release group. Analysis of variance confirmed this pattern: release location had a significant effect on MSMMR ($P < 0.05$), while year did not (P 0.2).

Reach-specific movement rates varied substantially from 15.3 $\text{km}\cdot\text{day}^{-1}$ in the Sacramento-San Joaquin River Delta to 89.1 $\text{km}\cdot\text{day}^{-1}$ in a reach of the upper river region (Table 5). The proportion of fish sampled varied due to differences in detection efficiencies throughout the watershed.

The distributions of movement rates per year and per region did not violate the assumptions of homogeneity of variances and of normal distributions were not violated, and therefore the mixed-effect ANOVA was performed. Results from the initial all-years mixed-effect ANOVA, including region and year factors, showed that region had a significant influence ($P < 0.001$) on the variation in movement rates, as well as the interaction between region and year (i.e. the relative movement rates among regions differed among years; Table 6). Year did not have a significant effect on movement rates (P 0.07), but still warrants further investigation (Fig. 2). Movement rates decreased as fish moved from upstream regions downstream toward ocean entry, with the fastest movement rates found in the upper river region, and the slowest in the Sacramento-San Joaquin River Delta (Fig. 3). The interaction between region and year suggested a similar trend in 2007 and 2008 of generally decreasing movement rates the further downstream the region is, but in 2009, movement rates were generally slower and more uniform among regions (Fig. 4). As expected, the random factor, individual fish, was significant ($P < 0.001$), suggesting that there was great variation in movement rates among individual fish.

Results from the 2008 and 2009-effect ANOVA included the additional factors of release month and release site (Table 7). Results from this analysis indicate a significant influence of region and the interaction between year and region ($P < 0.001$) as was the case for the three-year analysis. The large majority of interactions including the region factor were significant. The influence of year, release site, and release month on the variation in movement rates was not significant, although again year had a strong, but statistically insignificant, influence on movement rates (P 0.07).

Smolt movement varied substantially per hour, notably in the upper and middle river regions, where the majority of daily movement occured between midnight and 700 hours, then again from 1700 hours and midnight, suggesting a nocturnal movement (Fig. 5). The nocturnal pattern in arrivals seemed to lessen in strength the further downstream the region is found, to the point where in the estuary, smolts moved at all times of the day. To determine if the nocturnal pattern truly varied in strength per region, a Pearson's chi-squared test of independence was performed. Hour of arrival was therefore binned into two groups, day hours (arrival hours 7-17) and night hours (arrival hours 0-6, and 18-23) based on average sunrise and sunset during the time period of the study. A five-by-two contingency table of arrivals was created with the categorical factors of day/night and region. A Pearson's chi-squared test of independence indicated that the night/day arrival factor was significantly dependent on region ($P < 0.001$).

Hypothesis 2

Several variables tested had significant relationships with movement rate ($P < 0.001$; Table 8). Reach sinuosity had the strongest association with movement rates, suggesting that the more sinuous a river reach is, the faster a fish will travel through it. Width-to-depth ratio (WDR) had a negative relationship with movement rates, suggesting that the deeper and narrower reaches (low WDR) will have faster movement rates. Water velocity and river flow were both positively related to movement rates. Temperature was also positively related to movement rates, but was a relatively weak predictor of variability in movement rates. This suggests that smolts moved faster through faster flowing water, greater volume of water flow, and narrower-deeper channels.

All selected environmental variables were then tested for correlations among each other. No variables were found to be overly correlated using previously mentioned cutoff ($r^2 > 0.7$ and $P < 0.05$). However, while not significant, the negative relationship between WDR and sinuosity ($r^2=0.27$, $P < 0.001$) was the strongest correlation.

Mean sinuosity was seen to vary among region in a generally decreasing trend from the upper river down to the lower river (Table 9). Mean water velocity also followed this trend, with a sizeable decrease in regional mean velocity between the middle river and the lower river. Mean water velocity also varied among years, with a generally decreasing trend from 2007 to 2009.

DISCUSSION

Hypothesis 1

Mean successful migration movement rate (MSMMR) varied significantly by release location but did not vary significantly among the three years of the study. Effectively, movement rates were consistently slower the further downstream a group was released. Consequently, the mean total outmigration time for each group reflected this strong pattern: the further downstream a group was released, the longer the group took to reach the ocean. Therefore, smolts released further upstream, closer to their native nurseries, are exhibiting behavioral differences relative to the downstream released smolts with regard to migration that suggest that environmental cues that trigger migration are subdued or absent from the lower, more distant sites from their evolutionary migration origin.

Migration rates from the Battle Creek release site to the ocean in 2007 (23.53 $\mathrm{km \cdot day^{-1}}$) were very similar to migration rates of late-fall run Chinook salmon smolts released at the same site and recaptured at the beginning of the San Francisco Estuary in a previous study (20.63 $\mathrm{km \cdot day^{-1}}$, USFWS data 1998-2003, www.delta.dfg.ca.gov/usfws/maps/index.htm). The mean migration rate for yearling Chinook salmon smolts on the Columbia River, another large West Coast river, was 21.5 $\mathrm{km \cdot day^{-1}}$ (Giorgi et al. 1997). Although migration rates of yearling Chinook salmon on the Fraser River are not available in the literature, similarly sized sockeye salmon (*Oncorhynchus nerka*) smolts navigated the watershed at a rate of 15 to 30 $\mathrm{km \cdot day^{-1}}$ (Welch et al. 2009). The results for late-fall Chinook salmon smolts presented here in combination with those of yearlings from other studies strongly suggest that like-sized smolts exhibit very similar migration rates regardless of river they reside in.

Reach-specific movement rates displayed substantial variation among reaches and within reaches for some of the lower reaches. Specifically, the movement rates within the estuary have the largest variability. This is likely due to the influence of tidal dynamics on movement rates, as seen by Lacroix and McCurdy (1996) with Atlantic salmon (*Salmo salar*) smolts.

While mean movement rates appeared to be fastest in 2007, slower in 2008, and slowest in 2009, movement rates did not differ significantly among years (although there were greater differences than observed in most other factors). Coupled with the fact that MSMMR did not differ significantly among years, this could be misconstrued to suggest that yearly environmental variation has little effect on movement rates in general. However, the three years of the study were all similarly dry years resulting in low freshwater flows (DWR 2009. WSIHIST Water Year Hydrologic Classification Indices [http://cdec.water.ca.gov/cgi-progs/iodir/wsihist]). Therefore, movement rates and environmental associations found in this study may only be indicative of variation among similarly dry years.

The large majority of movement, particularly in the river regions, was nocturnal, which has been seen by other studies (McCormick et al. 1998, Ibbotson et al. 2006). This has often been suggested to be a predator avoidance strategy, particularly from visual predators like some fish and birds (McCormick et al. 1998, Ibbotson et al. 2006).

In addition to stealth by night movement, water turbidity has been shown to reduce predation (Gregory and Levings 1998), and warmer water temperatures allow for more efficient predator evasion in salmonid smolts due to increased neuromuscular escape responses. Also seen by Ibbotson et al. (2006), this is particularly interesting because the nocturnal migration pattern dissipates in the lower river region, which had higher turbidity and warmer water temperatures, suggesting smolts may only use night travel as a predator avoidance strategy until water turbidity and water temperature is protective enough to allow migration at all hours.

In conclusion, I find that hypothesis 1 is supported. There is evidence for both spatial (by region) and temporal (by hour and by year (although not significantly)) variation in movement rates for the three years of this study and it is likely that environmental variability is a contributor.

Hypothesis 2

River sinuosity had the strongest relationship with movement rates among the measured environmental variables. The relationship suggested that the more sinuous river reaches exhibited faster smolt movement rates. Sinuosity is associated with channel complexity and diverse flow velocities. In the Sacramento River, the most sinuous river reaches are also the most natural and unmodified reaches. Therefore, if a smolt were to seek the fastest water velocities in the river’s cross-section, it would benefit from more energy-efficient movement (Kemp et al. 2005) and expedite transit. Since some of the greatest river velocities occurred in the reaches with the greatest sinuosity, where late-fall run smolts moved the fastest, this association may be operative.

Width-to-depth ratios (WDR) were found to have a moderately strong negative relationship with movement rates, meaning that the narrower and deeper reaches would exhibit faster smolt movement. This relationship is counter-intuitive when considering that the lower river region had the slowest river movement rates and also had the lowest WDR. However, the upper river region did not have the highest mean WDR, suggesting that the fast movement rates in this region may be associated to medium to low WDR values, driving this relationship. Additionally, WDR was also found to associate negatively with sinuosity, suggesting that the narrower and deeper reachs (low WDR) are relatively more sinuous. The correlation between WDR and sinuosity (Pearson's correlation coefficient (r) -0.52), and between sinuosity and movement rates (r 0.53), were both substantially stronger than the correlation between WDR and movement rates (r -0.26), leading me to the conclusion that the counter-intuitive direction of the correlation between WDR and movement rates may be an indirect effect through the intermediary of the much stronger relationship between sinuosity and movement rate.

Flow has often been suggested to influence movement rates (Giorgi et al. 1997). In this study, flow was found to be positively related with movement rates. Flow generally increases in the downstream direction, in large part due to the progressive addition of flow from the numerous tributaries in this system. However, the mean flows experienced by smolts in this study were very similar across regions.

One possible interpretation of the relationship between flow and movement could be that it is the temporal (and not the spatial) variability in flow that drives this relationship. Salmonid smolts are known to initiate their downstream migration during storm events (McCormick et al. 1998), analogous with high flows. Additionally, there was evidence of increased watershed-wide smolt movements during particularly strong storm events. I therefore conclude that the relationship between flow and movement rate is potentially due to drastic increases in flow.

Movement rates and velocity were found to be positively correlated. Faster water velocities can help a smolt move downstream at faster rates by increasing passive transport. This relationship was believed to be the most important environmental factor *a priori,* however, the strength of the correlation was not as strong as some of the other relationships. A reason for this could be that the nocturnal behavior of smolts in the upper river decreases the total number of hours that smolts devote to migration. Although smolts moved the fastest in the upper regions of the river, movement rates would likely have been faster if the smolts travelled at all times of the day and benefitted from the maximum potential of the substantially faster water velocities.

Variation in water velocities and nocturnal movement were assessed in an attempt to explain regional differences in movement rates. I found that nocturnal movement decreases progressively as smolts moved further downstream toward the ocean, with smolts moving more continuously. However, lower river reaches also exhibit slower movement rates, probably in part due to the substantially slower water velocities. This could suggest a trade-off between predator avoidance via nocturnal travel upstream and increased continuous daily movement downstream when velocities do not provide relatively efficient passive transport. Although turbidity was not seen to influence movement rates directly in this study, turbidity may increase survival by decreasing predator efficiency (Michel unpubl. data). Thus, increased daylight migration (increasing daily travelled distance, thereby reducing temporal exposure to predators) coupled with increased turbidity may act in concert to improve predator avoidance during seaward migration.

Of the environmental variables found to have a significant relationship with movement rates, only water velocity was found to fluctuate similarly to the yearly fluctuations in movement rates. Mean water velocity declined between 2007 and 2009, while mean and region-specific movement rates followed the same trend. This evidence supports the *a priori* theory that water velocity may be one of the key factors influencing yearly differences in movement rates.

The evidence that fluctuations in river sinuosity and water velocities could explain spatial and temporal variation in movement rates, I find that hypothesis 2 is supported.

CONCLUSIONS

The relationship between movement patterns and migration strategies with environmental factors allows hypothesizing on which factors have the most important effect. Relating these same movement and migration patterns to immediate survival provides invaluable information on the success of the different strategies, and in turn provides evidence for how those strategies might have evolved.

Survival data from these same late-fall run individuals, with respect to release location shows that the furthest upstream release site group (rkm 518) experienced the worst survival, but the middle release site group (rkm 413) experienced the highest survival (Michel unpubl. data). Additionally, the smolts experienced relatively low survival in the upper and middle river regions, and high survival in the lower river region. When considered with the MSMMR of these same release groups, it becomes apparent that there could be tradeoff between the benefit of bypassing the upper river region and its high associated mortality, and the detriment of additional temporal exposure to predation of the groups released further downstream. It should be added that while releasing smolts downstream improves survival in some cases, it also increases straying of returning adults, which has been known to be detrimental to natural reproductive success (Quinn 1993).

This low survival in the upper reaches of the Sacramento River coincided with the location of the primarily nocturnal migration, while the high survival coincides with the temporally uniform timing of migration seen in the lower river reaches. Additionally, turbidity was found to have one of the strongest associations with survival rates (Michel unpubl. data). Taken together, these results suggest that the relatively clear waters of the upper and middle river regions have much higher predation rates, which in turn may have formed the nocturnal migration strategy to minimize mortality. The lower river region, being more turbid and therefore more hospitable to smolt survival (Gregory and Levings 1998), eased the nocturnal strategy to a more temporally uniform migration allowing smolts to travel larger distances per day.

The slowest movement rates were seen in the Sacramento-San Joaquin River Delta, a highly modified and complex system of sloughs and channels. Furthermore, water diversions in the southern delta remove nearly 40% of the historic flows through the delta, resulting in substantial modifications in flow dynamics and directions (Nichols et al. 1986). The result is a region in which smolts have a high susceptibility of entering the interior delta, predisposing them to longer routes, higher predation from invasive predators, and the risk of entrainment into water pump, inevitably leading to higher mortality rates (Perry et al. 2010). Interestingly, although movement rates were relatively slow compared to other regions, suggesting many smolts were diverted into the interior delta, the survival rate for these same smolts was still higher than in the San Francisco Estuary, and on par with survival rates from the upper river regions.

The delta has long been known to have an important nursery function, especially for subyearling fall run Chinook salmon (Kjelson et al. 1982). However, smolts in this study were in the delta for an average of 6.5 days, a period too short for significant nursery function. This may be because delta and estuarine residency is known to be shorter for yearling Chinook salmon smolts than for subyearlings in many watersheds along the West coast of North America (Healey 1991), but could also be an adaptation due to the above mentioned sources of mortality and the human modification of the delta, leading to dramatically decreased wetlands (Frayer et al. 1989) and potentially as a result, decreased benefits from foraging there.

This study has presented the spatial and temporal variability in movement rates and migration strategy, and supplied evidence that water velocity and nocturnal travel work cohesively in explaining yearly and regional variation in movement rates.

This study has also provided novel information on salmonid smolt migration, and will be valuable to resource managers. However, the study had some limitations that should not be overlooked. Perhaps most importantly, the study occurred during three years of very low precipitation and river flows for the Sacramento River Valley, with 2008 being deemed critically dry (DWR 2009. WSIHIST Water Year Hydrologic Classification Indices [http://cdec.water.ca.gov/cgi-progs/iodir/wsihist]). Therefore the movement dynamics and environmental associations may be different during years of substantially greater flow.

Another limitation of acoustic telemetry data is that one cannot positively know when a smolt has been eaten by a predator (Vogel 2010). While I attempted to filter the receiver detections to the best of my abilities, it is possible that some minor inaccuracies in movement rates exist from data recorded from predators retaining the tag gastrically. These data, if present, would not change mean calculated movement rates substantially, but does stress the need for tag technology that will allow detection of when a tagged smolt, or any tagged animal, has been consumed.

Finally, due to the limited availability of environmental data in the Sacramento – San Joaquin Delta and San Francisco Estuary, movement dynamics were associated with only environmental factors in the river reaches beyond tidal influence. Future work should explore these relationships in the delta and estuary using the methodology presented in this paper.

The results found in this study provide resource managers with valuable information that can be used to improve survival for the imperiled Sacramento River Chinook salmon populations. This study is the first in the Sacramento River watershed to provide reliable information on the total migration time and high-resolution reach specific movement rates for late-fall run Chinook salmon smolts. This information allows resource managers to better comprehend when and for how long smolts will be migrating, as well as smolt transit times in specific areas in the watershed, thus efficiently guiding the timing and scope of water and riparian development activities.

This study found significant evidence for an increasingly long total outmigration time and MSMMR for groups released progressively further from their native nurseries. This information is especially germane to the release strategies employed by Chinook salmon hatcheries in the Central Valley. A large portion of these hatchery-produced smolts are trucked and released in the estuary to reduce pre-ocean mortality and therefore maximize returns. However, if these smolts react similarly to this study's smolts when released downriver of their natal origins, they may be subject to high predation rates as they slowly acclimate and begin their outmigration. This may be evidence to discontinue the aforementioned hatchery release strategy.

This study also elucidated a strong nocturnal migration pattern during a portion of the outmigration. While other examples of nocturnal migration in salmonids exists in the literature (McCormick et al. 1998, Ibbotson et al. 2006), and may not be novel information to resource managers, the added complexity that the nocturnal migration pattern dissipates as the smolts progressively near the ocean is valuable information. Many detrimental anthropogenic impacts such as pile driving and dredging occur during the day based on the assumption that the fish migrate nocturnally (D. Hampton, NMFS Protected Resources Division, Sacramento, CA 95814, pers. comm.). This study shows that this assumption is not supported in the lower region of the river, as well as in the delta and estuary.

Finally, the hypothesis that water velocity and turbidity co-vary with (and perhaps govern) the extent to which smolts migrate nocturnally will be a useful tool in predicting the migrations of future cohorts facing environmental changes.

The imperiled Central Valley Chinook salmon stocks will require sound fisheries and resource managing for any hope of an eventual recovery, and this cannot be achieved without understanding the movement and migration dynamics and causal mechanisms of emigrating smolts, arguably the most vulnerable life stage. This study provides new insights on small scale temporal and spatial movement dynamics, the migration through the entire watershed, and finally provides suggestions on what and how environmental factors are influencing these dynamics.

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Table 1. Locations of acoustic monitors and tagged fish release locations.

Location	River km	Description
Battle Creek	534	Release site 2007
Jelly's Ferry	518	Monitor location & release site 2008/09
Bend Bridge	504	Monitor location
China Rapids	492	Monitor location
Above Thomes	456	Monitor location
Below GCID	421	Monitor location
Irvine Finch	412	Monitor location & release site 2008/09
Above Ord	389	Monitor location
Butte City Bridge	363	Monitor location & release site 2008/09
Above Colusa Bridge	325	Monitor location
Meridian Bridge	309	Monitor location
Above Feather River	226	Monitor location
I-80/50 Bridge Sacramento	189	Monitor location
Freeport	169	Monitor location
Chipps Island	70	Monitor location
Benicia Bridge	52	Monitor location
Carquinez Bridge	41	Monitor location
Richmond Bridge	15	Monitor location
Golden Gate East Line	2	Monitor location
Golden Gate West Line	1	Monitor location

Table 2. Means and standard errors for weight and fork length of acoustically-tagged smolts by year and for all years combined.

Year	Weight ± SE (g)*	Fork length ± SE (mm)*	Sample size
ALL	46.0 ± 0.4	161.5 ± 0.5	804
2007	46.6 ± 0.7^{a}	164.6 ± 0.8^{a}	200
2008	52.6 ± 0.8^{b}	168.7 ± 0.8^{b}	304
2009	38.9 ± 0.5^{c}	152.1 ± 0.5^{c}	300

*Size distributions with different superscripts are significantly different ($P < 0.05$)

Table 3. Sources of environmental data for this study.

Environmental variables	Data source *	Data Location
Water temperature (ºC)	UCD, BOR, DWR, USGS, USFWS	http://cdec.water.ca.gov/
Water turbidity (NTU)	BOR, DWR, USGS	http://cdec.water.ca.gov/
River flow ($m^3 \cdot sec^{-1}$)	BOR, DWR, USGS	http://cdec.water.ca.gov/
Channel water velocity ($m \cdot sec^{-1}$)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* †
Maximum river depth (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* †
River surface width (m)	HEC-RAS simulations using DWR bathymetric models	Ricky Doung, Todd Hillaire *pers. comm.* †

*Agency Acronyms: UCD= University of California - Davis, BOR= United States Bureau of Reclamation, DWR= California Department of Water Resources, USGS= United States Geological Survey, USFWS= United States Fish and Wildlife Service, USACE= United States Army Corps of Engineers

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Table 4. Mean total outmigration time in days and mean successful migration movement rate (MSMMR) for all years and all release groups.

Year	Release (rkm)*	# released	Mean total outmigration time (days) ± SE	MSMMR ($km \cdot day^{-1}$) ± SE
2007	534	200	24.2 ± 3.3	23.5 ± 3.6
2008	517	102	28.9 ± 2.8	18.9 ± 1.9
	413	101	30.2 ± 5.5	18.1 ± 3.3
	363	101	39.4 ± 3.0	15.6 ± 1.8
2009	517	100	24.5 ± 4.3	22.7 ± 3.1
	413	100	24.7 ± 2.4	18.1 ± 1.3
	363	100	27.1 ± 2.7	14.3 ± 1.3

*distance (river km (rkm)) from Golden Gate

Table 5. Mean movement rates (km·day^{-1}) and the respective proportions of fish sampled for each of the 17 reaches. Proportion sampled is the product of the detection efficiencies from the monitoring stations above and below each specific reach.

Region	Reach	Rkm from Golden Gate	Mean movement rate (km·day^{-1}) ± SE	Proportion sampled ± SE
Upper Sacramento River	1	518 - 504	69.5 ± 1.5	0.93 ± 0.01
	2	504 - 492	89.1 ± 1.7	0.93 ± 0.01
	3	492 - 456	41.2 ± 1.3	0.90 ± 0.02
Middle Sacramento River	4	456 - 421	35 ± 1.7	0.84 ± 0.03
	5	421 - 412	55.3 ± 2.6	0.86 ± 0.03
	6	412 - 389	36.9 ± 1.5	0.81 ± 0.03
	7	389 - 363	35.7 ± 1.7	0.80 ± 0.03
Lower Sacramento River	8	363 - 325	36 ± 1.4	0.48 ± 0.03
	9	325 - 309	56.4 ± 2.1	0.30 ± 0.02
	10	309 - 226	40.9 ± 1.3	0.41 ± 0.03
	11	226 - 189	34.1 ± 1.1	0.53 ± 0.03
	12	189 - 169	26.2 ± 1	0.62 ± 0.03
Sacramento/San Joaquin Delta	13	169 - 70	15.3 ± 0.8	0.73 ± 0.03
San Francisco Estuary	14	70 - 52	18.5 ± 2	0.77 ± 0.04
	15	52 - 41	31.2 ± 4.7	0.70 ± 0.04
	16	41 - 15	26.2 ± 4.2	0.55 ± 0.06
	17	15 - 2	32.8 ± 5.5	0.58 ± 0.07*

*Calculated using the Pt. Reyes Ocean Monitor Line and Golden Gate West Monitor Line

Table 6. Results from the 3-year linear mixed-effect ANOVA looking at the influence of region, year, the interactive term and individual fish on movement rates.

Source	Numerator df	Denominator df	F-Ratio	P
Region	4	534	2.696	<0.001
Year	2	956.953	107.462	0.07
Year x Region	8	534	6.875	<0.001
Individual Fish (random factor)	615	534	1.562	<0.001

Table 7. Results from the 2008-2009 linear mixed-effect ANOVA looking at the influence of region, year, release month, release site, all the interactive terms and individual fish on movement rates.

Source	Numerator df	Denominator df	F-Ratio	P
Region	4	453	3.224	<0.001
Year	1	787.872	1.398	0.07
Month	1	787.872	0.03	0.24
Site	2	807.501	100.287	0.97
Year x Region	4	453	0.223	<0.001
Month x Region	4	453	1.36	0.13
Site x Region	5	453	10.509	0.04
Month x Year	1	789.894	1.765	0.64
Site x Year	2	807.501	1.775	0.37
Site x Month	2	807.501	2.357	0.26
Month x Year x Region	4	453	0.281	0.11
Site x Year x Region	5	453	1.902	0.03
Site x Month x Region	5	453	2.538	0.10
Site x Month x Year	2	807.501	1.887	0.76
Site x Month x Year x Region	5	453	0.454	0.81
Individual Fish (random factor)	484	453	1.244	0.01

Table 8. Results from the Pearson's correlation analysis between all environmental variables and movement rates. P represents whether the correlation's slope is significantly different from zero.

Environmental Variable	Pearson's Correlation coefficient with Movement Rate (km·day^{-1})	P
Sinuosity	0.53	<0.001
WDR	-0.26	<0.001
Water Velocity (m·s^{-1})	0.21	<0.001
Flow (m^{3}·s^{-1})	0.21	<0.001
Temperature (Cº)	0.06	0.02
Turbidity (ntu)	0.03	0.18

Table 9. Mean and standard error by river region and by year for river sinuosity, river width-to-depth ratio (WDR), water velocity ($m \cdot s^{-1}$), and water flow($m^3 \cdot s^{-1}$). Sinuosity is a spatial variable only, so there are no year values.

Variable	Upper River	Middle River	Lower River	2007	2008	2009
Sinuosity	2.23 ± 0.02	1.57 ± 0.01	1.53 ± 0.01			
WDR	36.4 ± 0.7	42.0 ± 0.3	23.9 ± 0.3	24.0 ± 0.0	47.5 ± 0.5	30.8 ± 0.4
Velocity	0.91 ± 0.01	0.84 ± 0.00	0.29 ± 0.01	0.98 ± 0.01	0.84 ± 0.00	0.50 ± 0.01
Flow	161 ± 1	163 ± 1	159 ± 2	168 ± 1	161 ± 1	159 ± 1

Figure Captions

Fig. 1. Map of the study area, including the Sacramento River, Sacramento – San Joaquin River Delta, San Francisco Estuary, and Pacific Ocean. Bull's-eye icons signify a release locations, stars symbolizes major cities, and black dots symbolizes monitor locations used in final analysis. Shaded regions delimit (from North to South) the upper river, middle river, lower river, delta, and estuary.

Fig. 2. Movement rate distributions per year for all regions combined. These boxplots depict the general decrease in movement rates from 2007 to 2009. The bold horizontal lines that dissect the boxes represents the median values, while the upper and lower edges of the boxes represent the 75th and 25th percentiles of the movement data, respectively. The upper and lower ends of the vertical lines represent the maximum and minimum values of the movement data, unless outliers are present. Outliers are data points that are above the 75th percentile or below the 25th percentile by more than 1.5 times the inter-quartile range (the range from the 25th to 75th percentile) of each specific boxplot.

Fig. 3. Movement rate distributions per region for all years. These boxplots depicts the general decrease in movement rates from the upper river region to the delta. The boxplots are constructed in the same fashion as Fig. 2.

Fig. 4. Stacked boxplot of movement rate distributions per region by year. These boxplots depict the interaction of region and year. The boxplots are constructed in the same fashion as Fig. 2.

Fig. 5. Individual smolt arrivals to new monitor locations per hour, grouped by region. Each plot is a histogram, representing the percent of arrivals for each hour bin out of all arrivals for that region (N).

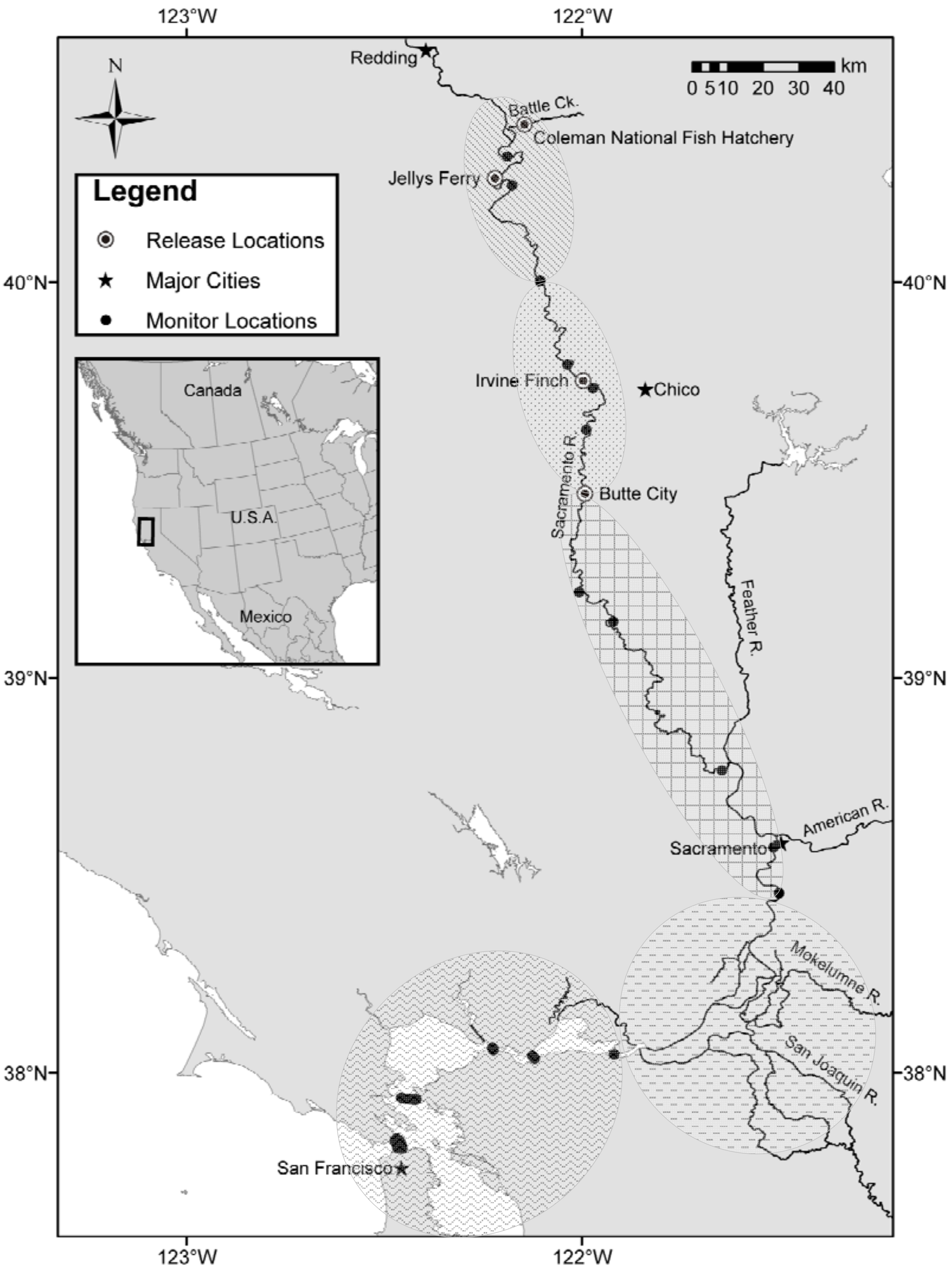
123°W
122°W
Redding
Battle Ck.
Coleman National Fish Hatchery
Jellys Ferry
Irvine Finch
Chico
Butte City
Sacramento R.
Feather R.
American R.
Sacramento
Mokelumne R.
San Joaquin R.
San Francisco
0 5 10 20 30 40 km
N
40°N
39°N
38°N
Legend
◉ Release Locations
★ Major Cities
● Monitor Locations
Canada
U.S.A.
Mexico

Fig. 1

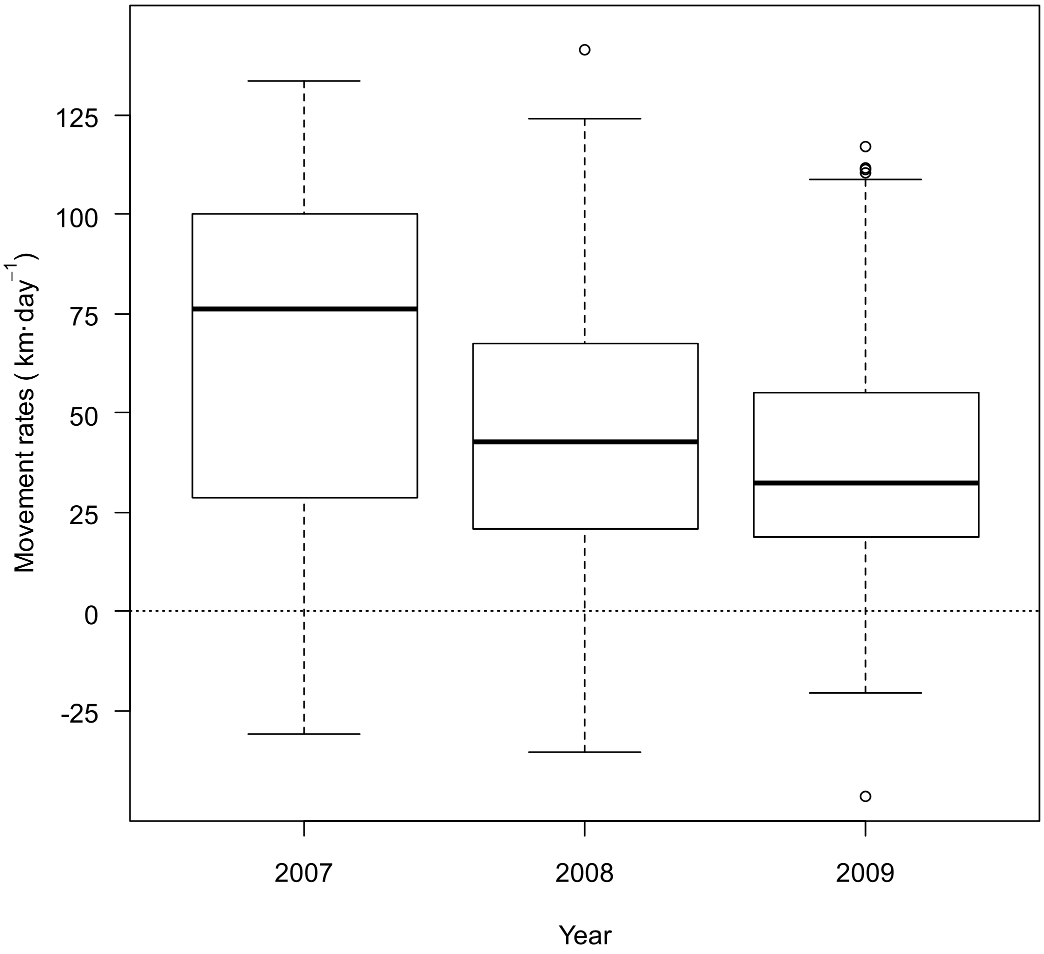
Movement rates (km·day^{-1})
125
100
75
50
25
0
-25
2007
2008
2009
Year

Fig. 2

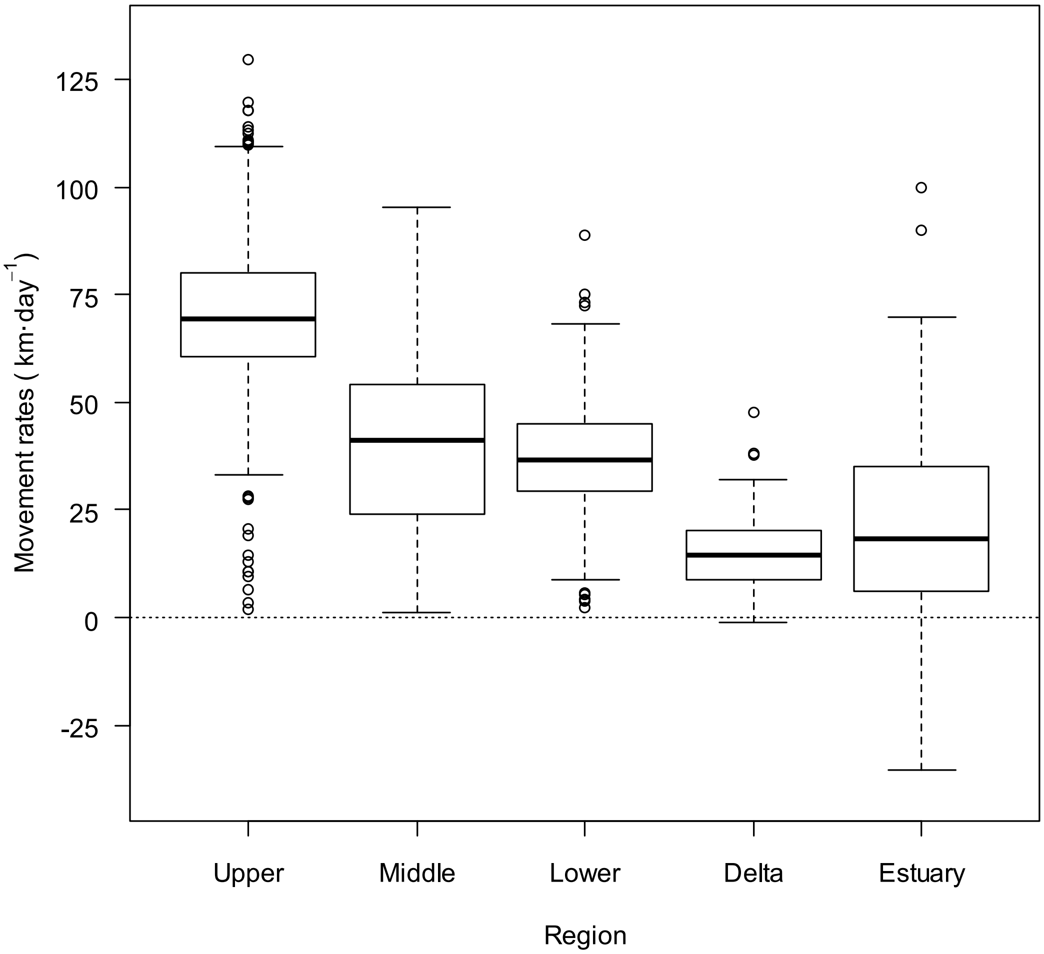
125
100
75
50
25
0
-25
Movement rates (km·day^{-1})
Upper
Middle
Lower
Delta
Estuary
Region

Fig. 3


2007
2008
2009
Movement rates ($km day^{-1}$)
125
100
75
50
25
0
-25
Upper
Middle
Lower
Delta
Estuary
Upper
Middle
Lower
Delta
Estuary
Upper
Middle
Lower
Delta
Estuary
Region

Fig. 4

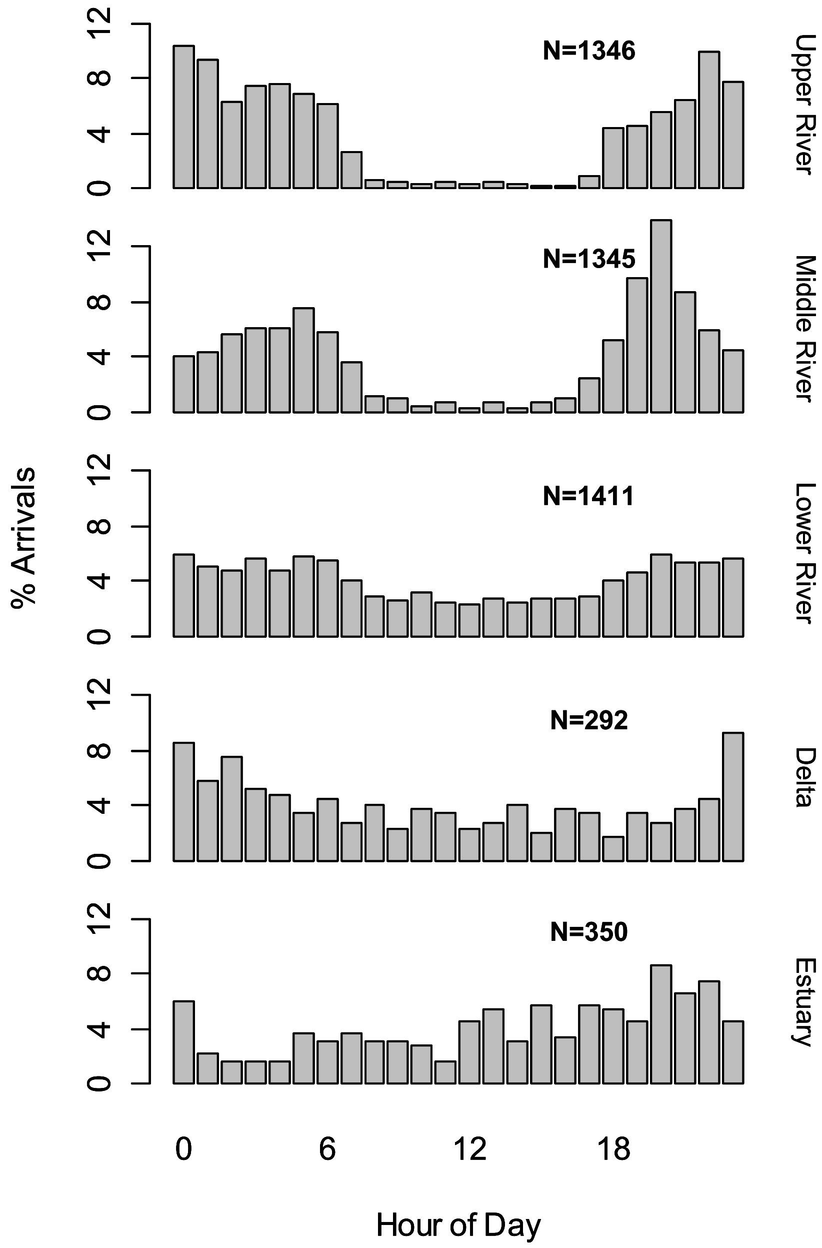
% Arrivals
0
4
8
12
N=1346
Upper River
N=1345
Middle River
N=1411
Lower River
N=292
Delta
N=350
Estuary
0
6
12
18
Hour of Day

Fig. 5

REFERENCE EXHIBIT G

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[Article]

Hierarchical Modeling of Juvenile Chinook Salmon Survival as a Function of Sacramento–San Joaquin Delta Water Exports

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Abstract.—A multiyear study was carried out in the Sacramento–San Joaquin Delta system to examine the relationship between the survival of out-migrating Chinook salmon *Oncorhynchus tshawytscha* and the amount of water exported from the system by the two major pumping stations in the southern portion of the delta. Paired releases of groups of coded-wire-tagged juvenile late-fall-run Chinook salmon were made at two locations in the delta, one in the main-stem Sacramento River and one in the interior portion of the delta where they were more likely to be directly affected by the pumping stations. Shortly after release, the fish were recovered downstream by a midwater trawl, and over a 2–4-year period the fish were recovered in ocean fishery catches and spawning ground surveys. A Bayesian hierarchical model for the recoveries was fit that explicitly accounted for the between-release variation in survival and capture probabilities as well as the sampling variation in the recoveries. The survival of the interior delta releases was considerably lower than that of main-steam releases (mean ratio of survival probabilities, 0.35). The ratio of survival probabilities was negatively associated with water export levels, but various model selection criteria gave more (or nearly equal) weight to simpler models that excluded exports. However, the signal-to-noise ratio, defined in terms of the export effect relative to environmental variation, was very low, and this could explain the indeterminacy in the results of the model selection procedures. Many more years of data would be needed to more precisely estimate the export effect. Whatever the factors that adversely affect survival through the interior delta, the fraction of out-migrants that enter the interior delta needs to be estimated in order to determine the overall effect of water exports on out-migrating Sacramento river Chinook salmon.

Survival experiments with juvenile Chinook salmon *Oncorhynchus tshawytscha* have been conducted in the Sacramento–San Joaquin Delta of California since the early 1970s (Kjelson et al. 1981, 1982; Kjelson and Brandes 1989; Brandes and McLain 2001). The experiments have involved the release, at multiple locations throughout the delta, of marked and tagged hatchery-reared juvenile Chinook salmon followed by later recovery of these fish. The survival of juvenile salmon through the delta is of particular interest because of the delta's role in water management in California. Two large pumping facilities, the Central Valley Project's C. W. "Bill" Jones Pumping Plant (CVP) and the State Water Project's Harvey Banks Pumping Plant (SWP), are located in the southern part of the delta (Figure 1) and provide water for municipal, agricultural, and domestic purposes to more than 23 million people throughout central and southern California. The delta is critical for the survival of salmon of Sacramento–San Joaquin origin, as all juvenile salmon must migrate through it to reach the Pacific Ocean. Two races of Central Valley Chinook salmon are listed under the Endangered Species Act (the winter run as endangered [NMFS 1997] and the spring run as threatened), and two others (the fall and late-fall runs) are considered species of concern. The role of CVP and SWP water exports on the survival of juvenile salmon through the delta is of great interest to managers and stakeholders, and this was the primary reason for the survival experiments.

Previous analyses of survival experiments involving juvenile fall-run Chinook salmon (Kjelson et al. 1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003), which out-migrate through the delta from March through June (Yoshiyama et al. 1998), have suggested that survival is negatively associated with water exports. These analyses included data from a very spatially dispersed set of release locations, at which many variables other than export levels may have affected survival.

In this paper we analyze release–recovery data from a more narrowly focused study of the effects of water exports, in which factors other than exports were to some degree controlled for by the temporal pairing of releases. Paired releases of juvenile late-fall-run Chinook salmon were made simultaneously in the interior delta and the main stem of the Sacramento River downstream from the Delta Cross Channel and Georgiana Slough (Figure 1). The interior delta is an area that out-migrating juvenile salmon can enter from the Sacramento River through either the Delta Cross

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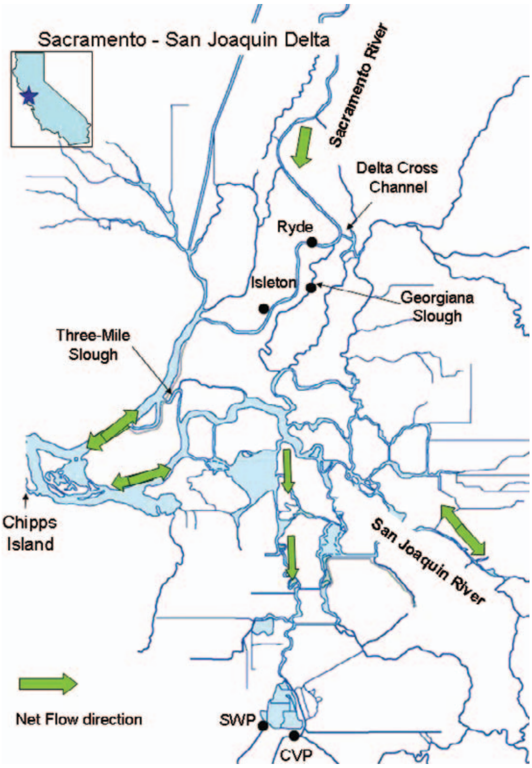


FIGURE 1.—Map of the Sacramento–San Joaquin Delta showing the Ryde and Georgiana Slough release locations, the Chipps Island recovery location, and the locations of two pumping stations with fish salvage facilities (SWP and CVP).

Channel (when the gates are open) or Georgiana Slough. Fish released directly into the interior delta are presumably more vulnerable to the influence of the CVP and SWP pumping facilities than fish released into the main stem. Unlike in the fall-run experiments (Newman and Rice 2002), the temporal pairing of releases controlled for the effects of all factors other than release location and exports on survival. One limitation of the study, however, is that the levels of exports cannot be fixed or controlled by researchers because water demands take precedence. Another limitation is that the overall effect of exports on out-migrating salmon cannot be determined without knowing the proportion of such salmon that enter the interior delta.

Brandes and McLain (2001) analyzed paired release–recovery data that involved releases of late-fall-run and fall-run fish. Their analytical procedure was to calculate freshwater recovery fractions (adjusted for estimates of capture efficiency) and regress those fractions against export levels. Based on the data available at the time, they found a statistically significant negative association between the survival of releases at Georgiana Slough (relative to that of releases at Ryde on the main-stem Sacramento River) and export levels (Figure 1).

One purpose of this paper was to update the analysis of Brandes and McLain (2001) incorporating more recent data but only using the late-fall-run stock. Late-fall-run fish are potential surrogates for winter-run Chinook salmon (Brandes and McLain 2001) since both runs out-migrate from November through May (Yoshiyama et al. 1998). A second purpose was to compare the results of the Brandes and McLain approach with those based on Bayesian hierarchical models (Carlin and Louis 1996; Gelman et al. 2004; for a fisheries release–recovery application, see Newman 2003). Hierarchical models offer several potential advantages for analyzing multirelease studies. One advantage is parsimony: rather than estimating release-pair-specific effects independently (e.g., n independent estimates of relative survival for n release pairs), one can specify a single distribution for the effects underlying the results for all release pairs. Another advantage is that such a "random effects" distribution characterizes the environmental variation in survival probabilities and the hierarchical approach makes this variation distinct from the sampling variation. A third advantage is that a hierarchical model provides a sensible means of combining data from multiple-year studies, in this case multiple sets of paired releases and recoveries (giving, for example, release pairs for which fewer fish were released less weight than those for which more fish were released).

Methods

Data

The paired release–recovery data, including the numbers of fish released, the numbers recovered at various locations, and the water export levels at the times of release, are given in Table 1. Fifteen paired groups of juvenile late-fall-run Chinook salmon yearlings (mean size, >100 mm) reared at Coleman National Fish Hatchery were released between 1993 and 2005 during the months of December and January. At the hatchery, each fish had its adipose fin clipped and a coded wire tag inserted into its snout; to read such tags after implantation requires sacrificing the fish. The tag codes were batch specific, that is, the same codes were used for thousands of fish, with unique tag codes for each release location. The fish were trucked from the hatchery to the interior delta (Georgiana Slough) and the main-stem Sacramento River (Ryde or Isleton) and releases at both locations made within a day or two.

Within a few weeks of release, recoveries were made

TABLE 1.—Release and recovery data for juvenile Chinook salmon in the Sacramento–San Joaquin Delta. Abbreviations are as follows: R is the number of fish released, CI and $\widehat{\mathrm{Oc}}$ are observed recoveries at Chipps Island and expanded recoveries in the ocean fisheries, $\widehat{\mathrm{FF}}$ is expanded recoveries at fish salvage facilities, and $\widehat{\mathrm{IL}}$ is expanded inland recoveries. Exports are 3-d averages (cfs) of the water exported from SWP and CVP, and E/F is the export–flow ratio over the same period.

		Georgiana Slough					Ryde						
Release date	Pair	R	CI	$\widehat{\mathrm{Oc}}$	$\widehat{\mathrm{FF}}$	$\widehat{\mathrm{IL}}$	R	CI	$\widehat{\mathrm{Oc}}$	$\widehat{\mathrm{FF}}$	$\widehat{\mathrm{IL}}$	E/F	Exports
Dec 2, 1993	1	33,608	5	79	248	12	34,650	37	293	10	36	0.68	10,434
Dec 5, 1994	2[a]	31,532	4	11	87	8	30,220	15	28	6	13	0.22	5,988
Jan 4–5, 1995	3[a]	31,328	2	102	837	53	31,557	13	266	231	138	0.40	10,403
Jan 10–11, 1996	4	33,670	5	146	768	9	30,281	21	239	12	23	0.55	9,523
Dec 4–5, 1997	5	61,276	2	7	153	4	46,756	22	42	18	11	0.51	10,570
Jan 13–14, 1997	6	66,803	18	240	24	51	49,059	48	167	0	70	0.06	3,887
Dec 1–2, 1998	7	69,180	12	172	28	44	48,207	30	183	0	102	0.04	1,868
Dec 29–30, 1998	8	68,843	12	151	48	54	48,804	17	156	0	88	0.09	1,984
Dec 10–11, 1999	9[a]	65,517	3	43	24	9	53,426	16	129	0	20	0.18	3,237
Dec 20–21, 1999	10[a]	64,515	21	149	82	32	49,341	19	160	4	66	0.26	4,010
Jan 3–5, 2002	11	77,053	18	240	390	116	52,327	34	521	18	418	0.12	7,789
Dec 5–6, 2002	12	90,219	1	68	700	11	49,629	18	148	42	34	0.46	5,007
Dec 9–10, 2003	13	68,703	5	51	306	8	45,981	13	127	24	69	0.18	4,016
Dec 8–9, 2004	14	72,082	10	11	0	1	50,397	28	20	0	0	0.25	6,092
Dec 8–9, 2005	15	70,414	6	35	165	1	51,017	23	49	12	1	0.68	10,837

[a] Ryde releases made at Isleton (see Figure 1).

in freshwater by a midwater trawl operating near Chipps Island (Figure 1). The trawl was towed at the surface almost daily for 4–6 weeks after the fish were released. Typically, ten 20-min tows were made each day between roughly 0700 and 1200 hours. Juvenile fish were also recovered at fish facilities located in front of the CVP and SWP pumping plants. These Chinook salmon were transported by truck and released at locations north of the pumps and nearer to the main stem of the Sacramento River upstream of Chipps Island, where they could be caught by the midwater trawl at Chipps Island. Then, over a 3–4-year period, adult fish were recovered from the landings of ocean fisheries. The total number of ocean fishery recoveries, summed over many landing areas and years, was estimated from a spatially and temporally stratified random sample of the landings and catches. The percentage of ocean catch sampled was roughly 20–25%. Additional recoveries of adult fish were made in freshwater fisheries, at hatcheries, and on spawning grounds (inland recoveries). The expanded ocean and inland recoveries were retrieved from a Web-based database query system administered by the Pacific States Marine Fisheries Commission (www.rmpc.org). The straying proportions for the Georgiana Slough and Ryde releases (i.e., the fractions of inland recoveries that were not recovered at Coleman National Fish Hatchery) varied considerably between release pairs, but within release pairs they were quite similar.

The combined water export levels (hereafter referred to as exports) from both the SWP and CVP facilities were averaged over a 3-d period starting the day after the release in Georgiana Slough. The choice of 3 d was somewhat arbitrary, although linear correlations of 3-d average export levels with those for 10 and 17 d were quite high (0.94 and 0.91, respectively). There is a certain degree of imprecision in defining an export variable with regard to fish out-migration because some fish take longer to out-migrate than others and the degree of exposure to the area influenced by the pumps will vary (for example, in group 1 of the Georgiana Slough release there was one recovery at the SWP fish facility 3 months after release). Furthermore, export levels are not necessarily constant, even within a 3-d period, and the day-to-day variation in export level is not captured by an average. The water volumes entering the interior delta are also affected by the position of the Delta Cross Channel gates, which when open increase the flow of water from the Sacramento River into the interior delta. The gates were open on the day of the Georgiana Slough releases in the first 2 years of the study (1993 and 1994) and for one of the 1999 releases (group 10), but otherwise closed. Recognizing that the amount of exports relative to total inflow from the Sacramento River (at Freeport) could be more important than absolute exports, we also examined the export-to-flow ratio as a covariate; the relationship between the ratios and the absolute values, however, was positive and linear ($r = 0.83$).

Assumptions and Notation

Within and between releases, the fate of an individual fish (live or die, be caught or not) was assumed to be independent of that of any other fish. For all fish released from a given location at a given time, the survival and capture probabilities were assumed to be identical. In recognition of the paired-release aspect of the study, we further assumed that within a release pair the probability of capture at Chipps Island and the recovery probabilities (complicated combinations of the survival and capture probabilities) in the ocean fishery and inland areas were identical. For example, for release pair 1 (Table 1) the capture probability is the same for a Ryde fish and a Georgiana Slough fish that has survived to Chipps Island, but that probability can differ from the probability for release pair 2.

We further assumed that only fish released in Georgiana Slough were affected by exports. Ryde is located 2.5 mi (1 mi = 1.61 km) downstream of the location on the main stem where water is diverted into Georgiana Slough, and releases at Ryde are further removed geographically from the export facilities. However, for 2 years sizeable numbers of Ryde fish were recovered at the fish facilities (Table 1); it may be that flood tides carried some of the Ryde releases into the interior delta at some upstream or downstream locations such as Three Mile Slough (Figure 1), a channel several miles downstream that connects the Sacramento and San Joaquin rivers.

For a given release pair t, the numbers released at Ryde and Georgiana Slough are denoted $R_{\mathrm{Ry},t}$ and $R_{\mathrm{GS},t}$ and the associated recoveries at Chipps Island $y_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $y_{\mathrm{GS}\rightarrow\mathrm{CI},t}$. Expanded ocean recoveries are denoted $\hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t}$ and $\hat{y}_{\mathrm{GS}\rightarrow\mathrm{Oc},t}$ and expanded inland recoveries $\hat{y}_{\mathrm{Ry}\rightarrow\mathrm{IL},t}$ and $\hat{y}_{\mathrm{GS}\rightarrow\mathrm{IL},t}$. The recovery fractions, defined as the ratios of the number of recoveries to the number released, are denoted $\hat{r}$, the subscripts indicating the release and recovery locations (e.g., $\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t} = \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t}/R_{\mathrm{Ry},t}$). The combined recovery fractions for more than one recovery location are denoted similarly (e.g., $\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI+Oc+IL},t} = [y_{\mathrm{Ry}\rightarrow\mathrm{CI},t} + \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc},t} + \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{IL},t}]/R_{\mathrm{Ry},t}$).

The notation for the probability that a Ryde release will be recovered at Chipps Island is $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and that for the probability that it will be recovered in either the ocean fisheries or inland recoveries is $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}$. The corresponding probabilities of recovery for Georgiana Slough releases are denoted $\theta_t r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $\theta_t r_{\mathrm{Ry}\rightarrow\mathrm{Oc},t}$, where θ_t is a release-pair-specific constant. Given the assumption that within a release pair the capture probabilities at Chipps Island are the same, θ_t is the ratio of the survival probability between Georgiana Slough and Chipps Island and the survival probability between Ryde and Chipps Island. How it relates to export levels is the primary management question.

Non-Bayesian, Nonhierarchical Models

Two nonhierarchical models were fit. Both somewhat mimic Brandes and McLain's (2001) analysis in that a two-step procedure was used, that is, an estimate of θ_t was first calculated and then regressed against exports. The first model is quite similar to Brandes and McLain's in that only recoveries at Chipps Island were used, that is, θ_t was estimated as the ratio of the recovery fractions at Chipps Island for the Georgiana Slough and Ryde releases,

$$\hat{\theta}_{1,t} = \frac{\hat{r}_{\mathrm{GS}\rightarrow\mathrm{CI},t}}{\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI},t}} \qquad (1)$$

In contrast to Brandes and McLain (2001), recoveries were not scaled by estimated gear efficiency because of the assumption that the capture probabilities were identical within a release pair. A simple linear regression model using standardized exports was fit, namely,

$$\hat{\theta}_{1,t} \sim \mathrm{Normal}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \sigma^2), \qquad (2)$$

where $\mathrm{Exp}_t^* = (\mathrm{Exp}_t - \overline{\mathrm{Exp}}/s_{\mathrm{Exp}}$, Exp_t is exports at time t, $\overline{\mathrm{Exp}}$ is the average export level, and s_{Exp} is the standard deviation of exports. Assuming independence and identical probabilities of survival and capture for all fish in a single release, the number of fish recovered at Chipps Island is a binomial random variable, that is, $y_{\mathrm{Ry}\rightarrow\mathrm{CI},t} \sim \mathrm{Binomial}(R_{\mathrm{Ry},t}, r_{\mathrm{Ry}\rightarrow\mathrm{CI},t})$. Given $R_{\mathrm{Ry},t}$ and $y_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$, $\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ is the maximum likelihood estimate (mle) of $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$; similarly, $\hat{r}_{\mathrm{GS}\rightarrow\mathrm{CI},t}$ is the mle of $\theta_t r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $\hat{\theta}_{1,t}$ is the mle for θ_t based on Chipps Island recoveries alone.

For the second nonhierarchical model, θ_t was estimated from Chipps Island, ocean, and inland recoveries combined, that is,

$$\hat{\theta}_{2,t} = \frac{\hat{r}_{\mathrm{GS}\rightarrow\mathrm{CI+Oc+IL},t}}{\hat{r}_{\mathrm{Ry}\rightarrow\mathrm{CI+Oc+IL},t}}. \qquad (3)$$

Implicit in this calculation is the assumption that within a release pair the Chipps Island capture, ocean recovery, and inland recovery probabilities are identical. If the total ocean and inland recoveries were known exactly and not estimated, the joint distribution of Chipps Island recoveries and the combined ocean and inland recoveries would be multinomial, and $\hat{\theta}_{2,t}$ would be the mle for θ_t. However, with the expanded recoveries, the distribution is more complex. To account for the differences in sampling variation and to somewhat duplicate the hierarchical model, a weighted regression of the log of $\hat{\theta}_{2,t}$ against standardized exports was fit, that is,

$$\log_e(\hat{\theta}_{2,t}) \sim \mathrm{Normal}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \mathrm{se}^2_{\log_e[\hat{\theta}_{2,t}]}\sigma^2). \quad (4)$$

The weights were the inverses of the squares of the standard errors of $\log_e(\hat{\theta}_{2,t})$, $\mathrm{se}_{\log_e[\hat{\theta}_{2,t}]}$, which were calculated using the delta method (see section 10.5 in Stuart and Ord 1987). The log transformation ensures that $\theta_{2,t}$ remains nonnegative.

The primary inferential aim for both models (equations 2 and 4) is to estimate the slope coefficient (β_1) and its standard error.

Hierarchical Models

Hierarchical models (Carlin and Louis 1996) consist of two or more levels, each level accounting for a different type of variation. For our data, the first level accounts for the sampling variation in the recoveries conditional on the survival and capture probabilities, the second level for the variation in the survival and capture probabilities between release pairs. The second level reflects what is sometimes referred to as random effects. The prior distributions for the fixed and unknown parameters of the model (in the second level) make up the third level of the model.

Bayesian hierarchical model.—A Bayesian hierarchical model (BHM) was formulated for the joint distribution of Chipps Island recoveries and the combined ocean and inland recoveries. The statistical distributions for the different levels of the hierarchical model are shown below. The first-level distributions are conditional on the second-level variables, and similarly for the second-level distributions.

Level 1:

$$y_{\mathrm{GS}\rightarrow\mathrm{CI},t}, \hat{y}_{\mathrm{GS}\rightarrow\mathrm{Oc+IL},t} \sim \mathrm{Multinomial}(R_{\mathrm{GS},t}, \theta_{3,t} r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}, \theta_{3,t} r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}) \tag{5}$$

$$y_{\mathrm{Ry}\rightarrow\mathrm{CI},t}, \hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t} \sim \mathrm{Multinomial}(R_{\mathrm{Ry},t}, r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}, r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}) \tag{6}$$

Level 2:

$$\log_e(\theta_{3,t}) \sim \mathrm{Normal}(\beta_0 + \beta_1 \mathrm{Exp}^*, \sigma_\theta^2) \tag{7}$$

$$\mathrm{logit}(r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}) \sim \mathrm{Normal}(\mu_{r_{\mathrm{Ry}\rightarrow\mathrm{CI}}}, \sigma^2_{r_{\mathrm{Ry}\rightarrow\mathrm{CI}}}) \tag{8}$$

$$\mathrm{logit}(r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}) \sim \mathrm{Normal}(\mu_{r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}}, \sigma^2_{r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}}) \tag{9}$$

Level 3:

$$\beta_0, \beta_1, \mu_{\mathrm{Ry}\rightarrow\mathrm{CI}}, \mu_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}} \sim \mathrm{Normal}(0, 1.0\mathrm{E}+6) \tag{10}$$

$$\sigma_\theta, \sigma_{r_{\mathrm{Ry}\rightarrow\mathrm{CI}}}, \sigma_{r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}} \sim \mathrm{Uniform}(0, 20) \tag{11}$$

As noted previously, the joint distributions for the Chipps Island recoveries and the combined expanded ocean and inland recoveries cannot be multinomial owing to estimation error in the expansions; thus, the level 1 formulation is an approximation. The log transformation of $\theta_{3,t}$ (in the level 2 model) ensures that $\theta_{3,t}$ is nonnegative. The logit transformations in level 2 force $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}$ to lie between 0 and 1; however, the resulting probabilities are so small that log transformations would have the same practical effect.

Unlike in the likelihood framework, the inferential objective in the Bayesian setting is to calculate the posterior distribution for the unknown parameters (Gelman et al. 2004), that is, to calculate

$$p(\Theta|\mathrm{Data}) \propto p(\mathrm{Data}|\Theta)p(\Theta),$$

where Θ is the vector of unknown constants (such as β_0 and β_1) and unknown random variables (such as θ_t) and $p(\Theta)$ is the prior distribution (here defined by level 3). In this case the primary interest is in the posterior distribution for β_1, and the probability that β_1 is negative is a measure of the degree of the negative association between exports and the relative survival of Georgiana Slough releases.

Sensitivity analysis.—The sensitivity of the BHM to the choice of distributions and functional forms was assessed by alternative formulations for each level. At level 1, to allow for the possible dependence between fish within a release as well as extramultinomial variation due to the fact that the ocean and inland recoveries are sample expansions, negative binomial distributions were used for the Chipps Island and expanded ocean and inland recoveries from a given release. For example, the negative binomial model for the recoveries at Chipps Island of releases from Ryde is

$$y_{\mathrm{Ry}\rightarrow\mathrm{CI}} \sim \text{Negative binomial}\left(k_{\mathrm{CI}}, \frac{k_{\mathrm{CI}}}{R_{\mathrm{Ry}} r_{\mathrm{Ry}\rightarrow\mathrm{CI}} + k_{\mathrm{CI}}}\right),$$

where k_{CI} is a nonnegative constant that affects the degree of overdispersion (relative to a Poisson, or indirectly a binomial, random variable). The larger it is, the less the overdispersion.

At level 2, several alternative models were fit. One model removed exports from the model for $\log_e(\theta_{3,t})$. A second used a logistic transformation of $\theta_{3,t}$, ensuring that $0 \leq \theta_{3,t} \leq 1$ (i.e., that the survival probability from Georgiana Slough to Chipps Island cannot exceed that from Ryde to Chipps Island). A third alternative was a multivariate normal (MVN) distribution for the joint distribution of $\theta_{3,t}$, $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$, and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},t}$, which allowed for correlation among these parameters within each release pair. In particular, $\theta_{3,t}$ was $\log_e$ transformed and, largely to facilitate fitting, an extension of a logistic model was used to transform $r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and

$r_{\text{Ry}\to\text{Oc+IL},t}$, that is (dropping the subscript t to reduce notation),

$$\begin{bmatrix}\theta^1\\ \theta^2\\ \theta^3\end{bmatrix} \sim \text{MVN}\left(\begin{bmatrix}\beta_0+\beta_1\text{Exp}^*\\ \mu_{\text{Ry}\to\text{CI}}\\ \mu_{\text{Ry}\to\text{Oc}}\end{bmatrix},\right.$$

$$\left.\boldsymbol{\Sigma} = \begin{bmatrix}\sigma_1^2 & \sigma_{1,2} & \sigma_{1,3}\\ \sigma_{2,1} & \sigma_2^2 & \sigma_{2,3}\\ \sigma_{3,1} & \sigma_{3,2} & \sigma_3^2\end{bmatrix}\right)$$

where

$$\theta^1 = \log_e(\theta_3)$$

$$\theta^2 = \log_e\left(\frac{r_{\text{Ry}\to\text{CI}}}{1 - r_{\text{Ry}\to\text{CI}} - r_{\text{Ry}\to\text{Oc+IL}}}\right)$$

and

$$\theta^3 = \log_e\left(\frac{r_{\text{Ry}\to\text{Oc+IL}}}{1 - r_{\text{Ry}\to\text{CI}} - r_{\text{Ry}\to\text{Oc+IL}}}\right).$$

A fourth alternative was to use the ratio of exports to total river flow instead of the absolute level of exports. A fifth alternative was to remove the random effects, that is, to make the level 2 models deterministic.

For level 3, various prior distributions were tried for the fixed parameters in level 2. We used the inverse gamma distributions instead of uniform distributions (equation 11) for the variances of the random effects, that is, σ_θ^2, $\sigma^2_{r_{\text{Ry}\to\text{CI}}}$, and $\sigma^2_{r_{\text{Ry}\to\text{Oc+IL}}}$. For the multivariate normal model, an inverse Wishart distribution was used as the prior for the variance–covariance matrix, $\boldsymbol{\Sigma}$.

Not all possible combinations of the models for each level were fit. During the fitting process it became clear that certain options at one level led to clearly poorly fitting models (e.g., removing the random effects at level 2 led to a drastic drop in model fit no matter what options were selected at the other levels).

Model fitting, assessment, and comparison.—To fit the BHMs we used the program WinBUGS (Lunn et al. 2000), which generated samples from the joint posterior distribution for the parameters, random effects, and expected numbers of recoveries. WinBUGS is based on a technique known as Markov chain–Monte Carlo (MCMC; Gilks et al. 1996), which is a computer simulation method in which samples are generated from a Markov chain that has a limiting distribution equal to the distribution of interest (in this case the joint posterior distribution).

By a limiting distribution it is meant that the samples do not initially come from the desired distribution but that when "enough" samples have been generated (the so-called burn-in period), all additional samples do come from the desired distribution. WinBUGS includes measures (e.g., the Brooks–Gelman–Rubin statistic; Brooks and Gelman 1998), based on the results of simulating from multiple Markov chains with differing initial values, for determining an adequate burn-in period. Informally stated, given widely different starting values, the point at which the chains begin to overlap (i.e., to begin mixing) is the necessary burn-in period; at that point, presumably, the samples are coming from the limiting distribution and are not stuck at some local mode of the posterior distribution. Values of the Brooks–Gelman–Rubin statistic that are near 1.0 are evidence for convergence, values below 1.1 often being adequate (Gelman et al. 2004:297). Three different chains with differing initial values were run in parallel and the summary statistics are based on the pooled output after burn-in.

For a given model, the goodness of fit was assessed by calculating Bayesian P-values (Gelman et al. 2004) for each of the observations. The P-value is the proportion of time a predicted value exceeds the observed value, that is,

$$\text{Bayesian } P\text{-value} = \frac{1}{L}\sum_{l=1}^{L} I(y_l^{\text{pred}} \geq y),$$

where $I(\bullet)$ is an indicator function that equals 1 when the condition inside $(\bullet)$ is met. The predicted value, y_l^{pred}, is found by simulating y from its probability distribution evaluated at the lth parameter value in the MCMC sample. Ideally, the observed values will lie in the central portion of the simulated posterior predictive distribution, equally distributed around the median predicted values. A Bayesian P-value near 0 or 1 is indicative of a poor fit for the particular observation.

The models were compared using the deviance information criterion (DIC; Spiegelhalter et al. 2002). The DIC can be viewed as a measure of overall model fit while penalizing model complexity. When two models are compared, the one with the lower DIC value is judged to have better predictive capabilities. Reversible jump MCMC (RJMCMC; Green 1995) was used to compare two models, one model with exports as a covariate (equation 7) and one without exports. Given the data, a set of models, and a corresponding set of prior probabilities that a given model is the correct model (the prior model probability), RJMCMC calculates posterior model probabilities.

Results

The recovery fractions for the Georgiana Slough releases were consistently less than those for the Ryde releases, with the exception of the fraction recovered at

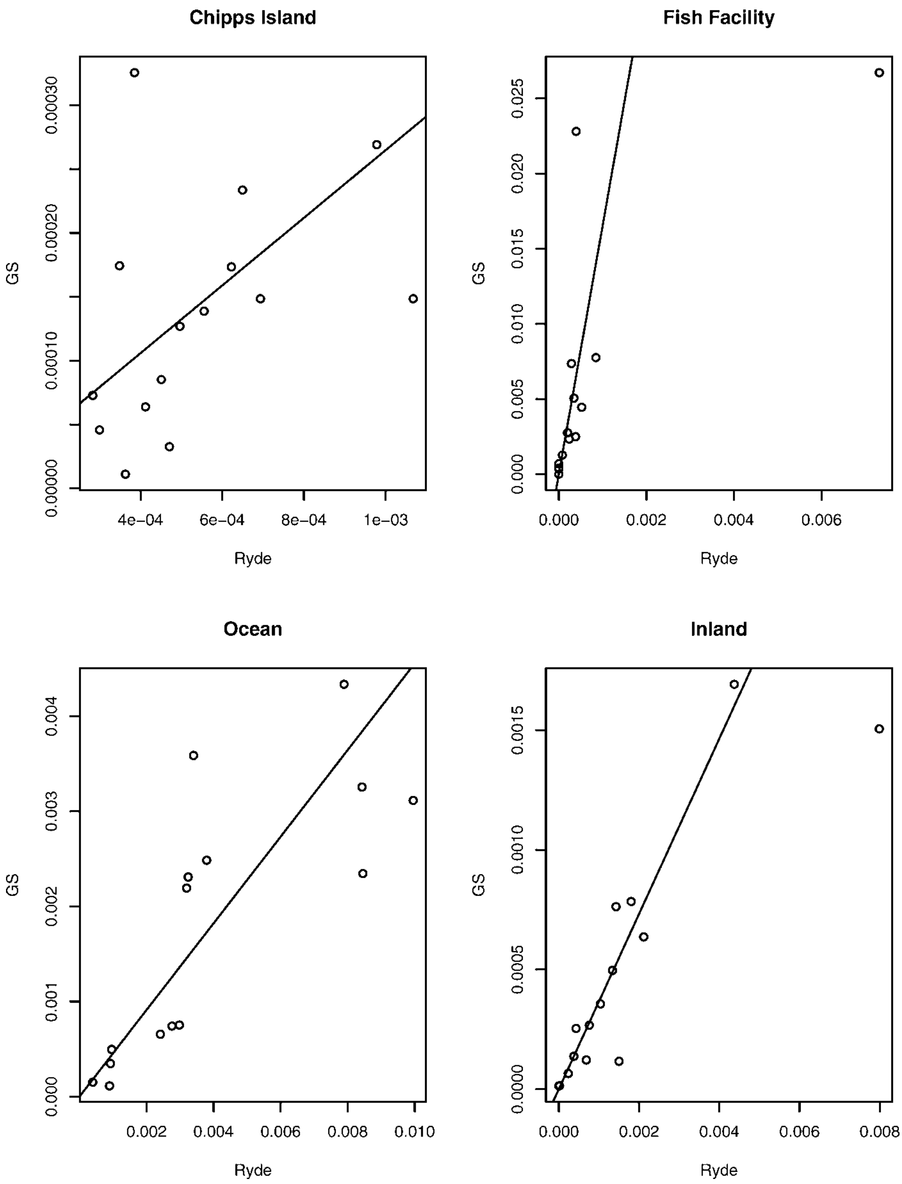
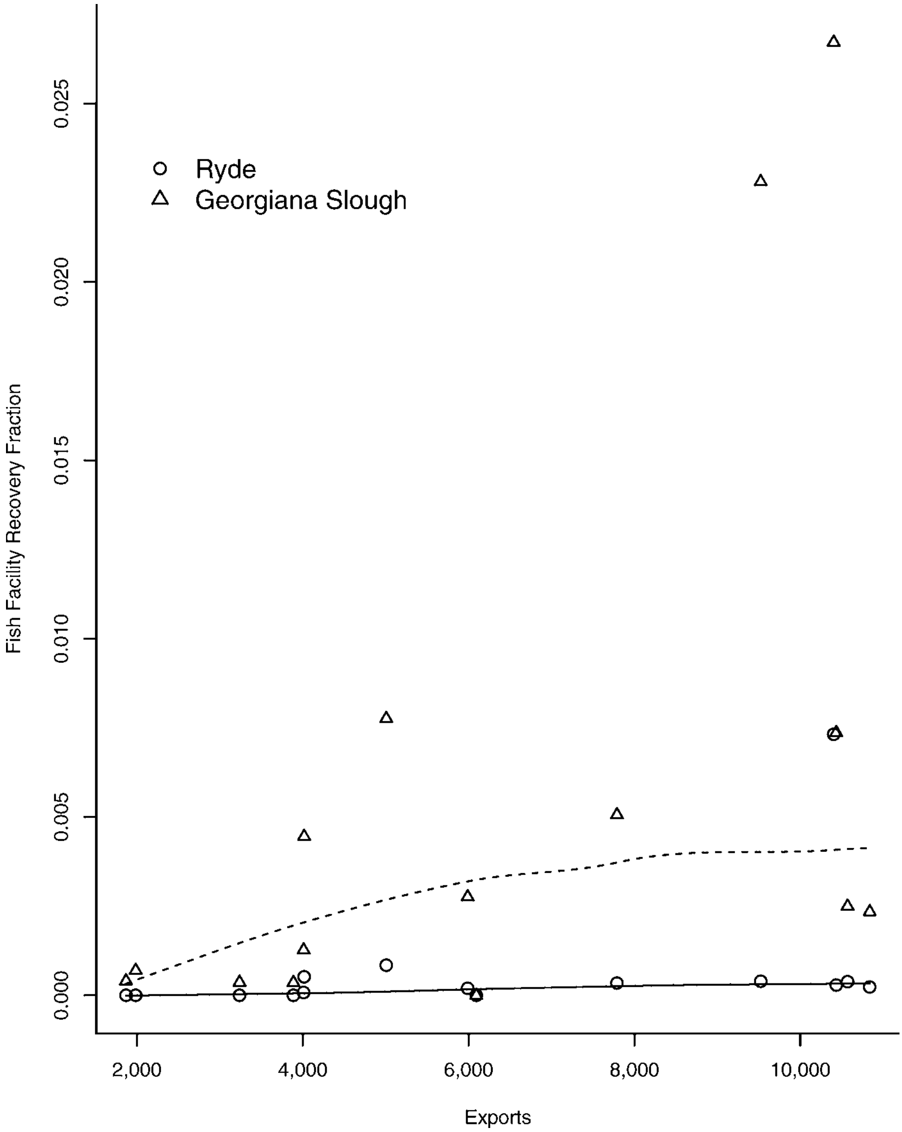


FIGURE 2.—Comparison of the recovery fractions at Chipps Island, in the ocean fisheries, at the fish salvage facilities, and among inland recoveries for Georgiana Slough and Ryde releases, by release pair. The straight lines have slopes equal to the means of the ratios of the recovery fractions.

the fish facilities (Figure 2). The means of the ratios of the recovery fractions equaled 0.26, 0.46, and 0.37 for the Chipps Island, ocean fisheries, and inland recoveries, respectively. Conversely, at the fish facilities, Georgiana Slough releases were about 16 times more likely to be recovered. Also, the fraction of fish facility recoveries from the Georgiana Slough releases tended to increase (from about 0.001 to 0.025) as exports increased from 2,000 cfs to 10,000 cfs (1 cfs = 0.028 m^3/s), although there was considerable variability at any given level of exports (Figure 3). This suggested a higher probability of ending up at the pumps with greater exports. In contrast, the fraction of the Ryde releases ending up at the fish facilities was less than 0.001 (group 3—a case with high exports—being an exception); these results are generally supportive of the assumption that Ryde releases were unaffected by exports.



?9 FIGURE 3.—Expanded recovery fractions at the SWP and CVP fish facilities versus export level. The lines are loess smooths for the Georgiana Slough (dashed) and Ryde releases (solid).

Nonhierarchical Analyses

The release-pair-specific point estimates, $\hat{\theta}_1$ and $\hat{\theta}_2$, and corresponding standard errors are shown in Table 2. As expected, given the additional information provided by the ocean and inland recoveries, the standard errors for $\hat{\theta}_2$ tended to be smaller than those for $\hat{\theta}_1$. The difference in standard errors was smaller for the most recent releases (groups 14 and 15), for which there is probably incomplete inland recovery information for the older-age returns. The variation in the estimates of θ_t was quite large between release groups, with values ranging from 0.13 to 0.80 (based on $\hat{\theta}_2$).

The fitted models of θ_t as a function of exports (equations 2 and 4) are

$$\hat{\theta}_{1,t} \approx \text{Normal}(0.265 - 0.086\text{Exp}_t^*, 0.18^2)$$

and

$$\log_e(\hat{\theta}_{2,t}) \approx \text{Normal}(-0.935 - 0.214\text{Exp}_t^*, 3.88^2).$$

The P-values for a one-sided test of the significance

TABLE 2.—Comparison of release-pair-specific fitted values of the ratio of the survival probability of Georgiana Slough releases to that of Ryde releases (θ). The non-Bayesian, nonhierarchical results are maximum likelihood estimates and standard errors based on Chipps Island recoveries alone ($\hat{\theta}_1$) and combined Chipps Island, ocean, and inland recoveries ($\hat{\theta}_2$). The Bayesian hierarchical values are the posterior distribution means and standard deviations from the model with a multivariate normal distribution at level 2 and θ modeled as a function of exports. See text for more details.

	Non-Bayesian, nonhierarchical				Bayesian hierarchical	
Group	$\hat{\theta}_1$	SE	$\hat{\theta}_2$	SE	$E(\theta_{3,t} \mid \text{data})$	SD
1	0.14	0.07	0.27	0.031	0.28	0.031
2	0.26	0.14	0.39	0.097	0.38	0.084
3	0.15	0.12	0.38	0.035	0.38	0.035
4	0.21	0.11	0.51	0.050	0.50	0.049
5	0.07	0.05	0.13	0.040	0.16	0.041
6	0.28	0.08	0.80	0.065	0.79	0.064
7	0.28	0.10	0.50	0.044	0.51	0.043
8	0.50	0.19	0.59	0.054	0.58	0.052
9	0.15	0.10	0.27	0.042	0.28	0.041
10	0.85	0.27	0.63	0.060	0.62	0.057
11	0.36	0.10	0.26	0.016	0.26	0.016
12	0.03	0.03	0.22	0.029	0.23	0.029
13	0.26	0.14	0.20	0.029	0.22	0.029
14	0.25	0.09	0.32	0.082	0.32	0.076
15	0.19	0.09	0.42	0.081	0.38	0.070

of the slope coefficient for exports with the alternative hypothesis that $\beta_1 < 0$ are 0.05 for the $\hat{\theta}_1$ model and 0.04 for the $\log_e(\hat{\theta}_2)$ model. Neither model fit particularly well, however; the R^2 values were 0.19 and 0.21 for the two models, respectively.

Bayesian Hierarchical Model

For each model the burn-in time was 50,000 iterations per chain; a further 150,000 iterations per chain were carried out, and every tenth realization was used for the posterior samples. The negative binomial model was an exception; owing to the somewhat slow computational speed for that model, the burn-in time was 50,000 iterations, and this was followed by 50,000 sample iterations. There were three types of evidence for convergence to the posterior distribution: Brooks–Gelman–Rubin statistics between 1.0 and 1.03 for all parameters; plots of the parameters for the three chains against the simulation number (trace plots) showing considerable overlap and movement in chain values (which would be consistent with good mixing); and DIC values that were stable between runs.

All of the BHMs with a multinomial distribution for the observations (level 1) and random effects (level 2) had nearly equal DIC values (models 1–6 in Table 3). Spiegelhalter et al. (2002) support the rule of thumb that models within 1–2 of the minimal DIC value deserve consideration (as used by Burnham and Anderson [1998] for the Akaike information criterion). Notably, this set included a model without exports. The results were robust to the choice of the prior for the standard deviation of the random effects (σ), either the uniform or inverse gamma distribution. Either covariate, exports or exports/flow, led to equivalent DIC values. The posterior means for $\theta_{3,t}$ were much the same for these models.

The Bayesian P-values were essentially identical for these multinomial, random-effect models. Fifty-three of the 60 observations (88%) had Bayesian P-values that fell within the middle 90% of the posterior predictive distributions. There were too few observed recoveries ($P = 0.02$–0.04) for two cases ($y_{\mathrm{Ry}\rightarrow\mathrm{CI},1}$ and $y_{\mathrm{Ry}\rightarrow\mathrm{CI},6}$) and too many observed recoveries ($P = 0.95$–1.00) for five others ($y_{\mathrm{GS}\rightarrow\mathrm{CI},5}$, $y_{\mathrm{GS}\rightarrow\mathrm{CI},9}$, $y_{\mathrm{GS}\rightarrow\mathrm{CI},12}$, $\hat{y}_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL},14}$, and $\hat{y}_{\mathrm{GS}\rightarrow\mathrm{Oc+IL},14}$).

Replacing the multinomial distribution with the negative binomial distribution (model 7) and excluding random effects (model 8) led to sizeable increases in the DIC values (Table 3), especially for the latter

TABLE 3.—Summary of Bayesian hierarchical models. The level 1 column specifies the distributions (Mn = multinomial, NB = negative binomial). The level 2 column shows models for $\theta_{3,t}$, N denoting the normal distribution and MVN the multivariate normal distribution; the models for the recovery probabilities ($r_{\mathrm{Ry}\rightarrow\mathrm{CI},t}$ and $r_{\mathrm{Ry}}\rightarrow$IL,$t$) are those shown in equations (8) and (9) in the text except for the MVN model (1) and the model without random effects (8). The level 3 column specifies the prior distribution for the random effects variance; U = uniform, IG = inverse gamma, and IW(I, 4) = inverse Wishart, I being the identity matrix.

Model	Level 1	Level 2	Level 3	$E(\beta_1)$	$\Pr(\beta_1 < 0)$	$E(\sigma_\theta)$	DIC
1	Mn	$\log_e(\theta_{3,t}), \ldots \sim .\mathrm{MVN}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \ldots, \Sigma)$	$\Sigma \sim \mathrm{IW}[I, 4]$	−0.194	0.92	0.53	460.0
2	Mn	$\log_e(\theta_{3,t}) \sim .N(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \sigma_\theta^2)$	$\sigma \sim \mathrm{U}(0, 20)$	−0.170	0.89	0.50	460.0
3	Mn	$\log_e(\theta_{3,t}) \sim .\mathrm{N}\left(\beta_0 + \beta_1 \frac{\mathrm{Exp}}{\mathrm{Flow}_t}, \sigma_\theta^2\right)$	$\sigma \sim \mathrm{U}(0, 20)$	−0.706	0.86	0.51	460.0
4	Mn	$\log_e(\theta_{3,t}) \sim .\mathrm{N}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \sigma_\theta^2)$	$\sigma^2 \sim \mathrm{IG}(0.001, 0.001)$	−0.166	0.90	0.48	459.9
5	Mn	$\mathrm{logit}(\theta_{3,t}) \sim .\mathrm{N}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \sigma_\theta^2)$	$\sigma \sim \mathrm{U}(0, 20)$	−0.297	0.88	0.89	460.0
6	Mn	$\log_e(\theta_{3,t}) \sim .\mathrm{N}(\beta_0, \sigma_\theta^2)$	$\sigma \sim \mathrm{U}(0, 20)$			0.51	460.1
7	NB	$\log_e(\theta_{3,t}) \sim .\mathrm{N}(\beta_0 + \beta_1 \mathrm{Exp}_t^*, \sigma_\theta^2)$	$\sigma \sim \mathrm{U}(0, 20)$	−0.168	0.89	0.46	487.0
8	Mn	$\log_e(\theta_{3,t}) = \beta_0 + \beta_1 \mathrm{Exp}_t^*$		−0.079	0.99		4,281.8

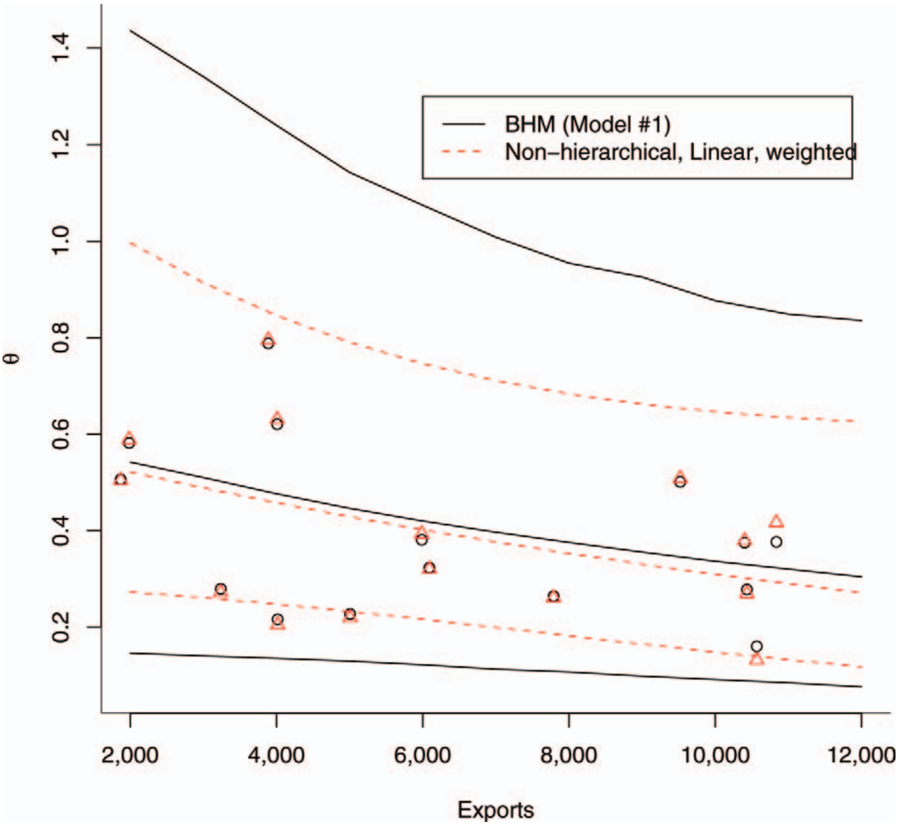


FIGURE 4.—Expected values and 2.5–97.5% prediction intervals for θ at different levels of exports produced by Bayesian hierarchical model (BHM) 1 (solid lines) and the nonhierarchical model (dashed lines) using Chipps Island and combined ocean and inland recoveries (equation 4). The circles denote posterior mean fitted values for θ from the BHM, the triangles maximum likelihood estimates.

model. Many of the Bayesian *P*-values for the nonrandom-effects model were close to 0 or 1. The negative binomial model's parameters, k_{CI} and k_{Oc}, were quite large (with posterior means of 214 and 279, respectively), providing little evidence for overdispersion.

Referring now to model 1 (the results for which are nearly identical to those for models 2–6), the recovery probabilities for Ryde releases at Chipps Island were an order of magnitude lower than those for the ocean fisheries and inland recoveries; the median for $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ was 0.0004, versus 0.0038 for $r_{\mathrm{Ry}\rightarrow\mathrm{Oc+IL}}$. Given that recovery probabilities are the product of survival and capture probabilities, an $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ of that value seems reasonable for the Chipps Island trawl based on independent estimates of Chipps Island trawl capture probabilities on the order of 0.001–0.002 (Newman 2003). The correlations between θ, $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$, and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc}}$ (on the transformed scales) were weakly positive: between θ and $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ the posterior mean for $\sigma_{1,2}$ was 0.21; between θ and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc}}$ $E[\sigma_{1,3}]$ was 0.18; and between $r_{\mathrm{Ry}\rightarrow\mathrm{CI}}$ and $r_{\mathrm{Ry}\rightarrow\mathrm{Oc}}$ $E[\sigma_{2,3}]$ was 0.25. Thus, within release pairs, when survival was higher for one segment it tended to be higher for the other segments.

For all models with exports the posterior mean value for β_1 was negative, indicating a negative association between θ and exports. For models 1–5, $\Pr(\beta_1 < 0)$ ranged from 0.86 to 0.92. The variation in the relationship with exports, however, was quite large, as both the size of $E(\sigma_\theta)$ and the plot of the predicted θ values against exports (Figure 4) indicate. While the plot shows a decline in the mean value of θ as exports increase (e.g., when exports are 2,000 cfs, the mean value of θ is 0.54, whereas when exports are 10,000 cfs, it is 0.34), the range of individual values is very wide. The upper bounds on θ for export levels less than 7,200 cfs exceed 1.0, allowing for the possibility that Georgiana Slough releases occasionally have higher survival than Ryde releases.

Given the similarity in DIC values among models 1–

6 and the fact that our primary interest was the effect of exports, we applied reversible jump MCMC to just two models that differed only with respect to the inclusion (model 2) or exclusion of exports (model 6). The posterior probability for the model including exports was only 1%, compared with 99% for the model without exports; thus, there is scant evidence for a relationship between θ and exports. However, such results could be due to the low signal-to-noise ratio, as measured by the ratio of the posterior mean for β_1 to the posterior means for σ_θ, $\sigma_{r_{\mathrm{Ry}\to\mathrm{CI}}}$, and $\sigma_{r_{\mathrm{Ry}\to\mathrm{OC+CI}}}$. Repeated simulations of 15 sets of recoveries with the actual release numbers and export levels were made with model 2 (equations 5–11) using the posterior mean values for the parameters (e.g., $E[\beta_1] = -0.17$). Despite the fact that the true model did have θ as a function of exports, RJMCMC typically yielded posterior probabilities for this model in the range of 1–3%. Even doubling the number of release pairs and extending the range of export levels to ±2 SDs of the observed values did not change these results. However, if the environmental variation were artificially decreased (e.g., by an order of magnitude), RJMCMC gave posterior probabilities for the correct model (the model with exports) ranging from 90% to 99%.

Nonhierarchical versus Hierarchical Models

The posterior means and standard deviations of θ_t from the BHMs (1–6) were quite similar to the (approximate) maximum likelihood estimates ($\hat{\theta}_{2,t}$) and the standard errors (Table 2). This indicates that the influence of the prior distributions on the Bayesian results was slight. The posterior standard deviations of θ_t were generally slightly less than the standard errors, presumably a result of the "borrowing of strength" from other release–recovery data that informs the estimates.

Model-based predictions of θ_t as a function of exports were quite similar for the BHM (equations 5–11) and the nonhierarchical model (equation 4), but the prediction intervals for the BHM were considerably wider (Figure 4). The observed variation in the estimates of θ_t (shown in Figure 4) seems more consistent with the wider BHM prediction intervals than the nonhierarchical model intervals.

Discussion

We conclude that, for a paired release the survival to Chipps Island of Georgiana Slough releases is considerably less than that of Ryde releases. The ratios of the recovery fractions of the two releases at Chipps Island, in the ocean fisheries, and at the inland sites were consistently much less than 1.0 (Figure 2), and the posterior means and maximum likelihood estimates of θ_t were at most 0.8 (Table 2). The posterior median of θ_t was 0.35 from a model without exports (BHM 6).

Factors other than exports that could cause lower relative survival for Georgiana Slough releases include water temperature, predation, and pollution (Moyle 1994). Higher water temperatures have been associated with higher mortality through the delta (Baker et al. 1995). For the paired releases we analyzed, however, the temperatures at release were very similar at Ryde and Georgiana Slough. Regarding predation, Stevens (1966) found more salmon in the stomachs of striped bass *Morone saxatilis* located in the so-called flooded-islands portion of the delta (south of the Georgiana Slough release point) than in the stomachs of striped bass in the Sacramento River.

Regarding the relationship between relative survival and export level, the point estimates of the effects of exports were consistently negative and for the BHMs the probability that the effects are negative was 86–92%. However, as a result of the low signal-to-noise ratio, the DIC values and posterior model probabilities indicate that the predictive ability of models without exports is equivalent to that of models with exports. The environmental variation is large enough that our failure to find a stronger association could be a function of inadequate sample size. Previous analyses (Newman 2008:72) of the relationship between the number of paired releases and the precision of the estimated slope parameter for exports showed that 100 paired releases were needed (based on $\beta_1 = -0.57$ for a logistic transformation of θ) to yield a coefficient of variation of 20%. The RJMCMC analysis of simulated data was consistent with those findings.

Exports do affect Georgiana Slough releases more than Ryde releases, as the fraction of Georgiana Slough releases recovered at the CVP and SWP fish salvage facilities increases with increasing exports (Figure 2). The intent of the salvage operations is to increase survival by relocating those fish away from the pumping facilities, and perhaps there is some mitigating effect. However, at the SWP facility there is an enclosed area, Clifton Court Forebay, where fish suffer mortality due to predators (Gingras 1997) before entering the salvage facilities. Experiments with marked salmon in the vicinity of the SWP fish facility have yielded estimates of "presalvage" mortality in the range of 63–99%, with an average of 85% (Gingras 1997), although the quality of these estimates has been called into question (Kimmerer 2008).

A tangential question is whether or not the fish facility recovery fractions are related to exports or the export–flow ratio (i.e., the absolute or relative level of exports). Over the range of values observed in these studies, exports and the export–flow ratio are linearly associated (Pearson correlation coefficient = 0.83), so that it is difficult to disentangle the effects of the two factors. Deliberate fixing of export levels at varying levels of flow would be one possible way of determining whether it is the absolute or the relative level of exports that affects the fraction of Georgiana Slough releases recovered at the fish salvage facilities. However, current water management policies and operational standards make such manipulations difficult to conduct. Export levels are largely determined by state and federal water project agencies based on water demand, conditions in the delta, water quality, and operational standards as well as endangered species biological opinions. Owing to the lack of randomization of export levels and the relatively low numbers of releases, the effects of exports may be confounded by other conditions that cause survival to increase or decrease. The pairing aspect of the design may control for such confounding factors, however.

Given the low signal-to-noise ratio, instead of repeating coded wire tag release–recovery experiments for many more years, we recommend releasing fish with acoustic tags and relocating them with strategically placed receivers. Such a system could provide more precise information about when and where mortality is occurring, yielding estimates of reach-specific survival (Muthukumarana et al. 2008). How much of an effect the interior delta mortality has on the total population of Sacramento River juvenile Chinook salmon (whatever the causes) depends on the fraction of the out-migrating population that moves into the interior delta. Using coded wire tag release–recovery data, Kimmerer (2008) estimated that the overall mortality is 10% at the highest export levels, assuming a presalvage mortality of 80% at the fish facilities. Pilot studies using acoustic tags have recently been carried out to estimate the proportion of out-migrants entering the delta (Perry et al. 2009, this issue), and once this proportion is identified, the benefits of preventing fish from entering the interior delta can be estimated more accurately.

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REFERENCE EXHIBIT H

Survival and Migration Route Probabilities of Juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta during the Winter of 2007-2008

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Abstract

Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) emigrating from natal tributaries of the Sacramento River may use a number of possible migration routes to negotiate the Sacramento–San Joaquin River Delta (hereafter, "the Delta"), each of which may influence their probability of surviving. In a previous report, we developed and applied a mark-recapture model to data from acoustically tagged juvenile late-fall Chinook salmon that migrated through the Delta during the winter of 2007. This study was repeated during the winter of 2008, and this report presents findings from our second year of research. First, population-level survival through the Delta (S_{Delta}) during 2008 was substantially lower than in 2007, and we found little difference in S_{Delta} between releases. For releases in December 2007, $\hat{S}_{\text{Delta}}$ was 0.174 ($\widehat{\text{SE}}$ =0.031) and for January 2008, $\hat{S}_{\text{Delta}}$ was 0.195 ($\widehat{\text{SE}}$ = 0.034), compared to 0.351 and 0.543 for the same release groups in 2007. In contrast to our previous study, we found that the fraction of the population entering the interior Delta was similar between releases (26.7% for December, 31.1% for January), despite the Delta Cross Channel being open during December and closed during January. However, similar to previous findings, survival of fish migrating through the interior Delta was significantly less than survival probabilities for fish remaining in the Sacramento River. The ratio of survival for fish migrating through the interior Delta relative to the Sacramento River was ≤35.2% ($\widehat{\text{SE}}$ ≤0.11) during both releases. Thus, migration routes through the interior Delta reduced population-level survival by a similar magnitude during both releases because differences in survival between routes remained constant, as did the fraction of fish entering the interior Delta. Reach-specific survival rates in the Sacramento River (expressed as a function of reach length) were higher than reaches within other migration routes. These findings indicated that variation in route-specific survival was driven by consistent differences among migration routes, rather than by specific reaches within a route. Our studies during 2006 and 2007 highlight the variation in survival and migration route probabilities that can be expected in future research, but nonetheless, consistent patterns in route-specific survival and migration are beginning to emerge.

Table of Contents

Table of Figures

Table of Tables

Acknowledgements

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Introduction

Many stocks of Chinook salmon (*Oncorhynchus tshawytscha*) in California, Washington, and Oregon are listed as threatened or endangered under the Endangered Species Act (Nehlsen et al. 1991; Myers et al. 1998). In the Central Valley of California, the winter, spring, and fall/late fall runs of Chinook salmon are federally listed as endangered, threatened, and a "species of concern," respectively (NMFS 1997). Recently, due to below-target returns of fall Chinook salmon to the Sacramento River, the National Marine Fisheries Service declared a Federal Disaster and closed the 2008 salmon fishery along the West Coast (NOAA 2008). Understanding factors affecting survival of salmon is therefore critical to devising effective recovery strategies for these populations.

An important stage in the life history of Chinook salmon is the period of migration from natal tributaries to the ocean, when juvenile salmon in the Sacramento River may suffer mortality from a host of anthropogenic and natural factors (Brandes and McLain 2001; Baker and Morhardt 2001; Williams 2006). Juvenile Chinook salmon emigrating from the Sacramento River must pass through the Sacramento-San Joaquin River Delta (hereafter, "the Delta"), a complex network of natural and man-made river channels linking the Sacramento River with San Francisco Bay (Nichols et al. 1986). Juvenile salmon may migrate through a number of routes on their journey to the ocean. For example, they may migrate within the mainstem Sacramento River leading directly into San Francisco Bay (see Route A in Figure 1). However, they may also migrate through longer secondary routes such as the interior Delta, the network of channels to the south of the mainstem Sacramento River (see Routes C and D in Figure 1).

Both human actions and natural processes affect the magnitude and distribution of Sacramento River flow among the channel network of the Delta. Inflow into the Delta from the Sacramento River is largely controlled by upstream releases of water from storage reservoirs. Within the Delta, water distribution is affected by two water pumping projects in the Southern Delta (the State Water Project and Central Valley Project). These projects pump water from the Delta for agricultural and municipal uses and can export up to 65% of the total inflow (Nichols et al. 1986). Associated with the water pumping projects is the Delta Cross Channel, a man-made channel that diverts river flow from the Sacramento River into the interior. In addition to these human influences on water flow through the Delta, natural processes include seasonal rainfall

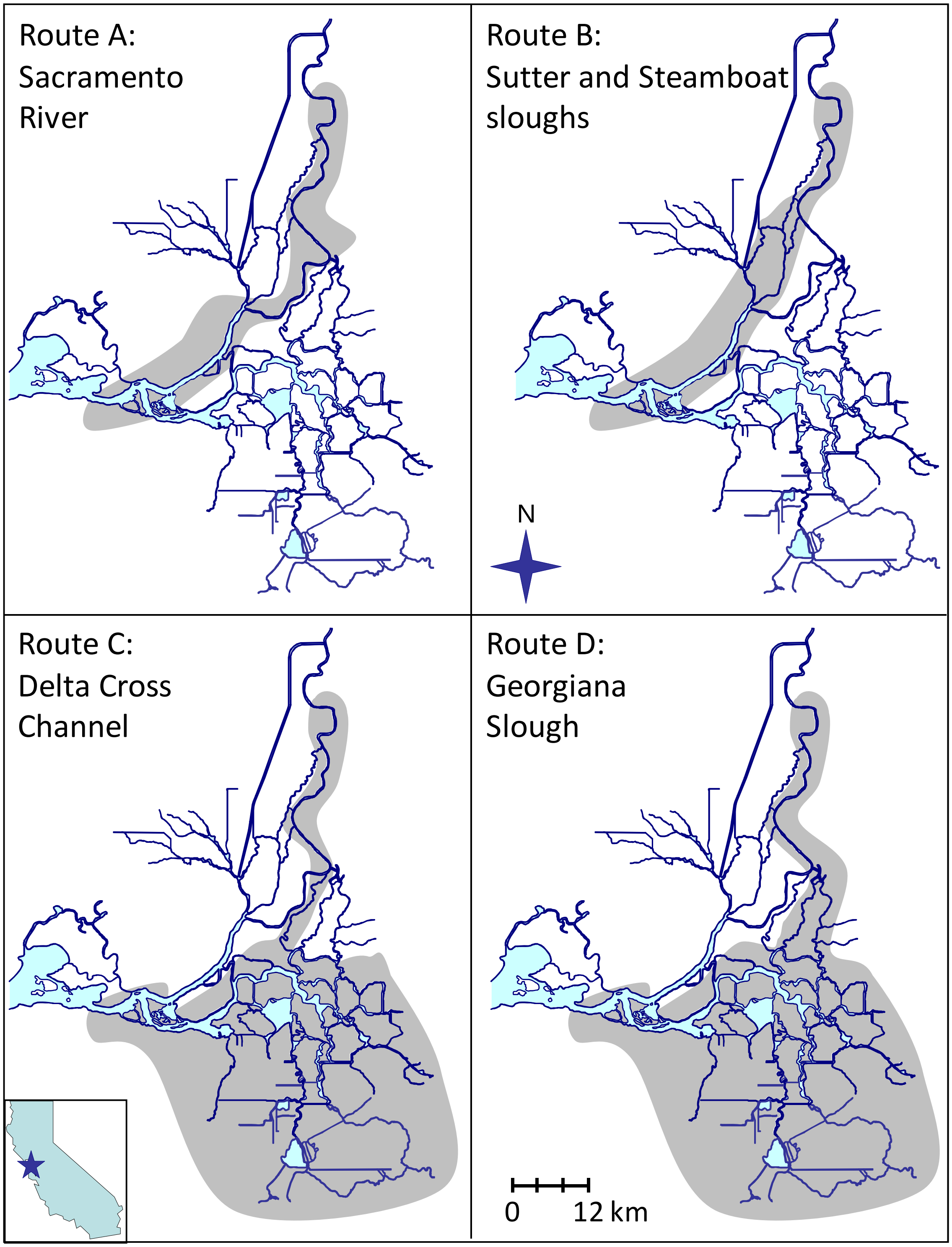

Figure 1.—Maps of the Sacramento–San Joaquin River Delta with shaded regions showing river reaches that comprise survival through the Delta for four different migration routes. For routes C and D, the interior Delta is the large shaded region at in southern-most section of the migration route.

and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and bi-weekly time scales.

As juvenile salmon disperse among the complex channel network of the Delta, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. For example, juvenile salmon entering the interior Delta must traverse longer migration routes and are exposed to entrainment at the water pumping projects, which may decrease survival of fish using this migratory pathway (Kjelson et al.1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003; Kimmerer 2008; Newman 2008, Newman and Brandes in press). However, whether low survival through a particular route has a large effect on survival of the population will depend on the fraction of the population migrating through that route (Newman and Brandes, in press; Perry et al. 2008, in press). Thus, population-level survival rates of juvenile salmon migrating through the Delta will be driven by 1) the survival rates arising from biotic and abiotic processes unique to each migration route, and 2) the proportion of the population using each migration route.

Currently, there is limited understanding of how water management actions in the Delta affect population distribution and route-specific survival of juvenile salmon. In a previous study, we developed a mark-recapture model to estimate the route-specific components of population-level survival for acoustically tagged late-fall Chinook salmonsmolts migrating through the Delta during the winter of 2006/2007 (hereafter “2007”, Perry et al. 2008, in press). Our study provided the first comprehensive estimates of route-specific survival through the Delta and the fraction of the population using each major migration route. Furthermore, we explicitly quantified the relative contribution of each migration route to population-level survival. As with other authors (Newman and Brandes in press), we found that survival through the interior Delta was lower than survival of fish using the Sacramento River. We also found that the proportion of the population entering the interior Delta differed between releases, which influenced population-level survival by shifting a fraction of the population from a low-survival migration route (the interior Delta) to a high-survival route (the Sacramento River). However, we also found that differences between releases in population-level survival were caused by changes in survival for given migration routes. Thus, variation in population-level survival was driven both by variation in movement among routes as well as survival within routes.

In this report, we estimate survival and migration route probabilities for acoustically tagged late-fall Chinook salmon migrating through the Delta during the winter of 2007/2008 (hereafter, “2008”). While design aspects of our previous study were maintained, we also incorporated a number of changes in study design based on insights from the first year of study. The most important limitation in our previous study was small total sample size, as well as small sample size for specific migration routes. For example, we found that up to 40% of fish migrated through Sutter and Steamboat Slough (Route B in Figure 1), which diverts fish around the two routes leading into the interior Delta (Routes C and D in Figure 1). This led to low sample size and poor precision of parameter estimates for routes through the interior Delta, which in turn led to low power to detect differences in survival among migration routes. Thus, we took two approaches to improve precision. First, the total sample size was tripled from 140 tagged fish in 2007 to 419 tagged fish in 2008. Second, because the interior Delta is an important migration route with many management concerns, we also released a subsample of fish directly into the interior Delta via Georgiana Slough (Route D in Figure 1).

We also added new telemetry stations which allowed us to better partition survival among specific reaches and to quantify movement among channels within major migration routes. For example, in our previous study we observed a substantial difference between releases in survival for Sutter and Steamboat sloughs. However, because this migration route encompassed numerous unmonitored river channels it was impossible to determine whether changes in route-specific survival were due to shifts in mortality within a particular reach, or occurred due to changes in survival over all reaches with this route. Therefore, we incorporated additional telemetry stations with this migration route (and others) to better partition within-route survival among specific reaches and channels.

We first report results for population-level survival through the Delta, route-specific survival through the Delta, and dispersal among migration routes, contrasting estimates from this study to those from 2007. Given more detailed information within migration routes, we then examined patterns in reach-specific survival to understand whether variation in route-specific survival through the Delta was driven by particular reaches within a route. Last, in addition to dispersal among the major migration routes shown in Figure 1, we explicitly accounted for movement among other channels within routes, and discuss the influence of these movements on population-level migration and survival dynamics.

Methods

Telemetry System

Telemetry stations were deployed to monitor movement of tagged fish among four major migration routes through the Delta (Figure 1): the mainstem Sacramento River (Route A), Steamboat and Sutter Slough (Route B), the interior Delta via the Delta Cross Channel (Route C), and the interior Delta via Georgiana Slough (Route D; Figure 1). Telemetry stations were labeled hierarchically to reflect the branching nature of channels at river junctions and their subsequent downstream convergence at the confluence of river channels (Figure 2). Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco Ltd., Model VR2) that identified individual fish based on the unique pattern of acoustic pulses emitted from a transmitter. Since the Sacramento River is the primary migration route, the *i*th telemetry station within this route is denoted as A_i from the release site to the last telemetry station in the Delta at Chipps Island (A_9). Sutter and Steamboat sloughs (labeled B_i) diverge from the Sacramento River at the first river junction and converge again with the Sacramento River upstream of A_7. We deployed numerous telemetry stations within Sutter and Steamboat sloughs to better quantify survival and movement within this region, relative to our previous study in 2007 (Perry et al. 2008, in press). Specifically, Sutter Slough and Miner Slough form a northern route and stations along this route are labeled B_{11} (entrance to Sutter Slough), B_{12}, and B_{13} (Miner Slough; Figure 2). A southern route is formed by Steamboat Slough and these stations are labeled as B_{21}, B_{22}, and B_{23}. The entrance to the interior Delta via the Delta Cross Channel was labeled as C_1 where it diverges from the Sacramento River at the second river junction. Telemetry stations within Georgiana Slough and the interior Delta were labeled as D_i beginning where Georgiana Slough diverges from the mainstem Sacramento River at the second river junction (D_1) until the convergence of the interior Delta with the Sacramento River at D_7. Following this hierarchy, routes A, B, C, and D contained 8, 6, 1, and 7 telemetry stations, whereas in 2007, the same routes contained 7, 1, 2, and 3 telemetry stations. In addition, to quantify movement between the lower Sacramento River and the lower San Joaquin River, we included a telemetry station within Three Mile Slough (E_1) for a total of 23 telemetry stations within the Delta. Parameter subscripting and coding of detection histories followed this hierarchical structure (see **Model Development** section below).

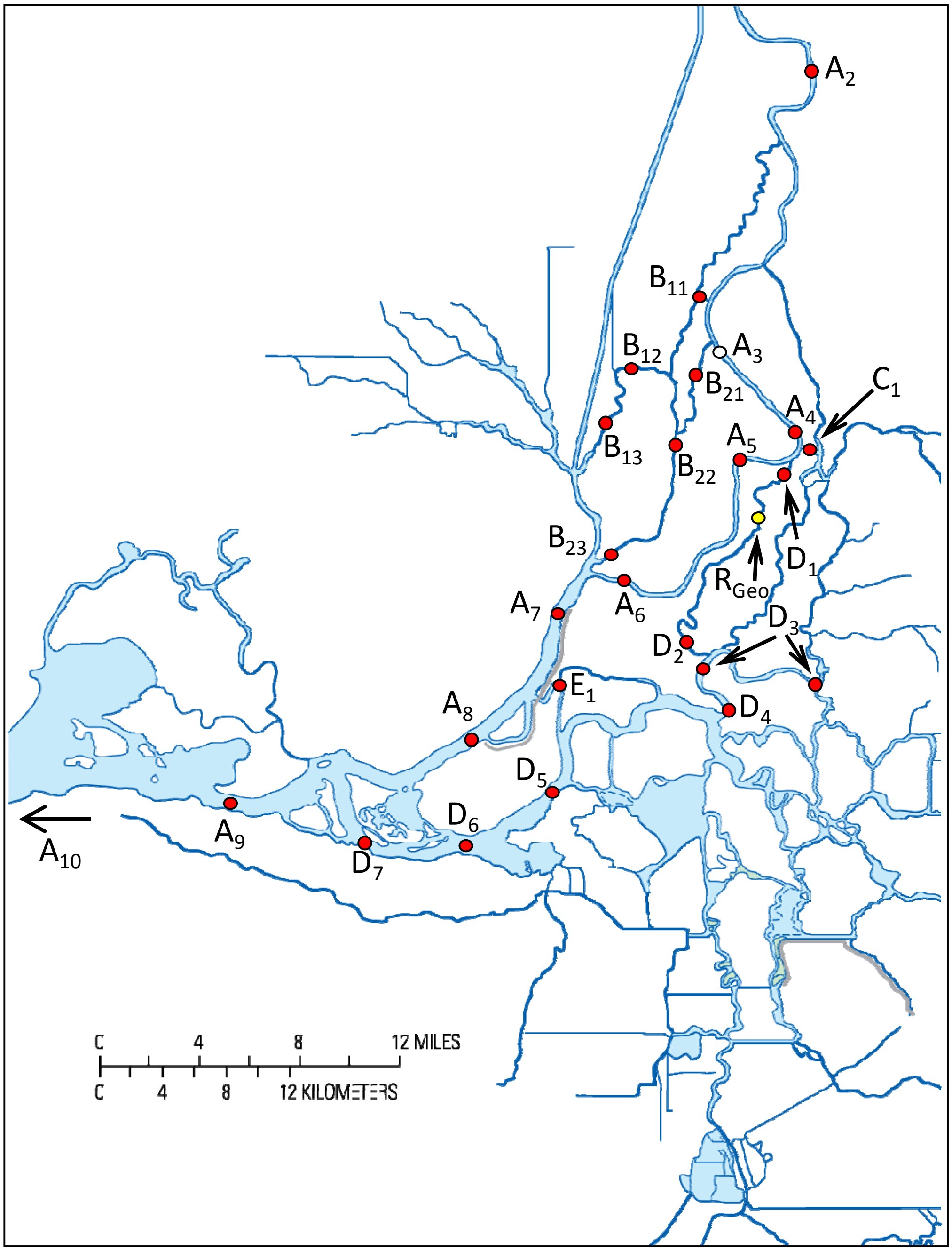

Figure 2.—Location of telemetry stations used to estimate survival and migration route probabilities within four major migration routes of the Sacramento–San Joaquin River Delta during the winter of 2007/2008. Red-filled circles labeled as h_i show the location of telemetry station *i* with route *h*. The Delta extends from station A_2 at Freeport to station A_9 at Chipps Island. The first river junction occurs where Sutter Slough (B_{11}) and Steamboat Slough (B_{12}) diverge from the Sacramento River at location A_3. Location A_3 is denoted by an unfilled circle to indicate that a telemetry station was not implemented at this location during the winter of 2007/2008. The second junction occurs where the Delta Cross Channel (C_1) and Georgiana Slough (D_1) diverge from the Sacramento River at station A_4. Station A_{10} pools all telemetry stations in San Francisco Bay downstream of A_9. The two site labeled D_3 were treated as a single station in the mark-recapture model. The Sacramento release site was 19 river kilometers

upriver of station A_2, and the Georgiana release site is noted as the yellow-filled circle labeled as R_{Geo}.

With this configuration of telemetry stations, survival in the final reach (downstream of A_8 and D_7) is confounded with detection probability at the last telemetry station (Skalski et al. 2001). Therefore, to estimate survival to the terminus of the Delta and detection probability at the last station in the Delta (A_9), we formed one additional telemetry station by pooling detections from numerous stations downstream of A_9 in San Francisco Bay (Figure 2). Most of these detections occurred at telemetry stations mounted to bridges that provided nearly complete cross-sectional coverage of San Francisco Bay, but single-monitor stations at other locations were also included.

Fish Tagging and Release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (approximately 340 river kilometers upstream of the release sites near Sacramento, CA). We used a 1.6-g tag with a 70-d expected battery life (Vemco Ltd., Model V7-2L-R64K). Except for a minimum size criteria of 140-mm fork length, fish were randomly selected for tagging resulting in a mean fork length of 155.0 mm (SD = 10.2) and mean weight of 42.0 g (SD = 9.6). The tag weight represented 3.8% of the mean fish weight (range = 1.9%–5.4%). Fish were fasted for 24 h prior to surgery to ensure they were in a post-absorptive state. To surgically implant transmitters, fish were anaesthetized and a small incision was made in the abdomen between the pectoral fins and the pelvic girdle. The transmitter was inserted into the peritoneal cavity, and the incision was closed with two interrupted sutures (4-0 nylon sutures with FS-2 cutting needle). Tagged fish were then returned to raceways and were allowed to recover for seven days prior to release.

To release fish, they were first transported to release sites at either the Sacramento River near Sacramento, CA (20 km upstream of A_2) or Georgiana slough (about 5 km downstream from D_1; Figure 2). Fish were then transferred to perforated 19-L buckets (2 fish per bucket) and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. Releases at Sacramento were conducted at roughly hourly intervals, whereas release at Georgiana Slough were conducted every other hour over a 24-h period. Each release was carried out over a 24-h period to distribute release times over the tidal and diel cycle. The total sample size for the study was 419 acoustically tagged fish, with 208 fish released in December when the Delta Cross Channel was open and 211 fish released in January when the Delta Cross Channel was closed (Table 1). For the first release, 28% of the fish were released into Georgiana Slough, but this fraction was increased to 38% for the second release in anticipation that a lower proportion of the Sacramento release group would enter the interior Delta with the Delta Cross Channel closed (Table 1). Fish were released into Georgiana Slough two days later than the Sacramento release group to match release times in Georgiana Slough with the travel time of fish from Sacramento to Georgiana Slough (R. Perry, unpublished data).

Table 1.—Summary of release dates, locations, and sample size of acoustically tagged late-fall Chinook salmon released into the Delta during the winter of 2007/2008.

Release date	Release number	Release location	Sample size
4 December 2007	1	Sacramento	149
6 December 2007	1	Georgiana Slough	59
15 January 2008	2	Sacramento	130
17 January 2008	2	Georgiana Slough	81

Model Development

We expanded upon the model developed by Perry et al. (2008, in press) to explicitly quantify more detail in reach-specific survival of juvenile salmon through regions such as Sutter Slough, Steamboat Slough, and the interior Delta. As in our previous model, we estimate detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (ψ_{hl}). However, to capture complexity in movement of fish among different channels we also estimated joint survival-entrainment probabilities ($\phi_{hi,jk}$). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station *i* within route *h* (*h* = A, B, C, D; Figure 2). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station *i* to *i*+1 within route *h* (i.e., to the next downstream telemetry station), conditional on surviving to station *i* (Figure 2 and 3). Route entrainment probabilities (ψ_{hl}) estimate the probability of a fish entering route *h* at junction *l* (*l* = 1, 2), conditional on fish migrating through junction *l* (Figures 2 and 3). Joint survival-entrainment probabilities ($\phi_{hi,jk}$) estimate the joint probability of surviving from site h_i to j_k and moving into route *j*. The $\phi_{hi,jk}$ parameters are estimated in reaches with river junctions that split into two channels, but where telemetry stations within each river channel are located some distance downstream the river junction. For example, fish passing station A_7 in the Sacramento River may enter Three Mile

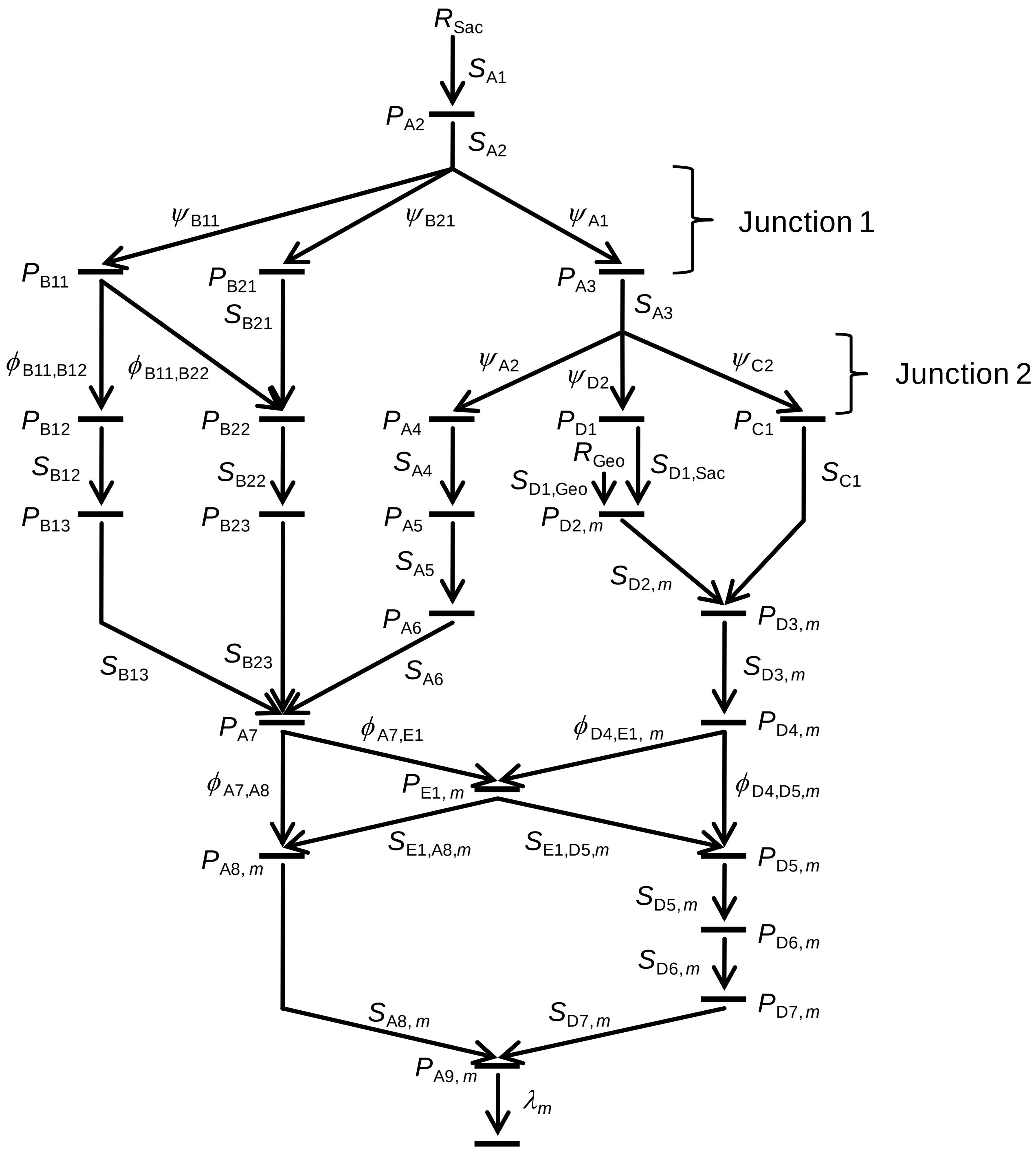

Figure 3.—Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), route entrainment (ψ_{hl}), and joint survival-entrainment ($\phi_{hi,\ jk}$) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made December 2007 and January 2008. Release sites are denoted by R_m (m = Sac (Sacramento)

and Geo (Georgiana Slough)), and parameters subscripted by *m* denote parameters which can be estimated separately for each release site.

Slough (E_1) or remain the Sacramento River for another 5.5 km below this junction to pass station A_8 (Figure 2). Thus $\phi_{A7,A8}$ is the joint probability of surviving from A_7 to its junction with Three Mile Slough, remaining in the Sacramento River at this junction, and then surviving from the junction to A_8.

In our 2007 study, telemetry arrays at the entrance to Sutter and Steamboat sloughs were pooled in the model to estimate a single route entrainment probability for both sloughs. For this study, however, telemetry stations within Sutter and Steamboat slough downstream of each entrance allowed us to estimate route entrainment probabilities separately for each slough (Figures 2 and 3). Thus, the parameter ψ_{B11} estimates the probability of being entrained into Sutter Slough at station B_{11} and ψ_{B21} estimates the probability of being entrained into Steamboat Slough at station B_{21}. Since route entrainment probabilities must sum to one at a given river junction, $1-\psi_{B11}-\psi_{B21}=\psi_{A1}$ is the probability of remaining in the Sacramento River at the first junction (Figures 2 and 3). As in 2007, the second junction was modeled as a three-branch junction where ψ_{A2}, ψ_{C2}, and $1-\psi_{A2}-\psi_{C2}=\psi_{D2}$ estimate the probabilities of remaining in the Sacramento River (Route A), being entrained into the Delta Cross Channel (Route C), and entering Georgiana Slough (Route D) at junction 2 (Figures 2 and 3).

Joint survival-entrainment probabilities were estimated for three reaches where 1) fish entering Sutter Slough (B_{11}) may subsequently continue down either Miner Slough (B_{12}) or Steamboat Slough (B_{22}), 2) fish entering the San Joaquin River at D_4 may subsequently exit this reach through either Three Mile Slough at E_1 or the San Joaquin River at B_5, and 3) fish passing A_7 in the Sacramento River may exit this reach at either E_1 or A_8 (Figures 2 and 3). Each of these reaches consist a single river channel, a junction where the channel splits, and then two separate channels through which fish migrate before being detected at telemetry stations in each channel. In these locations, interest may lie in estimating the proportion of fish entering each channel (i.e., the route entrainment probabilities, ψ_{hl}). However, when telemetry stations are located kilometers downstream of the river junction where fish enter one route or another, then estimates of ψ_{hl} may be biased if survival probabilities downstream of the junction differ between the two channels. However, the joint probability of surviving and migrating through a given channel (i.e., $\phi_{hi,jk}$) will remain unbiased in these circumstances. Although the $\phi_{hi,jk}$ parameters are difficult to interpret biologically, being the joint probability of entrainment and survival, their sum yields the total reach survival. Thus, in the three reaches where $\phi_{hi,jk}$ parameters are estimated, $S_{\mathrm{B11}} = \phi_{\mathrm{B11,B12}} + \phi_{\mathrm{B11,B22}}$, $S_{A7} = \phi_{\mathrm{A7,E1}} + \phi_{\mathrm{A7,A8}}$, and $S_{D4} = \phi_{\mathrm{D4,E1}} + \phi_{\mathrm{D4,D5}}$ are the probabilities of surviving from each upstream telemetry station to either of the next downstream stations.

Other than the differences noted above, our model structure for this study differed in two other aspects relative to our study conducted in 2007. First, in our previous study, about 14% of fish from one release passed the Delta Cross Channel when it was both open and closed, requiring us to incorporate a parameter to estimate the probability of fish passing the Delta Cross Channel under each condition (ω_{open}, see Perry et al. 2008, in press). However, for this study, only 3 fish (4%) released when the Delta Cross Channel was open passed the Delta Cross Channel after it had closed. Therefore, we did not include ω_{open} in the model. Second, having two release sites leads to two estimates of the same parameter for reaches within the interior Delta (e.g., $S_{\mathrm{D3},m} = S_{\mathrm{D3,Sac}}$ or $S_{\mathrm{D3,Geo}}$, Figure 3). With this model structure, the full model contains 75 unique parameters; 55 parameters from the Sacramento release and 20 for the Georgiana Slough release (Figure 3);

Parameter Estimation

Prior to parameter estimation, the records of tag-detections were processed to eliminate false positive detections using methods based on Skalski et al. (2002) and Pincock (2008). False positive detections of acoustic tags occur primarily when two or more tags are simultaneously present within the range of a given telemetry stations, and simultaneous tag transmissions "collide" to produce a valid tag code that is not actually present at the monitor (Pincock 2008). Our first criterion considered detections as valid if a minimum of two consecutive detections occurred within a 30-min period at a given telemetry station. Although this criterion minimized the probability of accepting a false positive detection, Pincock (2008) showed that a pair of false positive detections with a time interval <30 min occurred on average once every 30 d when simulating ten tags simultaneously present at a monitor. Thus, our second criterion considered records with two detections at a given location as valid only if these detections were consistent with the spatiotemporal history of a tagged fish moving through the system of telemetry stations (Skalski et al. 2002). The detection records of about 10% of tagged fish suggested they had been consumed by piscivorous predators as was evidenced by their directed upstream movement for long distance and against the flow. We truncated the detection record of these fish to the last known location of the live tagged fish. All other detections were considered to have been live juvenile salmon. In the lower Sacramento and San Joaquin rivers (sites A_7–A_8 and D_5–D_7), tag detection and discharge data showed that juvenile salmon were often advected upstream on the flood tides and downstream on the ebb tides. In these cases, we used the final downstream series of detections in forming the detection history.

Detection histories compactly describe the migration and detection process of fish moving through the network of telemetry stations. For example, a fish with the history AA0AAAAEDDDAA indicates it was released at Sacramento (“A”), detected in the Sacramento River at A_2 (“A”), and not detected in the Sacramento River at A_3 (“0”). This fish was subsequently detected at every other telemetry station as it emigrated from the Sacramento River (“AAAA”) through Three Mile Slough (“E”), down the San Joaquin River (“DDD”), and finally past Chipps Island into San Francisco Bay (“AA”). Each detection history represents one cell of a multinomial distribution where the probability of each cell is defined as a function of the detection, survival, route entrainment, and joint survival-entrainment probabilities (See Perry et al. 2008 for an example). Given these cell probabilities, the maximum likelihood estimates are found by maximizing the likelihood function of a multinomial distribution with respect to the parameters:

$$L_{km}\left(\underset{\sim}{\beta}\middle| R_{km}, n_{jkm}\right) \propto \prod_{j=1}^{J} \pi_{jkm}^{n_{jkm}}$$

where L_{km} is the likelihood for the kth release group ($k = 1, 2$) at the mth release site (m = Sacramento (Sac), Georgiana Slough (Geo)), R_{km} is the number of fish released for each release group and release site, n_{jkm} is the number of fish with the jth detection history in the kth release group at the mth release site, and π_{jkm} is the probability of the jth detection history in the kth release group at the mth release site expressed as a function of the parameters ($\underset{\sim}{\beta}$). The likelihood was numerically maximized with respect to the parameters using algorithms provided in the software programs R (R Development Core Team 2008) and USER (Lady et al. 2008). Parameters were estimated separately for each release (k) but simultaneously for both release sites by expressing the joint likelihood as the product of $L_{k,\mathrm{Sac}}$ and $L_{k,\mathrm{Geo}}$. The variance-covariance matrix was estimated as the inverse of the Hessian matrix. We used the delta method (Seber 1982) to estimate the variance of parameters that are functions of the maximum likelihood estimates (e.g., $\psi_{C2} = 1 - \psi_{B2} - \psi_{D2}$). Uncertainty in parameter estimates is presented both as standard errors and 95% profile likelihood confidence intervals.

Although we planned to have a telemetry station in the Sacramento River at junction 1 (A_3), this station was not implemented in 2008, so we set P_{A3} to zero. Absence of this telemetry station makes it impossible to uniquely estimate the parameters S_{A2}, S_{A3}, ψ_{B11}, and ψ_{B12}. However, these parameters can be estimated by assuming that $S_{\mathrm{A2}} = S_{\mathrm{A3}}$. This assumption was supported by estimates of S_{A2} and S_{A3} in 2007 (Perry et al. 2008, in press). Nonetheless, given that three of four releases thus far (in 2007 and 2008) have occurred without a telemetry station at A_3, we undertook a sensitivity analysis to examine the magnitude of bias introduced into route entrainment probabilities due to deviation from the assumption that $S_{\mathrm{A2}} = S_{\mathrm{A3}}$ (see Appendix 2). Since it is impossible to apportion mortality between the reach above and below A_3, we examined bias under the extreme scenarios where all mortality occurs either upstream of the first river junction (i.e., $S_{\mathrm{A3}} = 1$) or downstream of the first river junction (i.e., $S_{\mathrm{A2}} = 1$).

For each release, the full model was considered as the model with the fewest parameter constraints which still allowed all parameters to be uniquely estimated. When parameter estimates occur at the boundaries of one (or zero) they cannot be estimated through iterative maximum likelihood techniques and must be set to one (or zero). In our study, many detection probabilities were set to one because all fish passing a given location were known to have been detected at that location. In some cases, survival probabilities were fixed to one because all fish detected at a given telemetry station were also detected at the next downstream location. In addition, parameters for Route C (the Delta Cross Channel) were set to zero for the second release when the Delta Cross Channel was closed. A full detailing of parameter constraints applied under the full model can be found in Appendix Table 1.2.

The purpose of including a separate release into Georgiana Slough was to improve precision within the interior Delta by boosting the sample size of fish migrating through this region. Pooling data across release sites can improve precision but assumes that the fish released into the Sacramento River and Georgiana Slough experience similar survival and detection probabilities in reaches through which both release groups migrate. Therefore, we used likelihood ratio tests (Casella and Berger, 2002) to evaluate hypotheses about equality in detection and survival parameters between release sites. Lack of significance at $\alpha = 0.05$ indicates that the full model fits the data no better than the reduced model where parameters are set equal among releases, in which case the reduced model is selected over the full model. For each release, we first compared the full model to a reduced model where all parameters were set equal between releases. We then used parameter estimates from the selected model for estimating population-level and route-specific survival through the Delta.

Survival through the Delta

Survival through the Delta is defined as the probability of survival from the entrance to the Delta at station A_2 (Freeport) to the exit of the Delta at station A_9 (Chipps Island). Population-level survival through the Delta was estimated from the individual components as:

$$S_{\mathrm{Delta}} = \sum_{h=\mathrm{A}}^{\mathrm{D}} \psi_h S_h \qquad (1)$$

where S_h is the probability of surviving the Delta given the specific migration route taken through the Delta, and ψ_h is the probability of migrating through the Delta via one of four migration routes (A = Steamboat Slough, B = Sacramento River, C = Georgiana Slough, D = Delta Cross Channel). Thus, population survival through the Delta is a weighted average of the route-specific survival probabilities with weights proportional to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\psi_{\mathrm{A}} = \psi_{\mathrm{A1}} \psi_{\mathrm{A2}} \qquad (2)$$

$$\psi_{\mathrm{B}} = \psi_{\mathrm{B11}} + \psi_{\mathrm{B21}} \qquad (3)$$

$$\psi_{\mathrm{C}} = \psi_{\mathrm{A1}} \psi_{\mathrm{C2}} \qquad (4)$$

$$\psi_{\mathrm{D}} = \psi_{\mathrm{A1}} \psi_{\mathrm{D2}} \qquad (5)$$

For instance, consider a fish that migrates through the Delta via the Delta Cross Channel (Route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability ψ_{C2}. Thus, the probability of a fish migrating through the Delta via the Delta Cross Channel (ψ_{C}) is the product of these route entrainment probabilities, $\psi_{\mathrm{A1}}\psi_{\mathrm{C2}}$. Since route entrainment probabilities can be estimated separately for Sutter Slough and Steamboat Slough, the probability of migrating through either Sutter or Steamboat Slough (ψ_{B}) is the sum of the route-entrainment probabilities for each slough (ψ_{B11} and ψ_{B21})

When population level survival can be broken down into components of route-entrainment probabilities and reach specific survival, then survival through the Delta for a given migration route (S_h) is simply the product of the reach-specific survival probabilities that trace each migration path through the Delta between the points A_2 and A_9 (see Perry et al. 2008, in press). However, when joint survival-entrainment probabilities are included in the model, survival through a given route must take into account all possible within-route pathways that involve the $\phi_{hi,jk}$ parameters. For example, survival through the Delta for fish that remain in the Sacramento River through the first and second river junctions is expressed as:

$$S_{\mathrm{A}} = S_{\mathrm{A2}}S_{\mathrm{A3}}S_{\mathrm{A4}}S_{\mathrm{A5}}S_{\mathrm{A6}}\left(\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}\right)$$

The bracketed term is the weighted average survival between A_7 (Rio Vista) and A_9 (Chipps Island) with the $\phi_{hi,jk}$ parameters weighting survival of fish that remain in the Sacramento River ($\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}}$) and survival of fish that finish their migration in the lower San Joaquin after passing through Three Mile Slough ($\phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}$). Thus, Delta survival for Route A (the Sacramento River) includes some mortality of fish that enter the interior Delta, and it is impossible to factor out this mortality without explicitly estimating route entrainment probabilities at the junction of the Sacramento River with Three Mile Slough. Nonetheless, the $\phi_{hi,jk}$ parameters provide information about the relative contribution of the interior Delta to survival through Route A. For example, $\phi_{\mathrm{A7,E1}} \ll \phi_{\mathrm{A7,A8}}$ would suggest that movement through Three Mile Slough is a small component of the total survival for fish that migrated in the Sacramento River up to that point. Survival through the Delta for fish taking the Delta Cross

Channel (Route C) and Georgiana Slough (route D) is expressed similarly, and explicitly accounts for fish that pass through Three Mile Slough and finish their migration in the lower Sacramento River:

$$S_C = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{C1} S_{D3} \left(\phi_{D4,D5} S_{D5} S_{D6} S_{D7} + \phi_{\mathrm{D4,E1}} S_{\mathrm{E1,A8}} S_{\mathrm{D8}} \right),$$

and $$S_D = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{D1} S_{D2} S_{D3} \left(\phi_{D4,D5} S_{D5} S_{D6} S_{D7} + \phi_{\mathrm{D4,E1}} S_{\mathrm{E1,A8}} S_{\mathrm{A8}} \right).$$

To facilitate comparison with findings from our first year in 2007, we pooled Sutter and Steamboat Slough into a single migration route, but survival through the Delta can be estimated separately for fish that enter Sutter Slough and fish that enter Steamboat Slough:

$$S_B = \psi_{B11} S_{B1} + \psi_{B21} S_{B2}$$

where S_{B} is survival through the Delta for fish that enter either Sutter or Steamboat Slough, S_{B1} and S_{B2} are survival through the Delta for fish that enter Sutter Slough and Steamboat Slough, respectively, and where S_{B1} and S_{B2} are estimated as:

$$S_{B1} = S_{A2} \left(\phi_{B11,B12} S_{B12} S_{B13} + \phi_{B11,B22} S_{B22} S_{B23} \right) \left(\phi_{\mathrm{A7,A8}} S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}} S_{\mathrm{E1,D5}} S_{\mathrm{D5}} S_{\mathrm{D6}} S_{\mathrm{D7}} \right),$$

and $$S_{B2} = S_{A2} S_{B21} S_{B22} S_{B23} \left(\phi_{\mathrm{A7,A8}} S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}} S_{\mathrm{E1,D5}} S_{\mathrm{D5}} S_{\mathrm{D6}} S_{\mathrm{D7}} \right).$$

For fish entering Sutter Slough, note that the first bracketed term in S_{B1} accounts for survival of fish taking either Miner Slough ($S_{\mathrm{B12}} S_{\mathrm{B13}}$) or Steamboat Slough ($S_{\mathrm{B22}} S_{\mathrm{B23}}$) weighted by the joint probability of surviving and taking each of these routes ($\phi_{B11,B12}$ and $\phi_{B11,B22}$).

We used an approach similar to Newman and Brandes (in press) to quantify survival through each migration route relative to survival of fish that migrate within the Sacramento River:

$$\theta_h = \frac{S_h}{S_{\mathrm{A}}} \qquad h \neq \mathrm{A}$$

We measured each route relative to route A because the Sacramento River is considered the primary migration route. For Georgiana Slough, θ_{D} is nearly analogous to θ estimated by Newman and Brandes (in press), who estimated the ratio of recovery rates of coded wire tagged fish released into Georgiana Slough and the Sacramento River near A_4. Survival through the Delta for route h is equal to Route A when $\theta_h = 1$, and survival through route h is less (greater) than Route A when θ_h is less (greater) than one. We interpreted survival through route h as significantly different than Route A at $\alpha = 0.05$ when $\theta_h = 1$ fell outside the 95% profile likelihood confidence interval of $\hat{\theta}_h$.

To aid in interpreting differences in survival through the Delta among routes and between releases, we examined variation in reach-specific survival rates. Survival probabilities estimate the proportion of fish that survive through a given reach, but direct comparison of survival probabilities among reaches can be hampered by variation in the length of each reach. In our study, reach length varied from just a few kilometers to over 20 km. Therefore, we scaled survival probabilities relative to reach length by calculating survival rates per unit distance:

$$s_{hi} = \sqrt[x_{hi}]{S_{hi}}$$

where s_{hi} is the per-kilometer probability of surviving from telemetry station h_i to the next downstream station, x_{hi} is the distance (km) from telemetry station h_i to the next downstream telemetry station, and S_{hi} is the probability of surviving over x_{hi} kilometers. For reaches where more than one exit location is possible (reaches beginning at B_{11}, A_7, and D_4), we used the average distance to each of the exit points. The length of some reaches is ill-defined because fish may take multiple, unmonitored routes (e.g., the interior Delta between D_4 and D_5). For these reaches, reach length was calculated as the shortest distance between upstream and downstream telemetry stations (usually the main channel). If fish took longer routes which led to higher mortality, then survival probabilities (S_{hi}) scaled to the shortest possible migration route (s_{hi}) would appear low relative to other routes. Thus, this approach is of utility in identifying reaches of high mortality relative to the shortest possible pathway through a reach.

Results

River conditions and migration timing

River conditions differed for the two release groups and influenced their travel times through the Delta (Figure 4). For first release, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport was between 10,000 ft^3/s and 14,000 ft^3/s. The central 80% of this release group passed junction 2 (Stations A_4, C_1, and D_1; Figure 1) over a 5-day period between 7 December and 11 December. The Delta Cross Channel closed at 1138 hours on 14 December 2007 and remained closed for the balance of the study (Figure 4). In contrast, the second release group passed the two river junctions on the descending limb of a freshet, during which flows declined from about 19,000 ft^3/s to 14,000 ft^3/s. Under these flow conditions, the second release group passed junction 2 over a two-day period between 17 January and 19 January. Travel times from release to junction 2 were also shorter for the second release group, with a median travel time of 2.7 d for the first release compared to 1.5 d for the second release.

During their migration through the lower regions of the Delta, most of first release group experienced relatively low and stable discharge accompanied by declining water exports, whereas migration of the second release group coincided with a second freshet during which discharge increased to about 40,000 ft^3/s and exports remained stable (Figure 4). As a consequence, 80% of the first release group passed Chipps Island over a 29-d period (12 December to 10 January), but the central 80% of the second release group passed Chipps Island over only a 16-d period (24 January to 9 February). Although the median travel time from release to Chipps Island for the first release (9.7 d) was less than for the second release (12.9 d), the 90th percentile for the first release (35.9 d) was substantially longer than for the second release (23.9 d). These findings suggest that the main effect of the freshet during the second release was to compress the tail of the travel time distribution rather than shift its central tendency. For both releases, it was difficult to compare travel time among migration routes because ≤4 fish per route were detected at Chipps Island for all routes but the Sacramento River.

Route-specific survival through the Delta

Comparison of parameters between release sites (Sacramento and Georgiana Slough) suggested no difference in survival or detection probabilities, allowing us to set parameters equal between release sites to improve precision of survival estimates. For both releases, likelihood ratio tests were not significant (for December, $\chi_9^2=12.4$, $P = 0.192$; for January, $\chi_9^2=14.8$, $P = 0.097$), so the reduced model was used to estimate route-specific survival and S_{Delta}. We found little difference between releases in survival through the Delta. The probability of surviving through the Delta was 0.174 for the December release and 0.195 for the January release (Table 2). For the December release, fish remaining in the Sacramento River exhibited higher survival than all other routes ($S_A = 0.283$), whereas fish migrating through the interior Delta via the Delta Cross Channel and Georgiana Slough exhibited the lowest survival ($S_C = 0.041$, $S_D = 0.087$,

Table 2 and Figure 5). In contrast, for the January release, fish migrating through Sutter and Steamboat sloughs (S_{B} = 0.245) exhibited similar survival as fish migrating within the Sacramento River (S_{A} = 0.244), whereas survival through the interior Delta via Georgiana Slough remained lower than the other migration routes (S_{D} = 0.086). For both releases, separate estimates of route-specific survival for Sutter Slough and Steamboat Slough revealed fish entering Steamboat Slough exhibited survival that was about 9 percentage points higher than for fish that entering Sutter Slough (Table 2).

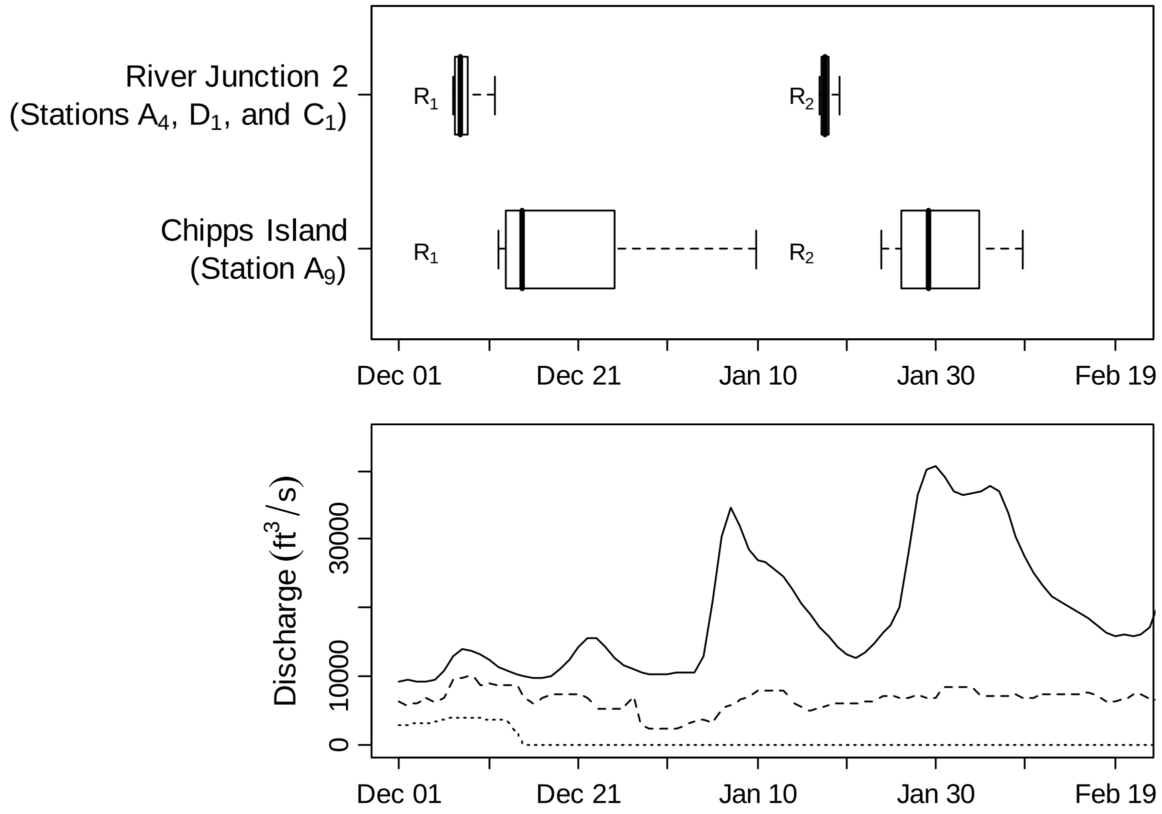

Figure 4.—River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during winter 2007/2008. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River (telemetry stations A4, C1, and D1) and at Chipps Island, the terminus of the Delta (telemetry station A9). The two release dates are shown as R_1 = 4 December 2006 for a release size of 149 tagged fish and R_2 = 15 January 2007 for a release size of 130 fish. Whiskers represent the 10th and 90th percentiles, the box encompasses the 25th to 75th percentiles, and the line bisecting the box is the median arrival date. River discharge (solid

line) is tidally filtered, daily discharge of the Sacramento River at Freeport (near telemetry station A2), Delta Cross Channel discharge (dotted line) is the tidally filtered daily discharge, and water exports (dashed line) are the total daily discharge of water exported from the Delta at the pumping projects.

Table 2.—Route-specific survival through the Sacramento–San Joaquin River Delta (S_h) and the probability of migrating through each route (ψ_h) for acoustically tagged fall-run juvenile Chinook salmon released in December 2007 (R_1) and January 2008 (R_2). Also shown is population survival through the Delta (S_{Delta}), which is the average of route-specific survival weighted by the probability of migrating through each route.

Migration route	$\hat{S}_h$ ($\widehat{\text{SE}}$)	95% Profile Likelihood Interval	$\hat{\psi}_h$ ($\widehat{\text{SE}}$)	95% Profile Likelihood Interval
R_1: December 2007				
A) Sacramento R.	0.283 (0.054)	0.187, 0.397	0.387 (0.044)	0.304, 0.475
B) Sutter & Steamboat S.	0.136 (0.039)	0.073, 0.225	0.345 (0.042)	0.267, 0.430
B_1) Sutter S.	0.107 (0.037)	0.050, 0.196	0.230 (0.037)	0.163, 0.308
B_2) Steamboat S.	0.193 (0.060)	0.095, 0.327	0.115 (0.028)	0.068, 0.178
C) Delta Cross Channel	0.041 (0.021)	0.013, 0.096	0.117 (0.029)	0.068, 0.182
D) Georgiana S.	0.087 (0.028)	0.043, 0.153	0.150 (0.033)	0.094, 0.221
S_{Delta} (All routes)	0.174 (0.031)	0.119, 0.242		
R_2: January 2008				
A) Sacramento R.	0.244 (0.048)	0.160, 0.346	0.490 (0.048)	0.397, 0.584
B) Sutter & Steamboat S.	0.245 (0.059)	0.143, 0.372	0.198 (0.037)	0.133, 0.278
B_1) Sutter S.	0.192 (0.070)	0.078, 0.343	0.086 (0.026)	0.044, 0.147
B_2) Steamboat S.	0.286 (0.070)	0.162, 0.430	0.112 (0.029)	0.033, 0.253
C) Delta Cross Channel	NA		0.000 (0.000)	
D) Georgiana S.	0.086 (0.023)	0.048, 0.140	0.311 (0.045)	0.229, 0.403
S_{Delta} (All routes)	0.195 (0.034)	0.135, 0.268		

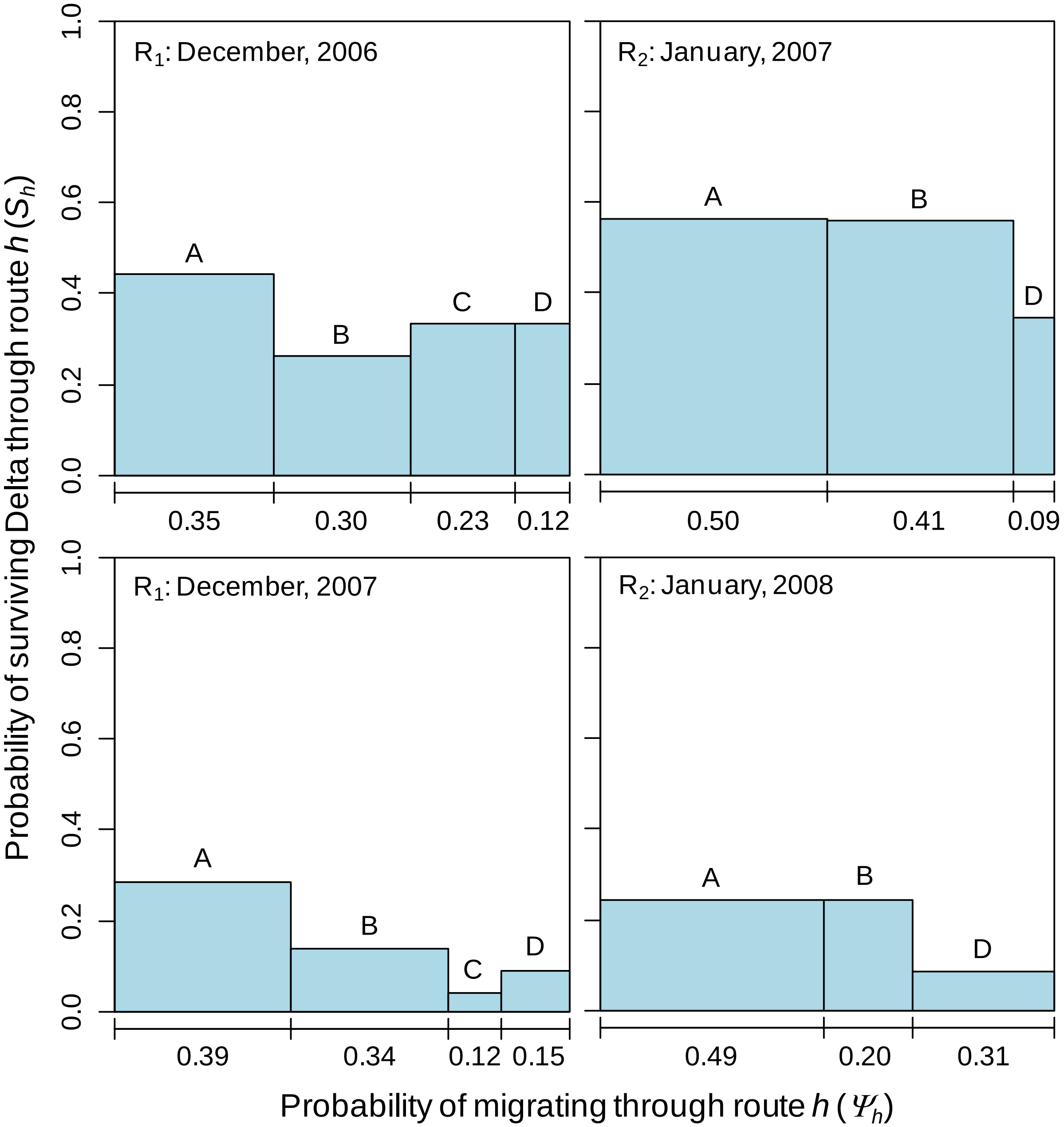

Figure 5.—Probability of surviving migration through the Sacramento-San Joaquin River Delta (S_h) for each of four migration routes for tagged late-fall juvenile Chinook salmon emigrating from the Sacramento River. The width of each bar shows the fraction of fish migrating through each route (ψ_h), and the total area under the bars yields S_{Delta}. The top panels show estimates from the winter of 2006/2007 (Perry et al. 2008, in press), and the bottom panels show estimates from this study during the winter of 2007/2008. Labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively.

We detected significant differences between survival for the Sacramento River and survival for other migration routes. For the December release, the ratio of survival for each major migration route relative to the Sacramento River (i.e., θ_h) ranged from 0.14 for the Delta Cross Channel to 0.48 for Sutter and Steamboat Slough, showing that survival through other routes was less than half that of the Sacramento River. Since $\theta_h = 1$ fell outside the 95% confidence intervals of $\hat{\theta}_h$ for all major routes, these findings support the hypothesis that all routes had significantly lower survival than the Sacramento River (Table 3). Considering Sutter Slough and Steamboat Slough separately, only the estimate of θ_{B2} for Steamboat Slough was not significantly different from one, likely due to small sample size and low precision for this secondary route. In contrast, in January, $\hat{\theta}_B = 1.005$ whereas $\hat{\theta}_D = 0.352$, showing that survival through the interior Delta (Route D) was only about one third that of other available routes. Survival for the interior Delta was significantly lower than for the Sacramento River for the January release, but survival for Sutter and Steamboat Slough (and each slough separately) was not significantly different than the Sacramento River (Table 3).

Table 3.—The ratio (θ_h) of survival through route h (S_h) to survival through the Sacramento River (S_A) for acoustically tagged fall-run juvenile Chinook salmon released in December 2007 and January 2008.

	R_1: December 2007		R_2: January 2008	
Migration route	$\hat{\theta}_h$ ($\widehat{SE}$)	95% Profile Likelihood Interval	$\hat{\theta}_h$ ($\widehat{SE}$)	95% Profile Likelihood Interval
B) Sutter & Sutter S.	0.481 (0.132)	0.265, 0.794	1.005 (0.215)	0.621, 1.480
B_1) Sutter S.	0.380 (0.127)	0.182, 0.689	0.787 (0.273)	0.330, 1.365
B_2) Steamboat S.	0.683 (0.205)	0.346, 1.153	1.172 (0.255)	0.698, 1.714
C) Delta Cross Channel	0.146 (0.077)	0.044, 0.363	NA	
D) Georgiana S.	0.307 (0.109)	0.145, 0.596	0.352 (0.110)	0.186, 0.642

Migration Routing

For some migration routes, we found that the proportion of the population migrating through a given route deviated from the fraction of mean discharge in a route. As juvenile salmon migrated past the first river junction, 34.5% of fish left the Sacramento River to migrate through Steamboat and Sutter Slough (ψ_B, Figure 5 and Table 2), about 10 percentage points higher than the fraction of total discharge entering this route (Figure 6). In contrast, for the

January release, only 19.8% of fish entered Sutter and Steamboat Slough ($\hat{\psi}_B$, Figure 5 and Table 2) despite 37% of river discharge entering this route (Figure 6). Route entrainment probabilities for each slough showed that the difference in $\hat{\psi}_B$ between releases occurred at the entrance to Sutter Slough (Table 2). In December, twice the fraction of fish entered Sutter Slough ($\hat{\psi}_{B11} = 0.230$) as compared to Steamboat Slough ($\hat{\psi}_{B21} = 0.115$), whereas in January, the proportion entering Sutter Slough declined to 0.086 while the fraction entering Steamboat Slough remained unchanged at 0.112 (Table 2). As a consequence, 65% of fish remained in Sacramento River at the first river junction during the December release, whereas 80% remained in the Sacramento River for the January release (see ψ_{A1} in Appendix Table 1.3). Thus, for the January release, a larger fraction of the population remained in the Sacramento River at the first junction, which increased exposure of the population to the second river junction where they could enter into the interior Delta.

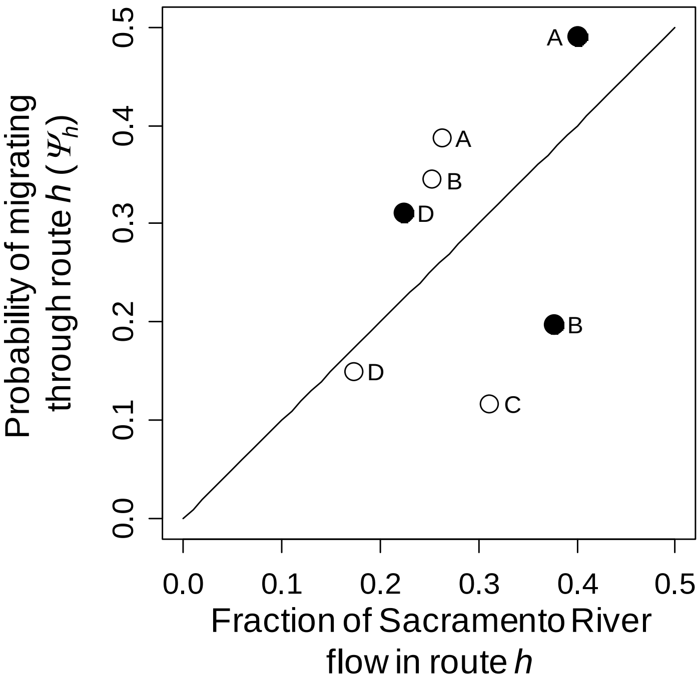

Figure 6.—The probability of migrating through route *h* (ψ_h) as a function of the proportion of total river flow in route *h* for tagged late-fall juvenile Chinook salmon released in December 2007 (open circles) and January 2008 (filled circles). Data labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively. The fraction of river flow in each route was calculated as the proportion of tidally filtered daily discharge of each route relative to the total discharge of the Sacramento River at Freeport. The reference line shows where the fraction of fish migrating through each route is equal to the proportion of flow in each route (i.e., a 1:1 ratio).

For the December release, of fish that arrived at the second river junction where the Delta Cross Channel is located, 18% entered the Delta Cross Channel, 23% entered Georgiana Slough, and 59.2% remained in the Sacramento River (see ψ_{C2}, ψ_{D2}, and ψ_{A2} in Appendix Table 1.3). In contrast, for the January release when the Delta Cross Channel was closed, 38.8% of fish arriving at the second river junction entered Georgiana Slough, with the remaining 61.2% migrating through the Sacramento River. Accounting for both river junctions, migration route probabilities for the December release indicated that 38.7% of the population migrated within the Sacramento River and 26.7% of the population entered the interior Delta. However, only 11.7% entered the interior Delta through the Delta Cross Channel even though 31% of the flow entered the Delta Cross Channel (Figures 5 and 6, Table 2). During January, nearly one third of the population was entrained into the interior Delta through Georgiana Slough (Figure 5, Table 2) despite the Delta Cross Channel being closed. Consequently, the fraction of the population entering the interior Delta was similar between release dates.

Relative Contributions to S_{Delta}

Estimates of S_{Delta} were driven by 1) variation among routes in survival through the Delta ($\hat{S}_h$) and 2) the relative contribution of each route-specific survival to $\hat{S}_{Delta}$ as measured by migration route probabilities ($\hat{\psi}_h$). For the December release, fish migrating within the Sacramento River exhibited the highest survival through the Delta ($\hat{S}_B$) relative to all other routes, but only 38.7% of the population migrated through this route ($\hat{\psi}_B$), representing a relatively small contribution to $\hat{S}_{Delta}$ (Figure 5, Table 2). In contrast, relative to survival in the Sacramento River, survival through all other routes reduced $\hat{S}_{Delta}$ and comprised 61.3% of the population ($\hat{\psi}_A + \hat{\psi}_C + \hat{\psi}_D$), thereby contributing substantially to $\hat{S}_{Delta}$ for the December release (Figure 5, Table 2). For the January release, 68.8% of the population ($\hat{\psi}_A + \hat{\psi}_B$) migrated through routes with the highest survival, and thus survival through these routes comprised the bulk of $\hat{S}_{Delta}$ for the January release (Figure 5, Table 2). In comparison, survival for the interior Delta via Georgiana Slough ($\hat{S}_C$) was lower than the other routes for the January release and accounted for 31.2% ($\hat{\psi}_C$) of the contribution to $\hat{S}_{Delta}$ (Figure 5, Table 2). Because the fraction of the population entering the interior Delta was similar for both releases, lower survival through the interior Delta reduced population-level survival by a similar magnitude for both releases.

Comparisons between 2007 and 2008

Some patterns in survival and migration route probabilities during 2008 differed considerably from 2007, whereas other patterns remained consistent. First, $\hat{S}_{\text{Delta}}$ for both releases in 2008 (Table 2) was lower than in 2007; $\hat{S}_{\text{Delta}}$ in 2007 was estimated at 0.351 and 0.543 for the December and January release groups (Perry et al. 2008, in press). Although $\hat{S}_{\text{Delta}}$ was lower in 2008 relative to 2007, the pattern of survival probabilities among routes was similar between releases and years (Figure 5). In both years, all routes exhibited lower survival than the Sacramento River during the December release, but only fish entering the interior Delta exhibited lower survival than the Sacramento River for the January release (Figure 5). Larger sample size and the additional release site in Georgiana Slough during 2008 improved precision of route-specific survival compared to our 2007 study, allowing us to detect differences in survival among routes. We also found notable differences between years in route entrainment probabilities at the two primary river junctions. In 2007, migration route probabilities were similar to the fraction of flow in each route, but migration route probabilities deviated from this pattern in 2008. Consequently, in 2008 we found little difference between releases in the fraction of fish entering the interior Delta, whereas in 2007, the fraction of fish was lower during the January release when the Delta Cross Channel was closed (Perry et al. 2008, in press).

Reach-specific patterns of survival and movement

We found high variation in survival rates among reaches, ranging from as low as 0.867 km^{-1} to 1.0 km^{-1} for a few reaches where all fish survived. To put the magnitude of these survival rates in perspective, only 24% of fish will survive a 10-km reach at a survival rate 0.867 km^{-1} (i.e., = $0.867^{10} = 0.247$) and only 6% will remain after 20 km. In contrast, at a survival rate of 0.99 km^{-1}, 90% of fish will survive 10 km and 82% will still be alive after 20 km. Reaches with the lowest survival rates occurred downstream of telemetry stations B_{13}, B_{23}, and A_6 (i.e., the Cache Slough to Rio Vista region, Figure 7). Two out of three of these reaches were among the four lowest survival rates observed in each release, highlighting a region of high local mortality relative to the length of these reaches. In contrast, other than survival probabilities that were fixed to one (Appendix Table 1.3), the highest survival rates in both releases occurred in the first two reaches of the Sacramento River (downstream of A_2 and the Sacramento release site, A_1). These reaches were relatively long (~20 km each) and survival probabilities were >0.91 (see S_{A1} and S_{A2} in Appendix Table 1.3), leading to high survival rates relative to reach length. Reach-specific survival rates were consistent with differences among routes in survival through the Delta. For the December release, 8 of the 11 reaches with the highest survival rates were comprised of all 8 reaches in the Sacramento River (Route A, Figure 7). These reaches exhibited survival rates ≥ 0.96 km^{-1}. The remaining 11 reaches with the lowest survival rates were comprised solely of the other three routes, with no particular route exhibiting consistently lower reach-specific survival rates. All of these reaches exhibited survival rates <0.96 km^{-1}. For the January release, the highest-ranking survival rates were still dominated by reaches within the Sacramento River (6 of the 11 lowest mortality rates), but two reaches of the Sacramento River ranked in highest 50 percent of mortality rates (reaches beginning at A_6 and A_8).

Between releases, most reach-specific survival rates within the Sacramento River (Route A) and interior Delta (Route D) changed by less than 0.03 km^{-1} (Figure 8), and this finding agrees with the similarity in route-specific survival between releases (Figure 5). Furthermore, variation in survival rates between releases was low relative to the large variation in survival rates among reaches, especially for the Sacramento River (Figure 8). However, survival rates for all but one reach within Sutter and Steamboat sloughs increased substantially from December to January (Figure 8), which is consistent with the observed increase in survival through the Delta for this route. Thus, the observed difference in route-specific survival for Sutter and Steamboat sloughs was driven by coincident changes in survival rates for most reaches within this route and not by changes in survival within a particular reach.

One reach of particular management interest occurs downstream of D_4 in the interior Delta (see Figure 2). Although only about 17 km long by way of the San Joaquin River, this reach encompasses a large network of channels and includes the pumping stations and fish salvage facilities in the southern Delta. This reach exhibited the lowest probability of survival of

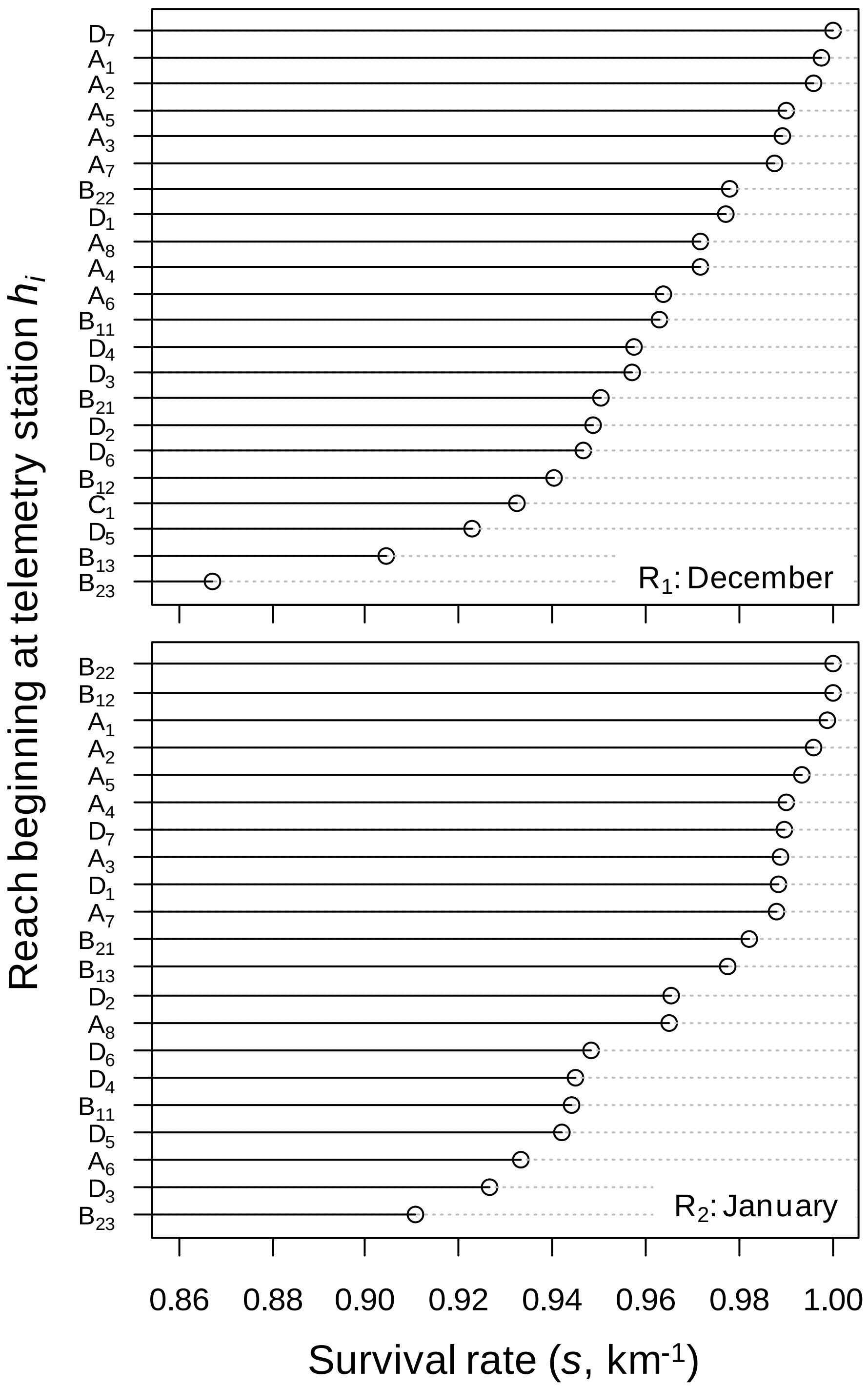

Figure 7.—Reach-specific survival rates plotted in ascending order for tagged late fall Chinook salmon released in December 2007 (top) and January 2008 (bottom). Survival rates scale survival probabilities (S_{hi}, Appendix Table 1.3) to the length of each reach from telemetry station h_i to the next downstream telemetry station.

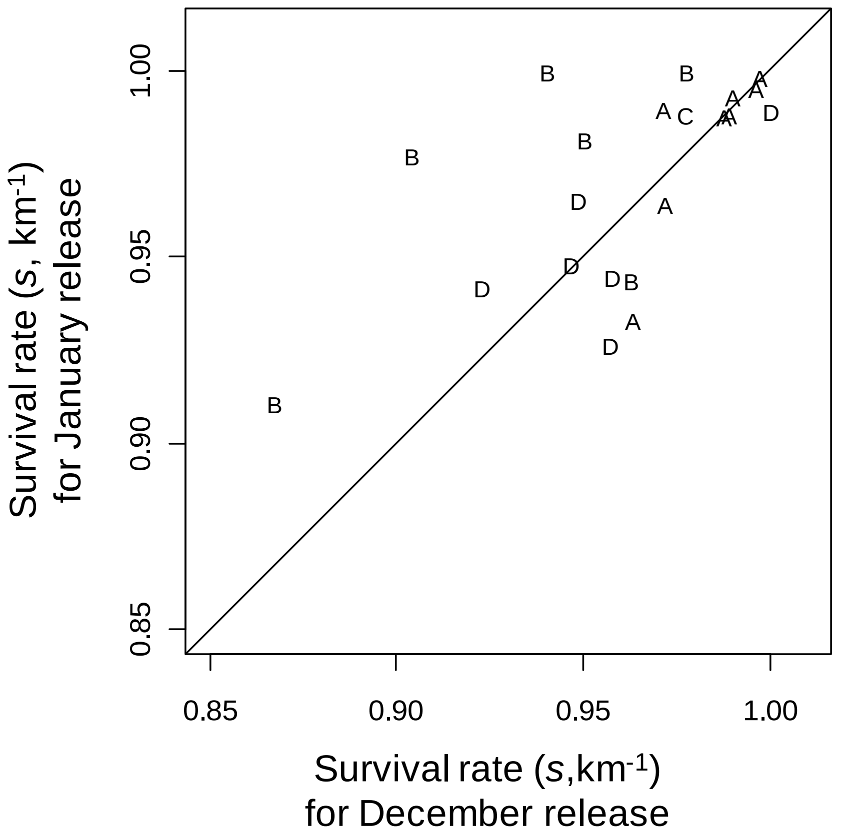

Figure 8.—Reach-specific survival rates for the December 2007 release compared to the January 2008 release for acoustically tagged late fall Chinook salmon migrating through the Sacramento-San Joaquin River Delta. The reference line shows where survival rates are equal between releases. Letters correspond to reaches within A = Sacramento River, B = Sutter and Steamboat sloughs, and D = the interior Delta via Georgiana Slough.

all reaches within the interior Delta, having observed survival probabilities of less than 50% (for R_1: $\hat{S}_{D4}$ = 0.484, $\widehat{SE}$ = 0.071; for R_2: $\hat{S}_{D4}$ = 0.395, $\widehat{SE}$ = 0.080; Appendix Table 1.3). However, when expressed as a function of reach length, other reaches within the interior Delta (Routes C and D) exhibited similar or lower survival rates than the reach downstream of D_4 (Figure 7). Direct mortality at the pumping stations appeared to contribute little to the estimate of S_{D4}. Both the State Water Project and Clifton Court Forebay were monitored by telemetry stations, but these stations could not be incorporated into the survival model because too few fish were detected at these locations to warrant parameter estimation. However, of the 76 fish passing D_4 that were never detected at or downstream of D_5 or E_1 (indicating probable mortality in this reach), only one fish was detected at the salvage facilities. Overall, six tagged fish were detected at the salvage facilities, and five of these were next detected at or downstream of D_5 or E_1 suggesting they had been salvaged at the fish facilities and transported to the lower Delta. Thus, mortality rates appear high in many reaches of the interior Delta relative the Sacramento River, not just the reach that includes a primary point source of known mortality (i.e., pumping stations and salvage facilities).

Although we could not estimate route entrainment probabilities at other junctions in the Delta, we explicitly accounted for observed movement among routes by estimating joint survival-entrainment probabilities. At the junction of Sutter Slough with Miner and Steamboat Slough (the reach downstream of B_{11}; Figure 2), $\hat{\phi}_{B11,B22}$ was about twice that of $\hat{\phi}_{B11,B12}$ during both releases (Appendix Table 1.3). If survival was similar for the two reaches downstream of the junction, then these findings suggest that about two-thirds of fish entering Sutter Slough migrated down Steamboat Slough and one-third traveled through Miner Slough.

For both releases we observed fish passing in both directions through Three Mile Slough (E_1 in Figure 2). However, Three Mile slough appears to play a relatively minor role in movement dynamics through the Delta relative to contribution of the major migration routes. In the Sacramento River, fish moving from A_7 to A_8 contributed a substantially larger fraction of the total survival through this reach (for R_1: $\hat{\phi}_{A7,A8} = 0.837$, $\widehat{SE} = 0.074$; for R_2: $\hat{\phi}_{A7,A8} = 0.781$, $\widehat{SE} = 0.070$) compared to fish moving from A_7 to E_1 (for R_1: $\hat{\phi}_{A7,E1} = 0.049$, $\widehat{SE} = 0.034$; for R_2: $\hat{\phi}_{A7,E1} = 0.109$, $\widehat{SE} = 0.046$). In the San Joaquin River, fish moving from D_4 to E_1 contributed more to the total reach survival for the first release compared to the second release. For the first release, $\hat{\phi}_{D4,E1} = 0.140$ ($\widehat{SE} = 0.049$) and $\hat{\phi}_{D4,D5} = 0.351$ ($\widehat{SE} = 0.070$), whereas for the second release $\hat{\phi}_{D4,E1} = 0.041$ ($\widehat{SE} = 0.023$) and $\hat{\phi}_{D4,D5} = 0.354$ ($\widehat{SE} = 0.079$). Whether a higher fraction of fish in the San Joaquin River passed through Three Mile Slough (E_1) during the first release is difficult to ascertain because lower survival in the San Joaquin River downstream of its junction with Three-Mile Slough may also account for the observed difference.

Discussion

In our previous study, $\hat{S}_{\text{Delta}}$ differed by nearly 20 percentage points between releases, and we attributed this observed difference to both a change in the proportion of fish entering the interior Delta and a change in survival within given migration routes (Perry et al. 2008, in press). In contrast, for this study, we attribute lack of an observed difference in $\hat{S}_{\text{Delta}}$ between releases to 1) less variation between releases in survival for given migration routes, relative to 2007, 2) lower-than-expected entrainment into the Delta Cross Channel, 3) a decline in the proportion of fish entering Sutter and Steamboat sloughs in January, and 4) little difference in the proportion of fish entering the interior Delta between releases. In 2007, survival through the Delta for both the Sacramento River and Sutter and Steamboat Slough increased substantially between December and January, partly driving the large observed difference in $\hat{S}_{\text{Delta}}$ between releases (Perry et al. 2008, in press). However, during 2008 only Sutter and Steamboat sloughs exhibited a sizeable increase in survival from December to January. However, although survival increased, the proportion of fish entering Sutter and Steamboat sloughs declined from 0.34 to 0.20 from December to January. Had the proportion of fish entering Sutter and Steamboat sloughs remained unchanged, population-level survival would have received a larger boost from the increase in survival observed for this route. Given that survival for routes through the interior Delta were significantly lower than the Sacramento River during both releases, the fraction of fish entering the interior Delta dictated the magnitude of decrease in population-level survival due to fish using this migration route. Thus, the magnitude of decrease in population-level survival attributed to the interior Delta remained unchanged between releases because similar fractions of the population entered the interior Delta during both releases. However, because maximum survival for any given route during both releases was <0.30, population-level survival would remain low regardless of the fraction of fish entrained in the interior Delta.

That estimates of population-level survival were ≤0.20 for an 80-km section of river begs the question of whether the untagged population also experienced such low survival. To put the magnitude of these estimates in perspective, survival of hatchery-reared juvenile Chinook salmon over 600 km and through eight dams of the Snake and Columbia rivers ranged from

31%-59% (Williams et al. 2001). Thus, the absolute magnitude of survival relative to the distance traveled is clearly low compared to a similarly developed river system. However, factors such as source of the study fish and the effects of the transmitter could have reduced survival probabilities relative to untagged fish. Fish in this study were obtained directly from Coleman National Fish Hatchery, tagged, and then released about 40 km upstream of the first channel junction in the Delta. Initial "culling" of unfit hatchery fish obtained directly from a hatchery, a process suggested by Muir et al. (2001) and Newman (2003), could have lead to lower absolute survival compared to a population that had migrated in-river from natal tributaries or hatcheries to the Delta. If this process were pronounced in our study, we might have expected 1) low survival in the first reach following release, and 2) fish released at Sacramento to have higher survival probabilities through the interior Delta relative to fish that were released directly into the interior Delta at Georgiana Slough. In contrast, survival probabilities for the first reach of the Sacramento River were higher than all other reaches within this route (see S_{A1}, Appendix Table 1.3). Furthermore, the model with equal survival probabilities between release sites was selected over the full model with different survival probabilities for each release, providing little evidence of a "culling" effect. As for the effect of the transmitter, Hockersmith et al. (2003) found no difference in survival between radio tagged and PIT-tagged juvenile Chinook salmon over a similar distance as that studied here. Thus, we found little evidence to suggest that the low population-level survival through the Delta was a function of the source of fish or tagging methodology used for the study.

The strength of inferences from our data to the untagged population depend on whether survival estimates are viewed from a relative or absolute point of view. Although we found no evidence that survival probabilities were lower than expected due to fish source or tagging method, we also have little basis with which to compare survival estimates from our study population to actively migrating populations of wild or hatchery origin in the Delta. However, regardless of the absolute magnitude of survival, differences among routes that influence survival should act similarly on all populations of salmon smolts migrating through the Delta. For example, while it is uncertain whether untagged fish migrating concurrently with tagged fish also exhibited population-level survival of less than 20%, both tagged and untagged fish migrating through the interior Delta likely experienced lower survival through the Delta relative to fish migrating within the Sacramento River. Therefore, the relative difference in survival among routes from our data should provide stronger inference to untagged populations than will inferences about the absolute magnitude of survival probabilities. From this perspective, although survival was low for all migration routes during 2008, survival for routes through the interior Delta was at most 35% that of survival for fish remaining in the Sacramento River (see θ_C and θ_D inTable 3). Future studies that include fish obtained from Coleman National Fish Hatchery paired with releases of in-river, actively migrating hatchery or wild fish would help to interpret the absolute magnitude of survival probabilities from this study in the context of other populations of interest.

The primary working hypothesis of management actions related to the operation of the Delta Cross Channel is that closing the Delta Cross Channel will increase population-level survival by reducing the fraction of the population entering the interior Delta where survival is lower than alternative migration routes. Implicit in this hypothesis is that the fraction of fish entering the interior Delta is proportional to the fraction of flow entering the interior Delta. However, in contrast to our previous findings, we found that the proportion of fish entering each migration route did not necessarily agree with the proportion of mean discharge entering a route. Furthermore, deviations from this "expected" relationship acted to decrease the proportion of fish entering the interior Delta during the December release, but increase it during the January release. Based on distribution of mean discharge, closing the Delta Cross Channel reduced the total fraction of flow entering the interior Delta from 48.4% during the December release to 22.5% during the January release. However, for the December release, the proportion of fish entering the Delta Cross Channel was only about one-third the proportion of flow entering this route, whereas the proportion of fish entering Georgiana Slough was similar to the proportion of flow (Figure 6). Thus, the proportion of fish entering the interior Delta was less than might otherwise be expected based only on the distribution of river flow during the December release. During the January release, only about 20% of fish entered Sutter and Steamboat Slough even though 37% of Sacramento River flow entered this route (Figure 6). Therefore, a higher fraction of fish remained in the Sacramento River relative to that expected based on the proportion of flow in this route, which in turn exposed a higher fraction of the population to entrainment into the interior Delta via Georgiana Slough. These findings show how variation in route entrainment probabilities at both major river junctions interacted to produce little observed difference between releases in the fraction of the population entering the Interior Delta, despite the Delta Cross Channel being open for the first release and closed for the second.

While dispersal of the population throughout the channel network of the Delta is likely driven in part by the distribution in mean river discharge among channels, our findings provide the first evidence that the distribution of fish entering each channel can deviate considerably from the distribution of flow entering each channel. Such deviation was expected by Burau et al. (2007), who identified a number of mechanisms likely to contribute to variation in route entrainment probabilities. First, flow distribution among the river channels at each junction varies with the tides on hourly time scales (Blake and Horn 2003). Thus, diel patterns in migration behavior (Wilder and Ingram 2006; Burau et al. 2007; Chapman et al. 2007) interacting with tidal fluctuations could produce route entrainment probabilities that deviate from that expected based on mean discharge. In addition, secondary circulation at river bends (Dinehart and Burau 2005) combined with swimming behavior of juvenile salmon could concentrate the lateral distribution of migrating fish along the outside of river bends where they become more (or less) likely to be entrained into a given channel at a river junction (Burau et al. 2007). These fine-scale processes are an active area of research in the Delta (Burau et al. 2007) and should provide new insights into the mechanisms driving variability in route entrainment probabilities at river junctions.

While some aspects of migration and survival dynamics differed greatly between years, other patterns remained consistent. Although population-level survival in 2008 was lower than in 2007, the pattern of survival among routes was similar. During both releases, survival of fish migrating through the interior Delta was significantly less than for fish that remained in Sacramento River, which is consistent our findings in 2007 (Perry et al. 2008, in press) and with the findings of previous studies (Brandes and McLain 2001; Newman and Rice 2002; Newman 2008, Brandes and Newman in press). This weight of evidence suggests that management actions that shift the distribution of the population from the interior Delta to the Sacramento River will improve population-level survival through the Delta. Similar to 2007, we also found that survival through the Delta for fish migrating in Sutter and Steamboat Sloughs was significantly lower than the Sacramento River during the December release, but was comparable to the Sacramento River during the January release. Higher total river discharge (Figure 4) in January combined with a higher fraction of that discharge entering Sutter and Steamboat sloughs

(Figure 6) could have improved migration conditions and reduced predation rates during the January release. Reach-specific survival rates increased for nearly all reaches of Sutter and Steamboat Slough (Figure 8), which is consistent with an increase in discharge through these reaches.

Quantifying survival rates per unit distance allowed us to identify patterns in reach-specific survival that generally followed the pattern of route-specific survival probabilities. Most reaches within the Sacramento River exhibited the highest survival rates during both releases, while most reaches within the interior Delta exhibited survival rates lower than the Sacramento River (Figure 7). These findings suggest that particular reaches within a route did not drive the observed differences in survival among migration routes. For instance, the lowest survival probabilities for the interior Delta were observed for the longest reach and included the most complex channel network with the pumping stations (see S_{D4} in Appendix Table 1.3). Yet survival rates for this reach were comparable to other reaches within this route when expressed as a function of reach length. In addition, we observed locally high mortality in the Cache Slough region downstream of stations B_{13}, B_{23}, and A_6 for both releases. Last, survival rates in Sutter and Steamboat sloughs increased in January for nearly all reaches within this route. These patterns of variation among reaches suggest that factors influencing survival are operating at a spatial scale larger than an individual reach.

Reach-specific survival rates expressed with respect to distance traveled changed little between releases relative to the variability observed among reaches, especially for the Sacramento River (Figure 9). These findings suggest that factors other than migration distance (e.g., travel time) may also influence mortality rates. In contrast, in the Columbia River, survival rates of juvenile Chinook salmon have been significantly related to migration distance, but only weakly correlated to travel time (Muir et al. 2001, Anderson et al. 2005). Anderson et al. (2005) offered a hypothesis explaining this apparently contradictory finding. When prey migrate through a “gauntlet” of predators, predator-prey encounter rates will be such that each prey encounters a predator at most once. Under these circumstances, predator-prey theory predicts that survival will be driven by distance traveled, but not by travel time. In contrast, when prey migration speeds are slow relative to predator swimming speeds such that multiple encounters are possible, then the situation reverses: the probability of survival becomes dependent on travel time. This hypothesis could partially explain the wide range in mortality rates among reaches within the Sacramento River, but low variability between releases (Figure 8). Within our study area the Sacramento River transitions from river-driven discharge in the uppermost reaches to tidally driven discharge in the lower reaches. Coincident with this transition, fish movement patterns shift from downstream-only movements to both upstream and downstream movements in the lower reaches of the Delta. Thus, in lower reaches of the Delta fish may pass through a given reach more than once, which could increase predator encounter rates relative to the length of each reach.

This research continues to provide critical information to understand factors influencing migration and survival dynamics of juvenile Chinook salmon migration through the Delta. Improved precision of parameter estimates allowed us detect statistically significant differences in survival among migration routes. While some findings were similar to our previous study, such as low survival through the Interior Delta relative to the Sacramento River, other findings deviated considerably between years. Survival through the Delta was less than 20% during 2008 (compared to 35%-54% in 2007), route-entrainment probabilities deviated from the fraction of mean river discharge entering each channel, and the proportion of the population entering the interior Delta was similar between releases despite closure of the Delta Cross Channel. Given the substantial variation in survival, route entrainment, and migration route probabilities observed among four releases and two years, we suspect that we are just beginning to unmask the temporal and spatial variability in migration and survival dynamics in the Delta. Nonetheless, even with such variability, patterns in survival and movement dynamics are beginning to emerge. With the addition of migration data collected during the winter of 2008/2009, we plan to formally model hypotheses about reach- and route-specific factors that influence survival and migration route probabilities. Such information should provide insights into management actions that will improve survival of juvenile salmon populations migrating through the Sacramento-San Joaquin River Delta.

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Appendix 1

Appendix Table 1.1.—Counts of detection histories for the model shown in Figure 3 for a release of $R_1 = 208$ fish on 4 December 2007 and $R_2 = 211$ fish on 16 January 2008. Counts for all other detection histories were zero and are not shown here. Each digit of the detection history indicates detection at telemetry stations within each of four migration routes (labeled A–D) and Three Mile Slough (E). A "0" indicating either a fish was not detected or a telemetry station within that route was not implemented at that position in the capture history (since some routes had more telemetry stations than others). Detection histories beginning with "0 0 0 D" indicate fish released in Georgiana Slough whereas those beginning with "A" are fish released into the Sacramento River.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
0 0 0 D 0 0 0 0 0 0 0 0 0	11	0 0 0 D 0 0 0 0 0 0 0 0 0 0	5
0 0 0 D D 0 0 0 0 0 0 0 0	5	0 0 0 D D 0 0 0 0 0 0 0 0	4
0 0 0 D D D 0 0 0 0 0 0 0	7	0 0 0 D D D 0 0 0 0 0 0 0	21
0 0 0 D D D D 0 0 0 0 0 0	20	0 0 0 D D D D 0 0 0 0 0 0	32
0 0 0 D D D D D 0 0 0 0 0	6	0 0 0 D D D D D 0 0 0 0 0	4
0 0 0 D D D D E 0 0 0 0 0	3	0 0 0 D D D D E 0 0 0 0 0	1
0 0 0 D D D D D 0 D 0 0 0	2	0 0 0 D D D D 0 0 D 0 0 0	1
0 0 0 D D D D D 0 D D A 0	1	0 0 0 D D D D D 0 D 0 0 0	2
0 0 0 D D D D E A 0 0 A A	2	0 0 0 D D D D 0 0 D D 0 0	1
0 0 0 D D D D D 0 0 D A A	1	0 0 0 D D D D 0 0 0 0 A 0	1
0 0 0 D D D D D 0 D D A A	1	0 0 0 D D D D E A 0 0 0 A	1
A 0 0 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D D 0 D D 0 A	1
A A 0 0 0 0 0 0 0 0 0 0 0	18	0 0 0 D D D D 0 0 0 0 A A	1
A 0 B1 0 0 0 0 0 0 0 0 0 0	1	0 0 0 D D D D D 0 0 0 A A	1
A A B1 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D E A 0 0 A A	1
A A B2 0 0 0 0 0 0 0 0 0 0	3	0 0 0 D D D D D 0 D 0 A A	2
A A 0 A 0 0 0 0 0 0 0 0 0	7	0 0 0 D D D 0 D 0 0 D A A	1
A A B1 B1 0 0 0 0 0 0 0 0 0	4	0 0 0 D D D D D 0 0 D A A	1
A A B1 B2 0 0 0 0 0 0 0 0 0	1	A 0 0 0 0 0 0 0 0 0 0 0 0	6
A 0 B2 B2 0 0 0 0 0 0 0 0 0	1	A A 0 0 0 0 0 0 0 0 0 0 0	16
A A B2 B2 0 0 0 0 0 0 0 0 0	2	A A B1 0 0 0 0 0 0 0 0 0 0	4
A 0 0 C 0 0 0 0 0 0 0 0 0	1	A A B2 0 0 0 0 0 0 0 0 0 0	1
A A 0 C 0 0 0 0 0 0 0 0 0	9	A A 0 A 0 0 0 0 0 0 0 0 0	3
A A 0 D 0 0 0 0 0 0 0 0 0	6	A 0 0 D 0 0 0 0 0 0 0 0 0	2
A 0 0 A A 0 0 0 0 0 0 0 0	1	A A 0 D 0 0 0 0 0 0 0 0 0	4
A A 0 A A 0 0 0 0 0 0 0 0	5	A 0 0 A A 0 0 0 0 0 0 0 0	1
A A B1 B1 B1 0 0 0 0 0 0 0 0	7	A A 0 A A 0 0 0 0 0 0 0 0	6
A A B1 B2 B2 0 0 0 0 0 0 0 0	4	A 0 B1 B1 B1 0 0 0 0 0 0 0 0	1
A A B2 B2 B2 0 0 0 0 0 0 0 0	2	A 0 B2 B2 B2 0 0 0 0 0 0 0 0	1
A A 0 D D 0 0 0 0 0 0 0 0	1	A A B2 B2 B2 0 0 0 0 0 0 0 0	3
A A 0 0 A A 0 0 0 0 0 0 0	1	A A 0 D D 0 0 0 0 0 0 0 0	3
A A 0 A A A 0 0 0 0 0 0 0	4	A A 0 A A A 0 0 0 0 0 0 0	10
A A 0 D D D 0 0 0 0 0 0 0	1	A 0 0 D D D 0 0 0 0 0 0 0	1

Appendix Table 1.1.—Continued.

A A 0 A A 0 A 0 0 0 0 0 0	1	A A 0 D D D 0 0 0 0 0 0 0	2
A A B1 B2 B2 0 A 0 0 0 0 0 0	1	A A B1 B2 B2 0 A 0 0 0 0 0 0	1
A A B2 B2 B2 0 A 0 0 0 0 0 0	1	A A B2 B2 B2 0 A 0 0 0 0 0 0	1
A A 0 A A A A 0 0 0 0 0 0	2	A 0 0 A A A A 0 0 0 0 0 0	1
A A 0 C 0 D D 0 0 0 0 0 0	3	A A 0 A A A A 0 0 0 0 0 0	2
A A 0 D D D D 0 0 0 0 0 0	3	A 0 0 D D D D 0 0 0 0 0 0	4
A A B2 B2 B2 0 0 A 0 0 0 0 0	1	A A 0 D D D D 0 0 0 0 0 0	12
A A 0 A A 0 A A 0 0 0 0 0	1	A A B1 B1 B1 0 0 A 0 0 0 0 0	1
A A B1 B1 B1 0 A A 0 0 0 0 0	1	A 0 B1 B2 B2 0 0 A 0 0 0 0 0	1
A A B2 B2 B2 0 A A 0 0 0 0 0	1	A A B2 B2 B2 0 0 A 0 0 0 0 0	1
A 0 0 A A A A A 0 0 0 0 0	1	A A 0 A A A 0 A 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 0 0	9	A A 0 A A 0 A A 0 0 0 0 0	1
A A 0 D D D D D 0 0 0 0 0	1	A A B1 B1 B1 0 A A 0 0 0 0 0	2
A A 0 D D D D E 0 0 0 0 0	1	A A B2 B2 B2 0 A A 0 0 0 0 0	3
A A 0 D D D D 0 0 D 0 0 0	1	A 0 0 A A A A A 0 0 0 0 0	1
A A 0 A A 0 0 A 0 0 0 A 0	1	A A 0 A A A A A 0 0 0 0 0	5
A A B1 B2 B2 0 A A 0 0 0 A 0	1	A A 0 D D D D D 0 0 0 0 0	2
A A B2 B2 B2 0 A A 0 0 0 A 0	1	A A 0 A A A A E 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 A 0	2	A A 0 A A 0 A E 0 D 0 0 0	1
A A B1 0 B1 0 0 E D D D A 0	1	A A 0 A A A A 0 0 0 0 A 0	1
A A 0 0 A 0 A 0 0 0 0 0 A	1	A A 0 A A A A A 0 0 0 A 0	3
A A 0 D D D D D 0 D D 0 A	2	A A 0 A A A A E 0 D 0 A 0	1
A A 0 A A A A E D D D 0 A	1	A A 0 D D D D D 0 D D A 0	1
A A 0 A A A A 0 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 0 A	1
A A B2 B2 B2 0 0 A 0 0 0 A A	1	A 0 0 A A 0 A E 0 D 0 0 A	1
A A 0 A A A 0 A 0 0 0 A A	2	A A 0 D D D D 0 0 0 0 A A	1
A A 0 A A 0 A A 0 0 0 A A	1	A A 0 A A A 0 A 0 0 0 A A	1
A A B1 B1 B1 0 A A 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 A A	3
A A B2 B2 B2 0 A A 0 0 0 A A	2	A 0 B2 B2 B2 0 A A 0 0 0 A A	1
A A 0 A A A A A 0 0 0 A A	5	A A B2 B2 B2 0 A A 0 0 0 A A	2
A A 0 C 0 D D E A 0 0 A A	1	A 0 0 A A A A A 0 0 0 A A	1
A A 0 D D D D D 0 0 D A A	1	A A 0 A A A A A 0 0 0 A A	5
A A 0 D D D D D 0 D D A A	1	A A 0 D D D D 0 0 0 D A A	1
Total released (R_k)	208		211

Appendix Table 1.2.—Parameter constraints applied under the full model for each release, representing the minimum estimable model with the maximum number of parameters. Parameters not shown below were estimable by iteratively maximizing the likelihood of the multinomial model. Constraints include parameters that had to be fixed to a constant value or set equal to other parameters because they could not be estimated from the data set of detection histories.

R_1: December 2007		R_2: January 2008	
Parameter	Constraint	Parameter	Constraint
S_{A3}	$= S_{\text{A2}}$	ψ_{C2}	$= 0$
$S_{\text{D7, Sac}}$	$= 1$	$\phi_{\text{D4,E1,Sac}}$	$= 0$
$S_{\text{E1,D5}}$	$= 1$	S_{A3}	$= S_{\text{A2}}$
P_{A3}	$= 0$	S_{B12}	$= 1$
P_{A5}	$= 1$	S_{B22}	$= 1$
$P_{\text{E1,Sac}}$	$= 1$	S_{C1}	$= 0$
P_{B11}	$= 1$	$S_{\text{D7,Sac}}$	$= 1$
P_{B21}	$= 1$	$S_{\text{E1,D5}}$	$= \phi_{\text{D4,D5,Geo}}$
P_{B22}	$= 1$	$S_{\text{E1,A8,Sac}}$	$= 0$
P_{B13}	$= 1$	P_{A3}	$= 0$
P_{B23}	$= 1$	P_{A4}	$= 1$
P_{C1}	$= 1$	P_{A5}	$= 1$
P_{D1}	$= 1$	P_{B11}	$= 1$
$P_{\text{D2,Sac}}$	$= 1$	P_{B12}	$= 1$
$P_{\text{D3,Sac}}$	$= 1$	P_{B13}	$= 1$
$P_{\text{D4,Sac}}$	$= 1$	P_{B21}	$= 1$
$P_{\text{D7,Sac}}$	$= 1$	P_{B22}	$= 1$
$S_{\text{D7,Geo}}$	$= 1$	P_{B23}	$= 1$
$P_{\text{D2,Geo}}$	$= 1$	P_{C1}	$= 0$
$P_{\text{D3,Geo}}$	$= 1$	P_{D1}	$= 1$
$P_{\text{D4,Geo}}$	$= 1$	$P_{\text{D2,Sac}}$	$= 1$
$P_{\text{D5,Geo}}$	$= 1$	$P_{\text{D3,Sac}}$	$= 1$
$P_{\text{D7,Geo}}$	$= 1$	$P_{\text{D4,Sac}}$	$= 1$
$P_{\text{A8,Geo}}$	$= 1$	$P_{\text{E1,Sac}}$	$= 1$
$P_{\text{A9,Geo}}$	$= 1$	$P_{\text{D2,Geo}}$	$= 1$
$P_{\text{E1,Geo}}$	$= 1$	$P_{\text{D3,Geo}}$	$= 1$
$S_{\text{A8,Geo}}$	$= 1$	$P_{\text{A8,Geo}}$	$= 1$
		$P_{\text{E1,Geo}}$	$= 1$
		$S_{\text{A8,Geo}}$	$= 1$

Appendix Table 1.3.—Parameter estimates under the reduced model for releases of acoustically tagged late-fall juvenile Chinook salmon in December, 2007 (R_1) and January, 2008 (R_2). Parameters not estimated are indicated by an “NA” in the estimate column, and parameters fixed at a constant value are noted by an “NA” in the profile likelihood column.

	R_1: December 2007		R_2: January 2008	
Parameter	Estimate ($\widehat{SE}$)	95% Profile likelihood interval	Estimate ($\widehat{SE}$)	95% Profile likelihood interval
S_{A1}	0.951 (0.019)	0.907, 0.981	0.975 (0.020)	0.927, 1.000
S_{A2}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A3}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A4}	0.841 (0.055)	0.715, 0.928	0.942 (0.032)	0.857, 0.985
S_{A5}	0.874 (0.062)	0.734, 0.984	0.914 (0.061)	0.785, 1.000
S_{A6}	0.843 (0.075)	0.671, 0.963	0.728 (0.078)	0.563, 0.864
S_{A7}	0.886 (0.068)	0.733, 1.000	0.890 (0.058)	0.758, 1.000
S_{A8}	0.618 (0.090)	0.441, 0.789	0.548 (0.087)	0.380, 0.716
S_{B11}	0.715 (0.087)	0.534, 0.876	0.600 (0.155)	0.299, 0.855
S_{B12}	0.692 (0.128)	0.423, 0.893	1.000	NA
S_{B13}	0.308 (0.149)	0.087, 0.623	0.765 (0.221)	0.282, 1.000
S_{B21}	0.800 (0.103)	0.560, 0.946	0.923 (0.074)	0.702, 0.995
S_{B22}	0.790 (0.094)	0.576, 0.929	1.000	NA
S_{B23}	0.616 (0.130)	0.360, 0.841	0.728 (0.123)	0.464, 0.921
S_{C1}	0.286 (0.121)	0.099, 0.545	NA	
$S_{D1,Sac}$	0.667 (0.111)	0.437, 0.852	0.818 (0.067)	0.665, 0.923
$S_{D1,Geo}$	0.814 (0.051)	0.702, 0.898	0.938 (0.027)	0.872, 0.977
S_{D2}	0.900 (0.039)	0.808, 0.959	0.932 (0.025)	0.873, 0.970
S_{D3}	0.862 (0.045)	0.758, 0.934	0.772 (0.051)	0.672, 0.885
S_{D4}	0.491 (0.073)	0.352, 0.635	0.395 (0.080)	0.262, 0.604
S_{D5}	0.658 (0.129)	0.411, 0.946	0.733 (0.180)	0.415, 1.000
S_{D6}	0.700 (0.145)	0.393, 0.915	0.709 (0.181)	0.155, 1.000
S_{D7}	1.000	NA	0.866 (0.159)	0.463, 1.000
$S_{E1,D5}$	1.000	NA	0.750 (0.288)	0.245, 1.000
$S_{E1,A8}$	0.433 (0.189)	0.130, 0.780	0.683 (0.279)	0.165, 1.000
ψ_{A1}	0.655 (0.042)	0.570, 0.733	0.802 (0.037)	0.722, 0.868
ψ_{B11}	0.230 (0.037)	0.163, 0.308	0.086 (0.026)	0.044, 0.147
ψ_{B21}	0.115 (0.028)	0.068, 0.178	0.112 (0.029)	0.063, 0.178
ψ_{A2}	0.592 (0.056)	0.481, 0.696	0.612 (0.053)	0.506, 0.711
ψ_{C2}	0.179 (0.043)	0.105, 0.273	0.000	NA
ψ_{D2}	0.230 (0.048)	0.146, 0.331	0.388 (0.053)	0.289, 0.494

Appendix Table 1.3.—Continued.

$\phi_{\mathrm{B11,B12}}$	0.482 (0.096)	0.305, 0.674	0.400 (0.155)	0.146, 0.700
$\phi_{\mathrm{B11,B22}}$	0.233 (0.077)	0.108, 0.403	0.200 (0.127)	0.036, 0.499
$\phi_{\mathrm{A7,A8}}$	0.837 (0.074)	0.679, 0.978	0.781 (0.07)	0.634, 0.914
$\phi_{\mathrm{A7,E1}}$	0.049 (0.034)	0.008, 0.143	0.109 (0.046)	0.040, 0.220
$\phi_{\mathrm{D4,D5}}$	0.351 (0.070)	0.225, 0.497	0.354 (0.079)	0.225, 0.564
$\phi_{\mathrm{D4,E1}}$	0.140 (0.049)	0.063, 0.253	0.041 (0.023)	0.010, 0.102
P_{A2}	0.959 (0.018)	0.915, 0.985	0.852 (0.034)	0.777, 0.910
P_{A3}	0	NA	0.000	NA
P_{A4}	0.949 (0.035)	0.850, 0.991	1.000	NA
P_{A5}	1.000	NA	1.000	NA
P_{A6}	0.821 (0.072)	0.655, 0.932	0.781 (0.073)	0.620, 0.899
P_{A7}	0.829 (0.064)	0.683, 0.928	0.850 (0.057)	0.719, 0.937
$P_{\mathrm{A8,Sac}}$	0.905 (0.064)	0.734, 0.983	0.950 (0.049)	0.798, 0.997
$P_{\mathrm{A8,Geo}}$	1.000	NA	0.950 (0.049)	0.798, 0.997
$P_{\mathrm{A9,Sac}}$	0.812 (0.084)	0.618, 0.937	0.846 (0.071)	0.678, 0.949
$P_{\mathrm{A9,Geo}}$	1.000	NA	0.846 (0.071)	0.678, 0.949
P_{B11}	1.000	NA	1.000	NA
P_{B12}	0.900 (0.095)	0.628, 0.994	1.000	NA
P_{B21}	1.000	NA	1.000	NA
P_{B22}	1.000	NA	1.000	NA
P_{B13}	1.000	NA	1.000	NA
P_{B23}	1.000	NA	1.000	NA
P_{C1}	1.000	NA	NA	
P_{D1}	1.000	NA	1.000	NA
P_{D2}	1.000	NA	1.000	NA
P_{D3}	1.000	NA	1.000	NA
P_{D4}	1.000	NA	0.958 (0.041)	0.829, 0.998
P_{D5}	0.922 (0.075)	0.699, 0.995	0.500 (0.118)	0.133, 0.872
P_{D6}	0.778 (0.139)	0.458, 0.959	0.500 (0.134)	0.255, 0.745
P_{D7}	1.000	NA	0.385 (0.135)	0.046, 0.848
P_{E1}	1.000	NA	1.000	NA
λ	0.748 (0.082)	0.570, 0.883	0.759 (0.080)	0.585, 0.888

Appendix 2

Evaluation of bias in survival and route entrainment probabilities

Since a telemetry station at location A_3 was not implemented during 2008, the parameters S_{A2}, S_{A3}, ψ_{B11}, and ψ_{B21} could not be uniquely estimated without imposing constraints on the parameters. Therefore, we estimated these parameters under the constraint that $S_{A2} = S_{A3}$. Although estimates from one release in 2007 showed little difference between S_{A2} and S_{A3} (Perry et al. 2008, in press), station A_3 has not been monitored for three of the four releases thus far. If S_{A2} is not equal to S_{A3}, then associated estimates of route entrainment and survival probabilities will be biased. Here we evaluate the magnitude of bias introduced by assuming $S_{A2} = S_{A3}$, when in fact S_{A2} differs from S_{A3}.

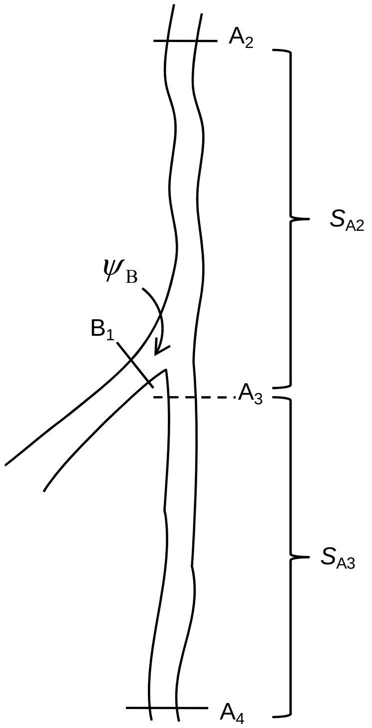
To illustrate the potential bias that might be incurred, we first simplified the problem by assuming a two-branch junction (Appendix Figure 2.1). We were interested not only in bias in ψ_B, but also in bias that might occur in the product $S_{A2}S_{A3}$. This product appears in equations for route specific survival through the Delta for Routes A, C, and D (i.e., S_h). Thus, bias in this product is more relevant than bias in each of the reach-specific survival probabilities. Appendix Figure 2.1 shows a schematic of the problem with the underlying survival and route entrainment parameters. Without a telemetry station at location A_3, only two parameters can be estimated from information provided by telemetry stations at B_1 and A_4. The two estimable parameters are the joint probabilities of the underlying parameters between stations A_2 and B_1, and between A_2 and A_4:

$$\phi_{A2,\,B1} = S_{A2}\psi_B \tag{A1}$$

$$\phi_{A2,\,A4} = S_{A2}S_{A3}\left(1-\psi_B\right) \tag{A2}$$

Where $\phi_{A2,\,B1}$ is the joint probability of surviving the first reach and entering channel B, and $\phi_{A2,\,A4}$ is the joint probability of surviving the first reach, remaining in channel A, and surviving the second reach. These two parameters can always be estimated without bias from the data, as can the total survival from A_2 to either of the downstream exit points:

$$S_{total} = \phi_{A2,\,B1} + \phi_{A2,\,A4} \tag{A3}$$



Appendix Figure 2.1.—Schematic of a two-branch river junction showing location of telemetry stations at A_2, B_2, and A_4. The dashed line notes lack of a telemetry station at A_3. Brackets show the probability of surviving between A_2 and A_3 and between A_3 and A_4. The probability of entering Channel B is Ψ_B, and the probability of remaining in Channel A is 1-Ψ_B.

To quantify bias, we substituted Eqns. A1 and A2 into Eqn. A3, set $S_{A3} = S_{A2}$, and then solved Eqn. A3 for S_{A2} and Eqn. A1 for ψ_B:

$$\tilde{S}_{A2} = \frac{\psi_B - \sqrt{\psi_B{}^2 - 4S_{total}(\psi_B - 1)}}{2(\psi_B - 1)} \tag{A4}$$

and $$\tilde{\psi}_B = \frac{\phi_{A2,\,B1}}{\tilde{S}_{A2}} \tag{A5}$$

Here, $\tilde{S}_{A2}$ and $\tilde{\psi}_B$ will be the biased estimates that result when assuming $S_{A2} = S_{A3}$ when in fact $S_{A2} \neq S_{A3}$; and S_{total} and $\phi_{A2,\,B1}$ are calculated based on the true values of S_{A2}, S_{A3}, and ψ_B.

Estimates of S_{total} from our data will be unbiased regardless of bias that might be present in estimates of S_{A2}, S_{A3}, or ψ_B, and we used this fact to establish the maximum possible bias that could arise by assuming $S_{A2} = S_{A3}$. For example, for the first release in December 2008, we estimated $\hat{\psi}_{\mathrm{B}} = 0.345$ and $\hat{S}_{A2} = \hat{S}_{A3} = 0.919$ (Appendix Table 1.3), resulting in $\hat{S}_{\mathrm{total}} = 0.87$. Now suppose $\hat{\psi}_{\mathrm{B}} = \tilde{\psi}_{\mathrm{B}} = 0.345$ is the biased estimate of ψ_{B}: What true values of ψ_{B} , S_{A2}, and S_{A3} could have produced the observed estimate, $\tilde{\psi}_{\mathrm{B}}$? First, the true parameter values ψ_{B} , S_{A2}, and S_{A3} are constrained such that $\hat{S}_{\mathrm{total}} = 0.87$ (according to Eqn. A3) and $\tilde{\psi}_{\mathrm{B}} = 0.345$ (according to Eqn. A5). Also, given that $\hat{S}_{\mathrm{total}} = 0.87$, S_{A2} and S_{A3} are further constrained such that all of the observed mortality could have occurred in either the first reach (i.e., $S_{A3} = 1$) or the second reach (i.e., $S_{A2} = 1$). Clearly, mortality will occur in both reaches, but we used these two scenarios to bound the extremes of bias that could possibly occur given that $\hat{S}_{\mathrm{total}} = 0.87$ and $\tilde{\psi}_{\mathrm{B}} = 0.345$. Thus, maximum bias is calculated by setting $S_{A2} = 1$ (or $S_{A3} = 1$), and then finding the true values of S_{A3} (or S_{A2}) and ψ_{B} that satisfy $S_{\mathrm{total}} = 0.87$ and $\tilde{\psi}_{\mathrm{B}} = 0.345$. Should the maximum possible bias be low under these extreme scenarios, then we can infer that the realized bias would be even less.

Under these extreme scenarios, we found that maximum possible bias was quite low. For the December release, maximum absolute bias in ψ_{B} was less than 0.028, and bias in $S_{A2}S_{A3}$ was less than 0.035 (Appendix Table 2.1). Maximum possible bias for the January release was even less (Appendix Table 2.1). These findings suggest that the realized bias in these parameters will be much less than the maximum possible bias, given that we know mortality occurs in both reaches, and that past evidence suggests little difference between S_{A2} and S_{A3} (Perry et al. 2008, in press). Our estimates are robust to deviations from $S_{A2} = S_{A3}$ partly due to the relatively high total survival (S_{total}) observed in this reach. Since S_{total} constrains the range of possible true values of S_{A2} and S_{A3}, as S_{total} decreases S_{A2} and S_{A3} may take on a wider range of values between 0 and 1. Thus, as S_{total} decreases, the possible maximum bias will increase under the extreme scenarios of all mortality occurring in either one reach or another.

Although this sensitivity analysis shows that bias was likely minimal, the appropriate course of action is to ensure a telemetry station is implemented at A_3 in future years. Given the influence of Sutter and Steamboat sloughs on migration dynamics through the entire Delta, this river junction is too important to rest future research on such assumptions.

Appendix Table 2.1.—Maximum possible bias induced by assuming $S_{A2} = S_{A3}$, when in fact, all mortality occurs in either the upstream reach or the downstream reach.

	True values				Estimates when assuming $S_{A2} = S_{A3}$		Bias	
Release	S_{A2}	S_{A3}	ψ_B	S_{total}	$\tilde{S}_{A2}$	$\tilde{\psi}_B$	$\psi_B - \tilde{\psi}_B$	$S_{A2}S_{A3} - \tilde{S}_{A2}^2$
R_1: December	0.870	1.000	0.364	0.870	0.918	0.345	-0.019	-0.025
	1.000	0.810	0.318	0.870	0.920	0.345	0.028	0.035
R_2: January	0.852	1.000	0.213	0.852	0.914	0.198	-0.014	-0.016
	1.000	0.819	0.182	0.852	0.915	0.198	0.017	0.017

REFERENCE EXHIBIT I

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[Article]

Estimating Survival and Migration Route Probabilities of Juvenile Chinook Salmon in the Sacramento–San Joaquin River Delta

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Abstract.—Juvenile Chinook salmon *Oncorhynchus tshawytscha* emigrating from natal tributaries of the Sacramento River must negotiate the Sacramento–San Joaquin River Delta, a complex network of natural and man-made channels linking the Sacramento River with San Francisco Bay. Natural processes and water management actions affect the fractions of the population using the different migration routes through the delta and survival within those routes. However, estimating these demographic parameters is difficult using traditional mark–recapture techniques, which depend on the physical recapture of fish (e.g., coded wire tags). Thus, our goals were to (1) develop a mark–recapture model to explicitly estimate the survival and migration route probabilities for each of four migration routes through the delta, (2) link these route-specific probabilities to population-level survival, and (3) apply this model to the first available acoustic telemetry data of smolt migration through the delta. The point estimate of survival through the delta for 64 tagged fish released in December 2006 ($\hat{S}_{\text{delta}} = 0.351$; SE = 0.101) was lower than that for 80 tagged fish released in January 2007 ($\hat{S}_{\text{delta}} = 0.543$; SE = 0.070). We attributed the observed difference in survival between releases to differences in survival for given migration routes and changes in the proportions of fish using the different routes. Our study shows how movements among, and survival within, migration routes interact to influence population-level survival through the delta. Thus, concurrent estimation of both route-specific migration and survival probabilities is critical to understanding the factors affecting population-level survival in a spatially complex environment such as the delta.

Many stocks of Chinook salmon *Oncorhynchus tshawytscha* in California, Washington, and Oregon are listed as threatened or endangered under the Endangered Species Act (Nehlsen et al. 1991; Myers et al. 1998). In the Central Valley of California, the winter, spring, and fall–late fall runs of Chinook salmon are federally listed as endangered, threatened, and a "species of concern," respectively (NMFS 1997). Recently, owing to below-target returns of fall Chinook salmon to the Sacramento River, the National Marine Fisheries Service declared a federal disaster and closed the 2008 salmon fishery along the West Coast (NOAA 2008). Understanding factors affecting survival of salmon is therefore critical to devising effective recovery strategies for these populations.

An important stage in the life history of Chinook salmon is the period of migration from natal tributaries to the ocean, when juvenile salmon in the Sacramento River may suffer mortality from a host of anthropogenic and natural factors (Baker and Morhardt 2001; Brandes and McLain 2001; Williams 2006). Juvenile Chinook salmon emigrating from the Sacramento River must pass through the Sacramento–San Joaquin River Delta, a complex network of natural and man-made river channels (Nichols et al. 1986). Juvenile salmon may migrate through a number of routes on their journey to the ocean. For example, they may migrate within the main-stem Sacramento River leading directly into San Francisco Bay (see route A in Figure 1). However, they may also migrate through longer secondary routes such as the interior delta, the network

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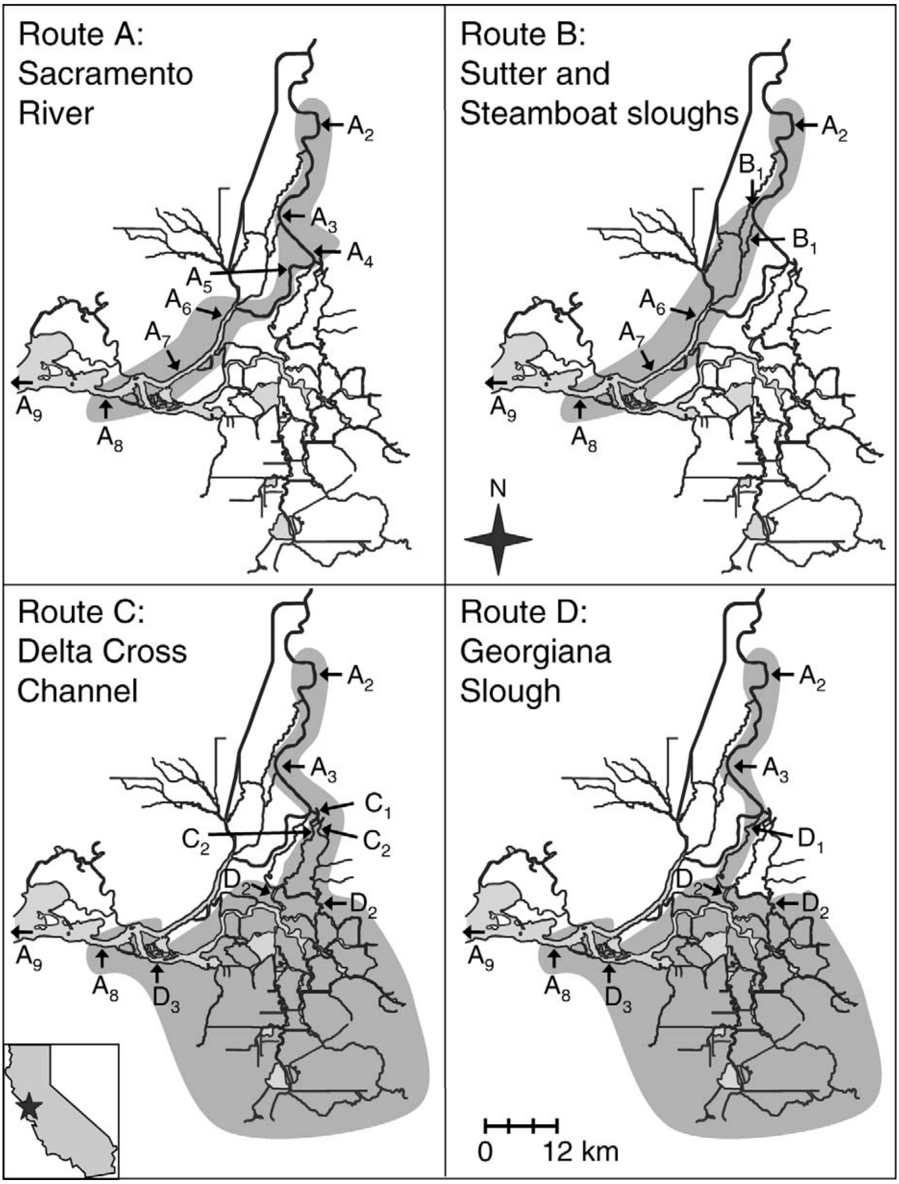

FIGURE 1.—Maps of the Sacramento–San Joaquin River Delta, with shaded regions showing the river reaches that comprise four different migration routes. Arrows show the locations of the telemetry stations specific to each route. The delta extends from station A_2 at Freeport to station A_8 at Chipps Island. The first river junction occurs where Sutter and Steamboat sloughs (B_1) diverge from the Sacramento River at station A_3. The second junction occurs where the Delta Cross Channel (C_1) and Georgiana Slough (D_1) diverge from the Sacramento River at station A_4. For routes C and D, the interior delta is the large shaded region to the south of station D_2. Telemetry stations with the same label (B_1, C_2, and D_2) were pooled as one station in the mark–recapture model. Station A_3 was not operational during the first release in December 2006. Station A_9 pools all of the telemetry stations in San Francisco Bay downstream of A_8. The release site (rkm 92) was 19 rkm upriver of station A_2 (rkm 73).

of channels to the south of the main-stem Sacramento River (see routes C and D in Figure 1).

Both human actions and natural processes affect the magnitude and distribution of Sacramento River flow among the channel network of the delta. Inflow into the delta from the Sacramento River is largely controlled by upstream releases of water from storage reservoirs. Within the delta, water distribution is affected by two water pumping projects in the southern delta (the State Water Project and Central Valley Project). These projects pump water from the delta for agricultural and municipal uses, and can export up to 50% of the total inflow (Nichols et al. 1986). Associated with the water pumping projects is the Delta Cross Channel, a man-made channel that diverts river flow from the Sacramento River into the interior delta (see C_1 in route C, Figure 1). In addition to these human influences on water flow through the delta, natural processes include seasonal rainfall and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and biweekly time scales.

As juvenile salmon migrate among the complex channel network of the delta, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and, ultimately, survival. For example, growth of juvenile salmon in the Yolo Bypass, a seasonally inundated flood plain, was significantly greater than in the main-stem Sacramento River (Sommer et al. 2001). In contrast, juvenile salmon entering the interior delta must traverse longer migration routes and are exposed to entrainment at the water pumping projects, both of which may decrease survival of fish using this migratory pathway (Brandes and McLain 2001; Newman and Rice 2002; Newman 2003; Kimmerer 2008; Newman and Brandes 2009, this issue). These examples show that population-level survival rates of juvenile salmon migrating through the delta will be driven by (1) the survival rates arising from the biotic and abiotic processes unique to each migration route, and (2) the proportion of the population using each migration route. In turn, natural and human-imposed variation in discharge and water distribution will affect population dispersal and survival rates within each channel, driving population-level survival through the delta.

Currently, there is limited understanding of how water management actions in the delta affect population distribution and route-specific survival of juvenile salmon. Evidence suggests that survival of fish migrating through the interior delta decreases with increasing water exports (Brandes and McLain 2001; Newman 2003). Water exports could decrease survival by increasing migration times through the interior Delta, by increasing encounter rates with predators, and by direct entrainment of fish at pumping facilities located in the interior delta. Operation of the Delta Cross Channel likely affects the proportion of the population entering the interior Delta. To date, the proportion of fish migrating through the interior delta has not been estimated, yet such estimates are critical to understand the relative effect of water management actions on the population as a whole (Newman and Brandes 2009). Thus, currently lacking is a population-level approach that quantifies dispersal of the population among migration routes and that measures survival within these routes to better understand the influence of management actions on population-level survival.

In this study, we develop a mark–recapture model for the delta to explicitly estimate the probability of migrating through each of four migration routes and the probability of surviving through each route. Next, we quantify population-level survival through the delta as a function of the route-specific migration and survival probabilities. We then apply this model to the first available acoustic telemetry data of juvenile late-fall run Chinook salmon. Acoustic telemetry is a passive "capture" technique enabling individual fish to be detected repeatedly by multiple telemetry stations as they migrate through the delta. Given estimates of route-specific survival and movement through the delta from the acoustic telemetry data, we then examine how each of these components interacted to affect survival of the population migrating through the delta.

Methods

Telemetry system

Telemetry stations were deployed in the delta to monitor movement of tagged fish among four major migration routes through the delta (Figure 1): the main-stem Sacramento River (route A); Sutter and Steamboat sloughs (route B); the interior delta via the Delta Cross Channel (route C); and the interior delta via Georgiana Slough (route D). Although there are numerous possible migration pathways, we focused on these routes because management actions likely have the largest influence on movement and survival among these routes. For example, fish may enter the interior delta from the Sacramento River through either the Delta Cross Channel or Georgiana Slough, where they subsequently become vulnerable to migration delays and entrainment at the water pumping projects. Steamboat and Sutter sloughs may be an important migration route because fish using this route bypass the Delta Cross Channel and Georgiana Slough (Figure 1). Thus, fish migrating through Steamboat and Sutter sloughs are unable to enter the interior delta through the Delta Cross Channel or Georgiana Slough.

Telemetry stations were labeled hierarchically to reflect the branching nature of channels at river junctions and their subsequent downstream convergence at the confluence of river channels (Figure 1). Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco, Ltd.; Model VR2), depending on the number of monitors needed to maximize detection probabilities at each station. Since the Sacramento River is the primary migration route, the *i*th telemetry station within this route was denoted as A_i from the release site (A_1 located at river kilometer [rkm] 92) to the last telemetry station in the delta at Chipps Island (A_8 at rkm −9; by convention, rkm 0 is defined at the southern tip of Sherman Island, which is 9 rkm upstream of station A_8). Migrating juvenile salmon first arrive at Sutter and Steamboat sloughs (B_1, rkm 43 and rkm 38), which diverge from the Sacramento River at the first river junction and converge again with the Sacramento River upstream of A_6 (rkm 19). Fish remaining in the Sacramento River then pass the Delta Cross Channel and Georgiana Slough at the second river junction. For the Delta Cross Channel, stations were labeled with C_i beginning where the Delta Cross Channel diverges from the Sacramento River at C_1 (rkm 60) and ending when these river channels converge with the interior delta at D_2 (rkm 40 and rkm 47). Telemetry stations within Georgiana Slough and the interior delta were labeled as D_i where Georgiana Slough branches off the main-stem Sacramento River (D_1, rkm 58) until convergence of the interior delta with the Sacramento River at D_3 (rkm 5). Following this hierarchy, routes A, B, C, and D contained eight, one, two, and three telemetry stations, respectively, for a total of 14 telemetry stations within the delta. Parameter subscripting and coding of detection histories followed this hierarchical structure (see the section on model development below). With this configuration of telemetry stations, survival in the final reach is confounded with detection probability at the last telemetry station (Skalski et al. 2001). Therefore, to estimate survival to the terminus of the delta and detection probability at the last station in the delta (A_8), we formed one additional telemetry station by pooling detections from numerous tag detecting monitors downstream of A_8 in San Francisco Bay. Most of these detections occurred at three primary stations that provided nearly complete cross-sectional coverage of San Francisco Bay at bridges located at rkm −37, rkm −64, and rkm −77, but single-monitor stations at other locations were also included.

Fish tagging and release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (rkm 431). For the first release in December, we used a 1.44-g tag (Vemco, Ltd.; Model V7–1 L-R64K, 40-d expected battery life), and for the second release in January we used a 1.58-g tag (Vemco, Ltd.; Model V7–2 L-R64K-2, 95-d expected battery life). Except for a minimum size criterion of 140-mm fork length (FL), fish were randomly selected for tagging, resulting in a mean FL of 164.6 mm (SD = 10.9) and mean weight of 53.5 g (SD = 12.6). The tag weight represented 2.7% of the mean fish weight (range = 1.3–3.8%) for the December release and 3.0% (range = 1.9–4.9%) for the January release. Although recommendations for maximum tag-to-body weight ratios have varied (Jepsen et al. 2004), we followed Adams et al. (1998) guidance for a maximum tag-to-body weight ratio of 5%. Fish were fasted for 24 h prior to surgery to ensure they were in a postabsorptive state. To surgically implant transmitters, fish were anesthetized in 90 mg/L tricaine methanesulfonate (MS-222) until they lost equilibrium. A fish was then placed in a light anesthetic bath (30 mg/L MS-222), ventral side up, and a small incision was made in the abdomen between the pectoral fins and the pelvic girdle. The transmitter was inserted into the peritoneal cavity, and the incision was closed with two interrupted sutures (4–0 nylon sutures with FS-2 cutting needle). Tagged fish were then returned to raceways and were allowed to recover for 7 d prior to release. All fish survived the recovery period. We observed no aberrant physiological or behavioral effects of tagging, based on laboratory studies examining growth, wound healing, and tag retention of late-fall Chinook salmon (A. Ammann, unpublished data).

Next, fish were transported to release sites in the Sacramento River near Sacramento, California (rkm 92). Fish were then transferred to net-pens (3-m square holding nets supported by pontoons) at the release site and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. Fish were transported and held in four separate groups, and each group was released at roughly 6-h intervals over a 24-h period on 5 December 2006 (release 1) and again on 17 January 2007 (release 2). Each release was carried out over a 24-h period to distribute tagged fish over the tidal and diel cycle. The total sample size consisted of 64 acoustically tagged fish in December 2006 and 80 acoustically tagged fish in January 2007.

Model development

We developed a mark–recapture model that estimates three sets of parameters: detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (ψ_{hl}). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h (h = A, B, C, D; Figure 2). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station i to $i + 1$ within route h, conditional on surviving to station i (Figure 2). Route entrainment probabilities (ψ_{hl}) estimate the probability of a fish entering route h at junction l (l = 1, 2), conditional on fish surviving to junction l (Figure 2). In addition, the parameter ω_{open} estimates the probability

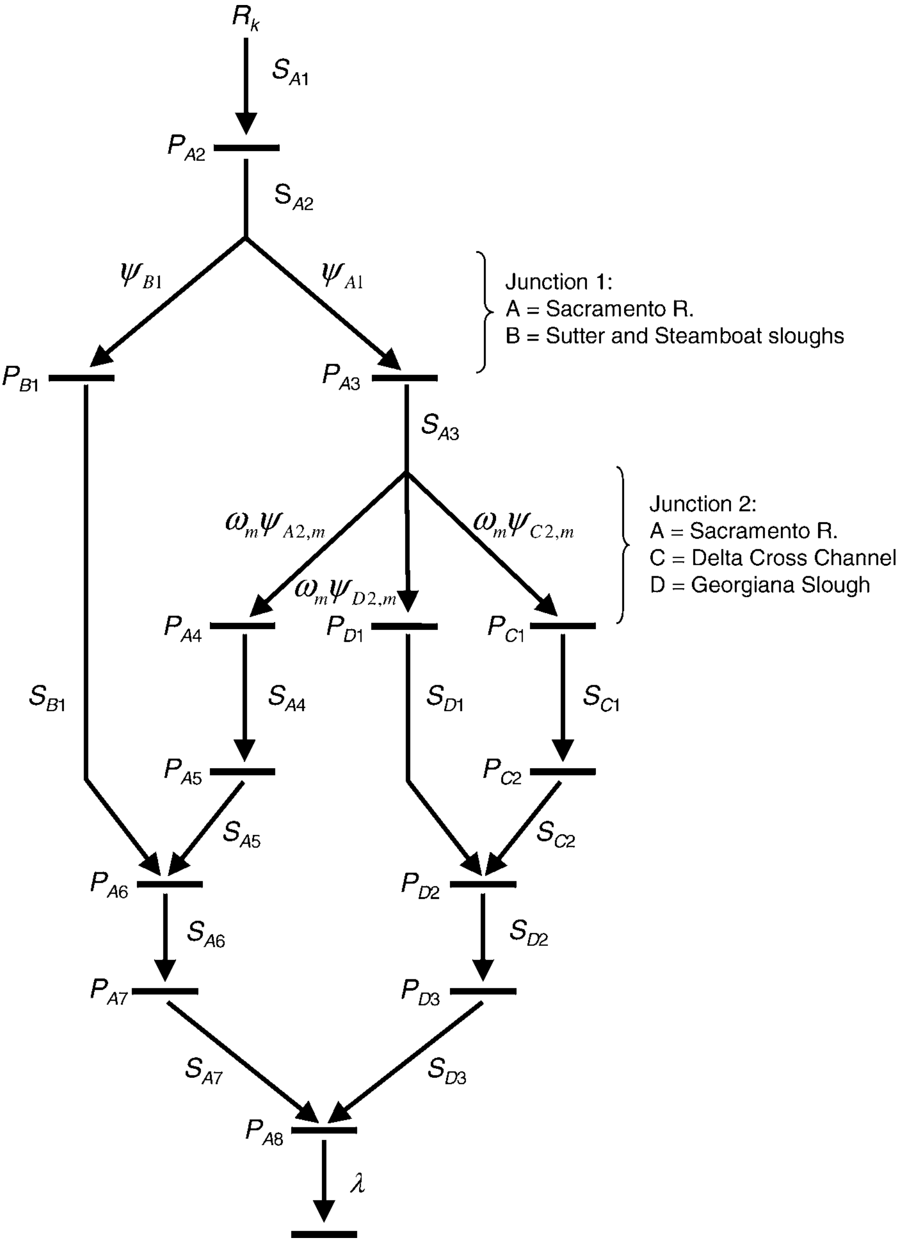

FIGURE 2.—Schematic of the mark–recapture model used to estimate survival (S_{hi}), detection (P_{hi}), and route entrainment (ψ_{hl}) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made on 5 December 2006 and 17 January 2007. See text and Figure 1 for additional information.

of fish passing junction 2 when the Delta Cross Channel was open. This model can be classified as a generalization of the standard Cormack–Jolly–Seber (CJS) mark–recapture model (Cormack 1964; Jolly 1965; Seber 1965) and a special case of a multistate mark–recapture model where the route entrainment probabilities represent a constrained matrix of state transition probabilities (Lebreton and Pradel 2002; Williams et al. 2002). Statistical assumptions associated with a model of this structure are detailed in Burnham et al. (1987) and Skalski et al. (2002).

The first river junction was modeled as a two-branch junction where detections at the entrance to either Sutter or Steamboat Slough (station B_1; Figure 1) were pooled to estimate a single route entrainment probability. Thus, the parameter ψ_{B1} estimates the probability of being entrained into either Sutter or Steamboat Slough at the first river junction (Figure 2). Conversely,

$$1 - \psi_{B1} = \psi_{A1}$$

is the probability of remaining in the Sacramento River at the first junction (Figure 2). The second junction was modeled as a three-branch junction, where

$$\psi_{A2}, \psi_{C2}, \quad \text{and} \quad 1 - \psi_{A2} - \psi_{C2} = \psi_{D2}$$

estimate the probabilities of remaining in the Sacramento River (route A), being entrained into the Delta Cross Channel (route C), and entering Georgiana Slough (route D) at junction 2 (Figure 2). Because ψ_{C2} equals 0 when the Delta Cross Channel is closed, route entrainment probabilities at junction 2 depend on the position of the Delta Cross Channel gate when fish migrate past this location (Figure 2).

While some survival probabilities estimate survival within a given river channel from telemetry station i to $i + 1$ (e.g., S_{A2}), others represent survival of fish migrating through a number of possible migration pathways. For example, fish entering Sutter or Steamboat Slough at B_1 may migrate through a northern or a southern channel (Figure 1). The parameter S_{B1}, estimating survival between sites B_1 and A_6, therefore represents an average of survival in each channel weighted by the proportion of fish using each channel. Note, however, that to separately estimate the underlying components of S_{B1}, additional telemetry stations would need to be placed at key channel junctions within this route. Similar survival probabilities include S_{C2} and S_{D2}, the latter of which encompasses much of the interior delta (Figure 1).

With this model structure, the full model contains 33 parameters: 13 detection probabilities, 13 survival probabilities, five route entrainment probabilities, and ω_{open} (Figure 2). The final parameter, λ, estimates the joint probabilities of surviving downstream of A_8 and being detected at telemetry stations comprising A_9. Thus, λ has little biological meaning but must be included in the model in order to estimate survival to the terminus of the delta at A_8.

Parameter estimation

Prior to parameter estimation, the records of tag detections were processed to eliminate false-positive detections using methods based on Skalski et al. (2002) and Pincock (2008). False-positive detections of acoustic tags occur primarily when two or more tags are simultaneously present within the range of a given monitor, and simultaneous tag transmissions "collide" to produce a valid tag code that is not actually present at the monitor (Pincock 2008). Our first criterion considered detections as valid if a minimum of two consecutive detections occurred within a 30-min period at a given telemetry station. Although this criterion minimizes the probability of accepting a false-positive detection, Pincock (2008) showed that a pair of false-positive detections with a time interval of less than 30 min occurred on average once every 30 d when simulating 10 tags simultaneously present at a monitor. Thus, our second criterion considered records with two detections at a given location as valid only if these detections were consistent with the spatiotemporal history of a tagged fish moving through the system of telemetry stations (Skalski et al. 2002). The detection records of five tagged fish suggested they had been consumed by piscivorous predators as was evidenced by their directed upstream movement for long distance and against the flow. We truncated the detection record of these fish to the last known location of the live tagged fish. All other detections were considered to have been live juvenile salmon. In the lower Sacramento River (sites A_6–A_8), tag detection and discharge data showed that juvenile salmon were often advected upstream on the flood tides and downstream on the ebb tides. In these cases, we used the final downstream series of detections in forming the detection history.

We used maximum likelihood techniques to estimate parameters based on a multinomial probability model that categorized each fish into a mutually exclusive and exhaustive detection history. Detection histories compactly describe the migration and detection process of fish moving through the network of telemetry stations. For example, the history 1A0AAAAAA indicates a fish was released ("1"), detected in the Sacramento River at A_2 ("A"), not detected in the Sacramento River at A_3 ("0"), and then subsequently detected at every other telemetry station in the Sacramento River ("AAAAAA"). This model has 912 possible detection histories, but with release sample sizes of $R_1 = 64$ and $R_2 = 80$ tagged fish, not all histories are observed.

Each detection history represents one of the 912 cells of a multinomial distribution where the probability of each cell is defined as a function of the detection, survival, and route entrainment probabilities. For example, the probability of history 1A0AAAAAA can be expressed as

$$S_{A1}P_{A2}S_{A2}\psi_{A1}(1 - P_{A3})S_{A3}\omega_{open}\psi_{A2,\,open}P_{A4}S_{A4}P_{A5} \\ \times S_{A5}P_{A6}S_{A6}P_{A7}S_{A7}P_{A8}\lambda.$$

In words, the probability of this detection history is the joint probability of surviving the first reach (S_{A1})

and being detected at A_2 (P_{A2}); surviving the second reach (S_{A2}), remaining in the Sacramento River at junction 1 (ψ_{A1}), and not being detected at A_3 ($1 - P_{A3}$); and surviving the third reach (S_{A3}), remaining in the Sacramento River at junction 2 ($\psi_{A2,\text{open}}$) when the Delta Cross Channel was open (ω_{open}), and surviving and being detected at all remaining stations in the Sacramento River (Figure 2).

Given the cell probabilities, the maximum likelihood estimates are found by maximizing the likelihood function of a multinomial distribution with respect to the parameters, that is,

$$L(\underset{\sim}{\theta} \mid R_k, n_j) \propto \prod_{j=1}^{912} \pi_j^{n_j}$$

where R_k is the number of fish released in the kth release-group ($k = 1, 2$), n_j is the number of fish with the jth detection history, and π_j is the probability of the jth detection history expressed as a function of the parameters ($\underset{\sim}{\theta}$). The likelihood was numerically maximized with respect to the parameters by using algorithms provided in the software programs R (R Development Core Team 2008) and USER (Lady et al. 2008). The variance–covariance matrix was estimated as the inverse of the Hessian matrix. We used the delta method (Seber 1982) to estimate the variance of parameters that are functions of the maximum likelihood estimates (e.g., $\psi_{D2} = 1 - \psi_{A2} - \psi_{C2}$). Uncertainty in parameter estimates is presented both as SEs and 95% profile likelihood confidence intervals.

Parameters were estimated separately for each release, but the model for each release was reduced from the full model because not all parameters could be estimated from the tag detection data. For the first release in December, P_{A3} equaled 0 because station A_3 was not operational, rendering limited ability to uniquely estimate the parameters S_{A2}, ψ_{B1}, and S_{A3}. However, S_{A2} and ψ_{B1} can be estimated under the assumption that S_{A2} equals S_{A3}, which was supported by the similarity of S_{A2} and S_{A3} measured during the second release (for R_2: $\hat{S}_{A2} = 0.959$, SE = 0.024; $\hat{S}_{A3} = 0.976$, SE = 0.025). The Delta Cross Channel gate was closed for the second release, so ω_{open} and ψ_{C2} were set to zero, which eliminated P_{C1}, S_{C1}, P_{C2}, and S_{C2} from the model. For both releases, a number of detection probabilities were set to 1 because of perfect detection data. Last, due to low detection frequencies in the interior delta, the parameters S_{D1} and S_{D2} could not be estimated for the first release, but the product $S_{D1}S_{D2}$ was estimable as a single parameter. Likewise, for the second release only the product $S_{D1}S_{D2}S_{D3}$ was estimable as a single parameter.

Survival through the delta.—Our model estimates the individual components that comprise survival of the population migrating through the delta, defined as survival of tagged fish from the entrance to the delta at station A_2 (Freeport, rkm 73) to the exit of the delta at station A_8 (Chipps Island, rkm −9). Population-level survival through the delta was estimated from the individual components as

$$S_{\text{delta}} = \sum_{h=A}^{D} \psi_h S_h \qquad (1)$$

where S_h is the probability of surviving the delta given the specific migration route taken through the delta, and ψ_h is the probability of migrating through the delta via one of four migration routes (A = Sacramento River, B = Sutter and Steamboat sloughs, C = Delta Cross Channel, D = Georgiana Slough). Thus, population survival through the delta is a weighted average of the route-specific survival probabilities with weights equal to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\psi_A = \psi_{A1}\psi_{A2} \qquad (2)$$

$$\psi_B = \psi_{B1} \qquad (3)$$

$$\psi_C = \psi_{A1}\psi_{C2} \qquad (4)$$

$$\psi_D = \psi_{A1}\psi_{D2} \qquad (5)$$

For instance, consider a fish that migrates through the delta via the Delta Cross Channel (route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability ψ_{C2}. Thus, the probability of a fish migrating through the delta via the Delta Cross Channel (ψ_C) is the product of these route entrainment probabilities, $\psi_{A1}\psi_{C2}$. For release 1, when the Delta Cross Channel was both open and closed, $\psi_{h2} = \omega_{\text{open}}\psi_{h2,\text{open}} + (1 - \omega_{\text{open}})\psi_{h2,\text{closed}}$.

Survival through the delta for a given migration route (S_h) is the product of the reach-specific survival probabilities that trace each migration path through the delta between points A_2 and A_8 (Figures 1, 2):

$$S_A = S_{A2}S_{A3}S_{A4}S_{A5}S_{A6}S_{A7} \qquad (6)$$

$$S_B = S_{A2}S_{B1}S_{A6}S_{A7} \qquad (7)$$

$$S_C = S_{A2}S_{A3}S_{C1}S_{C2}S_{D2}S_{D3} \qquad (8)$$

and

$$S_D = S_{A2}S_{A3}S_{D1}S_{D2}S_{D3}. \tag{9}$$

We also compared our estimates of S_{delta} described above with estimates produced by a standard three-station CJS model. We included telemetry stations A_2, A_8, and A_9 in this model. Here, S_{delta} is estimated directly from the model as the probability of surviving from station A_2 to A_8. We compared the two approaches to ensure they produced similar estimates and to examine the SEs produced under each approach. Given that the CJS model contained many fewer parameters (four for R_1 and five for R_2), we suspected that the CJS model might yield more precise estimates of S_{delta}.

Results

River Conditions and Migration Timing

For the first release in December, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport (U.S. Geological Survey [USGS] gauge 11447650 near station A_2; Figure 1) increased from 365 to 682 m^3/s (Figure 3). The Delta Cross Channel was open when most of these fish passed the second river junction (Figure 3). However, the Delta Cross Channel closed at 1000 hours on 15 December 2006 and remained closed for the balance of the study (Figure 3). River discharge receded to about 500 m^3/s when fish from the December release were migrating through the lower reaches of the delta (Figure 3). In contrast to December, river discharge for the January release was low and stable during much of the migration period (Figure 3). Daily discharge of the Sacramento River remained near 500 m^3/s until 9 February, after which discharge increased to 1,100 m^3/s. However, this increase in flow occurred after most fish had passed through the lower reaches of the delta (Figure 3). Water exports at the delta pumping stations were stable within each migration period, averaging 305 m^3/s for the December migration period and 193 m^3/s for the January period (Figure 3).

Coincident with lower river discharge, fish released in January took substantially longer to migrate through the delta and exhibited higher variation in travel times relative to fish released in December (Figure 3). Among routes, travel times for the December release from the release point to the lower delta (stations A_7 and D_3) were quickest for fish migrating through Sutter and Steamboat sloughs (median = 7 d; interquartile range (25th to 75th percentile) = 6.1–11.7 d; $n = 5$), followed by the Sacramento River (median = 10.7 d; interquartile range = 9.3–12.5 d; $n = 9$) and the interior delta via the Delta Cross Channel and Georgiana Slough (median = 13.8 d; interquartile range = 13.4–19.1 d; $n = 5$). For the January release, travel times were similar for fish migrating through the Sacramento River (median = 18.1 d; interquartile range = 13.2–23.9 d; $n = 19$) and Sutter and Steamboat sloughs (median = 17.8 d; interquartile range = 12.7–27.3 d; $n = 17$). We obtained travel times through the interior delta for only one fish in the January release, which took 33.9 d to travel from release to the lower delta.

Migration Routing

As juvenile salmon migrated past the first river junction, a large proportion of both release-groups left the Sacramento River and migrated through Sutter and Steamboat sloughs (for R_1: $\hat{\psi}_{B1} = 0.296$; for R_2: $\hat{\psi}_{B1} = 0.414$). For the December release, most fish remaining in Sacramento River encountered the second river junction when the Delta Cross Channel was open ($\hat{\omega}_{open} = 0.861$; SE = 0.058), and 39% percent of these fish were entrained into the Delta Cross Channel ($\hat{\psi}_{C2,open} = 0.387$; SE = 0.087). Regardless of release-group or position of the Delta Cross Channel gate, similar fractions of fish passing junction 2 were entrained into Georgiana Slough (for R_1: $\hat{\psi}_{D2,open} = 0.161$, SE = 0.066; $\hat{\psi}_{D2,closed} = 0.200$, SE = 0.179; for R_2: $\hat{\psi}_{D2,closed} = 0.150$, SE = 0.056). The remaining 45% of fish passing junction 2 when the Delta Cross Channel was open stayed in the Sacramento River ($\hat{\psi}_{A2,open} = 0.452$; SE = 0.089), whereas nearly twice that fraction remained in Sacramento River when the Delta Cross Channel was closed (for R_1: $\hat{\psi}_{A2,closed} = 0.800$, SE = 0.179; for R_2: $\hat{\psi}_{A2,closed} = 0.850$, SE = 0.056).

A substantial proportion of fish migrating past junction 2 entered the interior delta through the Delta Cross Channel and Georgiana Slough. However, a lower proportion of the population entered the interior delta because some fish bypassed the second river junction by migrating through Sutter and Steamboat sloughs (Figure 1). Accounting for population distribution among all routes, 23.5% were entrained into the Delta Cross Channel ($\hat{\psi}_C$), 11.7% entered Georgiana Slough ($\hat{\psi}_D$), and 35.2% migrated within the Sacramento River ($\hat{\psi}_A$) for the December release when the Delta Cross Channel was open during much of the migration period (Table 1). In contrast, 8.8% migrated through Georgiana Slough and 49.8% remained in the Sacramento River in January when the Delta Cross Channel was closed (Table 1). Because Sutter and Steamboat sloughs rejoin the Sacramento River upstream of telemetry station A_6, much of this migration route through the delta (route B) consists of the main-stem Sacramento River (Figure 1). Thus for the December release, 64.8% of fish took migration routes largely consisting of the Sacramento River ($\hat{\psi}_A$

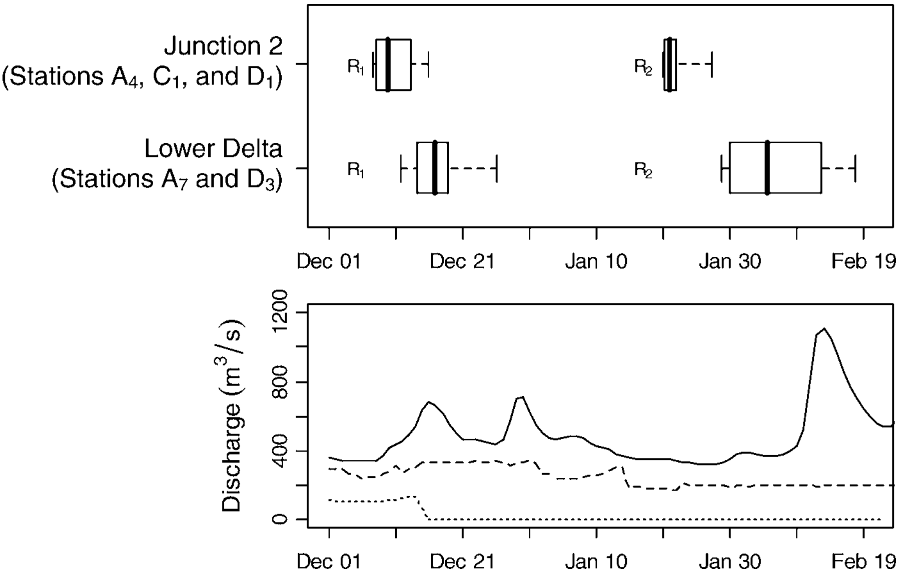

FIGURE 3.—In the upper panel are box plots showing the distribution of arrival dates at junction 2 on the Sacramento River and near the exit of the delta. The two release dates shown are 5 December 2006 (R_1; 64 tagged fish) and 17 January 2007 (R_2; 80 fish). The whiskers represent the 10th and 90th percentiles, the boxes encompass the 25th to 75th percentiles, and the lines within the boxes are the median arrival dates. The lower panel shows river discharge (solid line), which is the tidally filtered daily discharge of the Sacramento River at Freeport (near telemetry station A_2); the Delta Cross Channel discharge (dotted line), which is the tidally filtered daily discharge at that point; and water exports (dashed line), which are the total daily discharge of water from the delta at the pumping projects.

$+ \hat{\psi}_B$) and 35.2% were entrained into the interior delta via the Delta Cross Channel and Georgiana Slough ($\hat{\psi}_C + \hat{\psi}_D$; Table 1). In contrast, only 8.8% percent of fish were entrained into the interior delta through Georgiana Slough in January when the Delta Cross Channel was closed, the remaining 91.2% migrating mostly within the Sacramento River ($\hat{\psi}_A + \hat{\psi}_B$; Table 1).

We found that migration route probabilities (ψ_h) corresponded well with the fraction of total river discharge in each route (Figure 4). Distribution of river flow among the four migration routes was calculated as the fraction of mean discharge of each route relative to the mean discharge of the Sacramento River at Freeport (near station A_2), upstream of the two river junctions. Steamboat and Sutter sloughs diverted 33.4% and 37.6%, respectively, of the mean flow of the Sacramento River during the December and January migration period, accounting for the large proportion of

TABLE 1.—Route-specific survival through the Sacramento–San Joaquin River Delta ($\hat{S}_h$) and the probability of migrating through each route ($\hat{\psi}_h$) for acoustically tagged fall-run juvenile Chinook salmon released on 5 December 2006 and 17 January 2007. Also shown is population survival through the delta, which is the average of route-specific survival weighted by the probability of migrating through each route; NA = not applicable.

Migration route	$\hat{S}_h$ (SE)	95% profile likelihood interval	$\hat{\psi}_h$ (SE)	95% profile likelihood interval
		5 December 2006		
Sacramento River	0.443 (0.146)	0.222–0.910	0.352 (0.066)	0.231, 0.487
Steamboat and Sutter sloughs	0.263 (0.112)	0.102–0.607	0.296 (0.062)	0.186, 0.426
Delta Cross Channel	0.332 (0.152)	0.116–0.783	0.235 (0.059)	0.133, 0.361
Georgiana Slough	0.332 (0.179)	0.087–0.848	0.117 (0.045)	0.048, 0.223
All routes	0.351 (0.101)	0.200–0.692		
		17 January 2007		
Sacramento River	0.564 (0.086)	0.403–0.741	0.498 (0.060)	0.383, 0.614
Steamboat and Sutter sloughs	0.561 (0.092)	0.388–0.747	0.414 (0.059)	0.303, 0.531
Delta Cross Channel	NA		0.000	NA
Georgiana Slough	0.344 (0.200)	0.067–0.753	0.088 (0.034)	0.036, 0.170
All routes	0.543 (0.070)	0.416–0.691		

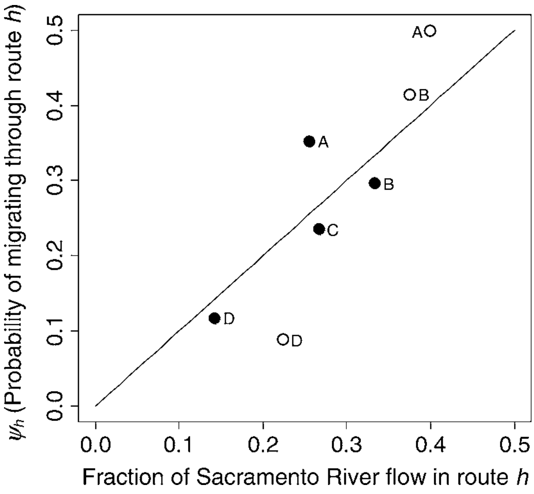

FIGURE 4.—The probability of migrating through route h as a function of the proportion of total river flow in route h for tagged late-fall juvenile Chinook salmon released on 5 December 2006 (filled symbols) and 17 January 2007 (open symbols). Data labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively. The 45° reference line shows where the fraction migrating through a particular route is equal to the proportion of flow in that route.

fish using this migration route (Figure 4). At the second river junction, operation of the Delta Cross Channel influenced the relative discharge of the Sacramento River as flow in the Sacramento River downstream of junction 2 represented 25.6% of its total discharge when the Delta Cross Channel was open (December release) compared with 40.0% when the Delta Cross Channel was closed (January release). The increase in relative flow of the Sacramento River due to closure of the Delta Cross Channel was accompanied by an increase in the fraction of fish migrating through this route (Figure 4). For both releases, the proportion of fish migrating within the Sacramento River was about 10% points higher than the fraction of flow remaining in the Sacramento River, and for the January release the fraction migrating through Georgiana Slough was about 10% lower than the fraction of flow (Figure 4).

Survival through the Delta

Overall, the estimate of survival through the Delta for the December release was lower than for January (for R_1: $\hat{S}_{\text{delta}} = 0.351$; for R_2: $\hat{S}_{\text{delta}} = 0.543$; Table 1) despite higher discharge and shorter travel times through the delta for the December release (Figure 2). The CJS model produced nearly the same point estimates and SEs (for R_1: $\hat{S}_{\text{delta}} = 0.351$, SE = 0.101; for R_2: $\hat{S}_{\text{delta}} = 0.536$, SE = 0.070). This finding supports the validity of our more complex model to reconstruct survival through the delta from the individual components of reach-specific survival and route entrainment probabilities, while also maintaining precision about $\hat{S}_{\text{delta}}$. Relative to the small sample size of this study, precision was favorable due to high detection probabilities at most telemetry stations (Table 2).

TABLE 2.—Maximum likelihood estimates of detection probabilities (P_{hi}) at the ith telemetry station within route h for acoustically tagged late-fall-run juvenile Chinook salmon released on 5 December 2006 and 17 January 2007. Detection probabilities not shown here were set to one because all fish known to pass a given telemetry station were detected at that station. For the first release, P_{A3} was set to zero because this station was not operational during the first release.

	5 December 2006		17 January 2007	
Parameter	Estimate	SE	Estimate	SE
P_{A2}			0.986	0.014
P_{A3}			0.975	0.025
P_{A4}			0.970	0.030
P_{A6}	0.857	0.094	0.641	0.077
P_{A7}			0.941	0.040
P_{A8}	0.500	0.158	0.645	0.088
P_{D2}	0.600	0.219		

Relative contributions to S_{delta}

Estimates of $\hat{S}_{\text{delta}}$ were driven by (1) variation among routes in survival through the delta ($\hat{S}_h$), and (2) the relative contribution of each route-specific survival to $\hat{S}_{\text{delta}}$ as measured by migration route probabilities ($\hat{\psi}_h$). For the December release, fish migrating within the Sacramento River exhibited the highest survival through the Delta ($\hat{S}_{\text{A}}$) relative to all other routes, but only 35% of the population migrated through this route ($\hat{\psi}_{\text{A}}$), representing a relatively small contribution to $\hat{S}_{\text{delta}}$ (Table 1). In contrast, relative to survival in the Sacramento River, survival through all other routes reduced $\hat{S}_{\text{delta}}$ and comprised 65% of the population ($\hat{\psi}_{\text{B}} + \hat{\psi}_{\text{C}} + \hat{\psi}_{\text{D}}$), thereby contributing substantially to $\hat{S}_{\text{delta}}$ for the December release (Table 1). For the January release, 91% of the population ($\hat{\psi}_{\text{A}} + \hat{\psi}_{\text{B}}$) migrated through routes with the highest survival, and thus survival through these routes comprised the bulk of $\hat{S}_{\text{delta}}$ for the January release (Table 1). In comparison, survival for the interior delta via Georgiana Slough ($\hat{S}_{\text{D}}$) was lower than the other routes, but this route accounted for only 9% of the population ($\hat{\psi}_{\text{D}}$), having little influence on $\hat{S}_{\text{delta}}$ (Table 1).

The observed difference in $\hat{S}_{\text{delta}}$ between releases can be attributed to (1) a change in the relative contribution of each route-specific survival to $\hat{S}_{\text{delta}}$, and (2) differences in survival for given migration routes. Survival estimates for interior Delta routes ($\hat{S}_{\mathrm{C}}$ and $\hat{S}_{\mathrm{D}}$) were lower than for the Sacramento River ($\hat{S}_{\mathrm{A}}$) during both releases but contributed only 9% for the January release when the Delta Cross Channel was closed, compared with 35% ($\hat{\psi}_{\mathrm{C}} + \hat{\psi}_{\mathrm{D}}$) for the December release when the Delta Cross Channel was open (Table 1). Thus, lower contribution of interior Delta routes to $\hat{S}_{\mathrm{delta}}$ partly accounts for the higher $\hat{S}_{\mathrm{delta}}$ observed for the January release. However, higher $\hat{S}_{\mathrm{delta}}$ for January was also a consequence of changes in route-specific survival for the Sacramento River and Sutter and Steamboat sloughs, both of which were higher for the January release compared with December. These findings show how both survival through given routes and population distribution among routes interacted to affect $\hat{S}_{\mathrm{delta}}$ during the two releases.

Discussion

Our study highlights the importance of quantifying both movement among migration routes and survival within routes to understand factors affecting population-level survival. Measuring survival through different migration routes (S_h) between the same beginning and end points (from telemetry station A_2 to A_8; Figure 1) provides direct insight into the effect of different migration routes on survival through the entire delta. Furthermore, the migration route probabilities (ψ_h) measure the contribution of each route-specific survival to the overall survival of the population migrating through the delta. Thus, our modeling approach provides a natural framework for understanding how these route-specific components interact to affect population-level survival through the delta. Operation of the Delta Cross Channel is an important water management action that may influence population-level survival by affecting the fraction of the population entering the interior delta where survival is typically lower than alternative migration routes (this study; Newman and Brandes 2009). Thus, without information about both population distribution among routes and survival within routes, it would be difficult to quantify how management actions affect these underlying components that give rise to population-level survival.

We show that route-specific survival and movement among migration routes interact to influence population-level survival, but the next challenge is to quantify the mechanisms causing variation in route-specific survival. Within each release, travel times for fish migrating through the interior delta were longer than alternative routes, possibly contributing to lower survival through the interior delta. Relative to the December release, however, survival for the January release was higher for two migration routes (Sacramento River and Sutter and Steamboat sloughs) despite lower discharge and longer travel times through these routes during January (Figure 3). Thus, instantaneous mortality rates (i.e., per time) in these two routes were lower in January than in December, suggesting that factors other than travel time also contribute to variation in survival within and among migration routes. Such factors may include variation in environmental conditions (e.g., water temperature, turbidity, tides) or temporal shifts in the spatial distribution of predators, both of which influence predator–prey interactions. Our study just begins to shed light on this variation, but with replication over a wide range of environmental conditions our framework will allow us to explicitly quantify mechanisms influencing the route-specific components of population survival.

Our findings are consistent with a series of studies that have estimated survival of juvenile salmon in the delta with coded wire tags (Brandes and McLain 2001; Newman and Rice 2002; Newman 2008; Newman and Brandes 2010). In general, similar to our study, these studies found that survival of fish released into the interior delta via Georgiana Slough was lower than survival of fish released into the Sacramento River downstream of Georgiana Slough (Newman 2008; Newman and Brandes 2009). Specifically, Newman and Brandes (2009) found that the ratio of survival for Georgiana Slough releases relative to Sacramento River releases was less than one for all release-groups, indicating significantly lower survival for fish migrating through the interior delta (see Table 2 *in* Newman and Brandes 2009). In our study, an analogous estimate is $S_{\mathrm{D1}}S_{\mathrm{D2}}S_{\mathrm{D3}}/S_{\mathrm{A5}}S_{\mathrm{A6}}S_{\mathrm{A7}}$ (i.e., survival from D_1 to A_8 relative to A_5 to A_8; Figure 1). The estimate of this ratio was 0.625 (SE = 0.352) for the December release and 0.591 (SE = 0.351) for the January release. Although the SEs indicate that these estimates do not differ from one (i.e., equal survival), the point estimates parallel the previous studies and fall well within their observed release-to-release variation. This evidence continues to support the hypothesis that survival for fish migrating through the interior delta is lower than for fish that remain in the Sacramento River. While past research has revealed differences in survival among migration routes, it was impossible to quantify how these survival differences influenced survival of the population. In contrast, our study builds on past research by explicitly estimating the relative contribution of route-specific survival to population-level survival, as quantified by migration route probabilities (ψ_h).

Given that 30–40% of the population migrated through Sutter and Steamboat sloughs (Table 1), this migration route plays a key role in population-level survival by reducing the probability of fish entering the interior Delta. Fish migrating through Sutter and Steamboat sloughs do not encounter the Delta Cross Channel or Georgiana Slough, which directly reduces the fraction of fish entering the interior Delta via these routes. This relation is couched explicitly in our model: the probability of migrating through the interior Delta can be expressed as

$$\psi_C + \psi_D = (1 - \psi_B)(\psi_{C2} + \psi_{D2}).$$

Note that the fraction entering the interior Delta ($\psi_C + \psi_D$) decreases as the fraction migrating through Sutter and Steamboat sloughs (ψ_B) increases. This relationship highlights a critical linkage among migration routes that drives the dispersal process of juvenile salmon migrating through the delta. Furthermore, closure of the Delta Cross Channel reduces channel capacity of the Sacramento River at the second river junction, which slightly increases the proportion of river flow diverted into Sutter and Steamboat sloughs at the first river junction (J. R. Burau, USGS, personal communication). Thus, in addition to eliminating a route through the interior delta, closure of the Delta Cross Channel may decrease the proportion of fish entrained into the interior delta by increasing the fraction of fish entering Sutter and Steamboat sloughs. However, whether population-level survival is increased by management actions that shift the population distribution among migration routes will depend on the relative difference in survival among alternative routes.

In general, migration route probabilities increased with the fraction of total river discharge in each migration route, but both the form of this relationship and the factors influencing migration route probabilities requires further study. Flow distribution among the river channels at each junction varies with the tides on hourly time scales. Thus, migration route probabilities in our model represent an average of time-specific route entrainment probabilities that depend on the flow distribution when each fish passes a river junction. Furthermore, the spatial distribution of migrating salmon across a river channel may deviate from the spatial distribution of flow, which could cause a disproportionate number of salmon to be entrained into a given river channel relative to the proportion of flow in that channel. For example, in the Columbia River, juvenile salmon pass through shallow spillways at dams in higher proportions than the fraction of flow passing through spillways (Plumb et al. 2003; Zabel et al. 2008) because of the surface-biased distribution of salmon. Similar behavioral processes at river junctions in the delta would manifest as consistently positive or negative deviations from the 1:1 line in Figure 4 (i.e., where the proportion of flow = proportion of fish in a given route). Given these processes and our initial findings, we hypothesize that (1) changes in the distribution of average river flow at river junctions will effect coincident changes in average migration route probabilities, (2) consistent deviations in migration route probabilities relative to flow distribution may arise from a mismatch in the spatial distribution of fish relative to flow, and (3) variability in release-specific migration route probabilities will be driven by the interaction between fish arrival timing at a river junction and hourly scale changes in flow distribution at river junctions. Thus, on average, we suspect that closure of the Delta Cross Channel will reduce the proportion of fish entrained into the interior delta by reducing the fraction of mean discharge entering the interior delta. However, hourly scale variation in flow distribution at river junctions will likely magnify release-to-release variation in migration route probabilities, requiring replication over a range of conditions to confirm whether migration route probabilities are indeed positively related to the proportion of average river flow entering a given migration route.

Strictly speaking, inferences from our study population apply directly to the population of hatchery-origin late fall Chinook salmon 140-mm FL or larger migrating through the delta between December and mid-February under the environmental conditions observed during our study. However, four distinct populations of juvenile Chinook salmon (fall, late fall, winter, and spring) of both hatchery and wild origin use the delta to varying degrees at different times of year during different life stages. Although our framework can be applied to any of these populations, inferences from our data should be considered in the context of the similarity of target populations to our study population. Between December and mid-February, most fish captured in midwater trawls in the lower delta at Chipps Island (near station A_8) range in size from about 110 to 200 mm (Brandes and McLain 2001) and likely represent actively migrating smolts from the late fall and winter run of Chinook salmon (Hedgecock et al. 2001). Fall-run fry (i.e., < 50-mm FL) begin appearing in the delta in January and overlap with the arrival of spring-run parr (>50-mm FL) in March, both of which rear and grow in the delta to sizes smaller than 120-mm FL until complete emigration by late June (as presumed by absence in catch data; Williams 2006 and references therein). Inferences from our data to fall-run fry and spring-run parr are not well supported due to differences in size, seasonal timing, and residence time in the delta. In addition, survival of hatchery-origin fish may differ from that of wild fish (Reisenbichler and McIntyre 1977; Kostow 2004), but factors influencing relative differences in survival among migration routes (e.g., interior delta relative to Sacramento River) are likely to act similarly on both wild and hatchery populations. Thus, inferences about such relative differences may provide critical information for better understanding mechanisms influencing population-level survival of both hatchery and wild populations.

Estimating both movement and survival rates among different habitats is difficult yet critically important because these demographic parameters can have important consequences on population dynamics and viability (Beissinger and McCullough 2002). In our study, strategically located telemetry stations yield information on the movement of individual fish, while the mark–recapture model allows unbiased estimation of demographic parameters by correcting for the imperfect detection probability of each telemetry station. Similar models have been applied extensively to estimate animal migration and survival rates among geographic areas over time (Hilborn 1990; Hestbeck et al. 1991; Williams et al. 2002), but relatively few studies have focused on survival through space among alternative migration pathways (but see Skalski et al. 2002). Our framework could be applied to any migrating fish population that uses a number of alternative migration routes and is particularly well suited to dendritic networks such as river systems and their estuaries. For example, by situating telemetry stations at appropriate tributary confluences in a main-stem river, our modeling framework could be used to estimate both reach-specific survival and dispersal of adult salmonids among spawning tributaries. Here, movement rates (ψ) estimate the proportion of the population using each tributary, providing important information about relative contribution of subpopulations in each tributary to the population as a whole. Our study shows how combining telemetry with mark–recapture models provides a powerful approach to estimate demographic parameters in spatially complex settings.

This study has provided the first quantitative glimpse into the migration dynamics of juvenile salmon smolts in the Sacramento River. Route-specific survival through the delta (S_h) measured the consequence of migrating through different routes on survival through the delta, while migration route probabilities (ψ_h) quantified the relative contribution of each route-specific survival to population-level survival. In years to come, increases in sample size and replication over variable environmental conditions will bolster inferences drawn from the acoustic tag data and increase understanding of the mechanisms influencing survival. Cumulative knowledge gained from this population-level approach will identify the key management actions in the delta that must be rectified if Sacramento River salmon populations are to recover.

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Rapid decline of California's native inland fishes: A status assessment

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ABSTRACT

A quantitative protocol was developed to determine conservation status of all 129 freshwater fishes native to California. Seven (5%) were extinct; 33 (26%) were found to be in danger of extinction in the near future (endangered); 33 (26%) were rated as sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable); 34 (26%) were rated as declining species but not in immediate danger of extinction. Only 22 (17%) species were found to be of least concern. Of 31 species officially listed under federal and state endangered species acts (ESAs), 17 (55%) were rated as endangered by our criteria, while 12 (39%) were rated vulnerable. Conversely, of the 33 species that received our endangered rating, only 17 (51%) were officially listed under the ESAs. Among the seven metrics used to assess extinction threat, climate change, area occupied and anthropogenic threats had the largest negative impacts on status. Of 15 categories of causes of decline, those most likely to diminish status were alien species, agriculture, and dams. Overall, 83% of California's freshwater fishes are extinct or at risk of becoming so, a 16% increase since 1995 and a 21% increase since 1989. The rapid decline of California's inland fishes is probably typical of declines in other regions that are less well documented, indicating a strong need for improved conservation of freshwater ecosystems.

1. Introduction

Extinction in freshwater environments is a world-wide crisis (Moyle and Williams, 1990; Saunders et al., 2002; Dudgeon et al., 2006) which is poorly documented (Strayer and Dudgeon, 2010; Vörösmarty et al., 2010). Loss of biodiversity seems to be occurring more rapidly from fresh water than from any other broad habitat type (Jenkins, 2003; Dudgeon et al., 2006). Driven by recent global assessments of mollusks (Bogan, 2008), crabs (Cumberlidge et al., 2009), amphibians (Stuart et al., 2004), and dragonflies (Clausnitzer et al., 2009), the number of freshwater species listed on International Union for the Conservation of Nature (IUCN) Red Lists has more than tripled since 2003 (Darwall et al., 2008). Nevertheless, the best-studied indicators of the problem remain freshwater fishes (Magurran, 2009) which account for about one-third of all described vertebrates, with roughly 13,000 species (Helfman, 2007; Lèvêque et al., 2008). In 1992, 20% of the world's freshwater fish fauna was estimated to be extinct or in serious decline (Moyle and Leidy, 1992). Less than 20 years later, 37% of the 3481 freshwater fish species evaluated globally by IUCN were regarded as extinct or imperiled (declining towards, or threatened, with extinction, Vié et al., 2009), although the IUCN database is likely biased towards including declining species. At the continental scale, 46% of 1187 described freshwater and diadromous fish species native to North America are extinct, imperiled, or have one subspecies or distinct population that is imperiled (Jelks et al., 2008) with the rate of extinction steadily increasing (Ricciardi and Rasmussen, 1999). Not surprisingly, the number of imperiled fish species is highly correlated with human population and economic growth (Limburg et al., 2011).

While large-scale assessments spotlight the global extent of the crisis, severity and causes are best understood through intensive studies of regional fish faunas because status can be repeatedly, systematically, and quantitatively documented over relatively short time periods. In this paper, we analyze the status of California's 129 native freshwater fishes. This regional fauna is reasonably well documented, occupies a wide variety of habitats, and exhibits a wide range of life history patterns including anadromy (Moyle, 2002; Moyle et al., 2008, 2010). Their status was previously analyzed in 1989 (Moyle and Williams, 1990) and 1995 (Moyle et al., 1995). Here, we use a new quantitative protocol to determine conservation status of each species. This protocol allows us to make status determinations independent of official agency designations and to find species needing protection that have been overlooked so far by state and federal agencies. Comparisons with official status designations also serve as a check on the usefulness of our protocol. In this paper, we answer the following questions:

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1. What is the status of California's inland fish fauna?
2. Are the fishes continuing to decline?
3. What factors are most strongly associated with declining status?
4. How do our results fit with official status designations?

1.1. The inland fishes of California

California's large size (411,000 km^2), length (1400 km and 10° latitude) and complex topography result in diverse habitats, including 50 isolated watersheds in which fish have evolved independently (Moyle, 2002, Moyle and Marchetti, 2006). For most of the state, the climate is Mediterranean; most precipitation falls in winter and spring, followed by long dry summers. This results in rivers that have high annual and seasonal variability in flows (Mount, 1995) and native fishes adapted to hydrologic extremes. There are 129 native inland fishes (defined as those breeding in fresh water) currently recognized (Appendix 1, which includes scientific names of fishes mentioned). Of these, 63% are endemic to the state and an additional 19% are also found in one adjacent state. Thus California's fishes fall within political and zoogeographic boundaries that largely coincide, important for a bioregional assessment (Moyle, 2002).

Conditions in California have produced an unusual number of anadromous fishes (24%) as well as fishes that thrive in isolated environments such as desert springs, intermittent streams, and alkaline lakes. Most fishes live in rivers of the Central Valley and North Coast, areas having the most water and most diverse aquatic habitats. Recent genetic and taxonomic studies have underscored the distinctiveness of California fishes and increased the number of taxa from 113 in 1989 (Moyle and Williams, 1990) to 129 in the present study.

Most California rivers have been dammed and diverted to move water from places of abundance to places of scarcity, where most Californians live (Hundley, 2001). Not surprisingly, native fishes have been in steady decline since the mid-19th century, although the first formal evaluation of their status was not conducted until 1989. At that time, 7 species (5%) were extinct, 15 (13%) were formally listed as Threatened or Endangered under the state or federal ESAs, and 51 (43%) were designated as Species of Special Concern by the State of California, indicating they were in decline or had small, vulnerable populations but were not yet threatened with immediate extinction (Moyle and Williams, 1990). The number of declining species has steadily increased so that in 1995, there were 18 (16%) listed and 51 (44%) in decline (Moyle et al., 1995). Today, the numbers are 30 (23%) listed and 70 (54%) in decline, meaning that 83% of California's native fishes have the potential to go extinct in coming decades or are already extinct (Appendix 1) (Fig. 1).

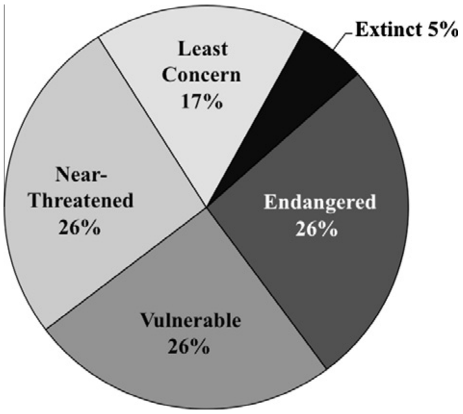

Fig. 1. Status of fishes ($N = 129$) native to inland waters of California in 2010. All threat categories are approximately equivalent to IUCN threat levels of the same name. Extinct = globally extinct or extirpated in the inland waters of California. Endangered = highly vulnerable to extinction in its native range, approximately equivalent to IUCN threat level of *endangered* or *critically endangered*. Vulnerable = could easily become threatened or endangered if current trends continue. Near threatened = populations in decline or highly fragmented. Least concern = no extinction threat for California populations.

2. Methods

2.1. Sources of information

Taxa used were those that qualified as species under the federal Endangered Species Act of 1973, so include species, subspecies, Evolutionarily Significant Units, and Distinct Population Segments recognized by one or more agencies. The biology and status of each species was determined from information in Moyle (2002), Moyle et al. (1995, 2008, 2010), additional reports and papers from intensive literature searches, and by personal communications with biologists working with each taxon. The information was summarized in standardized species accounts which included evaluation of status. All accounts were reviewed by experts on each species. In a few cases, information was updated by field investigations by the authors. The status of each species is as of December 31, 2010.

2.2. Quantitative evaluation of status

Species status was determined using seven metrics scored on a 1–5 scale (Table 1) where 1 was a low score indicating major negative impact on status and 5 was a high score, indicating either no or a positive impact on status. Scores were assigned according to a rubric which was standardized to each threat category (Table 2). Metrics were designed to capture all significant risk factors faced by freshwater fishes while keeping redundancy among metrics to a minimum. Principal component analysis revealed relatively equal weighting of all seven metrics on the final status scores (eigenvectors for principal component one: area occupied, 0.322; adult population, 0.398; intervention dependence, 0.405: tolerance 0.341: genetic risk 0.406; climate change 0.381: anthropogenic threats 0.382). For each species, the seven criteria were averaged to produce a single score for which the threat of near-term extinc-

Table 1
Metrics for determining the status of California fishes, with Sacramento splittail as example. Each metric is scored on a 1–5 scale where 1 is a major negative factor contributing to status, 5 is a factor with no or positive effects on status, and 2–4 are intermediate values. Scoring is described in Table 2.

Metric	Score	Justification
Area occupied	2	Two distinct populations in San Francisco Estuary, using different rivers for spawning
Estimated adult abundance	4	Large in upper estuary, likely small in lower
Intervention dependence	3	Floodplain areas need special management for spawning during droughts
Tolerance	5	One of the most physiologically tolerant native fishes
Genetic risk	3	Two populations; genetically fairly diverse
Climate change	1	Extremely vulnerable to droughts and sea level rise reducing habitat
Anthropogenic causes of decline	2	Multiple, see Table 3
Average	2.9	20/7
Certainty (1–4)	3	Well studied

tion increased as the score decreased. The scores were placed in categories following the IUCN categories for imperiled species (Vié et al., 2009). Fishes with scores between 1.0 and 1.9 were rated *endangered* and regarded as being in serious danger of extinction, while those scoring 4.0–5.0 were regarded as *least concern*. Species with scores of 2.0–2.9 were rated *vulnerable* and regarded as likely to become threatened or endangered in the near future, while those scoring between 3.0 and 3.9 were in decline but not yet in immediate danger of extinction and so were rated *near-threatened*. In order to simplify discussion, all species scoring between 1.0 and 3.9, were collectively referred to as ‘‘imperiled’’ because they either had declining populations or had small, isolated populations that increased their risk of extinction. The scores only apply within California, so rare species with wide distributions and high abundance outside the state (e.g., chum and pink salmon) might receive low scores within the state even if there is no danger of extinction as species.

2.3. Metrics used to score taxon status

2.3.1. Area occupied

We assumed that extinction threat was lower for species spread over many watersheds than for those with limited distributions. Inland fishes were scored by number and interconnectedness of large watersheds occupied. Anadromous fishes were scored on number of watersheds occupied (i.e., Functionally Independent Populations, Lindley et al., 2004, 2006).

2.3.2. Estimated adult abundance

In general, the more adult individuals in a population, the more likely it is to persist through time. However, quantitative population estimates are rare, especially for non-game fishes (Jelks et al., 2008). We therefore used order-of-magnitude estimates of average annual numbers of mature individuals at the time of the study as a proxy for population size (Table 2). While we recognized

Table 2
Scoring rubric for seven metrics used to evaluate status of native freshwater fishes of California. Final status score is the average score of all seven metrics.

1A. Area occupied: resident fish
1. 1 watershed/stream system in California only based on watershed designations in Moyle and Marchetti (2006)
2. 2–3 watersheds/stream systems without fluvial connections to each other
3. 3–5 watersheds/stream systems with or without fluvial connections
4. 6–10 watersheds/stream systems
5. More than 10 watersheds/stream systems

1B. Area occupied: anadromous fish
1. 0–1 apparent self-sustaining populations
2. 2–4 apparent self-sustaining populations
3. 5–7 apparent self-sustaining populations
4. 8–10 apparent self-sustaining populations
5. More than 10 apparent self-sustaining populations

2. Estimated adult abundance
1. ⩽500
2. 501–5000
3. 5001–50,000
4. 50,001–500,000
5. 500,000+

3. Dependence on human intervention for persistence
1. Captive broodstock program or similar extreme measures required to prevent extinction
2. Continuous active management of habitats (e.g., water addition to streams, establishment of refuge populations, or similar measures) required
3. Frequent (usually annual) management actions needed (e.g., management of barriers, special flows, removal of alien species)
4. Long-term habitat protection or improvements (e.g., habitat restoration) needed but no immediate threats need to be dealt with
5. Species has self-sustaining populations that require minimal intervention

4. Environmental tolerance under natural conditions
1. Extremely narrow physiological tolerance in all habitats
2. Narrow physiological tolerance to conditions in all existing habitats or broad physiological limits but species may exist at extreme edge of tolerances
3. Moderate physiological tolerance in all existing habitats
4. Broad physiological tolerance under most conditions likely to be encountered
5. Physiological tolerance rarely an issue for persistence

5. Genetic risks/problems
1. Genetic viability reduced by fragmentation, genetic drift, and isolation by distance, owing to very low levels of migration, and/or frequent hybridization with related fish
2. As above, but limited gene flow among populations, although hybridization can be a threat
3. Moderately diverse genetically, some gene flow among populations; hybridization risks low but present
4. Genetically diverse but limited gene flow to other populations, often due to recent reductions in connectivity
5. Genetically diverse with gene flow to other populations (good metapopulation structure)

6. Vulnerability to climate change
1. Vulnerable to extinction in all watersheds inhabited
2. Vulnerable in most watersheds inhabited (possible refuges present)
3. Vulnerable in portions of watersheds inhabited (e.g., headwaters, lowermost reaches of coastal streams)
4. Low vulnerability due to location, cold water sources and/or active management
5. Not vulnerable, most habitats will remain within tolerance ranges

7. Anthropogenic causes of decline
1. 1 or more causes rated critical or 3 or more threats rated high–indicating species could be pushed to extinction by one or more threats in the immediate future (within 10–25 years)
2. 1 or 2 causes rated high; species could be pushed to extinction in the foreseeable future (within 50 years)
3. No causes rated high but 5 or more threats rated medium; no single threat likely to cause extinction but all threats in aggregate could push species to extinction in the next century
4. 1–4 causes rated medium; no immediate extinction risk but taken in aggregate causes reduce population viability
5. 1 medium, all others low; known causes do not imperil the species

that the effect of adult population size upon persistence differs for large, long-lived species in contrast to small, short lived species (Flather et al., 2011), we rarely found this to be an issue for California fishes.

2.3.3. Dependence on human intervention for persistence

This metric scored how dependent a species was on direct human intervention for its continued survival. Thus, Eagle Lake rainbow trout received a score of '1' because it is completely dependent on artificial propagation for its persistence, while rough sculpin (a state listed species) scored a '4', because it needs only continued protection of its spring-fed streams (managed for trout fisheries) to maintain abundance.

2.3.4. Environmental tolerance under natural conditions

This metric measures overall physiological tolerance in relation to existing conditions in a species' range. Where possible this was based on results of laboratory or field studies of responses to ranges of temperature, salinity, dissolved oxygen and similar variables. However, if a species had fairly broad physiological tolerances in the laboratory but lived in waters (e.g., streams in southern California) where habitat conditions naturally approached the species limits of tolerance to temperature and other factors, its environmental tolerance was scored lower than that of a species likely to rarely encounter such conditions.

2.3.5. Genetic risks

This metric incorporates two concepts, hybridization and genetic bottlenecks. Hybridization with a related species, especially an introduced species, can result in sterility, reduced fitness and swamping of native genomes (Perry et al., 2002). Similarly, interbreeding between artificially propagated (hatchery) and wild individuals can reduce fitness of offspring (Araki et al., 2009).

In order to avoid over-weighting the impact of small population size on status, genetic impacts of small population size were not considered here. However, low genetic variation from hatchery management and/or other past reductions of effective population size may increase extinction threat (e.g., reduce the ability of species to adapt to environmental change) irrespective of current population size and so was included under this metric.

2.3.6. Vulnerability to climate change

Climate change is already having effects, as reflected in rising water temperatures and more variable stream flow; such effects are only likely to increase (Hayhoe et al., 2004; Anderson et al., 2008; Cayan et al., 2009). Vulnerability to future climate change was determined by examining geographic range of each species, its isolation (potential for finding refuges), and the types of habitat it inhabits. Species considered to have low vulnerability included those with broad thermal tolerances and those living in aquatic environments shielded (at least for now) from climate-driven change, such as spring-fed systems with constant sources of water (e.g., bigeye marbled sculpin and Saratoga Springs pupfish).

2.3.7. Anthropogenic causes of decline

We rated fifteen major categories of landscape-level factors likely to increase extinction risk as having no, low, medium, high or critical effect on species status, based on available information for each species summarized in Moyle (2002), and Moyle et al. (2008) (Table 3). A cause rated "critical" could push the species to extinction in three generations or 10 years which ever is less. A cause rated "high" could push the species to extinction in 10 generations or 11–50 years which ever is less. A cause rated "medium" was unlikely to drive a species to extinction by itself but contributed to increased extinction risk over the next century. A cause rated "low" could reduce populations but extinction was considered unlikely as a result. A cause rated "no" (no effect) has no known negative impact to the taxon under consideration.

For some species, a single threat was considered grave enough to cause extinction (e.g., hybridization for California golden trout), but for most species, number as well as severity of potential causes contributed to our final score (Table 2). We judged any species with even one critical rating as being in danger of extinction in the near future. The 15 causes of decline are summarized below.

2.4. Anthropogenic causes of decline

2.4.1. Large dams

Dams and their reservoirs had high impacts on status if they blocked access to much of the species range, caused major changes to physical habitat, or changed water quality and quantity. We regarded dams as having a low impact if they were present within the range of the species but their effects were small or beneficial.

2.4.2. Agriculture

Effects of agriculture were rated high if agricultural effluent polluted waterways of major importance to the species, if diversions severely reduced flow, if large amounts of silt flowed into streams from farmland, if pesticides had significant effects, and if other agricultural factors directly affected waters in which a species lives. We regarded agriculture as having a low impact if it was not pervasive in the species' range or was not known to be causing significant changes to a species' habitats.

Table 3
Ratings of major anthropogenic factors causing declines of freshwater fishes of California, using Sacramento splittail as an example. See text for definitions of ratings of causes.

Status metric	Rating	Explanation
Major dams	High	All waters have flows regulated by dams and diversions; frequency of flooding of spawning areas reduced
Agriculture	Medium	Pollution, channel modification, entrainment in major diversions
Grazing	Low	Little known impact but occurs in spawning areas
Rural residential	Low	Residences on the edges of rearing marshes
Urbanization	Medium	Most habitat is on urban fringes; sewage; water diversion and entrainment
Instream mining	Low	Some gravel mining in floodplain areas
Mining	Low	Legacy effects of gold mining, e.g. mercury
Transportation	Medium	Migratory corridors lined with roads and railroads,
Logging	No	No known impact
Fire	Low	Indirect impacts from marsh/floodplain fires possible
Estuarine alteration	High	Major habitat areas highly altered
Recreation	Low	Recreational boating etc. may affect habitat
Harvest	Medium	Some harvest for bait and of migrating adults for food
Hatcheries	No	No known impact
Alien species	Medium	Effects of new invaders unpredictable; predation and competition possible

2.4.3. Grazing

We separated livestock grazing from other agriculture because its effects are widespread on range and forest lands throughout California. Impacts were rated high where stream banks were trampled and riparian vegetation was removed, resulting in incised streams, drying of adjacent wetlands, and lowering of water tables. Removal of vegetation can also result in increased siltation, higher water temperatures, and decreased summer flows. Impacts were rated low where grazing was present but had minimal negative effects.

2.4.4. Rural residential

As California's human population grows, people spread across the landscape, often settling in diffuse patterns along or near streams. Rural development results in water removal, streambed alteration (to protect houses, create swimming holes, construct road crossings, etc.), and pollution (especially from septic systems). We rated such housing as having high effect on fishes where it was abundant and unregulated and caused major changes to streams. Where such housing was present but scattered, the effects were usually rated as low.

2.4.5. Urbanization

Streams that flow mostly through cities are generally highly altered to reduce flooding and remove water, while pollution is pervasive, from sewage, runoff, and storm drain discharges. Generally, the more the important waters for a species were encompassed by urban development, the higher we rated the effects of urbanization on the species.

2.4.6. Instream mining

The most severe instream mining in California took place during the 19th and early 20th centuries when miners buried (through hydraulic mining), excavated, and dredged riverbeds for gold. We often gave the legacy effects on fishes of mining medium or high ratings. Similar scores were given to species affected by legacy effects of instream gravel mining, which creates large pits in streambeds and alters stream banks. Such mining is largely banned (in favor of mining off-channel areas) today. Impacts of contemporary recreational and professional suction dredge mining resulted in some intermediate ratings.

2.4.7. Mining

The effects of hard-rock mining (mostly for gold and mercury) were rated according to how much of a species' habitat was affected by tailings and acidic mine drainage. We gave high ratings where major mines, even if abandoned, had toxic tailings poised on edges of waterways (e.g., Iron Mountain Mine near Redding, on the Sacramento River). Our low threat scores usually came from situations where old mines were present but effects on biota of nearby streams were not evident.

2.4.8. Transportation

Many rivers and creeks have roads and railroads running along one or both sides, confining stream channels and causing pollution from siltation, vehicle emissions, waste disposal, and accidents. In addition, culverts and other hydrologic modifications associated with transportation often restrict fish movements. Our ratings here were based on how much a species depended on streams altered by roads and railways and how severe the alterations were.

2.4.9. Logging

Timber harvest is a major use of forested California watersheds which support many native fishes, including anadromous salmonids. Logging was relatively unregulated until mid-20th century, resulting in major alteration and degradation of stream habitats. Although better regulated today, logging is still a pervasive activity resulting in siltation of streams and reduced habitat complexity. We gave high threat ratings to species dependent on streams degraded by either legacy or contemporary effects of logging. Low threat ratings were given where such effects are of small significance.

2.4.10. Fire

Wildfires are part of California's natural landscape but human activities have increased their intensity and frequency. High ratings were given where fish habitat was, or has the potential to be, seriously degraded by catastrophic wildfire, via post-fire erosion, loss of riparian canopy, increased temperature and spilled fire-fighting chemicals. We assigned low ratings to fishes that live in areas where wildfires occur but for various reasons, such as low fuel load, have minimal impact on streams.

2.4.11. Estuary alteration

Many California fishes depend on estuaries for at least part of their life cycle. All California estuaries are highly altered by human activity, including siltation, pollution, diking and draining, bridge construction, and removal of sandbars between the estuary and ocean. Thus, the more estuarine-dependent a fish species is, the more likely we were to assign a high rating to estuary alteration as a cause of decline.

2.4.12. Recreation

Recreational use of streams has greatly increased with the human population. We found recreational effects usually to be low, although they were often concentrated when stream flows were low. We rated recreation effects as high when a taxon depended on streams that are heavily disturbed (e.g., by off-road vehicles) or contains enough boaters and swimmers to disturb spawning or holding (e.g., salmon and steelhead).

2.4.13. Harvest

We rated harvest effects as high for fishes known to be subject to overharvest, especially large species (e.g., sturgeons) or species that become isolated and are therefore vulnerable to poaching (e.g., summer steelhead). We rated both legal and illegal harvest, although for most native resident fishes, legal fishing was rarely an issue.

2.4.14. Hatcheries

Most fishes are not supported by fish hatcheries but for those that are, hatchery fish often have negative effects on wild populations through competition for habitat and food, direct predation, and interbreeding which results in loss of genetic diversity (Moyle, 2002). We rated severity of these effects based in part on hatchery dependence and/or known interbreeding between wild and hatchery populations. We regarded conservation hatcheries that focus on rare species as having relatively low impacts because of their efforts to reduce negative hatchery effects as much as possible.

2.4.15. Alien species

Non-native species are present in every California watershed and their impacts on native species through hybridization, predation, competition, and disease are often severe (Moyle and Marchetti, 2006). We rated this category as high for a species if there were major direct or indirect impacts of alien invaders. We rated it as low if contact with alien species was infrequent or not known to be negative.

2.5. Certainty index

Because quality, amount and reliability of information varied among species, we developed a certainty index for our scores, on a 1–4 scale, where we scored status evaluations as follows:

1. Based on expert opinion (including our own) with little hard data.
2. Based on expert opinion supplemented with limited data and reports.
3. Based on extensive information found mainly in agency reports.
4. Based on reports from multiple sources including peer-reviewed literature.

This index lets managers know the risks involved in basing management decisions on our results.

3. Results

Of 129 freshwater fishes native to California, four are globally extinct (3%) and three (2%) are extirpated from the state (scores of 0). Another 33 (26%) are in danger of extinction in the near future if present trends continue (endangered, scores of 1.0–1.9) while 33 (26%) are sufficiently threatened to be on a trajectory towards extinction if present trends continue (vulnerable, scores of 2.0–2.9). Thirty-four (26%) are in long-term decline or have small isolated populations but do not face extinction in the foreseeable future, unless conditions change (near-threatened, scores of 3.0–3.9). The remaining 22 species (17%) are of least concern (4.0–5.0) (Fig. 1). The average status score of all extant taxa was 2.7. The certainty ratings of our status evaluations averaged 2.7 out of 4.0 (SD 1.2), with 66% of accounts based on extensive literature (4.0) and only 5% based mainly on our professional judgment (1.0).

Of the 31 species currently listed as Endangered or Threatened under federal and/or state endangered species acts, 17 had status scores of 1.0–1.9 and 12 had scores of 2.0–2.9 by our rating system (Appendix Table 1). Listed species made up half of the 33 species to which we gave status scores of 1.0–1.9 and 44% of extant species with scores <2.9. The number of listed species increased from 14 in 1989 to 18 in 1990 to 31 in 2010, a listing rate of about 0.8 species per year (Fig. 2). The total number of imperiled species increased from 55 to 100 in this same period (2.1 species per year) (Fig. 2). While the increase was partly the result of 14 taxa being added to the fauna, most of the increase reflects real declines in species status. Previous status determinations (Moyle and Williams, 1990; Moyle et al., 1995) were made without benefit of our systematic approach and were constrained by prior agency designations. However, because the senior author was in charge of all three assessments, the evaluations are fairly consistent.

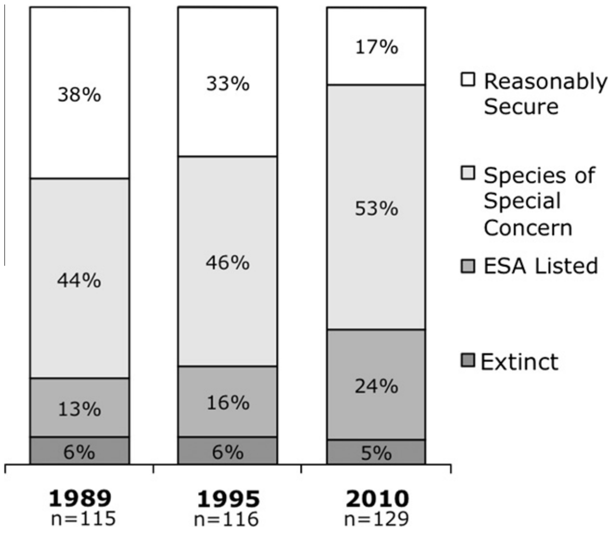

Fig. 2. Status of the native fishes of California from three surveys over 21 years, as shown by percentages of known species in conservation categories used by the state of California. Listed species are those listed under the state and federal endangered species acts as either Threatened or Endangered. Special Concern species are those in decline or in small isolated populations that are likely to be eligible for listing in the near future. For 2010, some Special Concern status determinations have not yet been officially recognized.

Table 4
Percentages of 122 extant California freshwater fishes assigned ratings of severity for 15 causes of fish declines. A cause rated 'critical' had the most severely negative effect on a species. See text for descriptions of causes and for definitions of critical, high, medium, and low rating levels.

Cause	Critical	High	Medium	Low	No effect
Percent of fish taxa with rating					
Major dams	3	21	32	27	17
Agriculture	1	17	50	25	7
Grazing	0	9	48	41	2
Rural residential	2	1	28	65	5
Urbanization	0	9	30	39	22
Instream mining	0	3	28	44	5
Mining	0	3	8	84	6
Transportation	0	4	46	48	3
Logging	2	4	27	55	12
Fire	0	4	42	50	4
Estuary alteration	2	10	22	7	61
Recreation	0	2	16	77	6
Harvest	1	8	13	29	49
Hatcheries	3	11	7	14	66
Alien species	11	23	35	30	1

In this status review, the metrics contributing most often to overall status scores of 1.0–2.9 were climate change (62% of species with such scores), anthropogenic threats (56%) and area occupied (55%). In contrast, fishes with scores of 4.0 and above had large populations, wide distributions, and high tolerance of environmental change. The anthropogenic threats that led to the most species with "critical" or "high" ratings were alien species (34%), dams (24%) and agriculture (18%) (Table 4). Twenty-five species (19%) had at least one "critical" rating, indicating high likelihood of extinction in the near future, while 63 species (49%) received at least one "high" rating. The largest number of "high" ratings awarded to a single species was six. All species had different combinations of causes of decline by kind and severity.

4. Discussion

4.1. What is the status of California's freshwater fish fauna?

In 1989, only 14 species were formally ESA listed as Threatened or Endangered (Moyle and Williams, 1990). Today, 31 species are formally listed and about one additional species is being listed every two years, despite a general slow-down in the listing process (Greenwald et al., 2006). In addition, seven species have gone extinct in the past 50 years. Clearly, the native fish fauna of California is in serious decline by official standards. However, our analysis indicates that the decline is more severe than recognized, with 107 (83%) of the native fishes prone to extinction. The major cause of decline is a growing human population that enjoys living in a mild Mediterranean climate where water is in short supply, especially in the dry summer season or during periods of drought. This shortage results in most waterways being dammed, diverted, polluted, or otherwise altered, with the additional threat of frequent invasions of alien fishes (Moyle, 2002; Moyle and Marchetti, 2006). The highly endemic fishes of the region are vulnerable to change because many are confined to limited geographic areas or to habitats where conditions are naturally stressful. However, even many wide-ranging species (e.g., all salmon species and steelhead rainbow trout) are imperiled (Moyle, 2002; Moyle et al., 2008). Native species that have managed to thrive under altered conditions are those that have naturally large ranges, broad habitat requirements, high tolerance of adverse conditions, and an ability to become part of new fish assemblages that include alien species (e.g., Tahoe sucker, Sacramento pikeminnow).

4.2. Are the fishes continuing to decline?

Today, 83% of California's freshwater fishes are imperiled or extinct, a 16% increase since the last assessment in 1995 and a 21% increase since 1989. The increase is partly the result of improved information, but declines of most species are also real, as illustrated below by coho salmon, Central Valley fall Chinook salmon, delta smelt, Clear Lake hitch, and Sacramento perch.

Coho salmon (Salmonidae) are native to hundreds of coastal streams from Monterey Bay north to the Oregon border and once supported sport and commercial fisheries (Moyle, 2002). In the 1940s, estimated numbers of adults spawning in California streams were 200,000–400,000 (Moyle et al., 2008). They were regarded by Moyle and Williams (1990) as being in sharp decline but still common. Subsequent studies documented their rapid disappearance from their native streams throughout the state and by 1996 the two Evolutionary Significant Units (ESUs) of coho salmon present in California had been listed as federal Threatened or Endangered species. Our analysis scored status of the Central Coast ESU as 1.1 and the Southern Oregon Northern California Coast ESU as 1.7. The 2010 federal ESA recovery plan for California coho salmon is consequently regarded as more an extinction prevention plan than a real plan for recovery (NMFS, 2010).

Central Valley fall Chinook salmon ESU once historically made up the largest run of salmon in the Sacramento and San Joaquin River basins, with runs once estimated to be around a million fish annually; adult populations through most of the 20th century were 200,000–400,000 fish. Moyle and Williams (1990) considered it to be abundant and perhaps even increasing in abundance. However, its status score here is 2.0, because of a recent precipitous population crash (Moyle et al., 2008) which is apparently the indirect result of the population being almost entirely composed of fish of hatchery origin (Barnett-Johnson et al., 2007).

Delta smelt (Osmeridae) are endemic to the San Francisco Estuary and require fresh water for spawning (Moyle, 2002). In the 1970s, they were still one of the most abundant fish in the upper estuary but declined rapidly so that Moyle and Williams (1990) indicated they merited listing as a threatened species. They were listed as Threatened by both state and federal governments in 1993. Nevertheless, their decline has continued as the result of major environmental changes to the upper estuary related to increasing water exports and other factors (Bennett, 2005), despite major efforts to curtail mortalities in recent years. With a 1-year life cycle, they may be on verge of extinction and accordingly were given a score of 1.4.

Clear Lake hitch (Cyprinidae) is endemic to Clear Lake, a large natural lake in the Coast Range of California (Moyle, 2002). Although the lake has been highly altered for human use and has been heavily invaded by alien species, hitch are one of the few native species that have persisted; Moyle and Williams (1990) found them to be abundant but possibly declining. However, dramatic reduction in numbers of individuals in spawning streams, presumably related to the expanding population of piscivorous Florida largemouth bass (*Micropterus floridae*) in the lake as well as continued environmental degradation, resulted in a status score of 1.9.

Sacramento perch (Centrarchidae) were once one of the most abundant fish in the Central Valley and subject to commercial fisheries in the 19th century (Moyle, 2002). Today they are extirpated from their native range largely from competition and predation by introduced centrarchids (Crain and Moyle, 2011). They have persisted only because they have been introduced into scattered reservoirs and lakes in other parts of California and the western USA. However, many introduced populations are now gone and most others are located in waters that are not secure (Crain and Moyle, 2011). Moyle and Williams (1990) indicated concern about its decline but thought it did not merit listing as a threatened species. Because so many populations have disappeared or declined since then, it scored 1.6 in our evaluation.

4.3. What factors are most strongly associated with conservation status?

The causes of the declines have their roots in the 19th and early 20th centuries when unrestricted mining, logging, and wetland conversion, combined with wide-scale dam building, severely altered most rivers, lakes, and estuaries. In addition, approximately 50 species of alien fishes were successfully introduced, many of them better suited to altered environments than native species (Moyle and Marchetti, 2006). Nevertheless, each native species has its own idiosyncratic response to this changing environment, as a result of its natural characteristics interacting with changes occurring in its particular habitats. Our analyses showed that each imperiled species has its own combination of causes of decline but most common were factors reflecting large-scale landscape changes (dams, agriculture, logging, urbanization, Table 4). An issue common to all species is climate change, which was often an important factor affecting our final status score for each species. Increases in water temperatures and variability in stream flows are becoming an increasingly important limiting factor for most species, but especially those relying on streams with perennial flows of cool (<20–22 °C) water. Thus a systematic conservation approach has to deal both with broad issues and those particular to each species.

4.4. How do our results fit with official status designations?

Of the 31 California fish species listed under the ESA, 94% fell into our two most at-risk status categories, indicating that our scoring system approximates the criteria used in official ESA listing determinations. However, only 51% of 33 species that we rated as endangered (scores <2.0) were officially listed under the ESA, indicating that official protection is not keeping pace with the rapid decline of California's inland fishes. That ESA designations are not concordant with current status is also born out by the fact that 12 (36%) of the 33 species we rated as vulnerable (scores of 2.0–2.9) and two (6%) of the species we rated as near-threatened (scores of 3.0–3.9) were listed as threatened or endangered under the ESA. The reasons for the discrepancies between our ratings and official status are complex but largely stem from better information being available now than at the time of listing. For example, the rough sculpin (score of 3.4) was one of the first fishes listed under state law, when little was known about its distribution and biology. Subsequent studies have indicated it is fairly widespread in spring streams of the Pit River watershed and is even expanding its range in reservoirs (Moyle, 2002). However, recent genetic studies suggest rough sculpin is actually two disjunct populations (A. Kinziger, pers. comm. 2010), perhaps species, which might qualify for listing if treated independently.

Rating the quality (certainty) of the information on which each species status score was based enables managers to determine which species need more study. Most of our species status determinations are based on strong published evidence. However, species with low certainty scores should be re-evaluated for status frequently.

5. Conclusions

The native inland fish fauna of California is in rapid decline and many species are likely to disappear from the state within the next century if present trends continue. Unfortunately, global climate change and human population growth are likely to increase fish extinction rates as competition with humans for increasingly scarce water intensifies, stream flows become more variable, and water quality, especially temperature, changes. For coldwater fishes, thermal refuges may disappear from streams in many areas, leaving no place to escape unfavorable conditions. The patterns of decline we see in California have been documented in freshwater fishes in other arid climates (Moyle and Leidy, 1992; Aparicio et al., 2000; Maceda-Veiga et al., 2010). However, the decline of California's inland fishes is likely characteristic of freshwater fishes and their ecosystems worldwide. As better information and similar systematic approaches are employed in other regions, we predict more imminent extinctions will be detected than are presently appreciated. Given trends of rapid decline that we have documented it is likely that many species will be lost before effective conservation plans can be implemented. There is, therefore, no time to be lost in designing and implementing conservation efforts for freshwater species in California and worldwide.

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Appendix

Table 1. List of all native fishes known to breed in the inland waters of California, ranked by level of extinction threat. Asterisks denotes taxon listed by federal or state Endangered Species Acts. Extinct= globally extinct or extirpated from the inland waters of California. Status scores of 1.0-1.9 are roughly equivalent to IUCN threat level of *endangered* or *critically endangered*; 2.0-2.9, IUCN threat level of *vulnerable*; 3.0-3.9, IUCN threat level of *Near Threatened;* 4.0-5.0, IUCN threat level of *Least Concern*.

Species	Status Score
Thicktail chub, Siphatales crassicauda	Extinct
High Rock Springs tui chub, *S. b. subsp.*	Extinct
Bonytail, *Gila elegans*	Extinct
Clear Lake splittail, *P. ciscoides*	Extinct
Colorado pikeminnow, *P. lucius*	Extinct
Bull trout, *Salvelinus confluentus*	Extinct
Tecopa pupfish, *C. n. calidae*	Extinct
Long Valley speckled dace, *R. o. subsp.*	1.0
Central coast coho salmon, *O. kisutch*	1.1*
Shoshone pupfish, *C. n. shoshone*	1.1
Razorback sucker, *Xyrauchen texanus*	1.3*
Pink salmon, *O. gorbuscha*	1.3
Shay Creek stickleback, *G. a. subsp.*	1.3
Owens tui chub, *S. b. snyderi*	1.4*
Mojave tui chub, *S. mohavensis*	1.4*
Delta smelt, *Hypomesus pacificus*	1.4*
Owens pupfish, *C. radiosus*	1.4*
Southern green sturgeon, *A. medirostris*	1.6*
Amargosa Canyon speckled dace, *R. o. nevadensis*	1.6
Santa Ana speckled dace, *R. o. subsp.*	1.6
Modoc sucker, *Catostomus microps*	1.6*
Flannelmouth sucker, *C. latipinnis*	1.6
Eulachon, *Thaleichthys pacificus*	1.6*
Upper Klamath-Trinity spring Chinook salmon, *O. tshawytscha*	1.6
Southern Oregon Northern California coast coho salmon, *O. kisutch*	1.6*
Chum salmon, *O. keta*	1.6
Sacramento perch, *Archoplites interruptus*	1.6
Lost River sucker, *C. luxatus*	1.7*
Santa Ana sucker, *C. santaanae*	1.7*
Central Valley late fall Chinook salmon, *O. tshawytscha*	1.7
Klamath Mountains Province summer steelhead, *O. mykiss*	1.7
Southern California steelhead, *O. mykiss*	1.7*
Paiute cutthroat trout, *O. c. seleneris*	1.7*
Clear Lake hitch, *L. e. chi*	1.9
Owens speckled dace, *R. o. subsp.*	1.9
Northern California coast summer steelhead, *O. mykiss*	1.9*
McCloud River redband trout, *O. m. stonei*	1.9
Kern River rainbow trout, *O. m. gilberti*	1.9
Desert pupfish, *Cyprinodon macularius*	1.9*
Unarmored threespine stickleback, *G. a. williamsoni*	1.9*
Kern brook lamprey, *L. hubbsi*	2.0
White sturgeon, *A. transmontanus*	2.0
Red Hills roach, *L. s. subsp.*	2.0
Klamath largescale sucker, *C. snyderi*	2.0
Shortnose sucker, *Chasmistes brevirostris*	2.0*
Longfin smelt, *Spirinchus thaleichthys*	2.0*
Central Valley winter Chinook salmon, *O. tshawytscha*	2.0*
Central Valley spring Chinook salmon, *O. tshawytscha*	2.0*
Central Valley fall Chinook salmon, *O. tshawytscha*	2.0
California golden trout, *O. m. aguabonita*	2.0
Little Kern golden trout, *O. m. whitei*	2.0*
Eagle Lake rainbow trout, *O. m. aquilarum*	2.1
Lahontan cutthroat trout, *O. c. henshawi*	2.1*
Cow Head tui chub, *S. t. vaccaceps*	2.1
Goose Lake sucker, *C. o. lacusanserinus*	2.1
Saratoga Springs pupfish, *C. n. nevadensis*	2.1
Arroyo chub, *Gila orcutti*	2.3
Amargosa River pupfish, *C. n. amargosae*	2.3
Lahontan Lake tui chub, *S. b. pectinifer*	2.4

(*continued on next page*)

Appendix (*continued*)

Species	Status Score
Cottonball Marsh pupfish, *C. s. milleri*	2.4*
Northern green sturgeon, *Acipenser medirostris*	2.4
Upper Klamath-Trinity fall Chinook salmon, *O. tshawytscha*	2.4
California Coast fall Chinook salmon, *O. tshawytscha*	2.4*
Central Valley steelhead, *O. mykiss*	2.4*
South Central California coast steelhead, *O. mykiss*	2.4*
Salt Creek pupfish, *C. s. salinus*	2.6
Goose Lake lamprey, *Entosphenus sp.*	2.6
Monterey hitch, *L. e. harengeus*	2.7
Central California coast winter steelhead, *O. mykiss*	2.7*
Bigeye marbled sculpin, *C. klamathensis macrops*	2.7
Sacramento splittail, *Pogonichthys macrolepidotus*	2.9
Tidewater goby, *Eucyclogobius newberryi*	2.9*
Northern Roach, *L. mitrulus*	2.9
Russian River roach, *L. s. subsp*	3.0
Navarro Roach, *L. s. navarroensis*	3.0
Gualala roach, *L. parvipinnus*	3.0
Tomales Roach, *L. s. subspecies*	3.0
Upper Klamath marbled sculpin, *C. k. klamathensis*	3.0
Clear Lake tule perch, *H. t. lagunae*	3.0
Western brook lamprey, *L. richardsoni*	3.1
Clear Lake roach, *L s. subsp.*	3.1
Clear Lake prickly sculpin, *C. a. subsp.*	3.1
Russian River tule perch, *H. t. pomo*	3.1
Eagle Lake tui chub, *S. b. subsp.*	3.3
Sacramento hitch, *Lavinia e. exilicauda*	3.3
Monterey roach, *L. s. subditus*	3.3
Mountain sucker, *C. platyrhynchus*	3.3
Northern California coast winter steelhead, *O. mykiss*	3.3
Goose Lake redband trout, *O. m. subsp.*	3.3
Lower Klamath marbled sculpin, *C.k. polyporus*	3.3
Blue chub, Gila coerulea	3.4
Central California roach, *L. s. symmetricus*	3.4
Pacific lamprey, *Entosphenus tridentata*	3.4
Goose Lake tui chub, *S. t. thalassinus*	3.4
Hardhead, *Mylopharodon conocephalus*	3.4
Coastal cutthroat trout, *O. clarki clarki*	3.4
Rough sculpin, *Cottus asperrimus*	3.4*
Riffle sculpin, *C. gulosus*	3.4
Sacramento tule perch, *Hysterocarpus t. traski*	3.4
River lamprey, *Lampetra ayersi*	3.6
Pit-Klamath brook lamprey, *L. lethophaga*	3.6
Southern Oregon Northern California coast fall Chinook salmon, *O. tshawytscha*	3.7
Klamath River lamprey, *E. similis*	3.9
Reticulate sculpin, *C. perplexus*	3.9
Owens sucker, *C. fumeiventris*	3.9
Mountain whitefish, *Prosopium williamsoni*	3.9
Klamath Mountains Province winter steelhead, *O. mykiss*	3.9
Pit River tui chub, *S. thalassinus subsp.*	4.0
Klamath tui chub, *S. b. bicolor*	4.1
Sacramento speckled dace, *Rhinichthys osculus subp.*	4.1
Monterey sucker, *C. o. mnioltiltus*	4.1
Klamath smallscale sucker, *C. rimiculus*	4.1
California killifish, *Fundulus parvipinnis*	4.1
Inland threespine stickleback, *G. a. microcephalus*	4.1
Humboldt sucker, *C. o. humboldtianus*	4.3
Pit sculpin, *C. pitensis*	4.3
Coastrange sculpin, *C. aleuticus*	4.4
Sacramento blackfish, *Orthodon microlepidotus*	4.4
Paiute sculpin, *C. beldingi*	4.4
Coastal threespine stickleback, *Gasterosteus a. aculeatus*	4.6
Lahontan stream tui chub, *S. b. obesus*	4.7
Sacramento pikeminow, *Ptychocheilus grandis*	4.7
Coastal rainbow trout, *O. m. irideus*	4.7
Coastal Prickly sculpin, *C. asper subsp.*	4.7
Lahontan redside, *Richardsonius egregius*	4.8
Lahontan speckled dace, *R. o. robustus*	4.8
Klamath speckled dace, *R. o. klamathensis*	4.8
Tahoe sucker, *Catostomus tahoensis*	5.0
Sacramento sucker, *C. o. occidentalis*	5.0

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Sensitivity of survival to migration routes used by juvenile Chinook salmon to negotiate the Sacramento-San Joaquin River Delta

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Abstract Populations of juvenile salmon emigrating from natal rivers to the ocean must often traverse different migratory pathways that may influence survival. In regulated rivers, migration routes may consist of a network of channels such as in the Sacramento-San Joaquin River Delta, or of different passage structures at hydroelectric dams (e.g., turbines or spillways). To increase overall survival, management actions in such systems often focus on altering the migration routing of fish to divert them away from low-survival routes and towards high-survival routes. Here, we use a 3-year data set of route-specific survival and movement of juvenile Chinook salmon in the Sacramento-San Joaquin Delta to quantify the sensitivity of survival to changes in migration routing at two major river junctions in the Sacramento River. Our analysis revealed that changes in overall survival in response to migration routing at one river junction depended not only differences in survival among alternative routes, but also on migration routing at the other river junction. Diverting fish away from a low-survival route at the downstream river junction increased population survival by less than expected, given the difference in survival among routes, because part of the population used an alternative migration route at the upstream river junction. We also show that management actions that influence only migration routing will likely increase survival by less than actions that alter both migration routing and route-specific survival. Our analysis provides an analytical framework to help fisheries managers quantify the suite of management actions likely to maximize increases in population level survival.

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Introduction

Population dynamics of migrating fish depend on how they use space over time. Populations may traverse different migratory pathways en route to their final destination. For example, variation in ocean currents may affect migration pathways of adult salmon returning to their natal rivers (Bracis 2010). In regulated rivers, migrating juvenile salmon may negotiate dams via alternative pathways such as spillways or turbines (Skalski et al. 2002, 2009). In estuaries and river deltas, complex channel networks offer an array of possible migration routes (Perry et al. 2010). In each of these examples, survival rates may vary among migration routes due to differences in migration timing, food resources, environmental conditions, or predator abundance. Thus, understanding variation in survival among migration routes can provide important insights about population dynamics.

The Sacramento-San Joaquin River Delta (hereafter, the Delta) is a complex network of natural and man-made channels through which juvenile salmon must navigate on their journey to the ocean (Fig. 1). As juvenile salmon enter the Delta from natal streams, they disperse among the Delta's complex channel network. This dispersal process is driven by the relative quantities of discharge entering each channel, the horizontal distribution of fish in the water column as they pass a channel junction (a main channel splitting into two or more channels), and by tidal cycles that alter flow patterns at river junctions. Once fish enter a given channel, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. Eventually, alternative migration routes converge at the exit of the Delta and the population once again comes together to migrate through San Francisco Bay.

Movement of juvenile salmon among migration pathways in the Delta is influenced by water management actions that route water from the Sacramento and San Joaquin Rivers into pumping stations in the southern Delta. In this paper, we focus on the influence of water management actions on juvenile salmon emigrating from the Sacramento River. Specifically, the Delta Cross Channel is a man-made gated channel that diverts water from the Sacramento River into the interior Delta, where it then flows towards the pumping stations to be exported for agricultural and domestic uses (Fig. 1). Juvenile salmon entering the interior Delta exhibit lower survival probabilities than other migration routes, presumably due to longer migration times, entrainment at the pumping stations, and exposure to predators (Brandes and McLain 2001; Newman and Brandes 2010; Perry 2010). Furthermore, overall survival through the Delta (the fraction surviving through all routes) has averaged less than 33% for migration years 2007–2009 (Perry 2010).

Recovering endangered salmon populations in the Central Valley requires actions that mitigate the effects of water management on juvenile salmon. Increasing juvenile salmon survival in the Delta may consist of actions aimed at either reducing mortality within migration routes or directing the population away from low-survival migration routes such as the interior Delta. Quantifying potential benefits of implementing recovery actions can help fisheries managers weigh the costs of a given action against benefits measured in terms of increasing overall survival. In this study, we examine how altering migration routing can influence the overall survival of juvenile salmon.

In the Delta, migration routing of juvenile salmon can be altered in at least three ways. First, physical barriers, such as closure of the Delta Cross Channel gates, keep fish from entering a given migration route. However, physical barriers also alter the distribution of water flow, which can have unforeseen consequences on both fisheries and water resources. For example, closure of the Delta Cross Channel gates significantly alters the flows of many channels both upstream and downstream of the Delta Cross Channel, which in turn may affect entrainment and survival rates of multiple migration pathways. Closing the cross-channel gates can also increase the rate of salinity intrusion into the central Delta, ultimately reducing water exports in order to comply with mandated salinity standards. As this example shows, simply closing off a channel in the Delta is nontrivial, which has spurred investigation of alternative approaches for altering migration routing of salmon. For instance, non-physical behavioral barriers such as bubble curtains and strobe lights can elicit an avoidance response from juvenile salmon (Coutant 2001) while allowing water to flow unrestricted into a given channel.

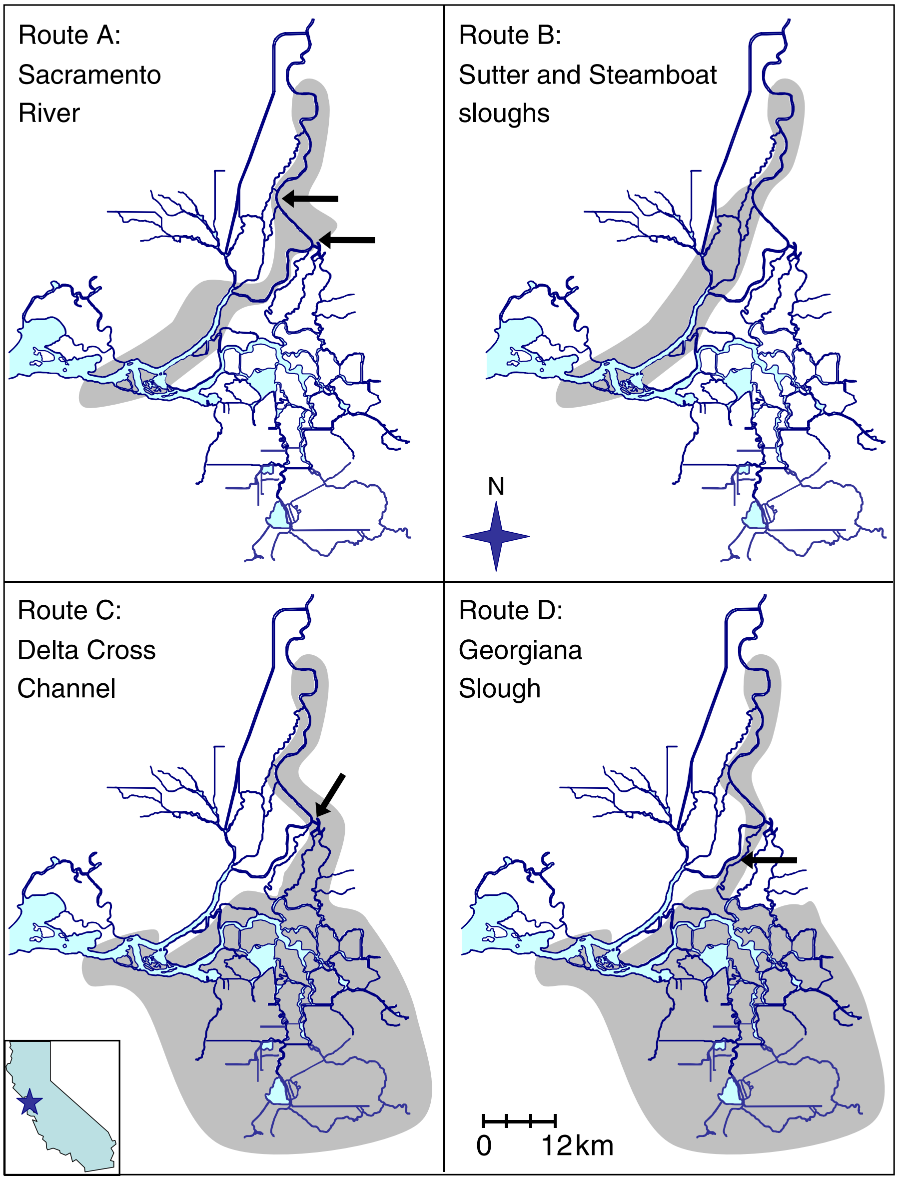


Fig. 1 Maps of the Sacramento–San Joaquin River Delta with shaded areas showing regions comprising survival through the Delta for four different migration routes. For each route, survival was estimated from Freeport on the Sacramento River (the northern most extent of the shaded area) to Chipps Island at the exit of the Delta (the western-most extent of the shaded area). In Route A, *arrows* show the two river junctions where migration routes diverge from the Sacramento River. For routes C and D, the interior Delta is the large shaded region to the south of the Sacramento River. The location of the Delta Cross Channel is indicated by the arrow in Route C. The Sacramento River release site (off the map) is 19 river kilometers upstream of Freeport, and the Georgiana Slough release site is shown by the arrow in Route D

Finally, behavioral responses to the hydrodynamics at junctions may play a role in the entrainment rates at a given river junction. Thus, structural changes in channel geometry at a river junction may provide a means of altering migration routing without changing the distribution of water flow. Currently, both physical and non-physical behavioral barriers are being investigated in the Delta in attempt to guide fish away from low-survival migration routes.

To quantify the influence of migration routing on overall survival, we used estimates of movement and reach-specific survival obtained from acoustically tagged juvenile salmon collected over 3 years. Biotelemetry techniques combined with mark-recapture statistical models provide a powerful tool to simultaneously quantify dispersal and survival of juvenile salmon migrating through the Delta. Uniquely identifiable transmitters provided detailed information about the temporal and spatial movements of individuals migrating through a series of monitoring stations in the Delta. This information was then synthesized using a multistate mark-recapture model that quantified dispersal of the population among migration routes and survival within these routes (Perry et al. 2010). Simultaneously estimating these quantities allowed overall survival to be derived from each of these components. For this exercise, we examined the sensitivity of overall survival to migration routing by altering the distribution of fish at critical river junctions and then used the observed route-specific survival estimates to quantify how such actions would affect overall survival in the Delta.

Methods

To examine how migration routing influences overall survival of juvenile Chinook salmon in the Delta (S_{Delta}), we used estimates of survival and routing probabilities provided by Perry et al. (2010) for the 2007 migration year and Perry (2010) for the 2008 and 2009 migration years. Route-specific survival, the fraction of fish migrating through each route, and overall survival were estimated from acoustic-tagged juvenile salmon using a multistate mark-recapture model applied to detection data from a system of telemetry stations situated throughout the Delta.

Telemetry system

Telemetry stations monitored movement of tagged fish among four primary migration routes through the Delta (Fig. 1): the mainstem Sacramento River (Route A); Sutter and Steamboat sloughs (Route B); the interior Delta via the Delta Cross Channel (Route C); and the interior Delta via Georgiana Slough (Route D). Each telemetry station consisted of single or multiple monitors (Vemco Ltd., Model VR2), depending on the number of monitors needed to maximize detection probabilities at each station. The number of telemetry stations varied among years (14, 23, and 20 stations in 2007, 2008, and 2009, respectively), but stations needed to estimate migration routing and survival to the terminus of the Delta remained constant among years. Detailed maps of the each year's telemetry system can be found in Perry (2010).

Fish tagging and release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery in Anderson, California. For the first release in December 2006, a 1.44-g tag (Vemco Ltd., Model V7-1L-R64K, 40-d expected battery life) was used. For all other releases, we used a 1.6-g tag (Vemco Ltd., Model V7-2L-R64K, 70-d expected battery life). Fish above 140 mm fork length were randomly selected for tagging. Transmitters were surgically implanted into fish using methods described by Perry et al. (2010).

To release tagged fish, they were first transported to release sites at either the Sacramento River near Sacramento, CA (all years) or Georgiana Slough (2008 and 2009; Fig. 1). The Georgiana Slough release site was added for 2008 and 2009 to increase the number of fish entering the interior Delta. In 2007 and 2008, fish were transferred to net pens (3-m square holding nets supported by pontoons) at the release site and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. For 2009, fish were transferred to perforated 121-L containers (2 fish per bucket) and held for 24 h in-river prior to release. Each release was carried out over a 24-h period to distribute tagged fish over the tidal and diel cycle. Two releases were performed in each migration year; one in December and another in January. For example, in migration year 2007, fish were released in December, 2006 when the Delta Cross Channel was open, and again in January, 2007 when the Delta Cross Channel was closed.

Linking migration routing to overall survival

The mark-recapture model described by Perry et al. (2010) estimates three sets of parameters: detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (Ψ_{hl}; Perry 2010; Perry et al. 2010). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h (h=A, B, C, D). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station i to $i+1$ within route h, conditional on surviving to station i. Route entrainment probabilities (Ψ_{hl}) estimate the probability of a fish entering route h at junction l (l=1, 2), conditional on fish surviving to junction l. Estimates of these parameters can be found in Perry (2010).

The first river junction was modeled as a two-branch junction where the entrance to Sutter and Steamboat Slough was pooled to estimate a single route entrainment probability. The parameter $\Psi_{\mathrm{B}1}$ estimates the probability of being entrained into either Sutter or Steamboat Slough at the first river junction (Fig. 2). Conversely, $1 - \Psi_{\mathrm{B}1} = \Psi_{\mathrm{A}1}$ is the probability

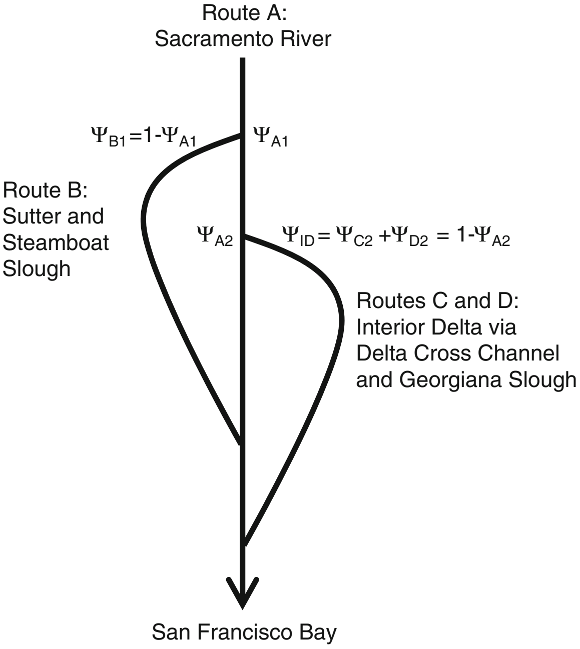


Fig. 2 Schematic showing the simplified routing structure and route entrainment probabilities (Ψ_{hl}) at each river junction

of remaining in the Sacramento River at the first junction. The second junction was modeled as a three-branch junction where Ψ_{A2}, Ψ_{C2}, and $1 - \Psi_{A2} - \Psi_{C2} = \Psi_{D2}$ estimate the probabilities of remaining in the Sacramento River (Route A), being entrained into the Delta Cross Channel (Route C), and entering Georgiana Slough (Route D) at junction 2.

The mark-recapture model estimates the individual components that comprise survival of the population migrating through the Delta, defined as survival of tagged fish from the entrance to the Delta at Freeport (rkm 73) to the exit of the Delta at station Chipps Island (rkm -9), a distance of 82 km by way of the Sacramento River. Overall survival through the Delta was estimated from the individual components as:

$$S_{\text{Delta}} = \sum_{h=\text{A}}^{\text{D}} \Psi_h S_h \qquad (1)$$

where S_h is the probability of surviving the Delta given the specific migration route used to negotiate the Delta, and Ψ_h is the probability of migrating through the Delta via one of four migration routes (A=Sacramento River, B=Sutter and Steamboat sloughs, C=Delta Cross Channel, D=Georgiana Slough). Overall survival through the Delta is a weighted average of the route-specific survival probabilities with weights equal to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\Psi_{\text{A}} = \Psi_{\text{A1}}\Psi_{\text{A2}} \qquad (2)$$

$$\Psi_{\text{B}} = \Psi_{\text{B1}} \qquad (3)$$

$$\Psi_{\text{C}} = \Psi_{\text{A1}}\Psi_{\text{C2}} \qquad (4)$$

$$\Psi_{\text{D}} = \Psi_{\text{A1}}\Psi_{\text{D2}} \qquad (5)$$

For instance, consider a fish that migrates through the Delta via the Delta Cross Channel (Route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability Ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability Ψ_{C2}. Thus, the probability of a fish migrating through the Delta via the Delta Cross Channel (Ψ_C) is the product of these route entrainment probabilities, $\Psi_{A1}\Psi_{C2}$.

Survival through the Delta for a given migration route (S_h) is the product of the reach-specific survival probabilities (S_{hi}) that trace each migration path between the entrance to the Delta and its terminus at Chipps Island. Thus, S_h is comparable among years even though annual differences in the telemetry system resulted in different reaches over which S_{hi} was estimated. Furthermore, S_h is directly comparable among routes because it estimates survival between the same starting and ending locations, but for fish migrating through different routes.

For our analysis, we focused on the probability of entering the interior Delta (Ψ_{ID}), which is the sum of the route entrainment probabilities for the Delta Cross Channel (Ψ_{C2}) and Georgiana Slough (Ψ_{D2}, Fig. 2). Survival through the interior Delta was estimated as the average survival of fish entering Routes C and D, weighted by the entrainment probabilities for each route. We aggregated Routes C and D for this analysis because survival estimates for fish entering the interior Delta were consistently lower than other routes (Fig. 3) regardless of whether fish entered the interior Delta via the Delta Cross Channel or Georgiana Slough. Thus, the specific

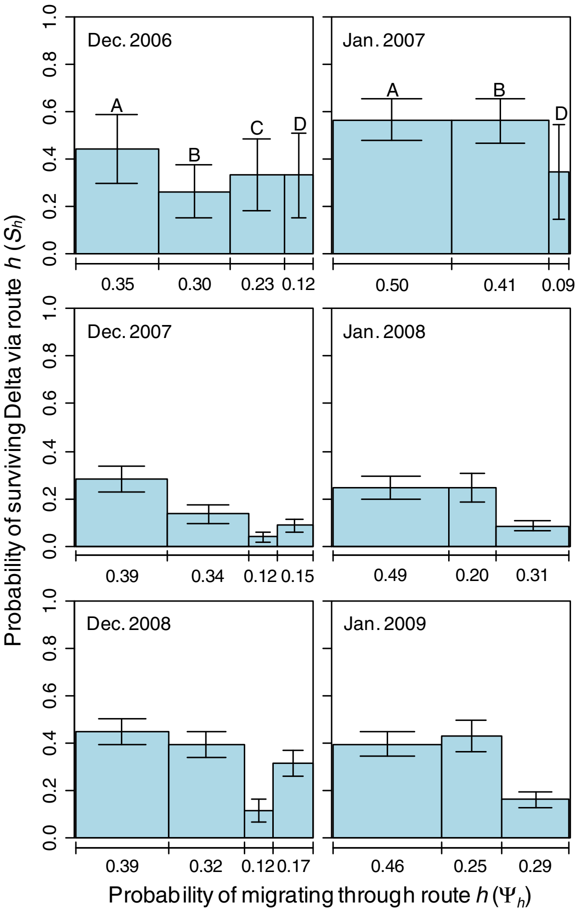


Fig. 3 Route-specific survival and the fraction of the population migrating through each migration route in the Sacramento – San Joaquin River Delta (from Perry et al. 2010; Perry 2010). Migration routes are labeled as follows: A=Sacramento River, B=Sutter and Steamboat sloughs, C=Delta Cross Channel, D=Georgiana Slough. Error bars show ±1 standard error

route used to enter the interior Delta is immaterial with respect to the sensitivity of overall survival to Ψ_{ID}.

Influence of migration routing on S_{Delta}

To quantify the influence of migration routing on S_{Delta}, we examined the change in S_{Delta} caused by varying route entrainment probabilities while holding constant the route-specific survival probabilities. Specifically, we examined the change in S_{Delta} when varying 1) the probability of fish entering Sutter and Steamboat sloughs (Ψ_{B1}), and 2) the conditional probability of entering the interior Delta (Ψ_{ID}), given fish that remained in the Sacramento River at its junction with Sutter and Steamboat Slough (Fig. 2). For each release group, we varied entrainment probabilities between zero and one at each river junction, and then recalculated S_{Delta}. We then quantified the predicted change in S_{Delta} relative to the observed estimate of S_{Delta} as both the absolute (i.e., additive) and relative (i.e., proportional) difference. This approach provides an understanding of how S_{Delta} might have changed had survival probabilities been the same but migration routing different for each release group.

To understand the response of S_{Delta} to changes in Ψ_{hl}, we also used demographic analysis techniques for matrix population models, which can be generalized to any transition matrix. For a Leslie matrix, sensitivity and elasticity measure the additive and proportional change in λ, the finite rate of population change, with respect to each demographic parameter in the model (Caswell 2001). In our case, S_{Delta} is analogous to λ in that it measures the rate of population change between the beginning and ending points of the Delta. Applying these techniques to our model, sensitivity is calculated as

$$s_{\Psi_{hl}} = \frac{\partial S_{\text{Delta}}}{\partial \Psi_{hl}} \tag{6}$$

and elasticity as

$$e_{\Psi_{hl}} = \frac{\Psi_{hl}}{S_{\text{Delta}}} \frac{\partial S_{\text{Delta}}}{\partial \Psi_{hl}}, \tag{7}$$

where $s_{\Psi_{hl}}$ and $e_{\Psi_{hl}}$ are sensitivity and elasticity with respect to a given route entrainment probability, Ψ_{hl}.

Sensitivity and elasticity can be interpreted in a number of ways to provide insights into how route entrainment probabilities affect S_{Delta}. First, sensitivity measures the slope of the relationship between absolute changes in S_{Delta} and Ψ_{hl}, while elasticity measures the slope of proportional changes in S_{Delta}. The steeper the slope, the larger will be the effect on S_{Delta} from a given change in Ψ_{hl}. Positive estimates indicate that increasing Ψ_{hl} will increase S_{Delta}, whereas negative values indicate that increasing Ψ_{hl} will reduce S_{Delta}. Second, sensitivity and elasticity can be interpreted as the additive and proportional change in S_{Delta}, respectively, when increasing Ψ_{hl} from zero to one. For example, if $s_{\Psi_{\text{ID}}} = -0.20$ then increasing Ψ_{ID} from zero to one will reduce S_{Delta} by 20 percentage points (e.g., from 0.50 to 0.30). In contrast, $e_{\Psi_{\text{ID}}} = -0.20$ indicates a 20% change in S_{Delta} (e.g., from 0.50 to 0.40). Last, applying Eq. 6 to S_{Delta} Eq. 1

yields a formula for the slope as a function of the route survival and entrainment parameters, elucidating which parameters affect the sensitivity of S_{Delta} to route entrainment probabilities. Although differences in survival among routes will certainly influence sensitivity of S_{Delta} to migration routing, sensitivity will also be a function of routing at both river junctions.

Last, we predicted S_{Delta} by varying both Ψ_{B1} and Ψ_{ID} simultaneously to quantify the range in overall survival that could be obtained by altering entrainment at both river junctions. Such insights will help fisheries managers better understand how to target management actions aimed at altering route entrainment probabilities in order to maximize overall survival in the Delta.

Results

Interannual patterns in route-specific survival and migration probabilities

We observed substantial variation in the magnitude of within-route survival among years, yet stable patterns of survival across routes over all years (Perry 2010; Perry et al. 2010). Among migration years, 2008 stands out as having the lowest survival at both the route scale and the Delta scale (Fig. 3). Survival through the Delta was <0.20 for 2008, but >0.33 for all other years and releases (Table 1). Over all years, estimates of S_{Delta} exceeded 0.40 for only one release group (Jan. 2007), and only during migration year 2007 did observed estimates of S_{Delta} differ considerably between releases (Table 1). For all releases, detection probabilities (P_{hi}) were high at most sites (median=1.0, mean=0.915, minimum=0.385), leading to favorable precision of survival probabilities relative to releases sample sizes (Table 1, Fig. 3).

Although rankings of route-specific survival vary somewhat across release groups, one pattern remained consistent: survival probabilities for the Sacramento River were always greater than survival for migration routes through the interior Delta (via Georgiana Slough and the Delta Cross Channel; Fig. 3). In addition, Sutter and Steamboat sloughs exhibited either similar survival to the Sacramento River (typically for January releases) or lower survival than the Sacramento River (typically for December releases; Fig. 1). Except for the Dec. 2007 release group, observed survival estimates for Sutter and Steamboat Sloughs were greater than for routes leading to the interior Delta.

Sensitivity of S_{Delta} to route entrainment probabilities

The effect of varying route entrainment probabilities on overall survival differed among river junctions. At the first river junction, sensitivity of S_{Delta} to entrainment into Sutter and Steamboat Slough (Ψ_{B1}) followed no consistent trend among releases. Increasing Ψ_{B1} decreased S_{Delta} for two of the releases, increased it for two releases, and resulted in a slight positive change in S_{Delta} for two releases (Table 1; Fig. 4a, b). In addition, the standard errors for sensitivity and elasticity of Ψ_{B1} indicate that the 95% confidence intervals overlap

Table 1 Sensitivity of S_{Delta} to route entrainment probabilities for Sutter and Steamboat sloughs and the interior Delta. Also shown is sample size and estimates of S_{Delta} for each release group (from Perry et al. 2010, Perry 2010). Standard errors are given in parentheses and were based on variances estimated using the Delta method

Release group	Number released	S_{Delta}	Sutter and Steamboat Slough, Ψ_{B1}		Interior Delta, $\Psi_{\mathrm{ID}} = \Psi_{\mathrm{C2}}+\Psi_{\mathrm{D2}}$	
			Sensitivity	Elasticity	Sensitivity	Elasticity
Dec. 2006	64	0.351 (0.101)	−0.125 (0.116)	−0.105 (0.098)	−0.078 (0.123)	−0.111 (0.175)
Jan. 2007	80	0.543 (0.070)	0.030 (0.101)	0.023 (0.077)	−0.129 (0.126)	−0.036 (0.038)
Dec. 2007	208	0.174 (0.031)	−0.059 (0.042)	−0.117 (0.085)	−0.142 (0.038)	−0.331 (0.085)
Jan. 2008	211	0.195 (0.034)	0.062 (0.051)	0.063 (0.052)	−0.127 (0.041)	−0.252 (0.073)
Dec. 2008	292	0.368 (0.037)	0.038 (0.058)	0.033 (0.050)	−0.148 (0.045)	−0.170 (0.053)
Jan. 2009	292	0.339 (0.035)	0.125 (0.071)	0.093 (0.054)	−0.176 (0.044)	−0.200 (0.054)

zero for all release groups (95% confidence interval=estimate ± 1.96*SE). In contrast, at the second river junction, increasing entrainment into the interior Delta (Ψ_{B1}) decreased S_{Delta} for every release group, and the confidence intervals for four of the six releases exclude zero (Table 1; Fig. 4c, d).

Changes in S_{Delta} in response to migration routing at a given junction are driven partly by differences in survival among migration routes and partly by entrainment probabilities at other river junctions. For example, for the two releases where S_{Delta} declined when increasing Ψ_{B1} (Dec. 2006 and Dec. 2007; Fig. 4a, b), the negative slope was driven by lower survival in Sutter and Steamboat Sloughs than in the Sacramento River (Fig. 3). For all other releases, survival was similar between the Sutter and Steamboat Sloughs (Route B) and the Sacramento River (Route A, Fig. 3), yet S_{Delta} responded positively to increasing the proportion of fish entering Sutter and Steamboat Slough (Table 1; Fig. 4a, 4a). Examining the equation for sensitivity of S_{Delta} with respect to Ψ_{B1} reveals why this pattern emerges:

$$s_{\Psi_{B1}} = (S_B - S_A) + \Psi_{ID}(S_A - S_{ID}).$$

The first term shows that sensitivity is partly a function of the difference in survival between the Sacramento River and Sutter and Steamboat sloughs (S_B-S_A). However, the second term in the equation shows

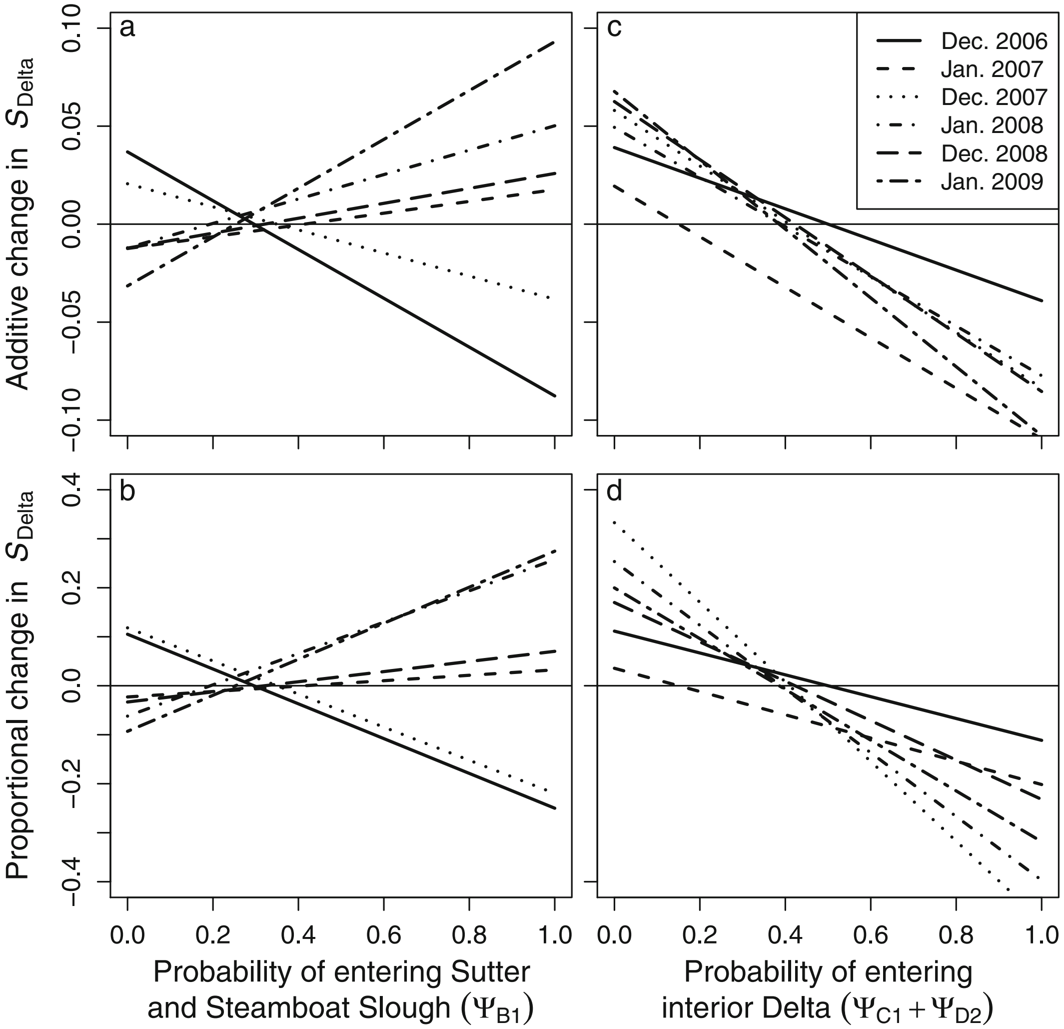


Fig. 4 Predicted change in estimates of S_{Delta} for each release group in response to varying route entrainment probabilities between zero and one

that sensitivity is also driven by 1) the probability of entrainment into the interior Delta (Ψ_{ID}), and 2) the difference in survival between the Sacramento River and interior Delta (S_{A}-S_{ID}). Consequently, when survival for Sutter and Steamboat sloughs is on par with the Sacramento River (S_{B} - $S_{\mathrm{A}} \approx 0$), increasing Ψ_{B1} increases S_{Delta} by routing fish away from the interior Delta where survival was lower than the Sacramento River.

At the second river junction, increasing entrainment into the interior Delta always reduced S_{Delta} because survival for the interior Delta (Routes C and D) was lower than the Sacramento River (Route A) for all release groups (Fig. 3). However, the magnitude of change in S_{Delta} depends on not only differences in survival between these routes, but also on the fraction of the population remaining in the Sacramento River at the first river junction:

$$s_{\Psi_{\mathrm{ID}}} = \Psi_{\mathrm{A1}}(S_{\mathrm{ID}} - S_{\mathrm{A}}).$$

Although the difference in survival between these routes determines the direction of change in S_{Delta}, Ψ_{A1} scales the magnitude of change. For example, for the Jan. 2009 release group, survival of fish entering the interior Delta was 0.235 less than the Sacramento River (i.e., S_{ID} – S_{A}=0.163–0.398). But because 25% of the tagged population entered Sutter and Steamboat Slough at the first river junction (Fig. 3), the maximum possible change in S_{Delta} is only 0.175 when changing Ψ_{ID} from one to zero (Table 1). These findings illustrate how the magnitude of change in S_{Delta} from altering entrainment at one river junction depends not only on differences in survival between alternative routes, but also on the fraction of the population passing the river junction.

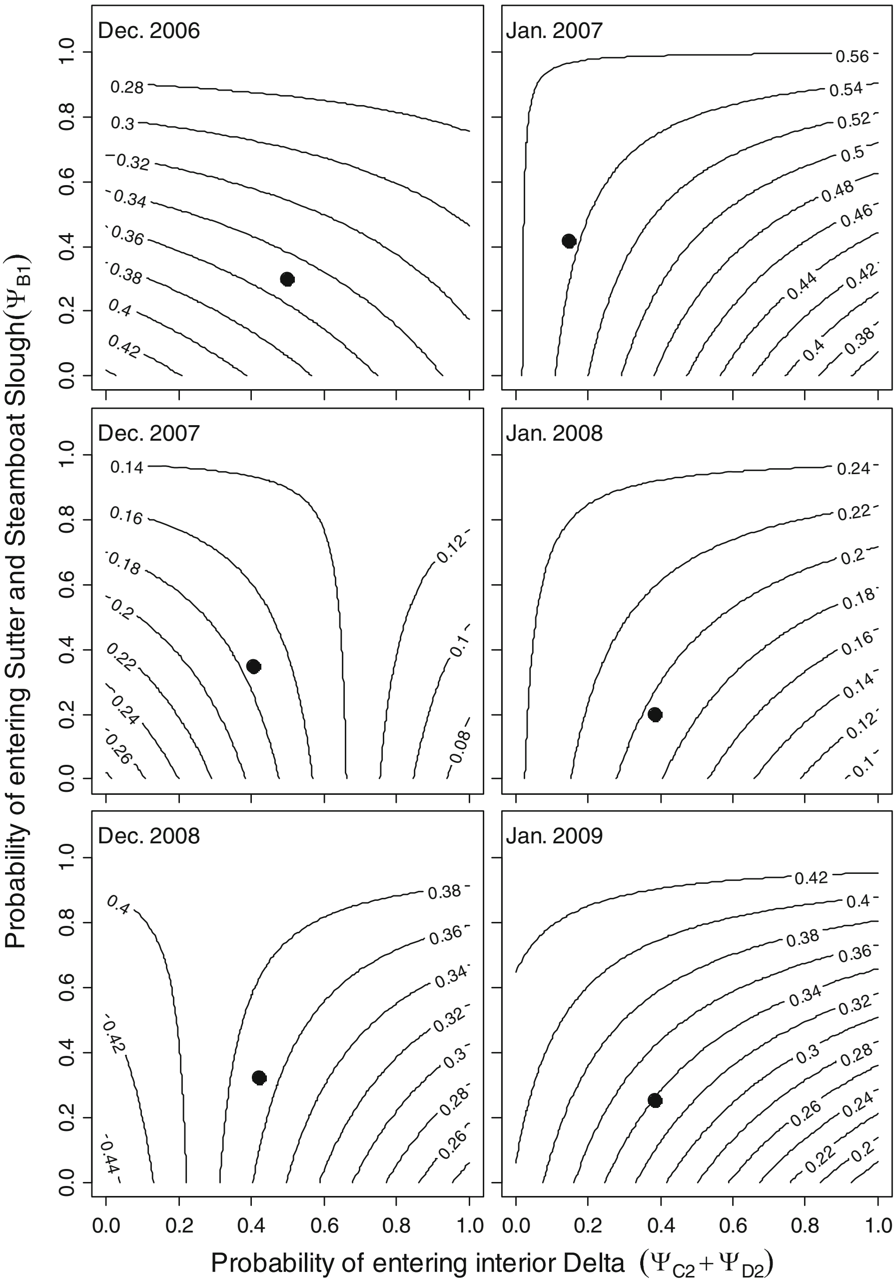
Eliminating entrainment into the interior Delta is expected to result in a 2–7 percentage point increase in overall survival (Fig. 4c). As discussed above, the magnitude of this change is, in part, due to only a fraction of the tagged population passing by this river junction. However, the small absolute increase in survival is also due to low survival probabilities observed in all routes. Route-specific survival for all routes was <0.5 for most release groups (Fig. 3). Thus, while shifting the distribution of fish among routes influences overall survival, the magnitude of absolute change in S_{Delta} is constrained by maximum survival observed in any given route. Further increases in S_{Delta} would require management actions that affect not only migration routing, but also survival within migration routes.

In contrast, proportional changes in S_{Delta} provide insight into the relative change in survival in response to altering route entrainment probabilities. S_{Delta} varied considerably among years (Table 1) even though relative differences in survival between the Sacramento River and interior Delta remained consistent among years (Fig. 3). Therefore, given interannual variation in overall survival, proportional changes in S_{Delta} allow comparison among release groups on a common relative scale. From this perspective, the relative change in S_{Delta} is considerably larger than the absolute change, increasing by 10–35% for five of the six releases in response to eliminating entrainment into the interior Delta. This analysis shows how understanding changes in S_{Delta} on both absolute and relative scales is important, particularly when overall survival is low and varies through time.

Altering entrainment at both river junctions simultaneously revealed that 1) overall survival could vary considerably in response to migration routing, 2) the optimal strategy for maximizing survival varied among releases, and 3) sensitivity of overall survival to entrainment at one junction depended the value of entrainment at the other river junction. Depending on release group, maximum S_{Delta} was 1.5 to 2.4 times the minimum survival (Fig. 5). Although survival can be maximized simply by directing fish to the highest-survival route, the set of entrainment probabilities that maximize survival varied among release groups. For December releases, since the Sacramento River (Route A) exhibited higher survival than other routes, overall survival is maximized when all fish remain in the Sacramento River (i.e., when Ψ_{B1}=0 and Ψ_{ID}=0; Fig. 5). However, for January release groups, overall survival is maximized by minimizing entrainment into the interior Delta but maximizing entrainment in Sutter and Steamboat Slough. Because survival in the Sacramento River was similar to Sutter and Steamboat Slough during January releases, diverting fish into Sutter and Steamboat Slough maximizes overall survival by routing fish away from the second river junction where they become exposed to entering the interior Delta.

Simultaneously altering entrainment probabilities at both river junctions illustrated how sensitivity of S_{Delta} to entrainment at one junction depends on the value of entrainment at the other river junction (Fig. 5). Vertical

Fig. 5 Contour plot showing overall survival through the Sacramento – San Joaquin River Delta (S_{Delta}) predicted as a function of entrainment probabilities into the interior Delta and Sutter and Steamboat Slough. *Filled circles* show the observed overall survival and route entrainment probabilities for each release group



contour lines in Fig. 5 indicate regions where S_{Delta} is insensitive to Ψ_{B1}, horizontal contour lines reveal insensitivity to Ψ_{ID}, and closely-spaced contour lines reveal regions of high sensitivity. For example, as entrainment into Sutter and Steamboat Slough increases, S_{Delta} becomes less sensitive to changes in Ψ_{ID} because most of the population is diverted away from the second river junction. For January releases, S_{Delta} is insensitive to Ψ_{B1} when Ψ_{ID} is low, as is indicated by the wide range of Ψ_{B1} that yields similar overall survival. These relationships help to understand how survival through Delta varies in response to migration routing.

Discussion

Our analysis reveals the magnitude of change in overall survival that might be expected from management actions that alter migration routing through the Delta. Given the substantial difference in survival between the interior Delta and the Sacramento River, we might have expected a larger boost in survival from eliminating entrainment into the interior Delta. In a simpler system with only one branching junction (e.g., a dam), change in overall survival with respect to migration routing is directly proportional to the difference in survival among migration routes. However, due to the channel complexity of the Delta, altering migration routing at one river junction yields changes in S_{Delta} that are less than proportional to the difference in survival between alternative migration routes. We showed that changes in S_{Delta} with respect to migration routing at one river junction depends also on migration routing at other river junctions. Therefore, by considering how management actions at multiple river junctions affect S_{Delta}, managers may be able to optimize the suite of actions required to maximize the expected increase in S_{Delta}. These are important insights about the magnitude of increase in S_{Delta} expected from management actions to alter migration routing.

The strength of inferences from acoustic tag data to the untagged population depend on whether survival estimates are viewed from a relative or absolute point of view. Potential tag effects on survival (Adams et al. 1998) or differences in survival between hatchery and wild fish (Reisenbichler and McIntyre 1977; Kostow 2004) could result in lower absolute survival of tagged fish relative to untagged fish. In our study, although it is unknown whether tagged fish of hatchery origin exhibit lower survival than untagged fish of wild origin, absolute changes in survival should be interpreted with caution (i.e., Fig. 4a, c). Regardless of the absolute magnitude of survival, however, differences among routes that influence survival should act similarly on all populations of salmon smolts migrating through the Delta. For example, both tagged and untagged fish migrating through the interior Delta likely experienced lower survival relative to fish migrating within the Sacramento River. Therefore, relative changes in survival in response to altering migration routing (i.e., Fig. 4c, d) should provide stronger inferences to untagged populations than will absolute change in survival probabilities.

We focused our analysis on river junctions where management actions are likely to have the largest influence on population survival. For example, we showed that Steamboat and Sutter Slough is an important migration route because fish using this route avoid entering the interior Delta where survival is lower than other routes. The Delta's channel geometry is hierarchical in nature such that secondary (and finer level) migration routes are nested within primary routes. At each secondary and tertiary river junction, the population divides into a smaller and smaller fraction of the whole. Therefore, management actions focused at secondary junctions will have less population-level influence than at primary river junctions simply because a small fraction of the population will be influenced. In contrast, management actions have the potential for influencing much of the population at the two primary river junctions examined in our analysis.

Sensitivity and elasticity measure changes in S_{Delta} with respect to migration routing at a junction while holding all other parameters constant. Thus, our analysis assumes that management actions alter only migration routing but not route-specific survival probabilities. This assumption may be violated in two ways. First, changing migration routing will alter the abundance of juvenile salmon in each route, which could cause a density dependent predator response. At very low prey densities, increasing smolt abundance within a route could increase predation rates via the predator's numerical or functional response to prey. In contrast, increasing smolt abundance to high levels within a route could reduce predation rates through predator swamping. Second, management actions that affect water routing at a particular junction (e.g., physical barriers) could influence route-specific survival or entrainment at other junctions by changing discharge and hydrodynamics within a migration route. For example, physical barriers alter discharge entering each channel, and juvenile salmon survival has been positively correlated with discharge in the Delta (Newman and Rice 2002; Perry 2010). Such simultaneous changes in migration routing and route-specific survival are not captured by our analysis.

In terms of the magnitude of change in population survival, managers must consider both the expected change in migration routing and the expected change in route-specific survival caused by implementation of physical and non-physical barriers. With respect to migration routing, physical barriers are 100% effective whereas non-physical barriers typically divert less than 100% of fish. Therefore, under the assumption of constant route-specific survival, non-physical barriers would realize only a fraction of the maximum possible increase in population survival. With respect to route-specific survival, physical barriers may yield a larger change in survival than non-physical barriers because physical barriers alter discharge and hydrodynamics of each migration route. However, the direction and magnitude of change in route-specific survival in response to physical and non-physical barriers is poorly understood. This uncertainty highlights the importance of quantifying simultaneous changes in both migration routing and route-specific survival in field studies evaluating physical and non-physical barriers in the Delta.

Our sensitivity analysis has application to other regulated river systems where managers must balance the costs of water management actions against benefits to fish populations. On the Columbia River, for example, millions of dollars are spent annually to evaluate survival of juvenile salmon migrating past dams. Management actions such as spilling water over dams results in foregone power generation but improves population survival of juvenile salmon by diverting them away from turbines. Our analytical approach could be used to quantify expected changes in population survival by implementing such actions, helping managers to better design dam operations to achieve recovery targets at minimum cost. More importantly, in the Delta and other regulated river systems, our analytical approach can be used to help design recovery actions before such actions are implemented. Given scarce resources with which to recover endangered salmon populations, such analyses can help direct resources towards actions most likely to yield the largest improvement in survival.

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Survival and Migration Dynamics of Juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) in the Sacramento-San Joaquin River Delta

Russell W. Perry

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

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University of Washington

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Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington
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This is to certify that I have examined this copy of a doctoral dissertation by

Russell W. Perry

and have found that it is complete and satisfactory in all respects,
and that any and all revisions required by the final
examining committee have been made.

Chair of the Supervisory Committee:

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Abstract

Survival and migration dynamics of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento-San Joaquin River Delta

Russell W. Perry

Chair of the Supervisory Committee:
Professor John R. Skalski
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Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) emigrating from natal tributaries of the Sacramento River must negotiate the Sacramento–San Joaquin River Delta, a complex network of natural and man-made channels linking the Sacramento River with San Francisco Bay. Natural processes and water management actions affect the fraction of the population using different migration routes through the Delta and survival within those routes. In this dissertation, my goals were to 1) develop a mark-recapture model to explicitly estimate survival and migration route probabilities for each of four migration routes through the Delta, 2) link these route-specific probabilities to population-level survival, and 3) apply this model to the first available acoustic telemetry data of smolt migration through the Delta, and 4) quantify the effect of river flow and tides on movement and survival.

I found that survival of juvenile salmon migrating through the interior Delta, where water pumping stations are located, was consistently less than for fish that migrated via the Sacramento River. Thus, movement of fish among migration routes in the Delta will influence population-level survival. To examine factors affecting migration routing, I used a multinomial model to quantify the effect of river flow, tides, and operation of a water diversion gate (the Delta Cross Channel) on entrainment of fish into the interior Delta. I found that the closing the Delta Cross Channel gate increased Sacramento River flow by about 30% but was expected to decrease entrainment into the interior Delta by only about 15%. I also found that river inflow affected entrainment by a similar magnitude as operation of the Delta Cross Channel gates. Flood tides causing upstream flow into the river junction increased the probability of fish entering the interior Delta, but increasing river flow dampens tidal fluctuations, thereby reducing entrainment probabilities. My study shows how movements among, and survival within, migration routes interact to influence population-level survival through the Delta. Models developed in this dissertation are critical for understanding how water management actions influence migration routing and population survival of juvenile salmon in the Sacramento–San Joaquin River Delta.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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I would like to thank John Skalski for being not only an advisor, but my mentor. The undending determination of Patricia Brandes ensured that I had a steady stream of data on which to base this dissertation. I thank Jim Anderson for providing a stimulating arena in which to discuss any topic under the sun, that is, as long as it could be expressed in scribbles on a white board. Jon Burau, Aaron Blake, and Christopher Holbrook provided many valuable insights that helped me to understand the dynamics of the Delta. Friends and colleagues of the USGS, Western Fisheries Research Center provided much needed support in the waning hours of this dissertation. I am grateful to staff of the USFWS, Stockton, CA; NOAA, Southwest Fisheries Science Center; and the UC Davis Biotelemetry Laboratory. This dissertation would not be possible without the hard work of many individuals to deploy and maintain telemetry stations, tag and release fish, and organize and disseminate the data. The U.S. Fish and Wildlife Service and the staff of Coleman National Fish Hatchery provided late-fall Chinook and logistical support for this research. Tagging of juvenile salmon, ultrasonic station deployment and interrogation, and tag-detection database maintenance were supported by a grant from the California Bay-Delta Authority by Agreement No. U-05-SC-047. Funding for this dissertation was provided by a research assistantship from the US Fish and Wildlife Service, a fellowship grant from the School of Aquatic and Fishery Sciences, and a CALFED Science Fellowship, Agreement No. U-04-SC-005 with the California Bay-Delta Authority.

DEDICATION

For my best friend Kari and my beautiful daughter Lilah

INTRODUCTION

1.1 Historical Background

1.1.1 The Central Valley and its Chinook salmon

Chinook salmon populations in the Central Valley of California once numbered up to two million spawning adults (Fisher, 1994) and represent the southern-most extant population of Chinook salmon in the Pacific Ocean (Moyle, 2002). Historical accounts attest to such great abundance, "The year 1878 was the year of the immense gathering of salmon in the McCloud", a tributary to the Sacramento River, "…I have never seen anything like it anywhere, not even on the tributaries of the Columbia…" (Stone, 1897 as quoted in Yoshiyama et al., 2001). Such historical abundance should come as little surprise given that the Central Valley of California drains 40% of California's landmass and discharges 47% of its water (Figure 1.1; Healy, 2008). The Central Valley watershed is comprised of the Sacramento River to north and San Joaquin River to the south, both of which converge in the Sacramento-San Joaquin River Delta (hereafter, "the Delta") to empty their fresh waters into San Francisco Bay (Figure 1.1). These two major rivers are fed by numerous tributaries with headwaters originating in the Sierra-Nevada and southern Cascade mountain ranges, and most of these tributaries once harbored populations of anadromous salmonids (Figure 1.1).

Four runs of salmon have evolved distinct life histories to capitalize on the diversity of habitat available in Central Valley rivers and streams. As is common in other areas of the northwest, the runs are named according the season in which the adults return to fresh water: winter, spring, fall, and late-fall. Each run's life history capitalizes on a spatiotemporal niche formed by temperature, elevation, and timing of life-history events (Moyle, 2002). Water temperatures in the lower watershed and Delta can often reach lethal limits for salmon during late spring and summer (Baker et al., 1995; Myrick and Cech , 2004), and life histories have

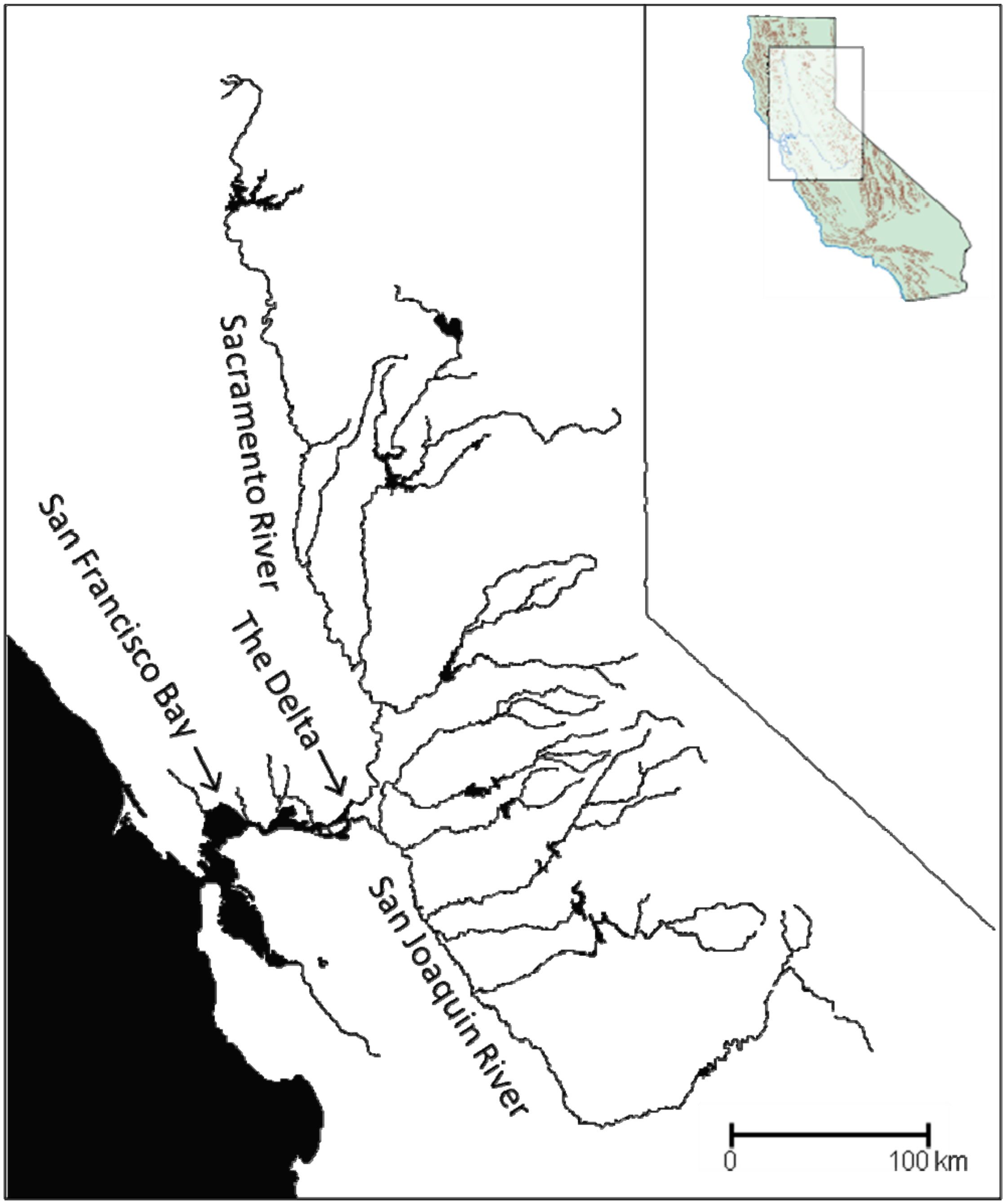

Figure 1.1. The Central Valley watershed of California.

evolved to avoid these locations during these seasons (Williams, 2006). In general, timing of adult returns is such that winter and spring runs spawn at higher elevations of the watershed, whereas fall and late-fall runs use the lowest reaches of the watershed for spawning. Spring-run adults arrive March through May, ascend the upper most-reaches and highest elevations of Central Valley rivers when spring run-off allows access, and remain in the stream until spawning in late summer (Moyle, 2002). Winter run arrive December through March, use lower elevations than the spring run, and consequently, spawn earlier than spring-run Chinook (May and June) when these reaches attain optimal spawning temperature (Moyle, 2002). Fall and late-fall run return in September – October and November – December destined for the lowest-elevation reaches and spawn soon after arriving at spawning grounds.

Such diversity in run timing, spawning, and habitat use dictates similar diversity in the life history patterns of juvenile Chinook salmon. Both ocean-type and stream-type forms are observed, with some runs exhibiting a mixture of both life history types (Moyle, 2002). Most spring-run juveniles exhibit the classic stream-type life history, but have shown considerable plasticity, with the in-stream rearing period ranging from 3 to 15 months (Moyle, 2002; Williams, 2006). Winter Chinook juveniles begin their migration shortly after emergence, but apparently rear extensively in the river for 5-10 months, as they are not observed in the Delta until they attain larger size (Moyle, 2002; Williams, 2006). Fall-run Chinook salmon exhibit both stream-type and ocean-type life history forms, with most juveniles entering and rearing in the Delta as fry and parr and some rearing in the river to emigrate as yearling smolts (Williams et al., 2006). Finally, juveniles of late-fall Chinook salmon typically emerge in the spring, rear in the stream during the summer, and then emigrate during the fall or winter. Although juveniles exhibit high life-history variation within and among runs, their common link is complete absence from lower-elevation rivers and the Delta between June and late September during periods of high water temperature (Williams, 2006).

Similar to many large West Coast rivers, salmon populations have declined substantially since the mid-1800s (Yoshiyama, 2001). All four runs of Chinook salmon in the Central Valley have been listed as either endangered (winter run), as threatened (spring run), or as a species of concern (fall/late-fall run) under federal and state endangered species legislation (Myers, 1998; Lindley, 2004). The winter run is the most imperiled, declining from an average of 86,509 spawners during the 1960s to only 191 spawners in 1991 (Fisher, 1994; Black, 1995). Returns have since increased to around 10,000 fish during the early 2000s (Williams, 2006). Spring-run salmon were completely extirpated from the San Joaquin River and now exist only in the mainstem Sacramento River and three of its tributaries. Both spring and winter run are particularly sensitive to catastrophic events due to a very restricted age-at-maturity distribution: 90% of adults return as 3-year old spawners (Fisher, 1994). The late-fall run has also been extirpated from the San Joaquin River, with the sole population now occurring in the mainstem Sacramento River. The fall run remains the healthiest population due to its reliance on lower-elevation mainstem rivers and tributaries, which were least affected by human alterations to the watershed. Annual escapement of the other runs now rarely exceeds 20,000 but fall-run escapement typically exceeds 100,000. A record 725,000 fall-run spawners returned in 2002, but returns in 2007 and 2008 dropped below conservation targets, spurring management concern for the once healthiest of Central Valley Chinook salmon populations (NOAA, 2008; Lindley et al., 2009). Most runs are now supported largely by hatcheries, instituted as mitigative and recovery measures when stocks began to decline due to human impacts (Moyle, 2002; Williams, 2006).

The decline of salmon populations began early in the settlement of the Central Valley. Hydraulic gold mining from the mid 1800s to 1884 completely eliminated salmon populations from many large tributaries of the Sacramento and San Joaquin rivers (Black, 1995; Yoshiyama, 2001). Extensive habitat loss occurred between 1900 and 1950 when hydroelectric and irrigation development rapidly transformed the watershed from a naturally functioning, snow-melt driven hydrologic cycle to a highly regulated water delivery system. Large dams completely eliminated all spawning habitat for the winter run, which now exists owing to cold-water releases from Keswick Dam, the upstream boundary of access to anadromous fish on the Sacramento River (Fisher, 1994; Yoshiyama, 2001). Eighty percent of the 6000 stream miles of former spawning habitat has been blocked from access to the spring run (Fisher, 1994). Dams were also responsible for complete elimination of spring and late-fall runs in the San Joaquin River (Yoshiyama, 2001). Commercial fisheries also contributed to the decline and major gill net fisheries targeting winter and spring runs operated through the late 1870s (Black, 1995). Following decline of these runs, much of the commercial fishery shifted to the ocean. However, the ocean fishery in southern Oregon and California was halted during 2008 and 2009 due to the collapse of the fall run (NOAA, 2008; Lindley et al., 2009). Because of its Mediterranean climate and variable rainfall, many irrigation canals were built to divert and reduce natural flows of Central Valley rivers for agricultural and municipal uses. Furthermore, with all water from the Sacramento River in the north and the San Joaquin River in the south funneling through the Delta, the Delta became the hub of the largest water delivery system in the world.

1.1.2 The Sacramento-San Joaquin River Delta

The Sacramento-San Joaquin River Delta is the largest wetland on the West Coast of the United States (Healy, 2008). Historically, the extensive freshwater and tidal wetlands once covered 2200 km^2 surrounding the confluence of the Sacramento and San Joaquin Rivers and upper San Francisco Bay (Nichols, 1986). As upland rivers entered the Delta, their flows dispersed through marshes, wetlands, and 700 miles of interconnected river channels, waterways, and sloughs (Figure 1.2). So unique is the Delta that it is home to a number of endemic fish species such as the Delta smelt (*Hypomesus transpacificus*). The Delta also provided a migration corridor for yearling Chinook smolts and critical habitat for subyearling Chinook salmon rearing in the shallow, productive wetlands and side channels of the Delta. The Delta played a critical role in the historical productivity of Chinook salmon populations of the Central Valley (Williams, 2006).

Degradation of the Delta occurred simultaneously with that of headwater tributaries as sediments from hydraulic mining washed downstream and settled in the slower water velocities of the Delta and San Francisco Bay. The Sacramento River's bed rose by six to seven feet at Sacramento (Black, 1995) and by over three feet in many bays (Nichols, 1986). Although mining ceased by 1884, not until the late 1920s did the river bed return to its pre-mining elevation (Nichols, 1986). Sedimentation of the Delta and San Francisco Bay reduced its capacity and substantially altered tidal and water circulation patterns on which the estuary ecosystem had evolved (Nichols, 1986). As the human population began to increase in the early 20th century, wetlands were filled and diked for agriculture, rivers were leveed for flood control, and channels were dredged for navigation. Only 125 km^2 of 2200 km^2 of wetlands

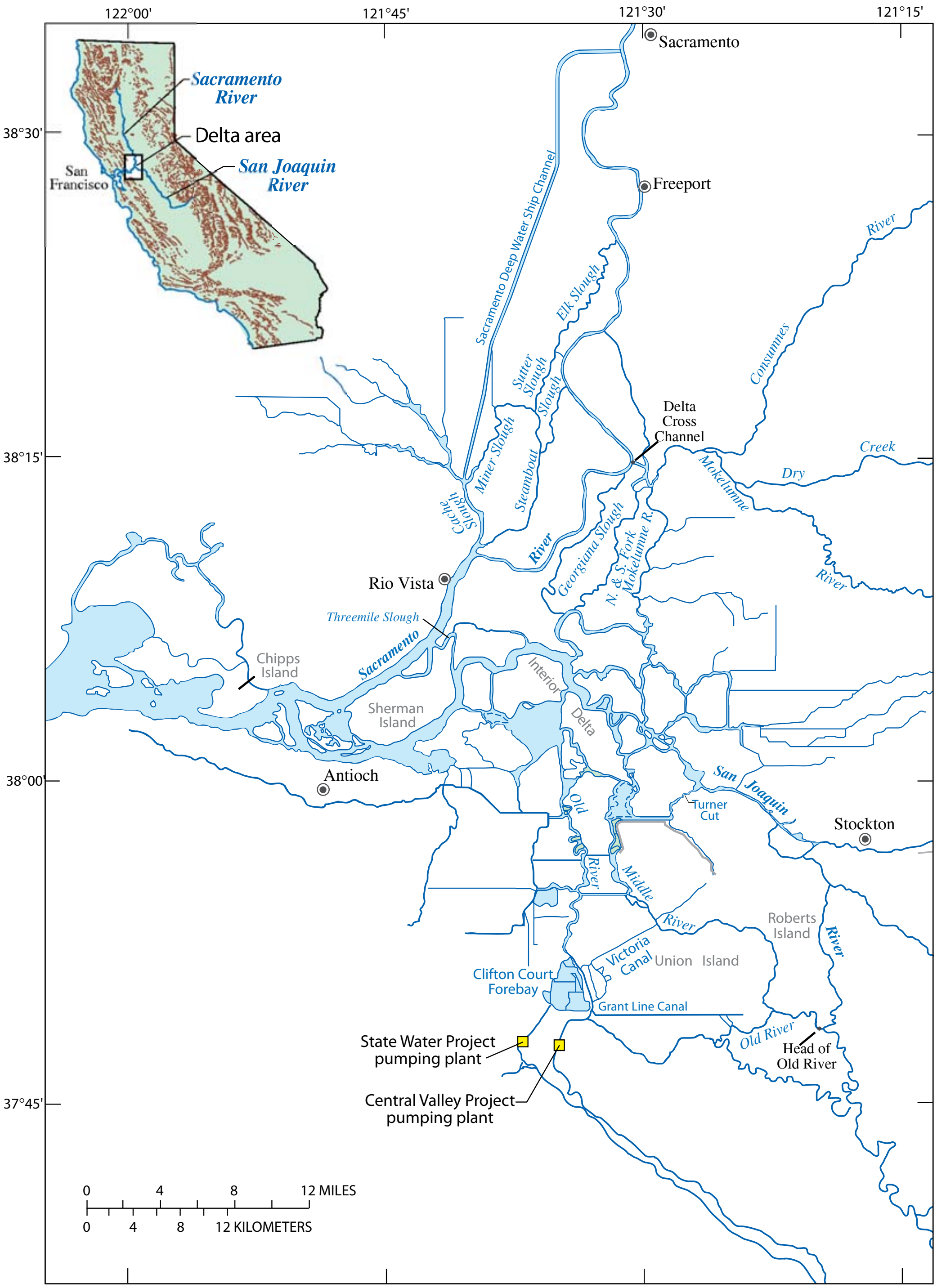

Figure 1.2. The Sacramento-San Joaquin River Delta.

(5.7%) remain intact today (Nichols, 1986). Changes in the structure of aquatic communities accompanied changes in the physical structure of the Delta. Due to both intentional and accidental introductions, over 130 invasive species have become established in the Delta (Healy et al. 2008). Invasive fish species now dominate both total biomass and abundance (Feyrer and Healy, 2003; Brown and Michniuk, 2007). However, the defining human alteration to today's Central Valley is the Central Valley Project and the State Water Project.

The Central Valley Project (CVP) and State Water Project (SWP) together form the world's largest water delivery system. Both projects form a system of reservoirs, pumping stations, and canals designed to move water from northern California, where most of the precipitation falls, to southern California which is much drier. The CVP is comprised of 20 dams and reservoirs, 11 powerplants, and 500 miles of canals (http://www.usbr.gov/dataweb/html/cvp.html; accessed May 2009). The SWP includes 34 storage facilities, 20 pumping plants, 5 hydroelectric generating plants, and over 700 miles of canals (http://www.water.ca.gov/swp/index.cfm; accessed May 2009). Since all water flowing into the Central Valley is funneled through the Delta, the Delta plays a prominent role as the hub of California's water delivery system. Both the CVP and the SWP pump large volumes of the water (termed "water exports") from two pumping stations located at the southern end of the Delta (Figure 1.2). Associated with these pumping stations is the Delta Cross Channel located on the Sacramento River in the northern Delta (Figure 1.2). The Delta Cross Channel is a man-made gated canal that diverts water from the mainstem Sacramento River into the central and southern Delta (hereafter, the "interior Delta"). Its purpose is to reduce salinities in the interior Delta to improve water quality at the pumping stations. This extensive water delivery system is critically important to state, national, and global economy, providing water to over 20 million Californians and to the world's fifth largest supplier of food and agricultural commodities (Culberson, 2008). Balancing human demands for water with maintenance of a functioning ecosystem capable of supporting healthy salmon populations has become a central challenge facing natural resource managers in the 21st century (Healy, 2008).

The influence of exporting water from the Delta on migrating juvenile salmon is profound. At times, the CVP and SWP can export up to 60% of the total inflow to the Delta, drawing water to the south and competing with flows heading towards the outlet of the Delta at

Chipps Island (Figure 1.2). Furthermore, when exports exceed inflow from the San Joaquin River, the net direction of flow is towards the pumps, rather than towards San Francisco Bay (Brandes and McLain, 2001). Thus, juvenile salmon emigrating from the San Joaquin and Sacramento rivers often become drawn towards the pumping stations rather the ocean (Brandes and McClain, 2001). This process increases their migration times and they become susceptible to entrainment into the intakes at the water pumping stations. Once at the pumping stations, predation rates are high and fish may be entrained into irrigation canals (Gringas, 1997; Kimmerer, 2008; Kimmerer and Nobriga, 2008; Clark et al., 2009). The role of the Delta on population-level survival has been recognized as critical to recovery of endangered salmon populations (CVPIA, 1992; Kimmerer et al., 2008; Lindley, 2009). Thus much research has focused on understanding the influence of exports and operation of the Delta Cross Channel on survival of endangered juvenile salmon migrating through the Delta.

1.2 Juvenile Salmon Survival in the Delta

1.2.1 State of Knowledge

The vast majority of research to quantify survival of juvenile salmon migrating through the Delta has been conducted by the U.S. Fish and Wildlife Service in Stockton, CA (http://www.fws.gov/Stockton; accessed May 2009). Studies since the 1970s through 2006 have focused on both the Sacramento and San Joaquin rivers and have employed mark-recapture methods using coded wire tags to estimate survival of subyearling fry and yearling smolts of Chinook salmon. In general, this methodology involves marking tens of thousands of fish, releasing them at various locations in the Delta, recapturing them using a mid-water trawl at the outlet of the Delta at Chipps Island (Figure 1.2), and recapturing them as adults in the commercial ocean fishery. Different release locations have served as reference points for comparing the relative probability of surviving through different migration routes. A variety of statistical methods have been used, ranging from analysis of survival “indices” based on expansion of trawl counts to sophisticated Bayesian hierarchical models that account for the multinomial structure of recapture data and for multiple sources of variation.

Early analyses of fry and smolt recaptures suggested that survival 1) differed among alternative migration routes through the Delta, 2) was affected by water exports, 3) depended on whether Delta Cross Channel gates were open or closed (Sacramento River), and 4) was influenced by presence or absence of a barrier blocking a migration pathway to the pumping stations (San Joaquin River). Fall-run fry releases occurred only in the Sacramento River through the 1980s and were recovered only in ocean fisheries (Brandes and McClain, 2001). Insights from these studies suggested that survival during dry years was higher for fish remaining in the Sacramento River relative to fish entering the interior Delta (Figure 2.1), but that survival was similar among migration routes during wet years. Brandes and McClain (2001) attributed this observation to the high inflows from rivers in wet years relative the amount of water exported at the pumping stations (the "export:inflow ratio").

The vast majority of mark-recapture studies have employed the use of fall-run and late-fall-run smolts, which can be captured by mid-water trawls at the outlet of the Delta. On the San Joaquin River, recovery rates of smolts migrating through the mainstem were higher than for smolts migrating through Old River, which took fish towards the pumping stations (Figure 1.2). In some years, a rock barrier was installed at the head of Old River to prevent smolts from entering this migration route, and recovery rates were compared with and without the barrier. Results from these experiments were statistically inconclusive, although Brandes and McClain (2001) presented several lines of supporting evidence that survival should increase with the rock barrier in place. Brandes and McClain (2001) also used the ratio of recovery rates of fish released into the upper San Joaquin River relative lower San Joaquin River near the terminus of the Delta to examine the relation between San Joaquin river flow and survival. The recovery ratio increased with flow, suggesting higher relative survival of the upstream release group as flows increased. Kjelson (1981) observed that coded-wire tag fish recovered at the pumping stations ("salvaged" fish) tended to increase with exports. Furthermore, Brandes and McClain (2001) noted that recovery rates of fish released into the San Joaquin River were much greater than that of fish released into the northern Delta, suggesting populations in the San Joaquin River were more susceptible to direct mortality at the pumping stations than populations from the Sacramento River.

For juvenile salmon smolts emigrating from the Sacramento River, studies with coded wire tags showed that river flow, water temperature, and migration routes through the interior Delta influenced survival (Kjelson et al., 1989; Brandes and McClain, 2001). First, recovery rates were positively related to river discharge of the Sacramento River and inversely related to temperatures. Second, for fish released upstream of the Delta Cross Channel, recovery rates were inversely correlated with the proportion of flow diverted into the interior Delta through the Delta Cross Channel and Georgiana Slough, suggesting diversion into the interior Delta reduced overall survival. Third, for paired releases into the interior Delta via Georgiana Slough or into the Sacramento River, fish entering the interior Delta survived at a lower rate. Finally, Brandes and McClain (2001) showed an inverse relationship between exports and recovery rates of fish released into the interior Delta. Taken together, this set of studies suggested a substantial negative effect of the Delta Cross Channel and water exports on survival of juvenile salmon.

Due to the implications of their findings, the statistical analyses of these studies (Kjelson et al., 1989; Brandes and McClain, 2001) were scrutinized and criticized on a number of counts (Williams, 2006; Brown and Kimmerer, 2006):

- Survival “indices”, either based on recapture rates or ratios of recaptures between locations, failed to account for the underlying variance structure in each point estimate. That is, each observation received equal weight in regression analysis even though the variance of each point estimate differed.
- Multiple linear regression assuming normally distributed errors was used to analyze the effect of covariates, even though the data arise from the multinomial distribution.
- Recapture counts in ocean fisheries were expanded to an estimate of total recaptures in the fisheries based on sampling rates at various ports, but the error associated with such expansion was not accounted for in analyses.
- Recapture counts at the Chipps Island trawl were expanded to an estimate of the flux of fish passing Chipps Island using the fraction of time sampled and the fraction of water volume sample. This approach involved a number of untenable

assumptions such as a uniform distribution of fish through space and time passing Chipps Island.

To address these concerns, K. B. Newman published a series of papers that directly modeled recaptures or ratios of recaptures using appropriate statistical models that explicitly accounted for the multinomial structure of the data (Newman and Rice, 2002; Newman, 2003; Newman, 2008; Newman and Brandes, 2010). These studies analyzed both paired and unpaired releases, but recognized that paired releases provided stronger inferences about survival. With unpaired releases, observed recaptures arise due to the joint probability of survival and capture and these processes are confounded. For paired releases (e.g., simultaneous releases into the interior Delta and the Sacramento River), the ratio of recovery rates yields the ratio of survival probabilities under the assumption of equal capture probabilities and equal post-Delta survival for the two release groups. Newman's earlier papers largely confirmed the findings of the Kjelson's and Brandes' studies conducted in the Sacramento River and showed a positive effect of river flow, a negative effect of water temperature (also found by Baker et al. 1995), a negative effect of an open Delta Cross Channel gate, and a negative but sometimes nonsignificant effect of exports on survival (Newman and Rice, 2002; Newman, 2003). His most recent analyses used paired releases within a Bayesian hierarchical framework to evaluate and summarize the major coded-wire tag experiments occurring in the Delta (Newman, 2008; Newman and Brandes, 2010). He found modest evidence that closure of the Delta Cross Channel gate improved survival, and estimated that mean survival of fish migrating through the interior Delta was only 35-44% that of fish remaining within the Sacramento River. Newman and Brandes (2010) found a high probability of a negative export effect on survival, but when compared against models with and without an export effect, other models explained the observed data just as well. The conclusions from Newman's series of papers support the initial findings from the earlier analyses, but do so using statistical models appropriate to the data structure of the mark-recapture studies.

These studies represent the bulk of research to estimate survival of juvenile salmon in the Delta and have provided important information about the effects of water management actions. Generalities that arise include:

1) Survival of fish migrating through the interior Delta, where pumping stations are located, is less than that of fish that remain in the Sacramento River.
2) Survival with the Delta Cross Channel open is less than when the Delta Cross Channel is closed, presumably because a larger fraction of the population remains within the Sacramento River when the Delta Cross Channel is closed.
3) Exports may have a negative effect on survival, but high unexplained natural variability muddles the underlying signal.

While thirty years of coded wire tag studies have certainly shed light on factors influencing survival of migrating salmon through the Delta, much remains to be learned.

1.2.2 Gaps in Knowledge

To better understand natural and anthropogenic factors influencing population-level survival of juvenile salmon migrating through the Delta, consider the underlying processes acting on the population as they migrate through the Delta. As the juvenile salmon population enters the Delta from mainstem rivers, it disperses among the Delta's complex channel network. The dispersal process will be driven by the relative quantities of discharge entering each channel, the horizontal distribution of fish as they pass a channel junction (a main channel splitting into two or more channels), and by tidal cycles that alter flow patterns at river junctions. Once fish enter a given channel, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. Eventually, alternative migration routes converge at the exit of the Delta and the population once again comes together to migrate through San Francisco Bay. This dispersal and migration process suggests that population-level survival of juvenile salmon migrating through the Delta will be driven by 1) the survival rates arising from the biotic and abiotic processes unique to each migration route, and 2) the proportion of the population using each migration route. In turn, natural and human-imposed variation in discharge and water distribution will affect population dispersal and survival rates within each channel, driving population-level survival through the Delta. It is this process that is the focus of my dissertation.

From this perspective, mark-recapture studies conducted thus far have provided insight into individual components of the dispersal-survival process, but many gaps remain to be filled. Some migration routes may be critical to population survival, yet have not been studied. For example, Sutter and Steamboat sloughs, upstream of the Delta Cross Channel, may be an important migration route because fish taking either of these routes do not encounter the Delta Cross Channel (Figure 1.2). However, migration through Sutter and Steamboat sloughs will increase population survival only if survival through these routes is higher than alternative routes. Considering all major migration routes is therefore crucial for understanding how each route affects population survival. Yet the single most important missing piece to this puzzle is an understanding of how juvenile salmon distribute among alternative migration routes once they enter the Delta. Even though survival may differ drastically among migration routes, the magnitude with which each route contributes to population survival will depend on the fraction of the population using each route. For example, although survival for fish entering the interior Delta is lower than for the Sacramento River, if 90% of fish remain in the Sacramento River then the interior Delta will have little influence on survival of the population. Current knowledge suggests survival is lower for fish migrating through the interior Delta, yet there is poor understanding of how such differences among migration routes affects population-level survival through the Delta.

Two recent studies examined important components of survival in the Delta, with the specific goal of placing findings in a population context. First, Kimmerer and Nobriga (2008) used particle tracking models to examine dispersal of juvenile salmon migrating through the Delta. Their findings provided insights into the distribution of possible fates of passively moving particles in response to tides, exports, and operation of the Delta Cross Channel. However, as recognized by Kimmerer and Nobriga (2008), a major assumption is that fish move as passive particles. Furthermore, their study did not incorporate differential "survival" of particles among different routes, which will substantially influence the distribution of possible fates of particles. Kimmerer (2008) also used existing coded-wire tag data to estimate a mean of 10% of the total number of fish surviving to Chipps Island, but such estimates are highly uncertain due to limitations of coded wire tags noted above. Such analyses begin to consider the population-level consequences of management actions, but still lack the ability to draw direct inference on the simultaneous dispersal-survival process of juvenile salmon in the Delta.

Currently lacking is a population-level approach that is capable of 1) quantifying dispersal of the population among migration routes, 2) estimating survival within these routes, and 3) explicitly linking each of these components to survival of the population. Water management actions in the Delta act on individual components of the population in different places at different times: e.g., some fraction of the population passes the Delta Cross Channel, of which some fraction enters the interior Delta, of which some fraction arrives at the pumping stations. Thus, a framework to estimate route-specific dispersal and survival will help fisheries managers better understand the how water management actions act on these individual components. But more importantly, such a framework would provide a means for explicitly relating each route-specific component back to the population of interest.

1.2.3 Filling in the Gaps

Although the framework above is conceptually appealing, feasible approaches to estimating the route-specific components of population survival are few. For example, to accomplish such a task with coded wire tags would require 1) releasing tagged fish upstream of the Delta and allowing them to naturally distribute among routes as they migrate through the Delta, 2) recapturing fish within each major migration route as they pass channel junctions, 3) recapturing fish at the convergence of major river channels, 4) recapturing fish as they exit the Delta, and 5) recapturing fish after they exit the Delta. While theoretically feasible, logistics and labor associated with such an effort detract from this approach. Furthermore, batch marks such as coded-wire tags (as opposed to individually identifiable tags) limit the statistical models that can be applied, the parameters that can be estimated, and the assumptions that can be tested (Skalski et al., 2009a). However, low capture probability is the biggest limitation with coded wire tags and other tags that require physical recapture of tagged fish. The precision of survival estimates is positively related to capture probability: the lower the capture probability, the poorer the precision (Burnham et al., 1987). In coded wire tag studies in the Delta, Newman (2008) estimated that median capture probabilities of the Chipps Island trawl were ≤0.0008, or 0.08% of the tagged fish passing Chipps Island being captured by the trawl.

Such low capture probabilities introduce high uncertainty in estimates of survival. For example, Newman (2008) estimated that 100 paired releases each with 150,000 coded-wire tagged fish would be needed to obtain a coefficient of variation of 20. Given that only one or two paired releases have been conducted each year in past studies, many years of study would be required before even moderate levels of precision were obtained.

Biotelemetry techniques combined with mark-recapture models offer one possible approach to simultaneously quantify dispersal and survival of juvenile salmon migrating through the Delta. This approach entails deployment of telemetry monitoring stations at key locations throughout the Delta, implanting small transmitters into juvenile salmon, and then tracking their migration through the Delta. A major impediment to estimating dispersal and survival through the Delta is the extreme spatial complexity of the Delta's channel network. However, in complex settings such as the Delta, biotelemetry has a number of advantages over traditional mark-recapture techniques that rely on the physical recapture of fish. First, uniquely identifiable transmitters provide detailed information about the temporal and spatial movements of individuals migrating through the Delta. Second, the "capture" process is passive, so that an individual may be "captured" numerous times as it migrates unimpeded through the Delta. Third, uniquely identifiable tags allow development of statistical models capable of estimating both survival and dispersal through the Delta. Fourth, the spatial arrangement of telemetry stations in Delta can be tailored to the Delta's complex channel structure to quantify both movement among and survival within given migration routes. Fifth, because detection probabilities are typically high (>0.75), small sample sizes can yield high precision of parameter estimates.

Telemetry techniques have long been used to quantify the temporal and spatial extents of fish migrations (Winter, 1996), but only recently has telemetry data been cast in a mark-recapture framework to explicitly estimate demographic parameters. Pollock et al. (1995) used telemetry to estimate survival over time, but here I am interested in estimating survival through space. Skalski et al. (1998, 2001) used mark-recapture models to estimate in-river survival of migrating juvenile salmon implanted with passive integrated transponders (PIT tags) and with radio-tags. These models are based on the classic models of Cormack (1964), Jolly (1965), and Seber (1965). As such, these models estimate survival through discrete reaches of river, but have limited application for the Delta where we must also estimate the proportion of fish using each migration route. Skalski et al. (2002) also developed a mark-recapture model to simultaneously estimate the probability of passing through a given route at a dam (e.g., turbines and spillway) and the probability of surviving each passage route. This model comes closer to that needed for the Delta because it estimates both movement among routes and survival within routes. However, the channel structure of the Delta is much more complex than that of fish passing through a single dam. The Delta has a hierarchical channel structure where a main channel splits in two or more channels, and nested within each of these channels may be additional junctions among which fish may disperse. Thus, although telemetry techniques offer promise, statistical models must be developed and tailored the Delta's complex channel network to estimate survival and dispersal of juvenile salmon in the Delta.

1.3 Goals of this Research

The overarching goal of my research is to use mark-recapture models to estimate 1) survival of juvenile salmon within specific migration routes of the Delta and 2) the proportion of fish using different migration routes through the Delta. Furthermore, as noted above, my goal is to link each of these components to population-level survival in the Delta to better understand how each migration route contributes to population survival. In 2006, a three-year research program was initiated to estimate watershed-scale survival of acoustically tagged juvenile salmon and steelhead in the Sacramento River (http://californiafishtracking.ucdavis.edu/; accessed December 2009). Although not specifically focused on the Delta, the infrastructure of acoustic telemetry stations from this research project afforded the opportunity for other studies to release acoustically tagged fish focused on their own research goals. As such, in 2006, I was funded through the CALFED Science Fellowship Program to assist the US Fish and Wildlife Service (USFWS) in developing the statistical models necessary to estimate dispersal and survival of juvenile salmon in the Delta.

The central interest of this work to fisheries managers is better understanding of the effect of water management actions on population-level survival of juvenile salmon migrating through the Delta. Thus, my goal is to provide a framework within which the effects of water management actions on specific components of the populations can be measured and related to the population at large. Given relatively small sample sizes, low release replication, a limited range of environmental conditions, and the novelty of acoustic telemetry in the Delta, my research just begins to shed light on the effects of water management actions on survival through the Delta. Nonetheless, I begin to uncover the dynamics of movement and survival of juvenile salmon in the Delta and provide an analytical framework within which effects of water management actions can be quantified.

In this dissertation, each chapter builds on the previous, beginning with building the statistical foundation of the mark-recapture models and culminating with a multiyear analysis of survival and dispersal through the Delta. In Chapter 2, I develop the foundation of mark-recapture models for the Delta, describing general model structure, detailing and assessing model assumptions, and examining requirements for identifiability of model parameters. In Chapter 3, I developed and applied the basic mark-recapture model that estimates both dispersal and survival among migration routes in the Delta to a small data set of acoustically tagged late-fall Chinook salmon released during the 2007 migration year (December 2006 – February 2007). Since such a study had never been conducted and sample size was small, the findings from Chapter 3 provided many new insights but also highlighted ways to improve the study. Thus, Chapter 4 expands the initial mark-recapture model and applies it to data from the 2008 migration year with the goals of 1) improving precision of parameter estimates both within and among migration routes, 2) obtaining more detailed information within migration routes, and 3) examining patterns of variation in reach-specific survival. In Chapter 5, I incorporate covariates into the mark-recapture model to quantify factors affecting survival during the three-year study. In Chapter 6, I analyzed the three-year data set to uncover factors affecting entrainment probabilities at an important river junction in Delta. Here, I examine how river flow, tidal fluctuations, and operation of the Delta Cross channel affect the probability of fish entering a particular migration route. In Chapter 7, I conclude with a discussion of the ramifications of my findings for management of the Delta and recovery of salmon populations. I also identify directions for future research to further improve knowledge of the complex migration and survival dynamics of juvenile salmon in the Delta.

Chapter 2

QUANTIFYING SURVIVAL IN THE DELTA: MODELING FRAMEWORK, ESTIMATION, AND ASSUMPTIONS

2.1 Introduction

In this chapter, my goal is to develop the basic building blocks for constructing statistical models to estimate survival of juvenile salmon migrating through the Delta. To develop these building blocks requires an understanding of the underlying problem at hand, the statistical methods to tackle the problem, and the assumptions involved with application of the statistical methods. Therefore, first I examine the role of the Delta in the context of the Chinook salmon's life cycle, showing how the Delta can be cast in terms of the demographic parameters of a matrix population model. Having set up the problem, I then discuss the class of statistical models that can be used to estimate the demographic parameters and the assumptions entailed with application of these models. Next I describe how the spatial structure of the Delta necessitates adapting the statistical models and how such adaptation can influence estimability of model parameters. Last, I discuss assumptions of these models with particular focus on how they apply to use of acoustic telemetry in the Delta.

In describing the models and assumptions, I used simple conceptual models of a river delta to focus on model construction techniques and assessment of assumptions. Given the channel complexity of the Delta and ability of telemetry to monitor any river channel, the range and scope of possible models that could be constructed is nearly limitless. Therefore, my goal here is to focus on the general techniques needed to construct any model, with particular emphasis on ensuring assumptions are fulfilled and parameters estimable. Given this "toolbox", it is then straightforward to tailor any model to the specific questions of a particular study to tackle the full channel complexity of the Delta.

2.2 A Matrix Population Model Perspective

2.2.1 The Delta in the life cycle of Chinook salmon

Recovery of endangered salmon populations in the Central Valley requires an understanding of how each life stage of the salmon's life cycle contributes to population growth rates. In turn, population growth rates are determined by vital rates of stage-specific survival and reproduction. Although my research focuses on one small aspect of the salmon's life cycle – the period of migration through the Sacramento-San Joaquin River Delta – this critical period could substantially influence population growth rates. To fully understand the influence of the Delta on population growth rates, the Delta must first be placed in the context of the salmon's life cycle. Here, I describe a generic stage-structured life-cycle of Chinook salmon in the Sacramento River (Figure 2.1). Using a simple representation of the Delta, I then show how the period of migration through the Delta can be explicitly included in the matrix representation of a salmon's life cycle.

Matrix population models provide a convenient mathematical framework for structuring the life cycle of pacific salmon and for examining the contribution of specific life stages to population growth rates (Caswell, 2001). Matrix population models have been used to examine the effects of climate change on population viability of salmon populations (Crozier and Zabel, 2006; Zabel et al., 2006; Crozier et al., 2008), to examine effects on population growth from improving survival during the freshwater migration phase (Kareiva et al., 2000), and to identify demographic parameters that most influence population growth rates (Wilson et al., 2003). Recently, an independent review panel recommended just such an approach to understand the influence of the CVP and SWP on endangered salmon populations in the Central Valley (CALFED Science Review Panel, 2008). Thus, understanding how the Delta fits into the life-cycle demographics of salmon is important to fully gauge the influence of this life stage on population dynamics. From this perspective, my research can be viewed as a focused effort to quantify demographic rates during a poorly understood, but possibly critical period of a salmon's life cycle that may be influenced by water management actions.

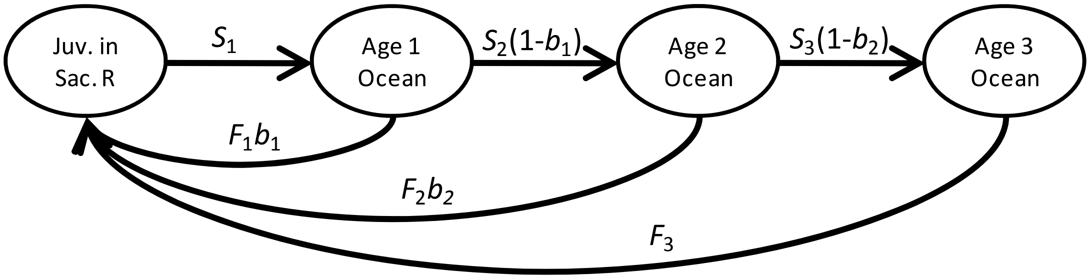

Figure 2.1. Stage-structured life cycle of salmon in the Sacramento River. Circles represent life stages, arrows represent transitions between time *t* and *t*+1, and demographic parameters of survival (S_i), breeding (b_j), and reproduction (F_j) govern the rate of transition between life stages.

I described a generic life cycle of Chinook salmon in the Central Valley using four life stages; the juvenile freshwater stage and three ocean age-classes (Figure 2.1). Transitions between life stages are governed by the probability of surviving, S_i, from life stage *i* to stage *i*+1 and the probability of returning to spawn after each year in the ocean, b_j. Each adult age class returning at time *t* contributes to the subsequent juvenile population at time *t*+1. I defined the juvenile life stage as ending when fish begin their downstream emigration from natal tributaries. Thus, F_j is the per-individual contribution of ocean age class *j* at time *t* to the population of emigrant juvenile salmon at time *t*+1. This life-cycle can be conveniently represented in matrix notation where the transition matrix **A** with entries a_{sr} represents the probability of transitioning from life stage *r* at time *t* (*r* indexes the columns) to life stage *s* at time *t*+1 (*s* indexes the rows):

$$\mathbf{A} = \begin{bmatrix} 0 & F_1b_1 & F_2b_2 & F_3 \\ S_1 & 0 & 0 & 0 \\ 0 & S_2(1-b_1) & 0 & 0 \\ 0 & 0 & S_3(1-b_3) & 0 \end{bmatrix}.$$

The demographic parameters forming the entries to the transition matrix are typically expressed as functions of more complex underlying processes. For example, each annual survival rate in the ocean may be expressed as a function of both fishing and natural mortality rates. Also, since F_j represents the contribution of spawning individuals to the juvenile emigrant population, F_j will be a function of 1) sex ratio, 2) survival of adults during the upstream migration, 3) age-specific fecundity, 4) egg-to-fry survival, and 5) fry-to-emigrant survival. Since fish pass through the Delta during their transition from the juvenile freshwater stage to the ocean age 1 stage (Figure 2.1), my goal is to express S_1 as a function of the underlying demographic rates driving survival of the population during the transition between these life stages.

Fish move over large distances through diverse environments during their transition from the freshwater to ocean environment. Demographic rates during transition between these life stages are therefore best conceptualized as a spatially-structured population model with the population being censused at different points in space. As an example, I have shown the simplest representation of the Delta that captures the essence of three major migration routes that fish could use during transition between the freshwater and ocean life stages (Figure 2.2). At the first river junction, fish can take migration route B which bypasses the second river junction, and then all routes converge at the exit of the Delta. This network structure is important because fish that take migration route B are "immune" from entering route C. Such structure emulates the Delta where fish entering Sutter and Steamboat sloughs (route B) bypass the entrance to the Interior Delta (route C, See Figure 3.1). To incorporate this channel structure into a population model, the population is tallied just downstream of each river junction to measure within-route survival and the proportion of the population using each migration route at each river junction (Ψ).

2.2.2 The Delta as a stage-structured population model

The life-stage transitions between the freshwater and ocean can be structured as a series of spatially-dependent transition matrices, $\mathbf{A}_t$, where stages are represented by each of the possible migration routes (Figure 2.2). For example, for the first reach, two transitions are possible: fish may survive the first reach and move into route B or they may survive and remain in route A (see $\mathbf{A}_1$ in Figure 2.2). However, in the next reach, transition matrix $\mathbf{A}_2$ differs due to the spatial structure of that reach. The change in population size between freshwater and ocean life stages, S_1 in original matrix population model (Figure 2.1), is the 1,1 element of the pre-multiplied transition matrices:

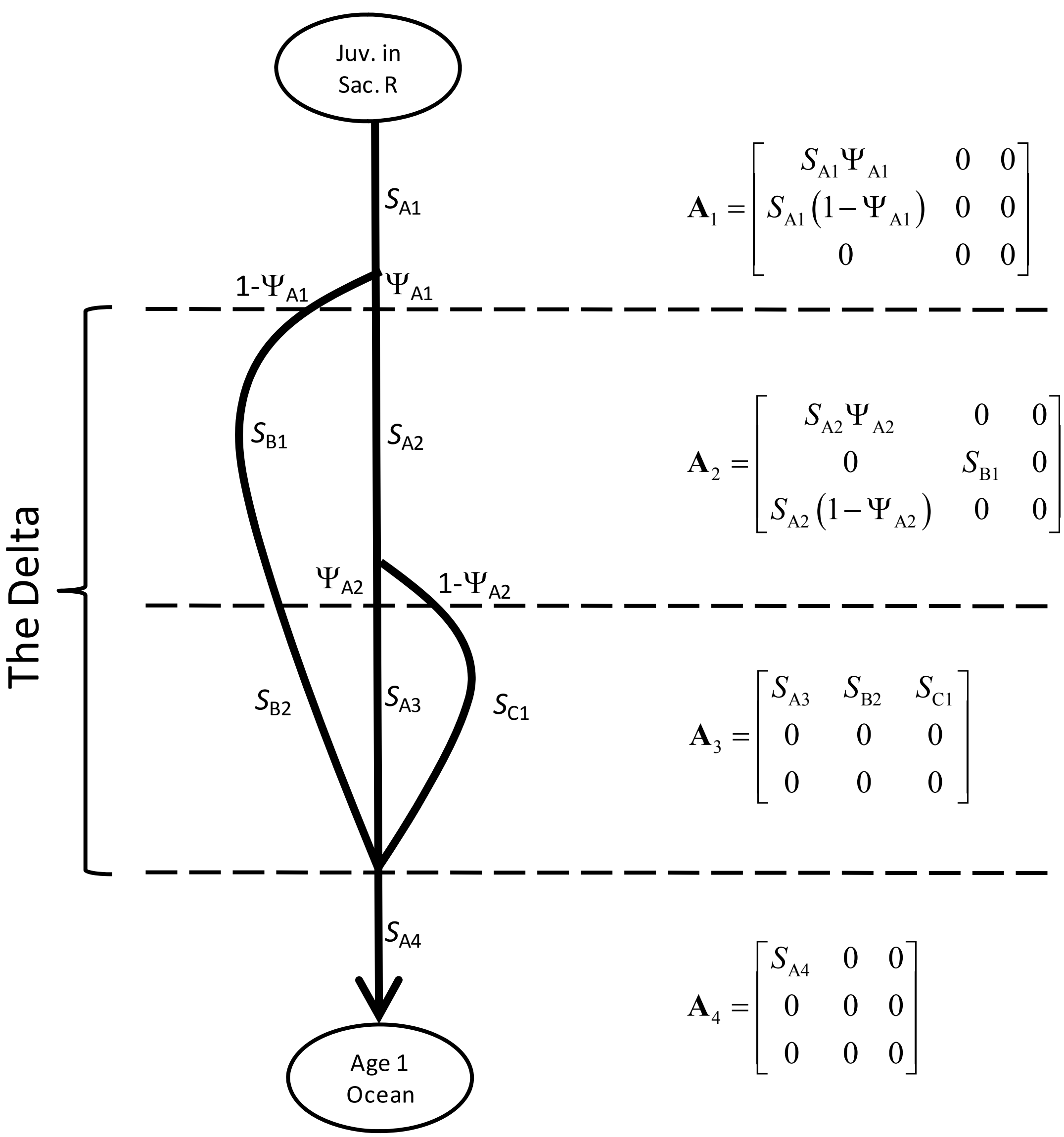

Figure 2.2. A simple representation of the Delta showing different migration routes that fish may take during their transition between freshwater and ocean life stages. Dashed lines mark the location of transitions among migration routes, with rates of transition governed by route-specific survival probabilities (S_{hi}) and probabilities of entering each migration route (Ψ_{hl}). Spatially dependent transition matrices ($\mathbf{A}_t$) show the probability of transitioning from route r (indexing the column) at location t to route s (indexing the row) at location t+1.

$$S_1 = (\mathbf{A}_1\mathbf{A}_2\mathbf{A}_3\mathbf{A}_4)_{1,1} = S_{\mathrm{A1}}\left((1-\Psi_{\mathrm{A1}})S_{\mathrm{B1}}S_{\mathrm{B2}} + S_{\mathrm{A2}}\left(\Psi_{\mathrm{A2}}S_{\mathrm{A3}} + (1-\Psi_{\mathrm{A2}})S_{\mathrm{C1}}\right)\right).$$

In essence, S_1 is the weighted average survival of fish that take different migration routes through the Delta where the weights are equal to the proportion of fish taking each unique migration route. Although the matrix notation used here may seem overly burdensome for describing the weighted average for such a simple example, it shows how this problem can be cast in terms of a matrix population model of a salmon's life cycle. Furthermore, as will be seen, this matrix representation will become very useful for constructing the likelihood of statistical models to estimate these parameters, especially when attempting to address the full spatial complexity of the Delta.

2.3 The Multistate Mark-Recapture Model

The central challenge of estimating parameters described in the population model above is sampling the population at different locations in the Delta. Acoustic telemetry provides a powerful technique for tracking the movements of individual fish. By placing autonomous telemetry stations at strategic locations in the Delta, detection data from the system of stations can be analyzed in mark-recapture statistical framework to estimate demographic parameters of interest (Skalski et al., 2001, 2002, 2009b). The Cormack-Jolly-Seber model has been used with telemetry data to estimate survival probabilities of juvenile salmon migrating to the ocean (LaCroix, 2008; Skalski et al., 2001). In our case, however, we are not only interested in estimating survival for each route, but also the proportion of fish using different migratory pathways. The multistate mark-recapture model provides just such a framework for estimating both survival and movement parameters.

Estimating movement rates among geographic areas from marked animals has received growing attention over the past 35 years. Arnason (1972) estimated movement rates and survival among two populations, and Arnason (1973) and Seber (1982) extended these models to three or more populations. Hilborn (1990) used a Poisson approximation to the multinomial distribution to estimate movement rates of skipjack tuna (*Katsuwonus pelamis*) from tag recovery data. Schwarz et al. (1993) fully generalized Arnason's models to allow for any number of recapture occasions and geographic locations for application to band recovery data. Brownie et al. (1993) further generalized the model for application to multiple recaptures, and also constructed models that allow for non-Markovian transitions. Since these seminal papers, the multistate mark-recapture model has been used to model not only movement among geographic locations, but transition rates among any set of discrete states where transitions are stochastic (Lebreton et al., 2002; Nichols and Kendal, 1995). For example, this model has been used to estimate transitions among weight classes (Letcher and Horton, 2009) and between breeding and non-breeding states (Nichols et al., 1994). Thus, the multi-state mark-recapture model has become a very flexible estimation framework for answering diverse questions about important demographic parameters influencing population dynamics of animals.

2.3.1 The multistate model as an estimation framework

To describe the multistate model here, I use the notation of Brownie et al. (1993), and this notation is later used for the models I constructed for the Delta. The fundamental parameters estimated by the multistate model are:

ϕ_i^{rs} = joint probability of surviving from sampling occasion i to i+1 and moving from state r at occasion i to state s at occasion i+1.

p_i^s = probability of capture in state s at occasion i.

Given the multiple states, it is convenient to express these parameters in matrix form, here using three states for simplicity:

$$\boldsymbol{\phi}_i = \begin{bmatrix} \phi_i^{11} & \phi_i^{12} & \phi_i^{13} \\ \phi_i^{21} & \phi_i^{22} & \phi_i^{23} \\ \phi_i^{31} & \phi_i^{32} & \phi_i^{33} \end{bmatrix},$$

$$\boldsymbol{p}_i = \begin{bmatrix} p_i^1 & 0 & 0 \\ 0 & p_i^2 & 0 \\ 0 & 0 & p_i^3 \end{bmatrix}.$$

As opposed to the matrix population model, r indexes the rows and s indexes the columns. Under the most general model when all states are sampled at every occasion and animals move among all states, the multistate model is directly analogous to a Cormack-Jolly-Seber (CJS) model generalized to allow movement among multiple states (Cormack, 1964; Jolly, 1965; Seber, 1965). As with the CJS model, all parameters can be estimated for all sampling periods except for the final period, when joint movement-survival probabilities (ϕ_i^{rs}) are confounded with detection probability. Since the multistate model follows directly from the CJS model, assumptions of the multistate model, in large part, mirror those of the CJS model (see below).

Summary statistics and the associated likelihood can be formed from either the multistate extension of the m_{ij}-array or the complete capture histories of individuals (Burnham et al., 1987; Williams et al., 2002). Below, I present the m_{ij}-array approach for the standard multistate model, but for dealing with the particulars of the Delta, I use complete capture histories. Sufficient statistics reduce to the numbers of animals initially marked in each state and frequencies of marked animals subsequently recaptured in each state:

$$\underset{\sim}{\mathrm{R}}_i = \begin{bmatrix} R_i^1 \\ R_i^2 \\ R_i^3 \end{bmatrix},$$

$$\mathbf{m}_{ij} = \begin{bmatrix} m_{ij}^{11} & m_{ij}^{12} & m_{ij}^{13} \\ m_{ij}^{21} & m_{ij}^{22} & m_{ij}^{23} \\ m_{ij}^{31} & m_{ij}^{32} & m_{ij}^{33} \end{bmatrix}.$$

Where R_i^r is the number of marked animals released at occasion i in state r, which includes both newly marked and recaptured/rereleased individuals; m_{ij}^{rs} is the number of individuals captured in state s during occasion j that were last captured and rereleased in state r at occasion i, and $i = 1, 2, \ldots, k$ capture occasions. Following the notation of m_{ij}-array for CJS models, each row of $\mathbf{m}_{ij}$-array forms a multinomial distribution conditional on the number of animals released at occasion i (Table 2.1).

Table 2.1 The multistate extension of the m_{ij} array for a 4-occasion experiment showing release frequencies ($\underset{\sim}{R}_1$) and recapture counts ($\mathbf{m}_{ij}$). Also shown under each recapture count matrix is the associated matrix of multinomial cell probabilities, where $\mathbf{q}_i = \mathbf{I}\text{-}\mathbf{p}_i$ and $\mathbf{I}$ is the identity matrix of appropriate dimension.

		Recapture occasion (*j*)		
Release occasion (*i*)	Number released	2	3	4
1	$\underset{\sim}{R}_1$	$\mathbf{m}_{12}$ $\boldsymbol{\phi}_1\mathbf{p}_2$	$\mathbf{m}_{13}$ $\boldsymbol{\phi}_1\mathbf{q}_2\boldsymbol{\phi}_2\mathbf{p}_3$	$\mathbf{m}_{14}$ $\boldsymbol{\phi}_1\mathbf{q}_2\boldsymbol{\phi}_2\mathbf{q}_3\boldsymbol{\phi}_3\mathbf{p}_4$
2	$\underset{\sim}{R}_2$		$\mathbf{m}_{23}$ $\boldsymbol{\phi}_2\mathbf{p}_3$	$\mathbf{m}_{24}$ $\boldsymbol{\phi}_2\mathbf{q}_3\boldsymbol{\phi}_3\mathbf{p}_4$
3	$\underset{\sim}{R}_3$			$\mathbf{m}_{34}$ $\boldsymbol{\phi}_3\mathbf{p}_4$

In the parameterization above, ϕ_i^{rs} includes the underlying probabilities of both surviving and moving between states. Interest lies in estimating these underlying parameters, but they can only be estimated by imposing the assumption that all mortality occurs while in state *r*, and movement to state *s* occurs "instantaneously" just prior sampling. Under this assumption, the model can be reparameterized as a function of S_i^r , the probability of surviving from occasion *i* to *i*+1 conditional on being in state *r* at occasion *i*; and Ψ_i^{rs} , the probability of transitioning from state *r* at occasion *i* to state *s* at *i*+1, conditional on surviving to *i*+1. Using the three-state example, the reparameterization is

$$S_i^r = \phi_i^{r1} + \phi_i^{r2} + \phi_i^{r3} \tag{2.1}$$

$$\text{and} \qquad \Psi_i^{rs} = \frac{\phi_i^{rs}}{S_i^r}. \tag{2.2}$$

These parameters can be estimated as derived parameters with maximum likelihood estimates of ϕ_i^{rs} , or the likelihood can be reparameterized directly in terms of S_i^r and Ψ_i^{rs} . As will be seen, I mix both parameterizations within the same model, separating S_i^r and Ψ_i^{rs} when the assumption that survival occurs first and transition occurs last is met, but estimating the joint movement-survival parameters (ϕ_i^{rs}) when this assumption cannot be fulfilled (e.g., see Chapter 4).

2.3.2 Assumptions of the multistate model

Assumptions of the multistate model are analogous that of the CJS model, with a number of additional assumptions as alluded to above.

A1: Inferences drawn from the sampled population apply to the population of interest.

A2: Marked animals have the same survival and movement probabilities as the unmarked population.

A3: The sampling occasion is instantaneous relative to the sampling period.

A4: Marks are not lost or misread.

A5: The states occupied at each occasion are known without error.

A6: The fate of one individual has no influence on the fate of other individuals.

A7: All individuals alive in state *s* at occasion *i* have the same probability of capture.

A8: All individuals alive in state *r* at occasion *i* have the same probability of transitioning to state *s* at occasion *i*+1.

A9: Joint movement-survival probabilities arise through a first-order Markov process. In other words, the probability of transition from state *r* at occasion *i* to state *s* at *i*+1 depends only the on the state occupied at occasion *i*.

A10: For S_i^r and Ψ_i^{rs} to remain unbiased, all mortality must occur in state *r* and then movement to state *s* occurs just prior to sampling.

Assumptions A1-A3 involve the interpretation of the parameters with respect to their strict definition. Assumption A1 should be obvious, but is important to explicitly acknowledge since the marked population can often differ from the population upon which inference is desired. For example, in my study, inferences about endangered winter-run Chinook salmon are desired, but because of their endangered status, this population is unavailable for sampling. Instead, hatchery-origin late-fall Chinook salmon are used as a surrogate for winter-run Chinook salmon because hatchery fish are readily available and emigrate during the same time period as winter-run Chinook. Strict inferences apply only to the untagged population that mirrors the tagged population, although insights about other populations may also be inferred from findings on the marked population. I expand the discussion on assumption A1 in

Chapters 3 and 4. Assumption A2 requires that handling or marking of the animal does not influence its subsequent survival. For acoustic tags, a maximum tag-to-body mass ratio of 5% is often recommended to ensure that assumption A2 is fulfilled (Adams et al. 1998a, 1998b; Perry et al., 2001). However, if such a size limit restricts study of only the largest fish in a population, there will be less overlap between the sampled population and the population of interest. Assumption A3 is required for precise definition of survival between occasion *i* and *i*+1. If the sampling occasions take place over a long period of time (e.g., 5 days) relative to the time between mid-points of sampling occasions (e.g., 7 days), then the concept of a discrete interval over which survival takes place begins to lose meaning, and sampling occasions become blurred with the intervals between sampling. I expand discussion of this assumption below with respect to using telemetry techniques to sample across space in the Delta.

Assumptions A4 and A5 are particularly important when using telemetry, and these assumptions may be violated in a number of ways. First, mark loss may occur not only through physical loss of the tag, but may also occur if the tag's battery expires before the end of the study. Both processes negatively bias estimates of survival since tag loss cannot be distinguished from mortality. Physical loss of tags can be estimated using double tagging experiments (Seber, 1982), while battery failure rates can be estimated by conducting controlled tag "survival" experiments (Townsend et al., 2006; Cowen and Schwartz, 2005). Environmental acoustic noise may be interpreted by telemetry equipment as a valid transmission from a transmitter, and these false-positive detections can introduce positive bias into survival estimates. False-positive detections can be removed by judicious screening of telemetry data prior to mark-recapture analysis, which I discuss further in Chapter 3. Since telemetry equipment indicates the presence of a live tag and not necessarily a live fish, care must be taken to ensure that dead fish with live tags are not interpreted as live fish. Such a process would lead to positive bias in survival estimates and can be evaluated by releasing a known subsample of dead individuals with live tags. Assumption A5 can be caused by violation of assumption A4 through false-positive detections and will cause bias in movement probabilities. Assumption A5 may also be violated by certain combinations of the detection process and movement process among states, which I discuss below with respect to monitoring river junctions with telemetry equipment.

Assumptions A6 through A10 arise due to the underlying statistical distributions and structural form of the model used to estimate the parameters. The multinomial distribution assumes that observations on individuals are independent (A6) and identically distributed (A7 and A8). Violation of these assumptions will introduce heterogeneity into model parameters, which typically does not bias parameter estimates but can lead to bias in variance estimates. The Markov assumption (A9) may be violated if prior history influences future survival. For example, if migration through one route reduces survival in downstream reaches relative to fish that traveled through a different migration route, then the Markov assumption will be violated. As with A7 and A8, violation of this assumption will introduce heterogeneity and the variance will be underestimated, but the expectation of the average survival over all prior histories will remain unbiased.

Assumption A10 is often difficult to assess when sampling over time, but is easier to validate when estimating survival over space such as in my study. When estimating survival for time periods, assumption A10 requires all animals move from state *r* to state *s* "instantaneously" just prior sampling. However, the more likely scenario is that animals transition among states at various times throughout the interval, which results in the estimated survival between occasion *i* and *i*+1 being dependent on a unknown mixture of survival while in state *r* and state *s*. In contrast, when sampling periods are composed of survival of a population moving through space, the location of transition from one river channel (i.e., state) to another is know perfectly. Thus, to fulfill assumption A10, the population should be sampled such that telemetry stations are situated just downstream of a river junction. This ensures that the survival process takes places first, and then the transition from one route to another occurs at the very end of a river reach. This assumption is discussed in detail below.

2.4 Survival through the Delta as a Constrained Multistate Model

In my study, unique migration routes constitute the states of a multistate model, but as seen Figure 2.2, the transition matrix is constrained in each sampling period by the spatial structure of the channel network. Thus, this particular problem can be cast as a matrix population model formed by spatially dependent transition matrices $\mathbf{A}_t$ with a constrained version of a multistate mark-recapture model to estimate the parameters. To maintain the link to matrix population models I retain the notation of section 2.2.1, but recognize that sampling occasions now refer to spatial locations indexed by *t*, and sampling periods represent river reaches between adjacent sampling occasions *t* and *t*+1.

As opposed to the fully generalized multistate model where all parameters are estimable in every occasion but the last, not all parameters in a constrained model may be estimable because transitions among each state do not occur during every sampling period. Furthermore, because the transition matrix varies across space, the structure of the multinomial likelihood must likewise accommodate the spatial structure of the Delta's channel network. Therefore, using the caricature of the Delta presented in Figure 2.2, I first develop an efficient method for constructing the likelihood of each capture history. Next, I discuss scenarios leading to inability to estimate parameters, minimal requirements to ensure parameter estimability, and approaches for determining whether all parameters are estimable in such models. Last, the spatial location of telemetry stations in the Delta directly affects the structure of the estimation model, the estimability of parameters, and validity of assumptions. Therefore, I explicitly show how a number of assumptions can be fulfilled or violated as a direct consequence of where telemetry stations are located relative to the parameters to be estimated.

2.4.1 Constructing the likelihood

Likelihoods for simple multinomial models with constrained state transitions can be constructed by specifying the probability function of each capture history "by hand" (e.g., see Chapter 3). However, given complex settings like the Delta, an efficient method of constructing the likelihood is needed to move beyond all but the simplest models of the Delta. For example, the model I present in Chapter 3 was comprised of nearly 1000 possible capture histories whereas the model in Chapter 4 had nearly 20,000 possible capture histories. Therefore, I adapted the methods of Fujiwara and Caswell (2002) to develop an efficient method of constructing the multinomial likelihood. Their approach proceeds by 1) defining transition matrices that include a "dead" state, 2) converting the state history vector defining the capture history into indicator matrices for each occasion, and 3) using matrix algebra to construct the likelihood contribution of each individual from the transition, indicator, and detection matrices.

The example in Figure 2.2 has $S = 3$ states comprised of migration routes A, B, and C, to which I add state “0” representing death or non-detection. To estimate the parameters of the first three transition matrices, $k = 4$ sampling occasions are needed, which includes the initial capture, tagging, and release upstream of the Delta and the three occasions marked by dashed lines in Figure 2.2. At locations where dashed lines intersect river channels, tagged fish are monitored for presence-absence by telemetry stations. Associated with each transition matrix is a diagonal matrix of detection probabilities for each telemetry station. Thus, for the simple population model in Figure 2.2, the transition and detection matrices are:

$$\mathbf{A}_1 = \begin{bmatrix} S_{\mathrm{A1}}\Psi_{\mathrm{A1}} & 0 & 0 & 0 \\ S_{\mathrm{A1}}\left(1-\Psi_{\mathrm{A1}}\right) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 1-S_{\mathrm{A1}} & 0 & 0 & 1 \end{bmatrix}, \qquad \mathbf{P}_2 = \begin{bmatrix} P_{\mathrm{A2}} & 0 & 0 & 0 \\ 0 & P_{\mathrm{B1}} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

$$\mathbf{A}_2 = \begin{bmatrix} S_{\mathrm{A2}}\Psi_{\mathrm{A2}} & 0 & 0 & 0 \\ 0 & S_{\mathrm{B1}} & 0 & 0 \\ S_{\mathrm{A2}}\left(1-\Psi_{\mathrm{A2}}\right) & 0 & 0 & 0 \\ 1-S_{\mathrm{A2}} & 1-S_{\mathrm{B1}} & 0 & 1 \end{bmatrix}, \qquad \mathbf{P}_3 = \begin{bmatrix} P_{\mathrm{A3}} & 0 & 0 & 0 \\ 0 & P_{\mathrm{B2}} & 0 & 0 \\ 0 & 0 & P_{\mathrm{C1}} & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}, \qquad (2.3)$$

$$\mathbf{A}_3 = \begin{bmatrix} S_{\mathrm{A3}} & S_{\mathrm{B2}} & S_{\mathrm{C1}} & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 1-S_{\mathrm{A3}} & 1-S_{\mathrm{B1}} & 1-S_{\mathrm{C1}} & 1 \end{bmatrix}, \qquad \mathbf{P}_4 = \begin{bmatrix} P_{\mathrm{A4}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}.$$

The $\left(S+1\right)\times\left(S+1\right)$ transition matrix $\mathbf{A}_t$ with entries a_{srt} defines the probability of transitioning from migration route r (indexing the columns, $r = 1, 2, \ldots, S+1$) at occasion t to migration route s (indexing the rows, $s = 1, 2, \ldots, S+1$) at occasion $t+1$. Note that I have separated the movement and survival process in this model; S_{hi} is the probability of survival from telemetry station i within route h ($h = \{\mathrm{A}, \mathrm{B}, \mathrm{C}\}$) to the next downstream sampling location, Ψ_{hl} is the probability of entering route h at river junction l conditional on surviving to junction l ($l = \{1, 2\}$), and P_{hi} is the probability of detection at the ith telemetry station within route *h*. The fourth row represents transitions to the death state, an absorbing state where $a_{SSt} = 1$ and the probability of detection in this state is zero (i.e., $P_{0t} = 0$). Adding the death state makes these matrices column stochastic, and because of the assumption of a first-order Markov process, each column forms a conditionally independent multinomial distribution where the probability of transition from state *r* at occasion *t* to state *s* at *t*+1 depends only on state *r* at occasion *t*.

Next, define the detection history as the *k*-dimension vector indicating whether each fish was observed in route *h* at occasion *t* ($t = 1, 2, \ldots, k$) or was not observed at occasion *t*. Likewise, let the state history represent the detection history in terms of the each route's index in the transition matrix. Thus, in the current example, route A = state 1, B = 2, C = 3, and 0 = 4. For example, the detection history AA0C can be represented as $\underset{\sim}{s} = \begin{bmatrix}1 & 1 & 4 & 3\end{bmatrix}^{\mathrm{T}}$. The next task is to translate the state history into indicator matrices for each occasion that will be used to select the appropriate entries in the transition and detection matrices. Let $\mathbf{E}_{mt}$ be the $(S+1)\times(S+1)$ matrix with a one in *s*th, *s*th position if the *m*th individual is detected in state *s* at occasion *t*:

$$\mathbf{E}_{mt} = \mathrm{D}\left(e_{\underset{\sim}{s}_t}\right).$$

Here, $\underset{\sim}{s}_t$ is the *t*th entry of the state history vector, $e_{\underset{\sim}{s}_t}$ is an S+1 length vector consisting of all zeros except for a one in the $\underset{\sim}{s}_t$th position, and $\mathrm{D}\left(e_{\underset{\sim}{s}_t}\right)$ is the diagonal matrix formed from this vector. The probability of a given detection history can now be formed as a function of the transition ($\mathbf{A}_t$), detection ($\mathbf{P}_t$), and indicator ($\mathbf{E}_{mt}$) matrices:

$$\pi_m = \underset{\sim}{1}^{\mathrm{T}}\left(\prod_{t=1}^{k-1}\mathbf{U}_{t+1}\mathbf{E}_{m,t+1}\mathbf{A}_t\right)\underset{\sim}{1} \tag{2.4}$$

where π_m is the probability of observing the detection history of the *m*th individual, $\underset{\sim}{1}$ is an S+1 vector of ones, $\mathbf{U}_{t+1} = \mathbf{P}_{t+1}$ if the *m*th fish is detected (i.e., $\underset{\sim}{s}_{t+1} \neq S+1$) at occasion *t*+1, and $\mathbf{U}_{t+1} = \mathbf{I}\text{-}\mathbf{P}_{t+1}$ if the *m*th fish is not detected (i.e., $\underset{\sim}{s}_{t+1} = S+1$) at occasion *t*+1. When a fish is detected in state *s* at *t*+1, $\mathbf{P}_{t+1}\mathbf{E}_{m,t+1}\mathbf{A}_t$ returns a matrix with a single entry representing the probability of surviving from *t* to *t*+1, of moving from state *r* to state *s*, and of being detected in state *s*. In contrast, when fish are not detected, $(\mathbf{I}\text{-}\mathbf{P}_{t+1})\mathbf{E}_{m,t+1}\mathbf{A}_t$ yields a matrix containing all possible transitions from state *r* at time *t* to state *s* at time *t*+1. Thus, when fish are not detected at various locations in the Delta, Eqn. 2.4 yields the sum of the probability of each possible pathway that the fish could have taken through the Delta, in addition to the possibility that the fish could have died. The complete likelihood of the parameters (θ) given the data set is simply the product of π_m over all fish:

$$L\left(\underset{\sim}{\theta}\right) \propto \prod_{m=1}^{M} \pi_m$$

since π_m is the likelihood contribution of the *m*th fish and fish are assumed independent (assumption A6).

The example shown in Figure 2.2 is extremely simple for illustration purposes, but the strength of constructing the likelihood using the approach above is the ability to design models that can be tailored to the spatial complexity of the Delta's channel network. Structuring the likelihood in this fashion has two major advantages: 1) The complex channel network of the Delta can be broken down into a series of simple transition matrices that describe transitions from one occasion to the next in terms of survival and movement probabilities, and 2) The matrix algebra expressed in Eqn. 2.4 can be easily coded into computer programs to automatically build the likelihood from the detection histories and transition matrices.

2.4.2 Assumptions in the context of acoustic telemetry in the Delta

In this section, I evaluate a number of assumptions in terms of their relevance to monitoring migration of tagged fish in the Delta. Specifically I evaluate assumptions A3 (sampling is instantaneous), A5 (states are known without error), and A10 (movement from state *r* to *s* occurs just before sampling). I focus on these assumptions because they have arisen frequently when either assisting in the design of the telemetry system or when analyzing data where one of these assumptions may have been violated. Furthermore, except for A3, these assumptions apply almost exclusively to the monitoring of river junctions where the goal is to assign fish to migration routes and estimate the proportion of fish using each route. Most of these assumptions can be fulfilled if they are explicitly evaluated when designing and situating the telemetry stations within channels at a river junction. Therefore, I use simple examples to show how these assumptions can be violated and how telemetry stations can be deployed such that assumptions are fulfilled.

Under assumption A5, the states occupied at each occasion are known without error. In terms of a river junction, this assumption means that there is no error in assigning fish to a migration route. This assumption may be violated in a number of ways. Consider the two examples in Figure 2.3 where the swimming path of a fish is shown relative to the detection zone of each telemetry station. In example A, the detection zone of the left channel extends into the right channel. Therefore, a fish taking the right channel could be detected by both telemetry stations, in which case no error would occur because the fish's migration route would be assigned based on the telemetry station where the fish was last detected. However, if the detection probability of the telemetry station in the right channel is imperfect and this fish were not detected (as indicated by the dashed line in Figure 2.3A), then this fish would be assigned to the left channel even though it had migrated through the right channel. This error could be identified if the fish were later detected at a downstream telemetry station within the right-hand migration route. However, if this fish had died before arriving at the next station then two types of bias will be introduced: 1) the probability of entering the left channel will be positively biased, and 2) the mortality that actually occurred in the right-hand channel will be assigned to the left hand channel, negatively biasing survival for the left hand channel.

This example shows that telemetry stations used to assign fish to a given migration route should have sufficient spatial specificity so as to detect only fish that have actually entered a given migration route. This can be accomplished by measuring the detection zone of each telemetry station and ensuring that only fish that have actually entered a specific migration route can be detected (Figure 2.3B). This approach will ensure that fish are not misassigned to a migration route regardless of whether they are detected at a given telemetry station. Even though the detection zones may be specific to a given channel, the swimming path of a fish may sometimes enter the mouth of one channel, but then swim out of that channel to enter the other channel. Again, the time series of detections would provide evidence of these events, in which case the telemetry stations should be situated some distance downstream of the river junction so as to detect only fish that are committed to a given route. Caution should be exercised; however, because moving the telemetry stations too far

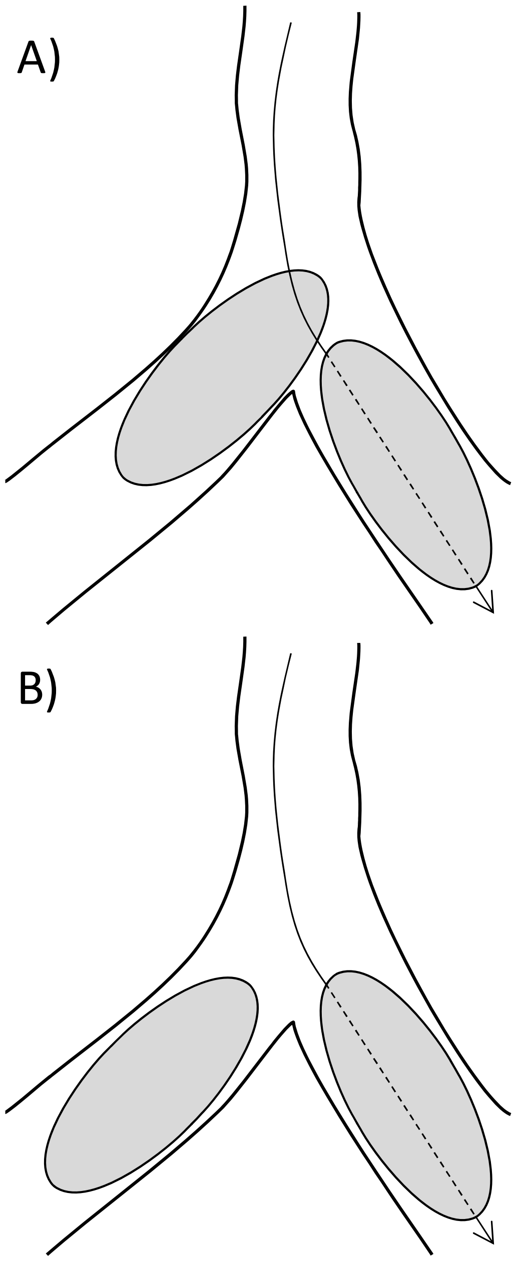

Figure 2.3. Schematic of a river junction under two scenarios with shaded ovals showing the detection zone of telemetry stations. The movement path of a fish is shown as a directed arrow. When the fish's path intersects the detection zone of each station, a solid line indicates the fish is detected and a dashed line indicates a fish is not detected. In scenario A, the fish would be wrongly assigned to the left-hand channel even though it remained in the right channel. In schematic B, no error would occur and mark-recapture models would account for the probability that the fish could have taken either route.

downstream of the river junction could violate assumption A10 (discussed next). Thus, design of the telemetry system involves a tradeoff between A5 and A10.

Although assumption A5 is important to facilitate system design, deployment, and testing of the telemetry system, perfect detection probabilities at a river junction will ensure that assumption A5 is fulfilled. That is, with perfect detection probabilities, the migration route of fish will be known without error regardless of complexity of movement paths through the telemetry stations at a river junction. Detection probabilities at river junctions were nearly perfect in all years at all river junctions in my study, implying that assumption A10 should take precedence over A5. However, planning of mark-recapture studies should occur with the expectation that detection probabilities will be imperfect, in which case consideration of assumption A5 is critical.

To separately estimate S_{hi} and Ψ_{hl} at a river junction, assumption A10 requires that all mortality occurs while in state r and then transition to state s occurs instantaneously just prior to sampling. In the spatial context of the Delta, this assumption means that all mortality should occur first within a reach, movement from one channel to another should occur last, and no mortality should occur between the point of entry to a channel and the location of the telemetry station within each channel. For example, consider a two-branch junction with the choice of placing hydrophones just downstream of a junction (points A_1 and B_1 in Figure 2.4) or some distance downstream of the river junction (points A_2 and B_2 in Figure 2.4). We might want to place the hydrophones at the downstream locations to ensure that fish were committed to a particular channel and not just temporarily “visiting” the entrance to that channel. This rationale is sound, but if mortality occurs downstream of the river junction, then the estimate of Ψ_h could be biased. Figure 2.4 shows the underlying survival probabilities upstream and downstream of the junction. The goal is to obtain unbiased estimates of survival and Ψ_h, the proportion of fish entering each channel.

First, consider the case when telemetry stations are placed at A_1 and B_1 (Figure 2.4). The mark-recapture model is capable of estimating two parameters between the upstream hydrophone (A_0) and the two downstream hydrophones (A_1 and B_1):

$$\hat{\phi}_{\mathrm{A0,B1}} = S_{\mathrm{A0}}\Psi_{\mathrm{B}}$$

$$\text{and} \qquad \hat{\phi}_{\mathrm{A0,B1}} = S_{\mathrm{A0}}\left(1-\Psi_{\mathrm{B}}\right).$$

These estimable parameters follow directly from the definitions of ϕ_i^{rs}, S_i^r, Ψ_i^{rs} in the multistate model described in Section 2.2.1 and Eqns. 2.1 and 2.2. Our primary interest is in estimating the underlying survival and route entrainment probabilities. These underlying parameters can be estimated as:

$$\hat{S}_{\mathrm{total}} = \hat{S}_{\mathrm{A0}} = \hat{\phi}_{\mathrm{A0,B1}} + \hat{\phi}_{\mathrm{A0,A1}} \tag{2.5}$$

because $\mathrm{E}\left(S_{\mathrm{A0}}\right) = \mathrm{E}\left(\phi_{\mathrm{A0,B1}} + \phi_{\mathrm{A0,A1}}\right) = S_{\mathrm{A0}}\Psi_{\mathrm{B}} + S_{\mathrm{A0}}\left(1-\Psi_{\mathrm{B}}\right) = S_{\mathrm{A0}}\left(\Psi_{\mathrm{B}} + 1 - \Psi_{\mathrm{B}}\right) = S_{\mathrm{A0}}$

and

$$\hat{\Psi}_{\mathrm{B}} = \frac{\hat{\phi}_{\mathrm{A0,B1}}}{\hat{S}_{\mathrm{total}}} \tag{2.6}$$

because

$$\mathrm{E}\left(\hat{\Psi}_{\mathrm{B}}\right) = \mathrm{E}\left(\frac{\phi_{\mathrm{A0,B1}}}{S_{\mathrm{total}}}\right) \doteq \frac{S_{\mathrm{A0}}\Psi_{\mathrm{B}}}{S_{\mathrm{A0}}} = \Psi_{\mathrm{B}}.$$

Thus, when telemetry stations are located just downstream of a river junction, all mortality occurs first, movement into each channel occurs last, assumption A10 is fulfilled, and the underlying true parameters of interest can be estimated without bias.

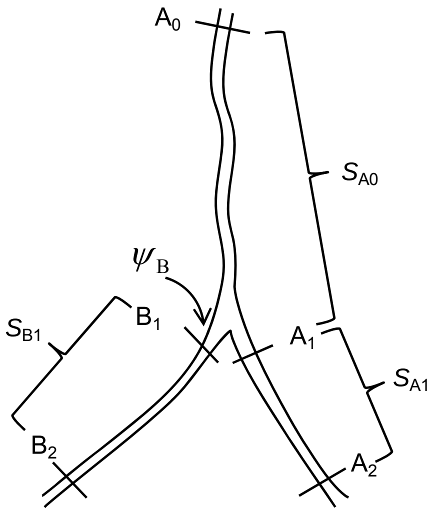

Figure 2.4. Schematic of a river junction showing potential locations of telemetry stations as hash marks across the river channel and brackets showing underlying survival probabilities between hash marks.

Now consider the case when telemetry stations are placed at the furthest downstream locations (A_2 and B_2) and *not* at A_1 and B_1 (Figure 2.4). In this case, the mark-recapture model is still capable of estimating only two parameters between the upstream hydrophone (A_0) and the two downstream hydrophones (A_2 and B_2), and these two parameters are functions of the underlying parameters:

$$\mathrm{E}\left(\hat{\phi}_{\mathrm{A0,B2}}\right)=S_{\mathrm{A0}}\Psi_{\mathrm{B}}S_{\mathrm{B1}}$$

$$\text{and} \qquad \mathrm{E}\left(\hat{\phi}_{\mathrm{A0,A2}}\right)=S_{\mathrm{A0}}\left(1-\Psi_{\mathrm{B}}\right)S_{\mathrm{A1}}.$$

Using Eqns. 2.5 and 2.6, however, results in

$$\mathrm{E}\left(\hat{S}_{\mathrm{total}}\right)=\mathrm{E}\left(\phi_{\mathrm{A0,B2}}+\phi_{\mathrm{A0,A2}}\right)=S_{\mathrm{A0}}\left(\Psi_{\mathrm{B}}S_{\mathrm{B1}}+\left(1-\Psi_{\mathrm{B}}\right)S_{\mathrm{A1}}\right)$$

$$\text{and} \qquad \mathrm{E}\left(\hat{\Psi}_{\mathrm{B}}\right)=\mathrm{E}\left(\frac{\phi_{\mathrm{A0,B2}}}{S_{\mathrm{total}}}\right)\doteq\frac{S_{\mathrm{A0}}\Psi_{\mathrm{B}}S_{\mathrm{B1}}}{S_{\mathrm{A0}}\left(\Psi_{\mathrm{B}}S_{\mathrm{B1}}+\left(1-\Psi_{\mathrm{B}}\right)S_{\mathrm{A1}}\right)}=\frac{\Psi_{\mathrm{B}}S_{\mathrm{B1}}}{\psi_{\mathrm{B}}S_{\mathrm{B1}}+(1-\Psi_{\mathrm{B}})S_{\mathrm{A1}}}. \qquad (2.7)$$

In this case, $\mathrm{E}(S_{\mathrm{total}})$ is unbiased and estimates a function of the underlying parameters representing the product of survival through the upstream reach and the weighted average survival through the two downstream channels. In essence, S_{total} estimates the probability of surviving from the upstream telemetry station to either of the downstream stations. However, when mortality occurs between the river junction and the downstream telemetry stations, $\mathrm{E}\left(\hat{\Psi}_{\mathrm{B}}\right)\neq\Psi_{\mathrm{B}}$, showing that $\hat{\Psi}_{\mathrm{B}}$ will likely be biased. In fact, the only situation when $\hat{\Psi}_{\mathrm{B}}$ will remain unbiased is when survival is equal in the two reaches downstream of the river junction. Setting $S_{\mathrm{A1}} = S_{\mathrm{B1}}$, we have

$$\mathrm{E}\left(\hat{\Psi}_{\mathrm{B}}\right)=\frac{\Psi_{\mathrm{B}}S_{\mathrm{B1}}}{\Psi_{\mathrm{B}}S_{\mathrm{B1}}+(1-\Psi_{\mathrm{B}})S_{\mathrm{A1}}}=\frac{\Psi_{\mathrm{B}}S_{\mathrm{B1}}}{\Psi_{\mathrm{B}}S_{\mathrm{B1}}+(1-\Psi_{\mathrm{B}})S_{\mathrm{B1}}}=\frac{\Psi_{\mathrm{B}}S_{\mathrm{B1}}}{S_{\mathrm{B1}}(\Psi_{\mathrm{B}}-1-\psi_{\mathrm{B}})}=\frac{\Psi_{\mathrm{B}}S_{\mathrm{B1}}}{S_{\mathrm{B1}}}=\Psi_{\mathrm{B}}.$$

Under any other circumstance, $\hat{\Psi}_{\mathrm{B}}$ will be biased when mortality occurs between the river junction and the next downstream hydrophone. For a concrete example, assume the following true parameter values: $S_{\mathrm{A0}} = 0.60$, $S_{\mathrm{A1}} = 0.97$, $S_{\mathrm{B1}} = 0.60$, and $\Psi_{\mathrm{B}} = 0.50$. With these true values, $\hat{\Psi}_{\mathrm{B}} = 0.382$ and Bias($\hat{\Psi}_{\mathrm{B}}$) = -0.118. The magnitude of bias will depend on the true value of $\hat{\Psi}_{\mathrm{B}}$ and the magnitude of the difference between S_{B1} and S_{A1}. When $S_{\mathrm{B1}} < S_{\mathrm{A1}}$, $\hat{\Psi}_{\mathrm{B}}$ will be negatively biased; when $S_{\mathrm{B1}} > S_{\mathrm{B2}}$, $\hat{\Psi}_{\mathrm{B}}$ will be positively biased; and as $S_{\mathrm{B1}} - S_{\mathrm{A1}}$

approaches zero, bias approaches zero. Bias with respect to $\hat{\Psi}_{\mathrm{B}}$ follows a parabolic function and approaches zero as $\hat{\Psi}_{\mathrm{B}}$ approaches either zero or one. Thus, absolute bias with respect to Ψ_{B} is at its maximum when

$$\frac{\partial}{\partial \Psi_{\mathrm{B}}}\left(\hat{\Psi}_{\mathrm{B}} - \Psi_{\mathrm{B}}\right) = 0,$$

which has the solution

$$\Psi_{\mathrm{B}} = \frac{S_{\mathrm{A2}} - \sqrt{S_{\mathrm{B1}} S_{\mathrm{A2}}}}{S_{\mathrm{A2}} - S_{\mathrm{B1}}}.$$

With the survival probabilities in the example above, absolute bias in $\hat{\Psi}_{\mathrm{B}}$ will be at its maximum value when the true value of Ψ_{B} is 0.56.

These examples show that if the goal is to estimate the proportion of fish entering a given river channel at a river junction, then telemetry stations must be positioned such that fish are detected as soon as possible after they enter a given river channel. Situating telemetry stations using these guidelines will ensure that little mortality occurs after fish enter a given channel and ensure that estimates of route entrainment probabilities remain unbiased. In cases when it is impossible to fulfill assumption A10, the best course of action is to estimate the ϕ parameters and S_{total} (see Eqns. 2.1, 2.2, 2.5, and 2.6). Although the ϕ parameters are difficult to interpret, being a combination of the underlying survival and movement probabilities, both ϕ and S_{total} will remain unbiased. I used this approach at a number of locations in the Delta where fish could take multiple pathways, but telemetry stations were located well downstream of the channel junctions (see Chapter 4).

How far downstream of a junction is too far (possible violation of assumption A10) and how close to a junction is too close (possible violation of assumption A5)? Spatial scale comes into play, as the realized bias in Ψ_{hl} through violation of A10 will depend on the rate of mortality with respect to distance. For example, if moving a telemetry station 500 m downstream of a junction avoids errors in assigning fish to migration routes, but survival is 0.98 through that 500 m stretch, then the realized bias will be extremely small. Using my earlier example from Figure 2.4 and setting $S_{\mathrm{B1}} = 0.98$ and $S_{\mathrm{A1}} = 1$ results in $\mathrm{E}(\Psi_{\mathrm{B}}) = 0.495$

when the true $\Psi_B = 0.5$ (using Eqn. 2.7). In this case, the tradeoff between fulfilling both assumptions A10 and A5 might warrant moving the telemetry station downstream by 500 m. Evaluating these assumptions will often require conceptual exercises such as the examples used here to first hypothesize the underlying parameter values and then calculate the bias. Empirically evaluating such questions by estimating survival over a 500 m reach could be difficult because the detection range of telemetry stations is often on the scale of hundreds of meters. In this case, the sampling occasion (i.e., detection range) cannot be considered instantaneous relative to the interval over which survival is estimated, which leads to violation of assumption A3.

Often researchers may be interested in estimating survival over small distances, or questions may arise about how best to monitor a complex channel junction. The appropriate spatial scale for monitoring can often be answered by considering assumption A3 and comparing the spatial scale of the detection zone to the spatial scale of the survival process. Such a situation occurs at the junction of Sutter Slough and Steamboat Slough with the Sacramento River (Figure 1.2). Sutter Slough branches off the Sacramento River and then 2 km downstream, Steamboat Slough splits off the Sacramento River (Figure 2.5). The question is whether this area should be modeled as 2 two-branch junctions or a single three-branch junction.

During the winter of 2007 (December 2006 – February 2007), telemetry stations were deployed just below each river junction, which allowed me to evaluate the best approach for modeling this junction. Assuming instantaneous sampling of fish passing detection stations (assumption A3), this reach could be modeled as two river junctions with survival to the first junction, entrainment probability for the first junction, survival from the first to the second junction, and then entrainment into the second junction (Figure 2.5). When analyzing the telemetry data, however, I found that detections of fish at the two telemetry stations in the mainstem river (just downstream of each junction) were often separated by only seconds. Since telemetry stations can detect tags for hundreds of meters, the short time difference between detections suggested that the detection range of these telemetry stations nearly overlapped (Figure 2.5). In this case, the spatial scale over which survival is to be estimated is on the same order of the survival process, making it impossible to accurately measure survival over such a short distance. Therefore, the best course of action was to model this reach as a single three-branch river junction since it was impossible to accurately estimate survival between the first and second river junction due to violation of assumption A3. When the scale of detection is on the order of hundreds of meters, assumption A3 suggests that the minimum spatial scale for estimating survival should be on the order of kilometers.

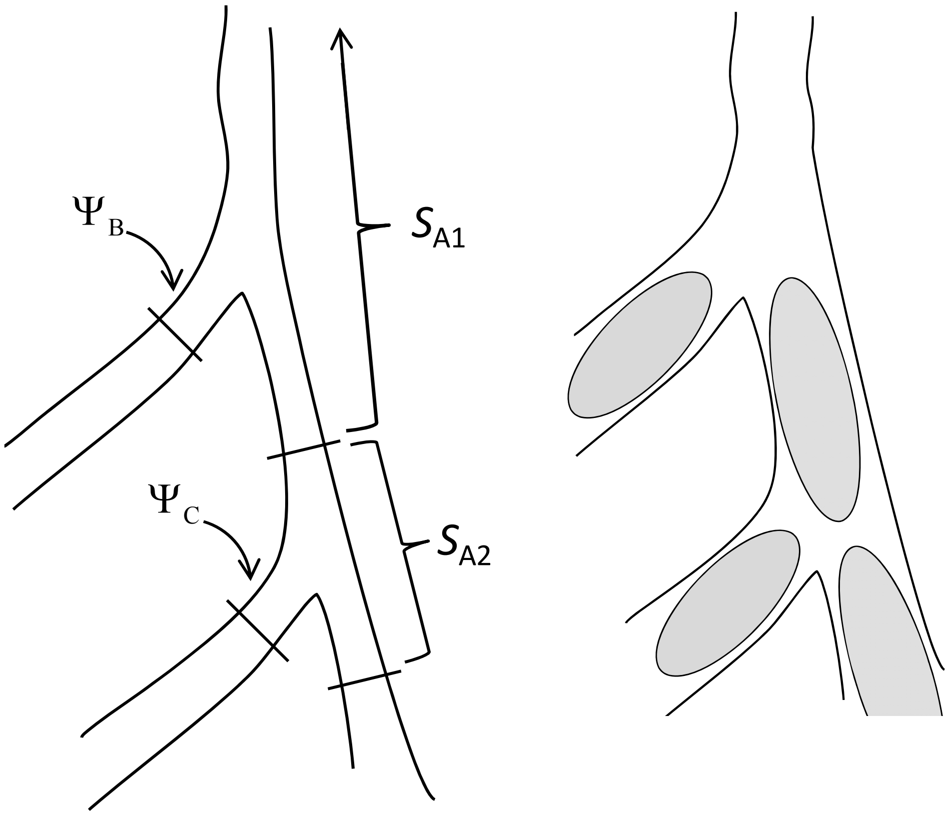

Figure 2.5. Schematic of the river junction at the Sacramento River with Sutter Slough and Steamboat Slough. Considering instantaneous sampling locations, this area could be modeled as 2 two-branch river junctions as shown at left. However, considering the detection zone of each telemetry station (shown as gray ovals on the right), indicates that the spatial scale of detection is on the same order of the survival process, suggesting this area should be modeled as a single three-branch river junction.

2.4.3 Parameter estimability under the constrained multistate model

Under the fully generalized multistate model described in Section 2.3, all parameters are estimable for all sampling periods but the last, but in a constrained model care is needed to ensure that all parameters are estimable. When the number of states sampled at each occasion varies, information contained in the recapture data may not be sufficient to separately estimate detection probabilities for each state and occasion. Inability to estimate detection probabilities typically leads to confounding between detection probabilities and survival and transition parameters, such as Ψ_{hl}. By contrast, ensuring detection probabilities are estimable at each telemetry station will also ensure that biological parameters can be estimated. Thus, understanding factors causing inability to estimate detection probabilities and features of system design that ensure identifiability of detection probabilities is crucial to designing a mark-recapture experiment that is capable of estimating the biological parameters of interest.

My goal in this section is to describe the techniques I used to evaluate identifiability of model parameters. Because the channel network of the Delta is hierarchical in nature, with secondary river junctions and migration routes nested within primary migration routes, ensuring estimability of parameters can be a difficult task. Therefore, I used both simulation and formal analytical techniques to evaluate parameter estimability of all models. Through this process, I identified a number of generalities for minimal requirements of system design that will ensure estimability of detection probabilities, and therefore, estimability of biological parameters. Such generalities will aid researchers during the initial design phase of a telemetry system, but only when a model is built, formally analyzed, and then fit to simulated data can we be absolutely certain that all parameters can be estimated from the mark-recapture data.

To simulate mark-recapture data, I built a mark-recapture model based on a given design of a telemetry system and then hypothesized a true set of parameter values for a given sample size of N fish. The probability of each detection history, π_i, was calculated from the hypothesized parameter values, and then the expected frequency of each capture history is calculated as $N\pi_i$. These expected frequencies were then used as the data set of detection history frequencies, the model was fit to the data to estimate the parameters, and the estimated parameters were compared to the true values. Substantial deviation between true and estimated values or nonsensical variance estimates provides evidence that a given parameter may not be estimable.

A more formal approach involves the use of computer algebra packages to identify unestimable parameters (Catchpole et al., 2002; Gimenez et al., 2004). This approach can be used to test for both “intrinsic and extrinsic parameter redundancy” (*sensu* Catchpole et al., 2002). Intrinsic redundancy is defined as inability to estimate some parameters due to the fundamental structure of the model and occurs independently of any particular data set. A classic example is the inability to separately estimate survival and capture probability in the last reach (or time-period) of a CJS model (Seber 1982). Intrinsic redundancy is evaluated by forming the matrix of derivatives of $\ln(\pi_i)$ with respect to θ_j (i.e., a matrix of derivatives of the log of each multinomial cell probability with respect to each parameter). The rank of this matrix yields the number of (theoretically) estimable parameters. The model is considered full rank and all parameters estimable if the number of parameters equals the rank of the derivative matrix.

Extrinsic redundancy is defined as the inability to estimate some parameters due to the structure of a particular data set and can occur when data are sparse or when parameter estimates occur on the boundary of zero or one. Extrinsic redundancy is evaluated as described above, except only multinomial cell probabilities with non-zero counts are used in forming the derivative matrix. For example, perfect detection probabilities cause extrinsic redundancy. Consider the maximum likelihood estimator of P_t for the CJS model:

$$\hat{P}_t = \frac{r_t}{r_t + z_t}$$

where r_t is the number of fish detected downstream of occasion t of those detected at occasion t and z_t is the number of fish not detected at t but detected downstream of t (Seber, 1982; Burnham et al., 1987). When all fish detected downstream of a particular station were also detected at that station, $z_t = 0$ and $\hat{P}_t = 1$. However, under these circumstances, the likelihood function has no unique maximum in the neighborhood of $P_t = 1$, causing inability to estimate P_t through iterative maximization of the likelihood. Thus, it is important to identify parameters on a boundary, and then set them to appropriate constant values prior to estimating parameters via optimization routines.

In constrained multistate models for the Delta, the ability to estimate route-specific biological parameters rests on whether route-specific detection probabilities can be estimated at river junctions. When detection probabilities at a river junction cannot be estimated for a particular route, survival and route entrainment probabilities become confounded with detection probability. Understanding minimal requirements for estimating detection probabilities at river junctions is therefore critical to designing studies capable of estimating biological parameters of interest.

If there are H routes at a river junction, then downstream of the river junction, at least H-1 routes must contain a telemetry station specific only to that route. To better understand this requirement, consider the example shown in Figure 2.6 where detection probabilities at the first two river junctions are defined as in Eqn. 2.6. For the first river junction, detection probabilities at both telemetry stations (P_{B1} and P_{A2}) can be estimated because each channel has a telemetry station unique to that channel at the next downstream occasion (i.e., location B_2 for P_{B1} and A_3 or C_1 for P_{A2}). For example, fish not detected at B_1 will be detected at B_2 providing the information needed to estimate P_{B1}. Given that both detection probabilities at the first junction are estimable, the probability of entering each route (Ψ_{A1} and 1-Ψ_{A1}) is also estimable.

However, for the second river junction, detection probabilities for route A and C (P_{A3} and P_{C1}) are confounded because the next downstream telemetry station (A_4) is not unique to either route. Because the final telemetry station at A_4 can detect fish from any route, detection data from A_4 provides no information with which to distinguish whether undetected fish were missed at A_3 or C_1. As a consequence, it is impossible to estimate separate detection probabilities for these sites. To ameliorate this problem, imagine that another telemetry station is located downstream of the second junction within route C. With this design, P_{C1} can now be estimated from the downstream telemetry station unique to route C. Even though the final telemetry station can detect fish from any route, given within-route telemetry stations for routes A and C, information from the final station can be used to estimate detection probability for route A at the second junction (P_{A3}). Thus, only two of the three downstream telemetry stations need be specific to a given river channel.

Interestingly, given the minimal requirements in the example above, all detection probabilities in Figure 2.6 become estimable even though it appears that three detection probabilities (P_{A3}, P_{B2}, and P_{C2}) must be estimated from a common telemetry station at the final occasion (A4). Given estimable route-specific detection and entrainment probabilities at each river junction, information at both *t*-1 (upstream) and *t*+1 (downstream) can be used to estimate detection probabilities at occasion *t*. For example, fish detected at B1 and then A4 must have passed B2 without being detected (Figure 2.3), allowing P_{B2} to be estimated. This example shows that ability to estimate detection probabilities at the river junctions ensures all subsequent parameters within a route become estimable.

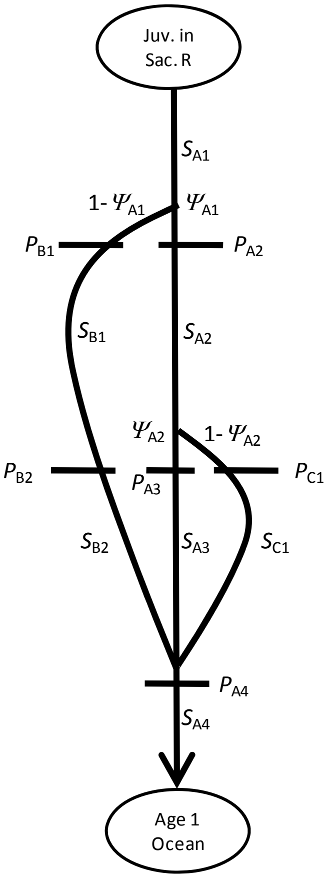

Figure 2.6. Schematic of the Delta with hash marks across the river channels showing locations where telemetry stations would be located according to Figure 2.2 to sample the population of tagged fish as it migrates through the Delta. Subscripts for detection probabilities identify each unique telemetry station within each route.

In designing models for the Delta, *H*-1 within-route telemetry stations downstream of a junction for *H* routes at a junction arose time and again as the minimal requirements for ensuring estimability of all parameters. This generality was confirmed by using the techniques described above to evaluate parameter estimability. Thus, the "*H*-1" rule of thumb can be used to help design mark-recapture experiments for the Delta. However, because of the hierarchical nature of the Delta's channel network, initial design of the telemetry system must be followed by formal testing of the model to ensure that all parameters are estimable *before* the study is implemented.

Chapter 3

ESTIMATING SURVIVAL AND MIGRATION ROUTE PROBABILITIES OF JUVENILE CHINOOK SALMON MIGRATING THROUGH THE SACRAMENTO-SAN JOAQUIN RIVER DELTA DURING WINTER 2007

3.1 Introduction

Many stocks of Chinook salmon (*Oncorhynchus tshawytscha*) in California, Washington, and Oregon are listed as threatened or endangered under the Endangered Species Act (Nehlsen et al., 1991; Myers et al., 1998). In the Central Valley of California, the winter, spring, and fall/late fall runs of Chinook salmon are federally listed as endangered, threatened, and a “species of concern,” respectively (NMFS, 1997). Recently, due to below-target returns of fall Chinook salmon to the Sacramento River, the National Marine Fisheries Service declared a Federal Disaster and closed the 2008 salmon fishery along the West Coast (NOAA, 2008). Understanding factors affecting survival of salmon is therefore critical to devising effective recovery strategies for these populations.

An important stage in the life history of Chinook salmon is the period of migration from natal tributaries to the ocean, when juvenile salmon in the Sacramento River may suffer mortality from a host of anthropogenic and natural factors (Brandes and McLain, 2001; Baker and Morhardt, 2001; Williams, 2006). Juvenile Chinook salmon emigrating from the Sacramento River must pass through the Sacramento-San Joaquin River Delta (hereafter, “the Delta”), a complex network of natural and man-made river channels (Nichols et al., 1986). Juvenile salmon may migrate through a number of routes on their journey to the ocean. For example, they may migrate within the mainstem Sacramento River leading directly into San Francisco Bay (see Route A in Figure 3.1). However, they may also migrate through longer secondary routes such as the interior Delta, the network of channels to the south of the mainstem Sacramento River (see Routes C and D in Figure 3.1).

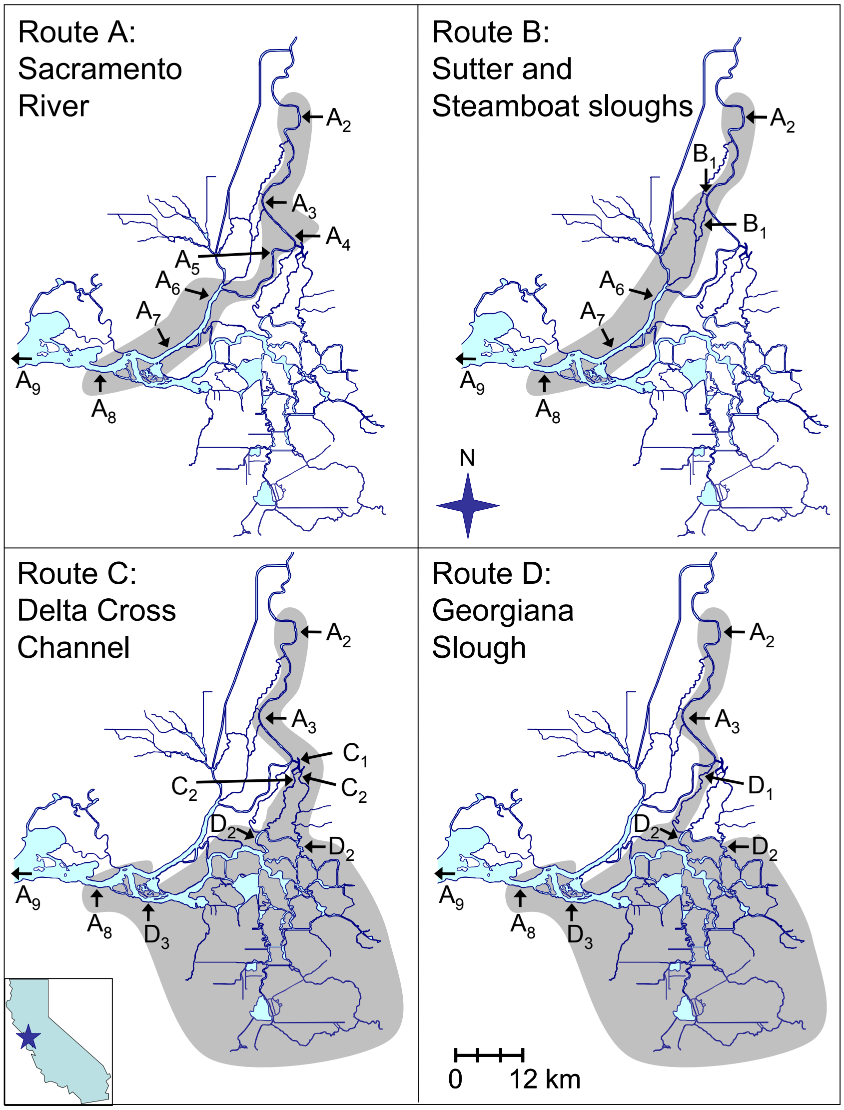

Figure 3.1. Maps of the Sacramento–San Joaquin River Delta with shaded regions showing river reaches that comprise survival through the Delta for four different migration routes. Arrows show the location of telemetry stations specific to each route. The Delta extends from station A_2 at Freeport to station A_8 at Chipps Island. The first river junction occurs where Sutter and Steamboat sloughs (B_1) diverge from the Sacramento River at station A_3. The second junction occurs where the Delta Cross Channel (C_1) and Georgiana Slough (D_1) diverge from the Sacramento River at station A_4. For routes C and D, the interior Delta is the large shaded region to the south of station D_2. Telemetry stations with the same label (B_1, C_2, and D_2) were pooled as one station in the mark-recapture model. Station A_3 was not operational during the first release in December, 2006. Station A_9 pools all telemetry stations in San Francisco Bay downstream of A_8. The release site (rkm 92) was 19 river kilometers upriver of station A_2 (rkm 73).

Both human actions and natural processes affect the magnitude and distribution of Sacramento River flow among the channel network of the Delta. Inflow into the Delta from the Sacramento River is largely controlled by upstream releases of water from storage reservoirs. Within the Delta, water distribution is affected by two water pumping projects in the southern Delta (the State Water Project and Central Valley Project). These projects pump water from the Delta for agricultural and municipal uses and can export up to 50% of the total inflow (Nichols et al., 1986). Associated with the water pumping projects is the Delta Cross Channel, a man-made channel that diverts river flow from the Sacramento River into the interior Delta (see C1 in Route C, Figure 3.1). In addition to these human influences on water flow through the Delta, natural processes include seasonal rainfall and snowmelt events in the winter and spring, respectively, and tidal cycles that vary on diel and bi-weekly time scales.

As juvenile salmon migrate among the complex channel network of the Delta, they are subject to channel-specific processes that affect their rate of migration, vulnerability to predation, feeding success, growth rates, and ultimately, survival. For example, growth of juvenile salmon in the Yolo Bypass, a seasonally inundated flood plain, was significantly greater than in the mainstem Sacramento River (Sommer et al., 2001). In contrast, juvenile salmon entering the interior Delta must traverse longer migration routes and are exposed to entrainment at the water pumping projects, both of which may decrease survival of fish using this migratory pathway (Brandes and McLain, 2001; Newman and Rice, 2002; Newman, 2003; Kimmerer, 2008; Newman and Brandes; 2010). These examples show that population-level survival rates of juvenile salmon migrating through the Delta will be driven by 1) the survival rates arising from the biotic and abiotic processes unique to each migration route, and 2) the proportion of the population using each migration route. In turn, natural and human-imposed variation in discharge and water distribution will affect population dispersal and survival rates within each channel, driving population-level survival through the Delta.

Currently, there is limited understanding of how water management actions in the Delta affect population distribution and route-specific survival of juvenile salmon. Evidence suggests that survival of fish migrating through the interior Delta decreases with increasing water exports (Brandes and McLain, 2001; Newman, 2003). Water exports could decrease survival by increasing migration times through the interior Delta, by increasing encounter rates with predators, and by direct entrainment of fish at pumping facilities located in the interior Delta. Operation of the Delta Cross Channel likely affects the proportion of the population entering the interior Delta. To date, the proportion of fish migrating through the interior Delta has not been estimated, yet such estimates are critical to understand the relative effect of water management actions on the population as a whole (Newman and Brandes, 2010). Thus, currently lacking is a population-level approach that quantifies dispersal of the population among migration routes and measures survival within these routes to better understand the influence of management actions on population-level survival.

In this chapter, I develop a mark-recapture model for the Delta to explicitly estimate the probability of migrating through each of four migration routes and the probability of surviving through each route. Next, I quantify population-level survival through the Delta as a function of the route-specific migration and survival probabilities. I then apply this model to the first available acoustic telemetry data of juvenile late-fall run Chinook salmon collected during the winter of 2006/2007 (hereafter, “2007”). Acoustic telemetry is a passive “capture” technique enabling individual fish to be detected repeatedly by multiple telemetry stations as they migrate through the Delta. Given estimates of route-specific survival and movement through the Delta from the acoustic telemetry data, I then examine how each of these components interacted to affect survival of the population migrating through the Delta.

3.2 Methods

3.2.1 Telemetry system

Telemetry stations were deployed in the Delta to monitor movement of tagged fish among four major migration routes through the Delta (Figure 3.1): the mainstem Sacramento River (Route A); Sutter and Steamboat sloughs (Route B); the interior Delta via the Delta Cross Channel (Route C); and the interior Delta via Georgiana Slough (Route D). Although there are numerous possible migration pathways, I focused on these routes because management actions likely have the largest influence on movement and survival among these routes. For example, fish may enter the interior Delta from the Sacramento River through either the Delta Cross Channel or Georgiana Slough where they subsequently become vulnerable to migration delays and entrainment at the water pumping projects. Steamboat and Sutter sloughs may be an important migration route because fish using this route bypass the Delta Cross Channel and Georgiana Slough (Figure 3.1). Thus, fish migrating through Steamboat and Sutter Slough are unable to enter the interior Delta through the Delta Cross Channel or Georgiana Slough.

Telemetry stations were labeled hierarchically to reflect the branching nature of channels at river junctions and their subsequent downstream convergence at the confluence of river channels (Figure 3.1). Each telemetry station consisted of single or multiple tag-detecting monitors (Vemco Ltd., Model VR2), depending on the number of monitors needed to maximize detection probabilities at each station. Since the Sacramento River is the primary migration route, the *i*th telemetry station within this route was denoted as A_i from the release site (A_1 located at river kilometer (rkm) 92) to the last telemetry station in the Delta at Chipps Island (A_8 at rkm -9; by convention, rkm 0 is defined at the southern tip of Sherman Island which is 9 river kilometers upstream of station A_8; see Figure 1.2). Migrating juvenile salmon first arrive at Sutter and Steamboat sloughs (B_1, rkm 43 and rkm 38), which diverge from the Sacramento River at the first river junction and converge again with the Sacramento River upstream of A_6 (rkm 19). Fish remaining in the Sacramento River then pass the Delta Cross Channel and Georgiana Slough at the second river junction. For the Delta Cross Channel, stations were labeled with C_i beginning where the Delta Cross Channel diverges from the Sacramento River at C_1 (rkm 60) and ending when these river channels converge with the interior Delta at D_2 (rkm 40 and rkm 47). Telemetry stations within Georgiana Slough and the interior Delta were labeled as D_i where Georgiana Slough branches off the mainstem Sacramento River (D_1, rkm 58) until convergence of the interior Delta with the Sacramento River at D_3 (rkm 5). Following this hierarchy, Routes A, B, C, and D contained 8, 1, 2, and 3 telemetry stations, respectively, for a total of 14 telemetry stations within the Delta. Parameter subscripting and coding of detection histories followed this hierarchical structure (see *Model Development* section below). With this configuration of telemetry stations, survival in the final reach is confounded with detection probability at the last telemetry station (Skalski et al., 2001). Therefore, to estimate survival to the terminus of the Delta and detection probability at the last station in the Delta (A_8), I formed one additional telemetry station by pooling detections from numerous tag detecting monitors downstream of A_8 in San Francisco Bay. Most of these detections occurred at three primary stations that provided nearly complete cross-sectional coverage of San Francisco Bay at bridges located at rkm -37, rkm -64, and rkm -77, but single-monitor stations at other locations were also included.

3.2.2 Fish tagging and release

Juvenile late fall Chinook salmon were obtained from and surgically tagged at the Coleman National Fish Hatchery (rkm 431). For the first release in December, a 1.44-g tag (Vemco Ltd., Model V7-1L-R64K, 40-d expected battery life) was used and for the second release in January a 1.58-g tag was used (Vemco Ltd., Model V7-2L-R64K-2, 95-d expected battery life). Except for a minimum size criterion of 140 mm fork length, fish were randomly selected for tagging resulting in a mean fork length of 164.6 mm (SD = 10.9) and mean weight of 53.5 g (SD = 12.6). The tag weight represented 2.7% of the mean fish weight (range = 1.3%–3.8%) for the December release and 3.0% (range = 1.9%–4.9%) for the January release. Although recommendations for maximum tag-to-body weight ratios have varied (Jepsen et al., 2004), a 5% maximum tag-to-body weight ratio was followed based on the guidance of Adams et al. (1998a). Fish were fasted for 24 h prior to surgery to ensure they were in a post-absorptive state. To surgically implant transmitters, fish were anaesthetized in 90 mg/l tricaine methanesulfonate (MS-222) until they lost equilibrium. A fish was then placed in a light anesthetic bath (30 mg/l MS-222), ventral side up, and a small incision was made in the abdomen between the pectoral fins and the pelvic girdle. The transmitter was inserted into the peritoneal cavity, and the incision was closed with two interrupted sutures (4-0 nylon sutures with FS-2 cutting needle). Tagged fish were then returned to raceways and were allowed to recover for seven days prior to release.

Next, fish were transported to release sites in the Sacramento River near Sacramento, CA (rkm 92). Fish were then transferred to net pens (3-m square holding nets supported by pontoons) at the release site and held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process. Fish were transported and held in four separate groups, and each group was released at roughly 6-h intervals over a 24-h period on 5 December 2006 (release 1) and again on 17 January 2007 (release 2). Each release was carried out over a

24-h period to distribute tagged fish over the tidal and diel cycle. The total sample size consisted of 64 acoustically tagged fish in December, 2006 and 80 acoustically tagged fish in January, 2007.

3.2.3 Model development

I developed a mark-recapture model that estimates three sets of parameters: detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (Ψ_{hl}). Detection probabilities (P_{hi}) estimate the probability of detecting a transmitter given a fish is alive and the transmitter operational at telemetry station i within route h (h = A, B, C, D; Figure 3.2). Survival probabilities (S_{hi}) estimate the probability of surviving from telemetry station i to i+1 within route h, conditional on surviving to station i (Figure 3.2). Route entrainment probabilities (Ψ_{hl}) estimate the probability of a fish entering route h at junction l (l = 1, 2), conditional on fish surviving to junction l (Figure 3.2). In addition, the parameter ω_{open} estimates the probability of fish passing junction 2 when the Delta Cross Channel was open. This model can be classified as a generalization of the standard Cormack-Jolly-Seber (CJS) mark-recapture model (Cormack, 1964; Jolly, 1965; Seber, 1965) and a special case of a multistate mark-recapture model where the route entrainment probabilities represent a constrained matrix of state transition probabilities (Lebreton and Pradel, 2002; Williams et al., 2002). Statistical assumptions associated with a model of this structure are detailed in Chapter 2.

The first river junction was modeled as a two-branch junction where detections at the entrance to either Sutter or Steamboat Slough (station B_1; Figure 3.1) were pooled to estimate a single route entrainment probability. Thus the parameter Ψ_{B1} estimates the probability of being entrained into either Sutter or Steamboat Slough at the first river junction (Figure 3.2). Conversely, $1 - \Psi_{B1} = \Psi_{A1}$ is the probability of remaining in the Sacramento River at the first junction (Figure 3.2). The second junction was modeled as a three-branch junction where $\Psi_{A2,}$ $\Psi_{C2,}$ and $1 - \Psi_{A2} - \Psi_{C2} = \Psi_{D2}$ estimate the probabilities of remaining in the Sacramento River (Route A), being entrained into the Delta Cross Channel (Route C), and entering Georgiana Slough (Route D) at junction 2 (Figure 3.2). Because $\Psi_{C2} = 0$ when the Delta Cross Channel is

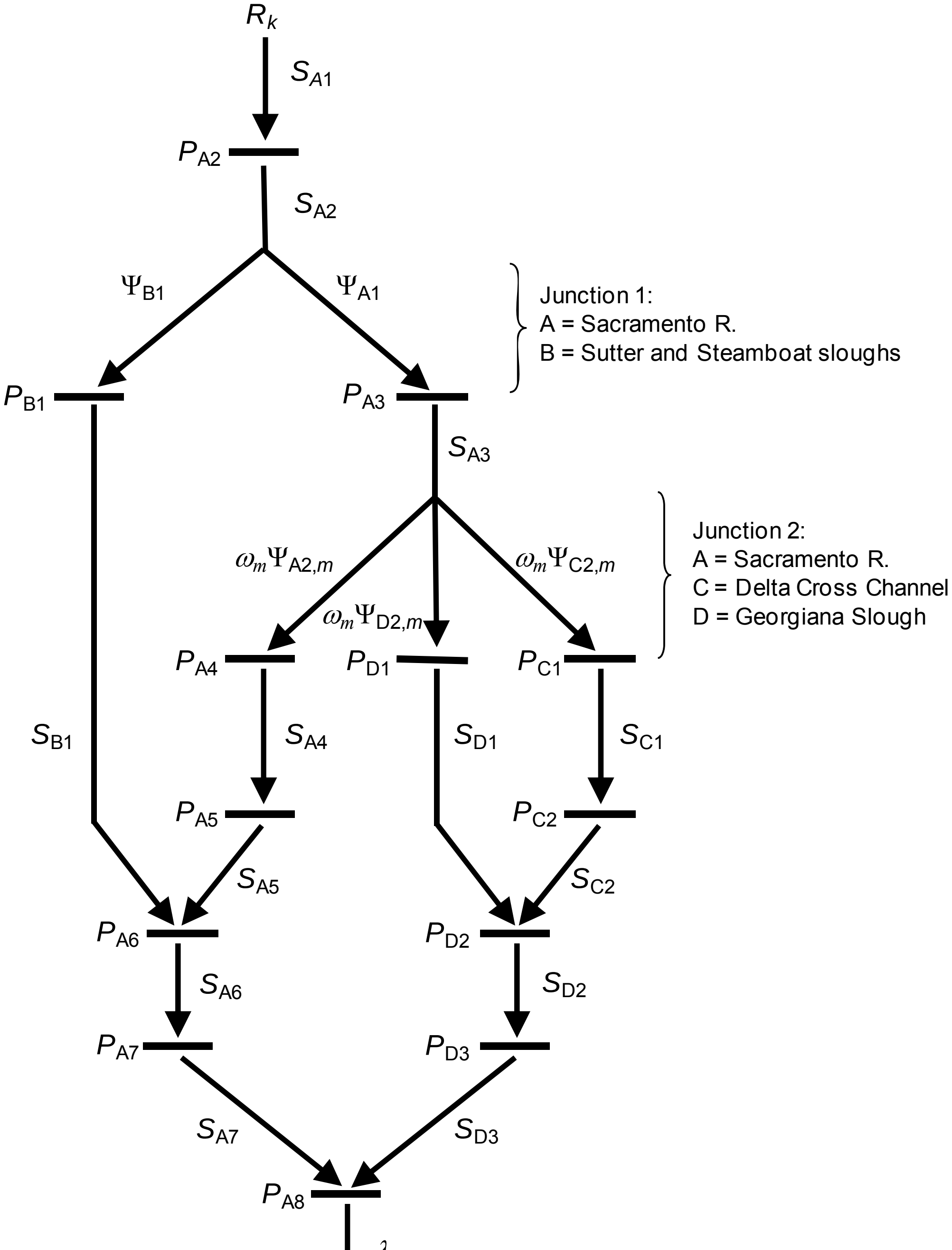

Figure 3.2. Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), and route entrainment (Ψ_{hl}) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made on 5 December 2006 and 17 January 2007.

closed, route entrainment probabilities at junction 2 depend on the position of the Delta Cross Channel gate when fish migrate past this location (Figure 3.2).

While some survival probabilities estimate survival within a given river channel from telemetry station *i* to *i*+1 (e.g., S_{A2}), others represent survival of fish migrating through a number of possible migration pathways. For example, fish entering Sutter or Steamboat Slough at B_1 may migrate through a northern or a southern channel (Figure 3.1). The parameter S_{B1}, estimating survival between sites B_1 and A_6, therefore represents an average of survival in each channel weighted by the proportion of fish using each channel. Note, however, that to separately estimate the underlying components of S_{B1}, additional telemetry stations would need to be placed at key channel junctions within this route. Similar survival probabilities include S_{C2} and S_{D2}, the latter of which encompasses much of the interior Delta (Figure 3.1).

With this model structure, the full model contains 33 parameters: 13 detection probabilities, 13 survival probabilities, 5 route entrainment probabilities, and ω_{open} (Figure 3.2). The final parameter, λ, estimates the joint probabilities of surviving downstream of A_8 and being detected at telemetry stations comprising A_9. Thus, λ has little biological meaning but must be included in the model in order to estimate survival to the terminus of the Delta at A_8.

3.2.4 Parameter estimation

Prior to parameter estimation, the records of tag-detections were processed to eliminate false positive detections using methods based on Skalski et al. (2002) and Pincock (2008). False positive detections of acoustic tags occur primarily when two or more tags are simultaneously present within the range of a given monitor, and simultaneous tag transmissions “collide” to produce a valid tag code that is not actually present at the monitor (Pincock 2008). My first criterion considered detections as valid if a minimum of two consecutive detections occurred within a 30-min period at a given telemetry station. Although this criterion minimizes the probability of accepting a false positive detection, Pincock (2008) showed that a pair of false positive detections with a time interval <30 min occurred on average once every 30 d when simulating ten tags simultaneously present at a monitor. Thus, my second criterion considered records with two detections at a given location as valid only if these detections were consistent with the spatiotemporal history of a tagged fish moving through the system of telemetry stations (Skalski et al., 2002). The detection records of five tagged fish suggested they had been consumed by piscivorous predators as was evidenced by their directed upstream movement for long distance and against the flow. We truncated the detection record of these fish to the last known location of the live tagged fish. All other detections were considered to have been live juvenile salmon. In the lower Sacramento River (sites A_6–A_8), tag detection and discharge data showed that juvenile salmon were often advected upstream on the flood tides and downstream on the ebb tides. In these cases, we used the final downstream series of detections in forming the detection history.

I used maximum likelihood techniques to estimate parameters based on a multinomial probability model that categorized each fish into a mutually exclusive and exhaustive detection history. Detection histories compactly describe the migration and detection process of fish moving through the network of telemetry stations. For example, the history 1A0AAAAAA indicates a fish was released ("1"), detected in the Sacramento River at A_2 ("A"), not detected in the Sacramento River at A_3 ("0"), and then subsequently detected at every other telemetry station in the Sacramento River ("AAAAAA"). This model has 912 possible detection histories, but with release sample sizes of $R_1 = 64$ and $R_2 = 80$ tagged fish, not all histories are observed.

Each detection history represents one of the 912 cells of a multinomial distribution where the probability of each cell is defined as a function of the detection, survival, and route entrainment probabilities. For example, the probability of history 1A0AAAAAA can be expressed as:

$$S_{A1}P_{A2}S_{A2}\Psi_{A1}\,(1\text{-}P_{A3})S_{A3}\,\omega_{\text{open}}\Psi_{A2,\text{open}}P_{A4}S_{A4}P_{A5}S_{A5}P_{A6}S_{A6}P_{A7}S_{A7}P_{A8}\lambda$$

In words, the probability of this detection history is the joint probability of surviving the first reach (S_{A1}) and being detected at A_2 (P_{A2}); surviving the second reach (S_{A2}), remaining in the Sacramento River at junction 1 (Ψ_{A1}), and not being detected at A_3 ($1–P_{A3}$); and surviving the third reach (S_{A3}), remaining in the Sacramento River at junction 2 ($\Psi_{A2,\text{open}}$) when the Delta Cross Channel was open (ω_{open}), and surviving and being detected at all remaining stations in the Sacramento River (Figure 3.2).

Given the cell probabilities, the maximum likelihood estimates are found by maximizing the likelihood function of a multinomial distribution with respect to the parameters:

$$L\left(\underset{\sim}{\theta} \mid R_k, n_j\right) \propto \prod_{j=1}^{912} \pi_j^{n_j}$$

where R_k is the number of fish released in the kth release group ($k = 1, 2$), n_j is the number of fish with the jth detection history, and π_j is the probability of the jth detection history expressed as a function of the parameters ($\underset{\sim}{\theta}$). The likelihood was numerically maximized with respect to the parameters by using algorithms provided in the software programs R (R Development Core Team, 2008) and USER (Lady et al., 2008). The variance-covariance matrix was estimated as the inverse of the Hessian matrix. I used the delta method (Seber, 1982) to estimate the variance of parameters that are functions of the maximum likelihood estimates (e.g., $\Psi_{\mathrm{D2}} = 1 - \Psi_{\mathrm{A2}} - \Psi_{\mathrm{C2}}$). Uncertainty in parameter estimates is presented both as standard errors and 95% profile likelihood confidence intervals.

Parameters were estimated separately for each release, but the model for each release was reduced from the full model because not all parameters could be estimated from the tag detection data. For the first release in December, $P_{\mathrm{A3}} = 0$ because station A_3 was not operational, rendering limited ability to uniquely estimate the parameters S_{A2}, Ψ_{B1}, and S_{A3}. However, S_{A2} and Ψ_{B1} can be estimated under the assumption that $S_{\mathrm{A2}} = S_{\mathrm{A3}}$, which was supported by the similarity of S_{A2} and S_{A3} measured during the second release (for R_2: $\hat{S}_{\mathrm{A2}} = 0.959$, $\widehat{\mathrm{SE}} = 0.024$; $\hat{S}_{\mathrm{A3}} = 0.976$, $\widehat{\mathrm{SE}} = 0.025$). The Delta Cross Channel gate was closed for the second release, so ω_{open} and Ψ_{C2} were set to zero, which eliminated P_{C1}, S_{C1}, P_{C2}, and S_{C2} from the model. For both releases, a number of detection probabilities were set to 1 because of perfect detection data. Last, due to low detection frequencies in the interior Delta, the parameters S_{D1} and S_{D2} could not be estimated for the first release, but the product $S_{\mathrm{D1}}S_{\mathrm{D2}}$ was estimable as a single parameter. Likewise, for the second release only the product $S_{\mathrm{D1}}S_{\mathrm{D2}}S_{\mathrm{D3}}$ was estimable as a single parameter.

3.2.5 Survival through the Delta

This mark-recapture model estimates the individual components that comprise survival of the population migrating through the Delta, defined as survival of tagged fish from the entrance to the Delta at station A_2 (Freeport, rkm 73) to the exit of the Delta at station A_8 (Chipps Island, rkm -9). Population-level survival through the Delta was estimated from the individual components as:

$$S_{\text{Delta}} = \sum_{h=\text{A}}^{\text{D}} \Psi_h S_h \tag{3.1}$$

where S_h is the probability of surviving the Delta given the specific migration route taken through the Delta, and Ψ_h is the probability of migrating through the Delta via one of four migration routes (A = Sacramento River, B = Sutter and Steamboat sloughs, C = Delta Cross Channel, D = Georgiana Slough). Thus, population survival through the Delta is a weighted average of the route-specific survival probabilities with weights equal to the fraction of fish migrating through each route.

Migration route probabilities are a function of the route entrainment probabilities at each of the two river junctions:

$$\Psi_{\text{A}} = \Psi_{\text{A1}}\Psi_{\text{A2}} \tag{3.2}$$

$$\Psi_{\text{B}} = \Psi_{\text{B1}} \tag{3.3}$$

$$\Psi_{\text{C}} = \Psi_{\text{A1}}\Psi_{\text{C2}} \tag{3.4}$$

$$\Psi_{\text{D}} = \Psi_{\text{A1}}\Psi_{\text{D2}} \tag{3.5}$$

For instance, consider a fish that migrates through the Delta via the Delta Cross Channel (Route C). To enter the Delta Cross Channel, this fish first remains in the Sacramento River at junction 1 with probability Ψ_{A1}, after which it enters the Delta Cross Channel at the second river junction with probability Ψ_{C2}. Thus, the probability of a fish migrating through the Delta via the Delta Cross Channel (Ψ_{C}) is the product of these route entrainment probabilities, $\Psi_{\text{A1}}\Psi_{\text{C2}}$. However, for release 1, when the Delta Cross Channel was both open and closed, $\Psi_{h2} = \omega_{\text{open}}\Psi_{h2,\text{open}} + (1- \omega_{\text{open}})\, \Psi_{h2,\text{closed}}$.

Survival through the Delta for a given migration route (S_h) is the product of the reach-specific survival probabilities that trace each migration path through the Delta between points A_2 and A_8 (Figure 3.1, Figure 3.2):

$$S_{\mathrm{A}} = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{\mathrm{A4}} S_{\mathrm{A5}} S_{\mathrm{A6}} S_{\mathrm{A7}} \tag{3.6}$$

$$S_{\mathrm{B}} = S_{\mathrm{A2}} S_{\mathrm{B1}} S_{\mathrm{A6}} S_{\mathrm{A7}} \tag{3.7}$$

$$S_{\mathrm{C}} = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{\mathrm{C1}} S_{\mathrm{C2}} S_{\mathrm{D2}} S_{\mathrm{D3}} \tag{3.8}$$

$$S_{\mathrm{D}} = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{\mathrm{D1}} S_{\mathrm{D2}} S_{\mathrm{D3}} \tag{3.9}$$

I also compared our estimates of S_{Delta} described above to estimates produced by a standard three-station CJS model. We included telemetry stations A_2, A_8, and A_9 in this model. Here, S_{Delta} is estimated directly from the model as the probability of surviving from station A_2 to A_8. I compared the two approaches to ensure they produced similar estimates and to examine the standard errors produced under each approach. Given that the CJS model contained many fewer parameters (4 for R_1 and 5 for R_2), I suspected that the CJS model might yield more precise estimates of S_{Delta}.

3.3 Results

3.3.1 River conditions and migration timing

For the first release in December, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport (US Geological Survey gauge 11447650 near station A_2; Figure 3.1) increased from 12,900 ft^3/s to 24,100 ft^3/s (Figure 3.3). The Delta Cross Channel was open when most of these fish passed the second river junction (Figure 3.3). However, the Delta Cross Channel closed at 1000 hours on 15 December 2006 and remained closed for the balance of the study (Figure 3.3). River discharge receded to about 12,000 ft^3/s when fish from the December release were migrating through the lower reaches of the Delta (Figure 3.3). In contrast to December, river discharge for the January release was low and stable during much of the migration period (Figure 3.3). Daily discharge of the Sacramento River remained near 12,000 ft^3/s until 9 February, after which discharge increased to 39,000 ft^3/s. However, this increase in flow occurred after most fish had passed through the lower reaches of the Delta (Figure 3.3). Water exports at the Delta pumping stations were stable within each migration period and averaged 10,789 ft^3/s for the December migration period and 6,823 ft^3/s for the January (Figure 3.3).

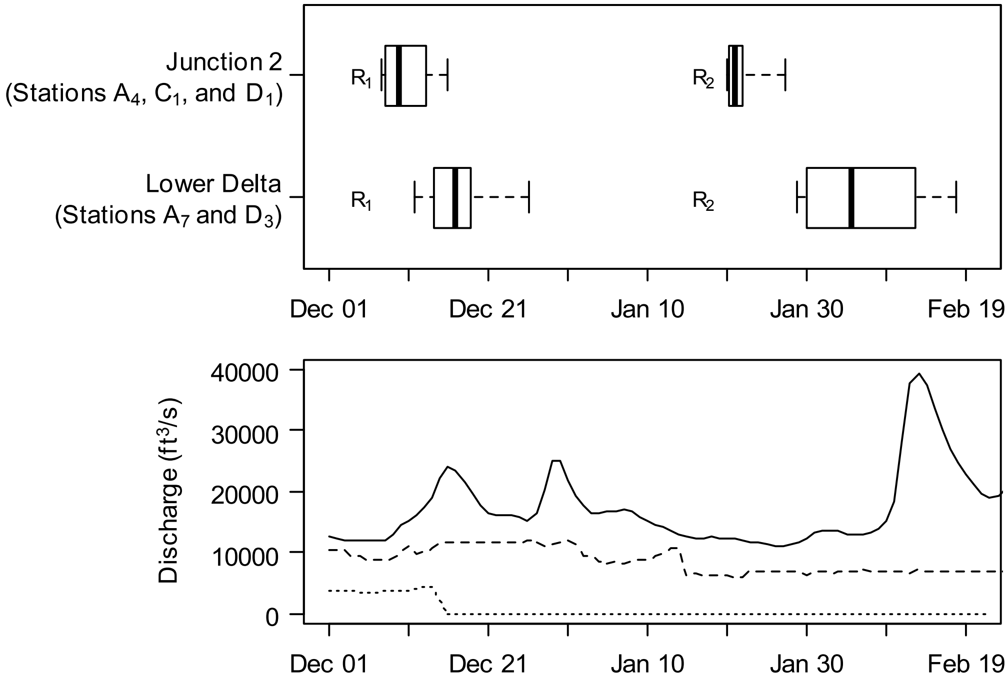

Figure 3.3. River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during winter 2006/2007. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River and near the exit of the Delta. The two release dates are shown as R_1 = 5 December 2006 for a release size of 64 tagged fish and R_2 = 17 January 2007 for a release size of 80 fish. Whiskers represent the 10th and 90th percentiles, the box encompasses the 25th to 75th percentiles, and the line bisecting the box is the median arrival date. River discharge (solid line) is tidally filtered, daily discharge of the Sacramento River at Freeport (near telemetry station A_2), Delta Cross Channel discharge (dotted line) is the tidally filtered daily discharge, and water exports (dashed line) are the total daily discharge of water exported from the Delta at the pumping projects.

Coincident with lower river discharge, fish released in January took substantially longer to migrate through the Delta and exhibited higher variation in travel times relative to fish released in December (Figure 3.3). Among routes, travel times for the December release from the release point to the lower Delta (stations A_7 and D_3) were quickest for fish migrating through Sutter and Steamboat sloughs (median = 7 d, interquartile range (25th – 75$^{\text{th}}$ percentile) = 6.1 – 11.7 d, n = 5) followed by the Sacramento River (median = 10.7 d, interquartile range = 9.3 – 12.5 d, n = 9) and the interior Delta via the Delta Cross Channel and Georgiana Slough (median = 13.8 d, interquartile range = 13.4 – 19.1 d, n = 5). For the January release, travel times were similar for fish migrating through the Sacramento River (median = 18.1 d, interquartile range = 13.2 – 23.9 d, n = 19) and Sutter and Steamboat Sloughs (median = 17.8 d, interquartile range = 12.7 – 27.3 d, n = 17). Travel times through the interior Delta were measured for only one fish in the January release, which took 33.9 d to travel from release to the lower Delta.

3.3.2 Migration routing

As juvenile salmon migrated past the first river junction, a large proportion of both release groups left the Sacramento River and migrated through Sutter and Steamboat sloughs (for R_1: $\hat{\Psi}_{\text{B1}} = 0.296$; for R_2: $\hat{\Psi}_{\text{B1}} = 0.414$). For the December release, most fish remaining in Sacramento River encountered the second river junction when the Delta Cross Channel was open ($\hat{\omega}_{\text{open}} = 0.861$, $\widehat{\text{SE}} = 0.058$), and 39% percent of these fish were entrained into the Delta Cross Channel ($\hat{\Psi}_{\text{C2,open}} = 0.387$, $\widehat{\text{SE}} = 0.087$). Regardless of release group or position of the Delta Cross Channel gate, similar fractions of fish passing junction 2 were entrained into Georgiana Slough (for R_1: $\hat{\Psi}_{\text{D2,open}} = 0.161$, $\widehat{\text{SE}} = 0.066$; $\hat{\Psi}_{\text{D2,closed}} = 0.200$, $\widehat{\text{SE}} = 0.179$; for R_2: $\hat{\Psi}_{\text{D2,closed}} = 0.150$, $\widehat{\text{SE}} = 0.056$). The remaining 45% of fish passing junction 2 when the Delta Cross Channel was open stayed in the Sacramento River ($\hat{\Psi}_{\text{A2,open}} = 0.452$, $\widehat{\text{SE}} =$ 0.089), whereas nearly twice that fraction remained in Sacramento River when the Delta Cross Channel was closed (for R_1: $\hat{\Psi}_{\text{A2,closed}} = 0.800$, $\widehat{\text{SE}} = 0.179$; for R_2: $\hat{\Psi}_{\text{A2,closed}} = 0.850$, $\widehat{\text{SE}} =$ 0.056).

A substantial proportion of fish migrating past junction 2 entered the interior Delta through the Delta Cross Channel and Georgiana Slough. However, a lower proportion of the population entered the interior Delta because some fish bypassed the second river junction by migrating through Sutter and Steamboat sloughs (Figure 3.1). Accounting for population distribution among all routes, 23.5% were entrained into the Delta Cross Channel ($\hat{\Psi}_C$), 11.7% entered Georgiana Slough ($\hat{\Psi}_D$), and 35.2% migrated within the Sacramento River ($\hat{\Psi}_A$) for the December release when the Delta Cross Channel was open during much of the migration period (Table 3.1). In contrast, 8.8% migrated through Georgiana Slough and 49.8% remained in the Sacramento River in January when the Delta Cross Channel was closed (Table 3.1). Because Sutter and Steamboat sloughs rejoin the Sacramento River upstream of telemetry station A_6, much of this migration route through the Delta (Route B) consists of the mainstem Sacramento River (Figure 3.1). Thus for the December release, 64.8% of fish took migration routes largely consisting of the Sacramento River ($\hat{\Psi}_A + \hat{\Psi}_B$) and 35.2% were entrained into the interior Delta via the Delta Cross Channel and Georgiana Slough ($\hat{\Psi}_C + \hat{\Psi}_D$; Table 3.1). In contrast, only 8.8% percent of fish were entrained into the interior Delta through Georgiana Slough in January when the Delta Cross Channel was closed, with the remaining 91.2% migrating mostly within the Sacramento River ($\hat{\Psi}_A + \hat{\Psi}_B$; Table 3.1).

I found that migration route probabilities (Ψ_h) corresponded well with the fraction of total river discharge in each route (Figure 3.4). Distribution of river flow among the four migration routes was calculated as the fraction of mean discharge of each route relative to the mean discharge of the Sacramento River at Freeport (near station A_2), upstream of the two river junctions. Steamboat and Sutter Slough diverted 33.4% and 37.6% of the mean flow of the Sacramento River during the December and January migration period, accounting for the large proportion of fish using this migration route (Figure 3.4). At the second river junction, operation of the Delta Cross Channel influenced the relative discharge of the Sacramento River, with flow in the Sacramento River downstream of junction 2 representing 25.6% of its total discharge when the Delta Cross Channel was open (December release) compared to 40.0% when the Delta Cross Channel was closed (January release). The increase in relative flow of the Sacramento River due to closure of the Delta Cross Channel was accompanied by an increase in the fraction of fish migrating through this route (Figure 3.4). For both releases the proportion of fish migrating within the Sacramento River was about 10 percentage points higher than the fraction of flow remaining in the Sacramento River, and for the January release the fraction migrating through Georgiana Slough was about 10% lower than the fraction of flow (Figure 3.4).

Table 3.1. Route-specific survival through the Sacramento–San Joaquin River Delta ($\hat{S}_h$) and the probability of migrating through each route ($\hat{\Psi}_h$) for acoustically tagged fall-run juvenile Chinook salmon released on 5 December 2006 (R_1) and 17 January 2007 (R_2). Also shown is population survival through the Delta (S_{Delta}), which is the average of route-specific survival weighted by the probability of migrating through each route.

Migration route	$\hat{S}_h$ ($\widehat{\text{SE}}$)	95% Profile Likelihood Interval	$\hat{\Psi}_h$ ($\widehat{\text{SE}}$)	95% Profile Likelihood Interval
R_1: December, 2006				
A) Sacramento R.	0.443 (0.146)	0.222, 0.910	0.352 (0.066)	0.231, 0.487
B) Steamboat & Sutter S.	0.263 (0.112)	0.102, 0.607	0.296 (0.062)	0.186, 0.426
C) Delta Cross Channel	0.332 (0.152)	0.116, 0.783	0.235 (0.059)	0.133, 0.361
D) Georgiana S.	0.332 (0.179)	0.087, 0.848	0.117 (0.045)	0.048, 0.223
S_{Delta} (All routes)	0.351 (0.101)	0.200, 0.692		
R_2: January, 2007				
A) Sacramento R.	0.564 (0.086)	0.403, 0.741	0.498 (0.060)	0.383, 0.614
B) Steamboat & Sutter S.	0.561 (0.092)	0.388, 0.747	0.414 (0.059)	0.303, 0.531
C) Delta Cross Channel	NA		0.000	NA
D) Georgiana S.	0.344 (0.200)	0.067, 0.753	0.088 (0.034)	0.036, 0.170
S_{Delta} (All routes)	0.543 (0.070)	0.416, 0.691		

3.3.3 Survival through the Delta

Overall, the estimate of survival through the Delta for the December release was lower than for January (for R_1: $\hat{S}_{\text{Delta}} = 0.351$, for R_2: $\hat{S}_{\text{Delta}} = 0.543$, Table 3.1) despite higher discharge and shorter travel times through the Delta for the December release (Figure 3.2). The CJS model produced nearly the same point estimates and standard errors (for R_1: $\hat{S}_{\text{Delta}} = 0.351$, $\widehat{\text{SE}} = 0.101$; for R_2: $\hat{S}_{\text{Delta}} = 0.536$, $\widehat{\text{SE}} = 0.070$). This finding supports the validity of our more complex model to reconstruct survival through the Delta from the individual components of reach-specific survival and route entrainment probabilities, while also maintaining precision about $\hat{S}_{\text{Delta}}$. Relative to the small sample size of this study, precision was favorable due to high detection probabilities at most telemetry stations (Appendix Table 1.2).

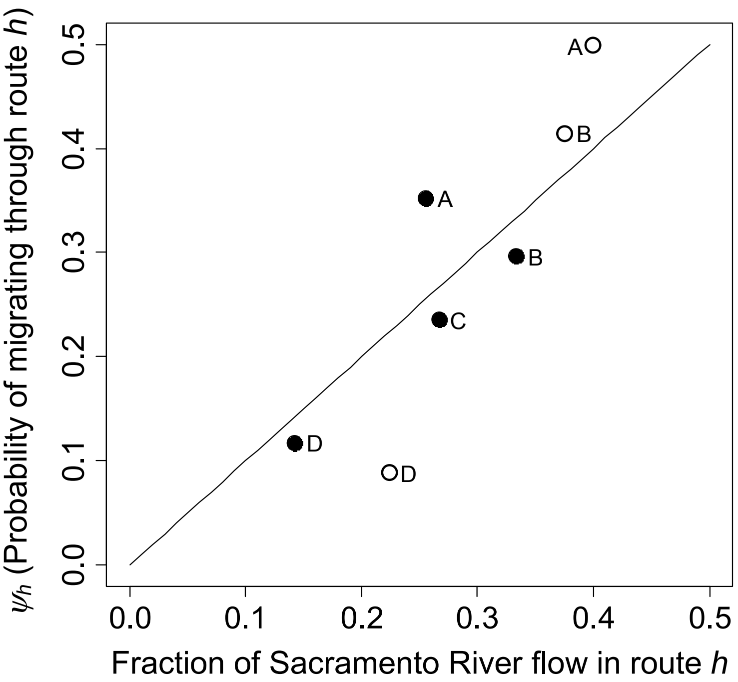

Figure 3.4. The probability of migrating through route *h* (Ψ_h) as a function of the proportion of total river flow in route *h* for tagged late-fall juvenile Chinook salmon released on 5 December 2006 (filled symbols) and 17 January 2007 (open symbols). Data labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively. The reference line shows where the fraction migrating through each route is equal to the proportion of flow in each route (i.e., 1:1 ratio).

3.3.4 Relative contributions to S_{Delta}

Estimates of S_{Delta} were driven by 1) variation among routes in survival through the Delta (S_{h}) and 2) the relative contribution of each route-specific survival to S_{Delta} as measured by migration route probabilities (Ψ_h). For the December release, fish migrating within the Sacramento River exhibited the highest survival through the Delta ($\hat{S}_{\text{A}}$) relative to all other routes, but only 35% of the population migrated through this route ($\hat{\Psi}_{\text{A}}$), representing a relatively small contribution to $\hat{S}_{\text{Delta}}$ (Figure 3.5, Table 3.1). In contrast, relative to survival in the Sacramento River, survival through all other routes reduced $\hat{S}_{\text{Delta}}$ and comprised 65% of the population ($\hat{\Psi}_{\text{B}} + \hat{\Psi}_{\text{C}} + \hat{\Psi}_{\text{D}}$), thereby contributing substantially to $\hat{S}_{\text{Delta}}$ for the December release (Figure 3.5, Table 3.1). For the January release, 91% of the population ($\hat{\Psi}_{\text{A}} + \hat{\Psi}_{\text{B}}$) migrated through routes with the highest survival, and thus survival through these routes comprised the bulk of $\hat{S}_{\text{Delta}}$ for the January release (Figure 3.5, Table 3.1). In comparison, survival for the interior Delta via Georgiana Slough ($\hat{S}_{\text{D}}$) was lower than the other routes, but this route accounted for only 9% of the population ($\hat{\Psi}_{\text{D}}$), having little influence on $\hat{S}_{\text{Delta}}$ (Figure 3.5, Table 3.1).

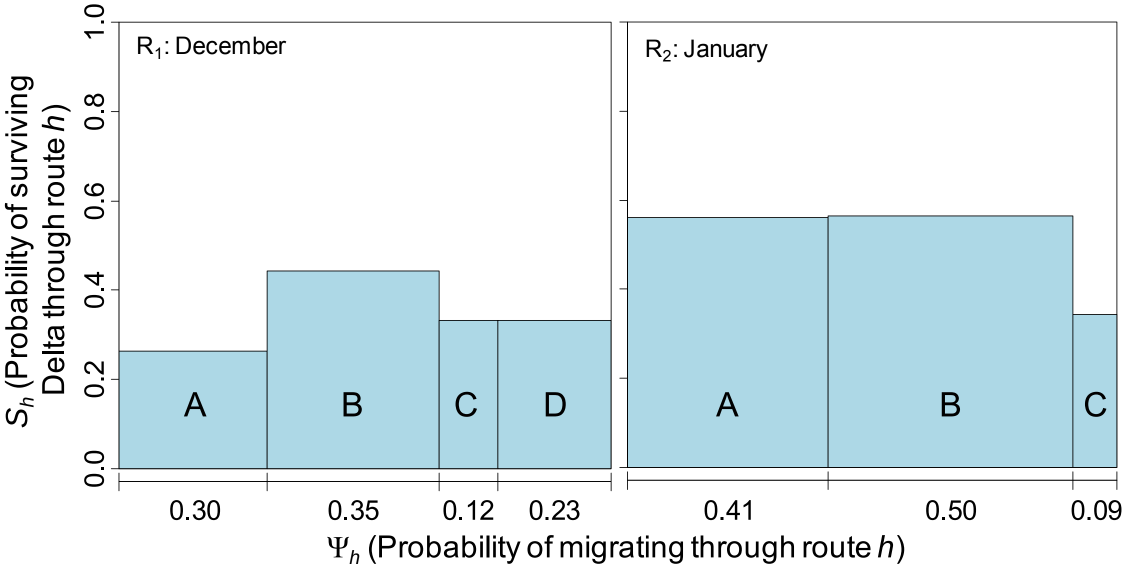

Figure 3.5. Probability of surviving migration through the Sacramento-San Joaquin River Delta (S_h) for each of four migration routes for tagged late-fall juvenile Chinook salmon released on 5 December 2006 (R_1) and 17 January 2007 (R_2). The width of each bar shows the fraction of fish migrating through each route (Ψ_h), and the total area of the bars yields S_{Delta}. Labels A–D represent Steamboat and Sutter sloughs, the Sacramento River, Georgiana Slough, and the Delta Cross Channel, respectively.

The observed difference in $\hat{S}_{\text{Delta}}$ between releases can be attributed to 1) a change in the relative contribution of each route-specific survival to $\hat{S}_{\text{Delta}}$, and 2) differences in survival for given migration routes. Survival estimates for interior Delta routes ($\hat{S}_{\text{C}}$ and $\hat{S}_{\text{D}}$) were lower than for the Sacramento River ($\hat{S}_{\text{A}}$) during both releases but contributed only 9% for the January release when the Delta Cross Channel was closed, compared to 35% ($\hat{\Psi}_{\text{C}} + \hat{\Psi}_{\text{D}}$) for the December release when the Delta Cross Channel was open (Figure 3.5, Table 3.1). Thus, lower contribution of interior Delta routes to $\hat{S}_{\text{Delta}}$ partly accounts for the higher $\hat{S}_{\text{Delta}}$ observed for the January release. However, higher $\hat{S}_{\text{Delta}}$ for January was also a consequence of changes in route-specific survival for the Sacramento River and Sutter and Steamboat sloughs, both of which were higher for the January release compared to December. These findings show how both survival through given routes and population distribution among routes interacted to affect $\hat{S}_{\text{Delta}}$ during the two releases.

3.4 Discussion

My study highlights the importance of quantifying both movement among migration routes and survival within routes to understand factors affecting population-level survival. Measuring survival through different migration routes (S_h) between the same beginning and end points (from telemetry station A_2 to A_8; Figure 3.1) provides direct insight into the effect of different migration routes on survival through the entire Delta. Furthermore, the migration route probabilities (Ψ_{h}) measure the contribution of each route-specific survival to the overall survival of the population migrating through the Delta. Thus, my modeling approach provides a natural framework for understanding how these route-specific components interact to affect population-level survival through the Delta. Operation of the Delta Cross Channel is an important water management action that may influence population-level survival by affecting the fraction of the population entering the interior Delta where survival is typically lower than alternative migration routes (this study, Newman and Brandes, 2010). Thus, without information about both population distribution among routes and survival within routes, it would be difficult to quantify how management actions affect these underlying components that give rise to population-level survival.

I show that route-specific survival and movement among migration routes interact to influence population-level survival, but the next challenge is to quantify the mechanisms causing variation in route-specific survival. Within each release, travel times for fish migrating through the interior Delta were longer than alternative routes, possibly contributing to lower survival through the interior Delta. Relative to the December release, however, survival for the January release was higher for two migration routes (Sacramento River and Sutter and Steamboat sloughs) despite lower discharge and longer travel times through these routes during January (Figure 3.3). Thus, instantaneous mortality rates (i.e., per time) in these two routes were lower in January than in December suggesting that factors other than travel time also contribute to variation in survival within and among migration routes. Such factors may include variation in environmental conditions (e.g., water temperature, turbidity, tides) or temporal shifts in the spatial distribution of predators, both of which influence predator-prey interactions. This first year of study just begins to shed light on this variation, but with replication over a wide range of environmental conditions my analytical framework will allow researchers to explicitly quantify mechanisms influencing the route-specific components of population survival.

My findings are consistent with a series of studies that have estimated survival of juvenile salmon in the Delta with coded wire tags (Brandes and McLain, 2001; Newman and Rice, 2002; Newman, 2008; Newman and Brandes, 2010). In general, similar to my analysis, these studies found that survival of fish released into the interior Delta via Georgiana Slough was lower than survival of fish released into the Sacramento River downstream of Georgiana Slough (Newman, 2008; Newman and Brandes, 2010). Specifically, Newman and Brandes (2010) found that the ratio of survival for Georgiana Slough releases relative to Sacramento River releases was less than one for all release groups, indicating significantly lower survival for fish migrating through the interior Delta (see Table 2 in Newman and Brandes). In my analysis, an analogous estimate is $S_{D1}S_{D2}S_{D3}/S_{A5}S_{A6}S_{A7}$ (i.e., survival from D_1 to A_8 relative to A_5 to A_8; Figure 3.1). The estimate of this ratio was 0.625 ($\widehat{\text{SE}}$ = 0.352) for the December release and 0.591 ($\widehat{\text{SE}}$ = 0.351) for the January release. Although the standard errors indicate that these estimates do not differ from one (i.e., equal survival), the point estimates parallel the previous studies and fall well within their observed release-to-release variation. This evidence continues to support the hypothesis that survival for fish migrating through the interior Delta is lower than for fish that remain in the Sacramento River. While past research has revealed differences in survival among migration routes, it was impossible to quantify how these survival differences influenced survival of the population. In contrast, my study builds on past research by explicitly estimating the relative contribution of route-specific survival to population-level survival, as quantified by migration route probabilities (Ψ_h).

Given that 30-40% of the population migrated through Sutter and Steamboat sloughs (Table 3.1), this migration route plays a key role in population-level survival by reducing the probability of fish entering the interior Delta. Fish migrating through Sutter and Steamboat sloughs do not encounter the Delta Cross Channel or Georgiana Slough, which directly reduces the fraction of fish entering the interior Delta via these routes. This relation is couched explicitly in my model: the probability of migrating through the interior Delta can be expressed as $\Psi_C + \Psi_D = (1 - \Psi_B)(\Psi_{C2} + \Psi_{D2})$. Note that the fraction entering the interior Delta ($\Psi_C + \Psi_D$) decreases as the fraction migrating through Sutter and Steamboat sloughs (Ψ_B) increases. This relationship highlights a critical linkage among migration routes that drives the dispersal process of juvenile salmon migrating through the Delta. Furthermore, closure of the Delta Cross Channel reduces channel capacity of the Sacramento River at the second river junction, which slightly increases the proportion of river flow diverted into Sutter and Steamboat sloughs at the first river junction (J.R. Burau, US Geological Survey, personal communication). Thus, in addition to eliminating a route through the interior Delta, closure of the Delta Cross Channel may decrease the proportion of fish entrained into the interior Delta by increasing the fraction of fish entering Sutter and Steamboat sloughs. However, whether population-level survival is increased by management actions that shift the population distribution among migration routes will depend on the relative difference in survival among alternative routes.

In general, migration route probabilities increased with the fraction of total river discharge in each migration route, but both the form of this relationship and the factors influencing migration route probabilities requires further study. Flow distribution among the river channels at each junction varies with the tides on hourly time scales. Thus, migration route probabilities in my mark-recapture model represent an average of time-specific route entrainment probabilities that depend on the flow distribution when each fish passes a river junction. Furthermore, the spatial distribution of migrating salmon across a river channel may deviate from the spatial distribution of flow, which could cause a disproportionate number of salmon to be entrained into a given river channel relative to the proportion of flow in that channel. For example, in the Columbia River, juvenile salmon pass through shallow spillways at dams in higher proportions than the fraction of flow passing through spillways (Plumb et al., 2003; Zabel et al., 2008) because of the surface-biased distribution of salmon. Similar behavioral processes at river junctions in the Delta would manifest as consistently positive or negative deviations from the 1:1 line in Figure 3.4 (i.e., where the proportion of flow = proportion of fish in a given route). Given these processes and my initial findings, I hypothesize that 1) changes in the distribution of average river flow at river junctions will effect coincident changes in average migration route probabilities, 2) consistent deviations in migration route probabilities relative to flow distribution may arise from a mismatch in the spatial distribution of fish relative to flow, and 3) variability in release-specific migration route probabilities will be driven by the interaction between fish arrival timing at a river junction and hourly-scale changes in flow distribution at river junctions. In Chapter 6, I examine these hypotheses in detail by evaluating the effects of hydraulic variables on route entrainment probabilities of individuals when they migrated past the Delta Cross Channel and Georgiana Slough.

Strictly speaking, inferences from our study population apply directly to the population of hatchery-origin late fall Chinook salmon ≥140mm FL migrating through the Delta between December and mid-February under the environmental conditions observed during our study. However, four distinct populations of juvenile Chinook salmon (fall, late fall, winter, and spring) of both hatchery and wild origin use the Delta to varying degrees at different times of year during different life stages. Although our framework can be applied to any of these populations, inferences from our data should be considered in the context of the similarity of target populations to our study population. Between December and mid-February, most fish captured in midwater trawls in the lower Delta at Chipps Island (near station A_8) range in size from about 110 mm to 200 mm (Brandes and McLain, 2001) and likely represent actively migrating smolts from the late fall and winter run of Chinook salmon (Hedgecock, 2001). Fall run fry (i.e., < 50 mm FL) begin appearing in the Delta in January and overlap with the arrival of spring run parr (>50 mm FL) in March, both of which rear and grow in the Delta to sizes <120 mm FL until complete emigration by late June (as presumed by absence in catch data; Williams, 2006 and references therein). Inferences from our data to fall run fry and spring run parr are not well supported due to differences in size, seasonal timing, and residence time in the Delta. In addition, survival of hatchery-origin fish may differ from wild fish (Reisenbichler and McIntyre, 1977; Kostow, 2004), but factors influencing relative differences in survival among migration routes (e.g., interior Delta relative to Sacramento River) are likely to act similarly on both wild and hatchery populations. Thus inferences about such relative differences may provide critical information for better understanding mechanisms influencing population-level survival of both hatchery and wild populations.

Estimating both movement and survival rates among different habitats is difficult yet critically important because these demographic parameters can have important consequences on population dynamics and viability (Beissinger and McCullough, 2002). In our study, strategically located telemetry stations yield information on the movement of individual fish, while the mark-recapture model allows unbiased estimation of demographic parameters by correcting for the imperfect detection probability of each telemetry station. Similar models have been applied extensively to estimate animal migration and survival rates among geographic areas over time (Hilborn et al., 1990; Hestbeck et al., 1991; Williams et al., 2002), but relatively few studies have focused on survival through space among alternative migration pathways (but see Skalski et al., 2002). Our framework could be applied to any migrating fish population that uses a number of alternative migration routes and is particularly well suited to dendritic networks such as river systems and their estuaries. For example, by situating telemetry stations at appropriate tributary confluences in a mainstem river, our modeling framework could be used to estimate both reach-specific survival and dispersal of adult salmonids among spawning tributaries. Here, movement rates (Ψ) estimate the proportion of the population using each tributary, providing important information about relative contribution of sub-populations in each tributary to the population as a whole. Our study shows how combining telemetry with mark-recapture models provides a powerful approach to estimate demographic parameters in spatially complex settings.

This study has provided the first quantitative glimpse into the migration dynamics of juvenile salmon smolts in the Sacramento River. Route-specific survival through the Delta (S_h) measured the consequence of migrating through different routes on survival through the Delta, while migration route probabilities (Ψ_h) quantified the relative contribution of each route-specific survival to population-level survival. In years to come, increases in sample size and replication over variable environmental conditions will bolster inferences drawn from the acoustic-tag data and increase understanding of the mechanisms influencing survival. Cumulative knowledge gained from this population-level approach will identify the key management actions in the Delta that must be rectified if Sacramento River salmon populations are to recover.

Chapter 4

IMPROVING THE PRECISION AND SPATIAL RESOLUTION OF REACH SURVIVAL IN THE SACRAMENTO-SAN JOAQUIN RIVER DELTA IN WINTER 2008

4.1 Introduction

In the previous chapter, I developed a mark-recapture model to estimate the route-specific components of population-level survival for acoustically tagged late-fall Chinook salmon smolts migrating through the Sacramento–San Joaquin River Delta. The model was applied to data from tagged salmon that migrated through the Delta during the winter of 2006/2007 (hereafter “2007”, Perry et al., 2008, 2010). This analysis provided the first quantitative estimates of route-specific survival through the Delta and the fraction of the population using each migration route. Furthermore, I explicitly quantified the relative contribution of each migration route to population-level survival. As with other authors (Newman and Brandes, 2010), I found that survival through the interior Delta was lower than survival of fish using the Sacramento River. I also found that the proportion of the population entering the interior Delta differed between releases, which influenced population-level survival by shifting a fraction of the population from a low-survival migration route (the interior Delta) to a high-survival route (the Sacramento River). However, I also found that differences between releases in population-level survival were caused by changes in survival for given migration routes. Thus, variation in population-level survival was driven both by variation in movement among routes as well as survival within routes.

In this chapter, I expand the model presented in Chapter 3 with the goal of increasing spatial resolution and improving precision of the subsequent study conducted during winter of 2007/2008 (hereafter “2008”). While many design aspects were maintained, I worked closely with the US Fish and Wildlife Service to incorporate a number of changes in study design based on insights from the first year of study. The most important limitation in 2007 was small total sample size, as well as small sample size for specific migration routes. For example, because up to 40% of fish migrated through Sutter and Steamboat Slough at the first river junction (Route B in Figure 3.1), only 60% of fish remained in Sacramento River to pass the second river junction (Routes C and D leading to the interior Delta; Figure 3.1). This led to low sample size and poor precision of parameter estimates for routes through the interior Delta, which in turn led to low power to detect differences in survival among migration routes. Thus, I recommended two approaches to improve precision. First, the total sample size was tripled from 144 tagged fish in 2007 to 419 tagged fish in 2008. Second, because the interior Delta is an important migration route with many management concerns, we also released a subsample of fish directly into the interior Delta via Georgiana Slough (Route D in Figure 3.1).

To improve spatial resolution, many new telemetry stations were added, allowing survival to be better partitioned among specific reaches and to better quantify movement among channels within major migration routes. For example, in 2007, I observed a substantial difference between releases in survival for Sutter and Steamboat sloughs. However, because this migration route encompassed numerous unmonitored river channels it was impossible to determine whether changes in route-specific survival were due to shifts in mortality within a particular reach, or occurred due to changes in survival over all reaches with this route. Therefore, additional telemetry stations within this migration route allowed me to quantify the contribution of within-route reaches to overall route survival.

I first report results for population-level survival through the Delta, route-specific survival through the Delta, and dispersal among migration routes, contrasting estimates from this study to those from 2007. Given more detailed information within migration routes, I then examined patterns in reach-specific survival to understand whether variation in route-specific survival through the Delta was driven by particular reaches within a route. Last, in addition to dispersal among the major migration routes shown in Figure 3.1, I explicitly accounted for movement among other channels within routes, and discuss the influence of these movements on population-level migration and survival dynamics.

4.2 Methods

4.2.1 Telemetry system and fish tagging

The telemetry system, fish tagging, and fish releases followed the methods described in Chapter 3; therefore, only major departures from Chapter 3 are noted here. Telemetry stations were deployed to monitor movement of tagged fish among four major migration routes through the Delta (Figure 3.1): the mainstem Sacramento River (Route A), Steamboat and Sutter Slough (Route B), the interior Delta via the Delta Cross Channel (Route C), and the interior Delta via Georgiana Slough (Route D). Numerous telemetry stations were deployed within Sutter and Steamboat sloughs to better quantify survival and movement within this region, relative to the study in 2007 (see Chapter 3). Sutter Slough is labeled as B_1, the first sub-route within route B, and Steamboat Slough as B_2, the second sub-route. Specifically, Sutter Slough and Miner Slough form a northern route and stations along this route are labeled B_{11} (entrance to Sutter Slough), B_{12}, and B_{13} (Miner Slough; Figure 1.2 and 4.1). Steamboat Slough forms the southern route and these stations are labeled as B_{21}, B_{22}, and B_{23}. Relative to 2007, additional telemetry stations were also installed within the interior Delta (D_i). Routes A, B, C, and D contained 8, 6, 1, and 7 telemetry stations, whereas in 2007, the same routes contained 7, 1, 2, and 3 telemetry stations. In addition, to quantify movement between the lower Sacramento River and the lower San Joaquin River, we included a telemetry station within Three Mile Slough (E_1) for a total of 23 telemetry stations within the Delta.

In 2008, a 1.6-g tag with a 70-d expected battery life was used (Vemco Ltd., Model V7-2L-R64K), and fish had a mean fork length of 155.0 mm (SD = 10.2) and mean weight of 42.0 g (SD = 9.6). The tag weight represented 3.8% of the mean fish weight (range = 1.9%–5.4%). To release fish, they were first transported to release sites at either the Sacramento River near Sacramento, CA (20 km upstream of A_2) or Georgiana slough (about 5 km downstream from D_1; Figure 4.1). Fish were then transferred to perforated 19-L buckets (2 fish per bucket), held for 24 h in the Sacramento River prior to release to allow recovery from the transportation process, and then released at roughly hourly intervals over a 24-h period. The total sample size for the study was 419 acoustically tagged fish, with 208 fish released in

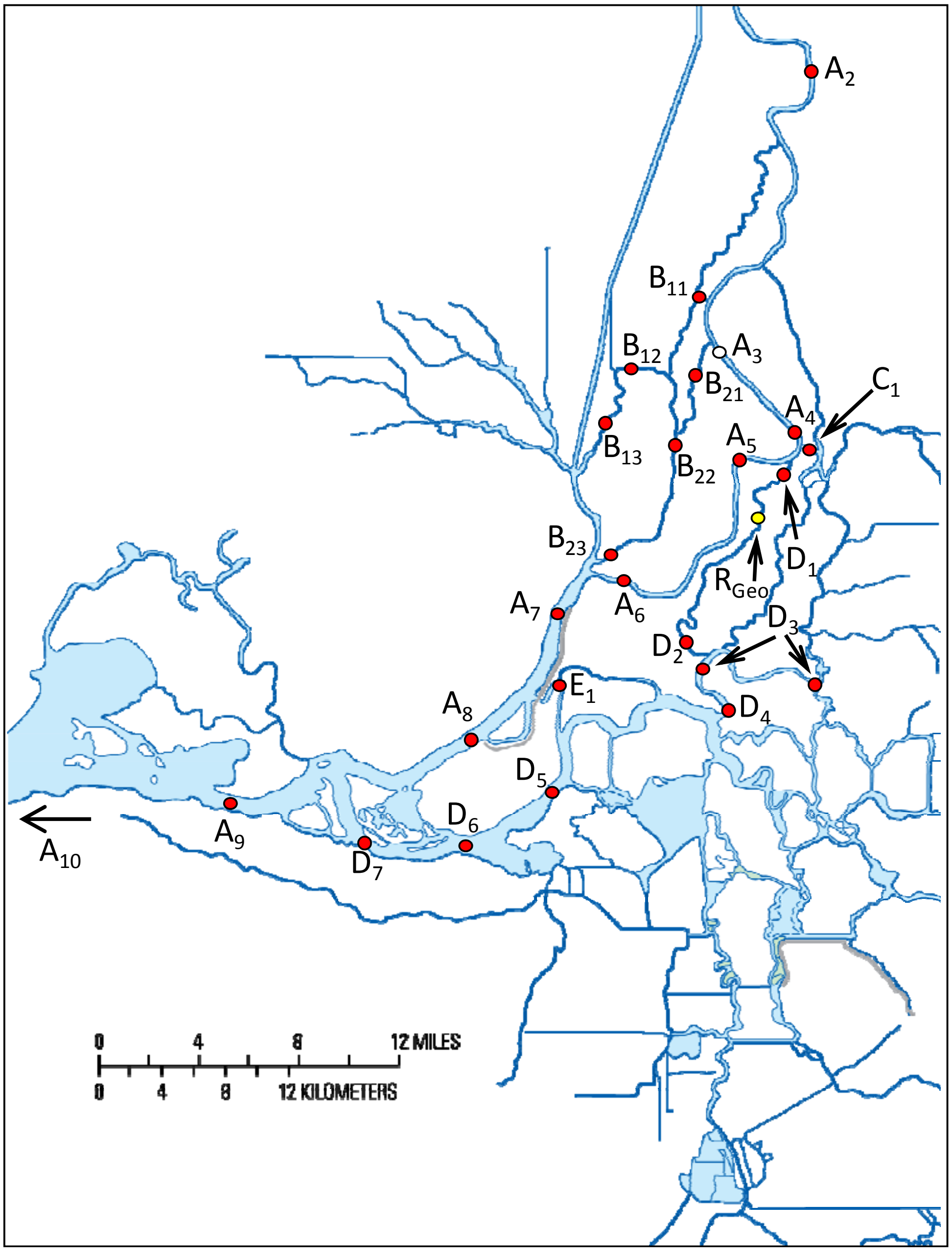

Figure 4.1. Location of telemetry stations used to estimate survival and migration route probabilities within four major migration routes of the Sacramento–San Joaquin River Delta during the winter of 2007/2008. Red-filled circles labeled as h_i show the location of telemetry station i with route h. Location A_3 is denoted by an unfilled circle to indicate that a telemetry station was not implemented at this location during the winter of 2007/2008. Station A_{10} pools all telemetry stations in San Francisco Bay downstream of A_9. The Sacramento release site was 19 river kilometers upriver of station A_2, and the Georgiana release site is noted as the yellow-filled circle labeled as R_{Geo}.

December when the Delta Cross Channel was open and 211 fish released in January when the Delta Cross Channel was closed (Table 4.1). For the first release, 28% of the fish were released into Georgiana Slough, but this fraction was increased to 38% for the second release in anticipation that a lower proportion of the Sacramento release group would enter the interior Delta with the Delta Cross Channel closed (Table 4.1). Fish were released into Georgiana Slough two days later than the Sacramento release group to match release times in Georgiana Slough with the travel time of fish from Sacramento to Georgiana Slough (R. Perry, unpublished data).

Table 4.1. Summary of release dates, locations, and sample size of acoustically tagged late-fall Chinook salmon released into the Delta during the winter of 2007/2008.

Release date	Release number	Release location	Sample size
4 December 2007	1	Sacramento	149
6 December 2007	1	Georgiana Slough	59
15 January 2008	2	Sacramento	130
17 January 2008	2	Georgiana Slough	81

4.2.2 Model development

As in my previous model, I estimated detection (P_{hi}), survival (S_{hi}), and route entrainment probabilities (Ψ_{hl}). However, to capture complexity in movement of fish among different channels I also estimated joint survival-entrainment probabilities ($\phi_{hi,jk}$) as described in Chapter 2 (Figure 4.2). Joint survival-entrainment probabilities ($\phi_{hi,jk}$) estimate the joint probability of surviving from site h_i to j_k and moving into route j. The $\phi_{hi,jk}$ parameters are estimated in reaches with river junctions that split into two channels, but where telemetry stations within each river channel are located some distance downstream the river junction. For example, fish passing station A_7 in the Sacramento River may enter Three Mile Slough (E_1) or remain the Sacramento River for another 5.5 km below this junction to pass station A_8 (Figure 4.2). Thus $\phi_{A7,A8}$ is the joint probability of surviving from A_7 to its junction with Three Mile Slough, remaining in the Sacramento River at this junction, and then surviving from the junction to A_8.

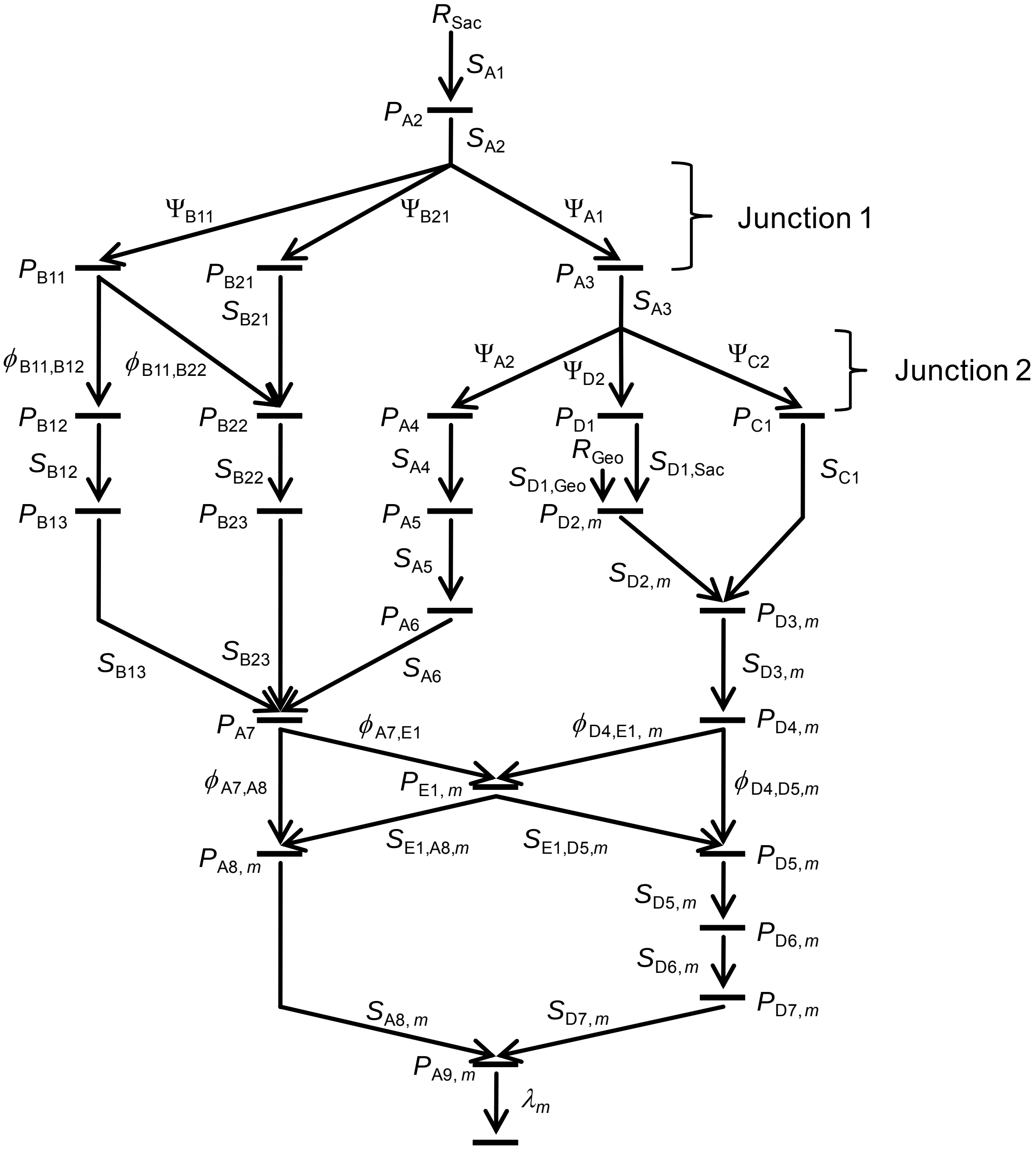

Figure 4.2. Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), route entrainment (Ψ_{hl}), and joint survival-entrainment ($\phi_{hi,jk}$) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made in December 2007 and January 2008. Release sites are denoted by R_m (m = Sac (Sacramento) and Geo (Georgiana Slough)), and parameters subscripted by m denote parameters which can be estimated separately for each release site.

In the 2007 study, telemetry arrays at the entrance to Sutter and Steamboat sloughs were pooled in the model to estimate a single route entrainment probability for both sloughs because within-route telemetry stations were not present. For this analysis, however, telemetry stations within Sutter and Steamboat slough downstream of each entrance allowed me to estimate route entrainment probabilities separately for each slough (Figures 4.1 and 4.2). Thus, the parameter Ψ_{B11} estimates the probability of being entrained into Sutter Slough at station B_{11} and Ψ_{B21} estimates the probability of being entrained into Steamboat Slough at station B_{21}. The probability of remaining in the Sacramento River at the first junction is $1 - \Psi_{B11} - \Psi_{B21} = \Psi_{A1}$ (Figures 4.1 and 4.2).

Joint survival-entrainment probabilities were estimated for three reaches where 1) fish entering Sutter Slough (B_{11}) may subsequently continue down either Miner Slough (B_{12}) or Steamboat Slough (B_{22}), 2) fish entering the San Joaquin River at D_4 may subsequently exit this reach through either Three Mile Slough at E_1 or the San Joaquin River at B_5, and 3) fish passing A_7 in the Sacramento River may exit this reach at either E_1 or A_8 (Figures 4.1 and 4.2). Each of these reaches consist a single river channel, a junction where the channel splits, and then two separate channels through which fish migrate before being detected at telemetry stations in each channel. In these locations, interest may lie in estimating the proportion of fish entering each channel, but as discussed in Chapter 2, Ψ_{hl} may be biased if survival probabilities downstream of the junction differ between the two channels. However, the joint probability of surviving and migrating through a given channel (i.e., $\phi_{hi,jk}$) will remain unbiased in these circumstances. Although the $\phi_{hi,jk}$ parameters are difficult to interpret biologically, being the joint probability of entrainment and survival, their sum yields the total reach survival. Thus, in the three reaches where $\phi_{hi,jk}$ parameters are estimated, $S_{B11} = \phi_{B11,B12} + \phi_{B11,B22}$, $S_{A7} = \phi_{A7,E1} + \phi_{A7,A8}$, and $S_{D4} = \phi_{D4,E1} + \phi_{D4,D5}$ are the probabilities of surviving from each upstream telemetry station to either of the next downstream stations.

Other than the differences noted above, the model structure for 2008 differed in two other aspects compared to 2007. First, in 2007, fish from a given release passed the Delta Cross Channel when it was both open and closed, requiring us to incorporate a parameter to estimate the probability of fish passing the Delta Cross Channel under each condition (ω_{open}, see Chapter 3). However, for this study, only 3 fish released when the Delta Cross Channel was open passed the Delta Cross Channel after it had closed. Therefore, we did not include ω_{open} in the model because its effect on the route entrainment probabilities is minimal. Second, having two release sites leads to two estimates of the same parameter for reaches within the interior Delta (e.g., $S_{\mathrm{D3},m} = S_{\mathrm{D3,Sac}}$ or $S_{\mathrm{D3,Geo}}$; Figure 4.2). With this model structure, the full model contains 75 unique parameters; 55 parameters from the Sacramento release and 20 for the Georgiana Slough release (Figure 4.2).

4.2.3 Parameter estimation

Prior to parameter estimation, the records of tag-detections were processed to eliminate false positive detections as described in Chapter 3. The detection records of about 10% of tagged fish suggested they had been consumed by piscivorous predators as was evidenced by their directed upstream movement for long distance and against the flow. We truncated the detection record of these fish to the last known location of the live tagged fish. All other detections were considered to have been live juvenile salmon. In the lower Sacramento and San Joaquin rivers (sites A_7–A_8 and D_5–D_7), tag detection and discharge data showed that juvenile salmon were often advected upstream on the flood tides and downstream on the ebb tides. In these cases, we used the final downstream series of detections in forming the detection history.

Parameters were estimated using the maximum likelihood techniques described in Chapter 3, and the likelihood of each capture history was formed by adapting the methods of Fujiwara and Caswell (2002), as described in Chapter 2. Detection histories for 2008 were able to describe detailed movements of fish through the Delta. For example, a fish with the history AA0AAAAEDDDAA indicates it was released at Sacramento (“A”), detected in the Sacramento River at A_2 (“A”), and not detected in the Sacramento River at A_3 (“0”). This fish was subsequently detected at every other telemetry station as it emigrated from the Sacramento River (“AAAA”) through Three Mile Slough (“E”), down the San Joaquin River (“DDD”), and finally past Chipps Island into San Francisco Bay (“AA”). Parameters were estimated separately for each release (k) but simultaneously for both release sites by expressing the joint likelihood as the product of $L_{k,\mathrm{Sac}}$ and $L_{k,\mathrm{Geo}}$ (Sac = Sacramento release site, Geo = Georgiana Slough release site).

Although I suggested a telemetry station be deployed in the Sacramento River at junction 1 (station A_3), this station was not implemented in 2008, so I set P_{A3} to zero. Absence of this telemetry station makes it impossible to uniquely estimate the parameters S_{A2}, S_{A3}, Ψ_{B11}, and Ψ_{B11}. However, these parameters can be estimated by assuming that $S_{A2} = S_{A3}$. This assumption was supported by estimates of S_{A2} and S_{A3} in 2007 (See Chapter 3 and Appendix Table 1.2). Nonetheless, given that three of four releases thus far (in 2007 and 2008) occurred without a telemetry station at A_3, I undertook a sensitivity analysis to examine the magnitude of bias introduced into route entrainment probabilities due to deviation from the assumption that $S_{A2} = S_{A3}$ (see Appendix 2). Since it is impossible to apportion mortality between the reach above and below A_3, I examined bias under the extreme scenarios where all mortality occurs either upstream of the first river junction (i.e., $S_{A3} = 1$) or downstream of the first river junction (i.e., $S_{A2} = 1$).

For each release, the full model was considered as the model with the fewest parameter constraints which still allowed all parameters to be uniquely estimated. When parameter estimates occur at the boundaries of one (or zero) they cannot be estimated through iterative maximum likelihood techniques and must be set to one (or zero). In our study, many detection probabilities were set to one because all fish passing a given location were known to have been detected at that location. In some cases, survival probabilities were fixed to one because all fish detected at a given telemetry station were also detected at the next downstream location. In addition, parameters for Route C (the Delta Cross Channel) were set to zero for the second release when the Delta Cross Channel was closed. A full detailing of parameter constraints applied under the full model can be found in Appendix Table 3.2.

The purpose of including a separate release into Georgiana Slough was to improve precision within the interior Delta by boosting the sample size of fish migrating through this region. Pooling data across release sites can improve precision but assumes that the fish released into the Sacramento River and Georgiana Slough experience similar survival and detection probabilities in reaches through which both release groups migrate. Therefore, I used likelihood ratio tests (Casella and Berger, 2002) to evaluate hypotheses about equality in detection and survival parameters between release sites. Lack of significance at $\alpha = 0.05$ indicated that the full model fit the data no better than the reduced model where parameters were set equal among releases, in which case the reduced model was selected over the full model. For each release, I first compared the full model to a reduced model where all parameters were set equal between releases. I then used parameter estimates from the selected model for estimating population-level and route-specific survival through the Delta.

4.2.4 Survival through the Delta

Population-level survival through the Delta was estimated using Eqn. 3.1, which is a weighted average of the route-specific survival probabilities (S_h) with weights proportional to the fraction of fish migrating through each route (Ψ_h).

Migration route probabilities Ψ_h are a function of the route entrainment probabilities (Ψ_{hl}) and estimate the probability of migrating through the Delta via particular migration route. I estimated the same migration route probabilities as described in Eqns. 3.1-3.4, except that $\Psi_{\mathrm{B}} = \Psi_{\mathrm{B11}} + \Psi_{\mathrm{B21}}$. Since route entrainment probabilities can be estimated separately for Sutter Slough and Steamboat Slough, the probability of migrating through either Sutter or Steamboat Slough (Ψ_{B}) is the sum of the route-entrainment probabilities for each slough (Ψ_{B11} and Ψ_{B21})

When population level survival can be broken down into components of route-entrainment probabilities and reach specific survival, then survival through the Delta for a given migration route (S_h) is simply the product of the reach-specific survival probabilities that trace each migration path through the Delta between the points A_2 and A_9 (see Eqns 3.6-3.9). However, when joint survival-entrainment probabilities are included in the model, survival through a given route must take into account all possible within-route pathways that involve the $\phi_{hi,jk}$ parameters. For example, survival through the Delta for fish that remain in the Sacramento River through the first and second river junctions is expressed as:

$$S_{\mathrm{A}} = S_{\mathrm{A2}} S_{\mathrm{A3}} S_{\mathrm{A4}} S_{\mathrm{A5}} S_{\mathrm{A6}} \left(\phi_{\mathrm{A7,A8}} S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}} S_{\mathrm{E1,D5}} S_{\mathrm{D5}} S_{\mathrm{D6}} S_{\mathrm{D7}} \right)$$

The bracketed term is the weighted average survival between A_7 (Rio Vista) and A_9 (Chipps Island) with the $\phi_{hi,jk}$ parameters weighting survival of fish that remain in the Sacramento River ($\phi_{\mathrm{A7,A8}} S_{\mathrm{A8}}$) and survival of fish that finish their migration in the lower San

Joaquin after passing through Three Mile Slough ($\phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}$). Thus, survival through the Delta for Route A (the Sacramento River) includes some mortality of fish that enter the interior Delta, and it is impossible to factor out this mortality without explicitly estimating route entrainment probabilities at the junction of the Sacramento River with Three Mile Slough. Nonetheless, the $\phi_{hi,jk}$ parameters provide information about the relative contribution of the interior Delta to survival through Route A. For example, $\phi_{\mathrm{A7,E1}} \ll \phi_{\mathrm{A7,A8}}$ would suggest that movement through Three Mile Slough is a small component of the total survival for fish that migrated in the Sacramento River up to that point. Survival through the Delta for fish taking the Delta Cross Channel (Route C) and Georgiana Slough (route D) is expressed similarly, and explicitly accounts for fish that pass through Three Mile Slough and finish their migration in the lower Sacramento River:

$$S_{\mathrm{C}} = S_{\mathrm{A2}}S_{\mathrm{A3}}S_{\mathrm{C1}}S_{\mathrm{D3}}\left(\phi_{\mathrm{D4,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}} + \phi_{\mathrm{D4,E1}}S_{\mathrm{E1,A8}}S_{\mathrm{D8}}\right),$$

and $$S_{\mathrm{D}} = S_{\mathrm{A2}}S_{\mathrm{A3}}S_{\mathrm{D1}}S_{\mathrm{D2}}S_{\mathrm{D3}}\left(\phi_{\mathrm{D4,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}} + \phi_{\mathrm{D4,E1}}S_{\mathrm{E1,A8}}S_{\mathrm{D8}}\right).$$

To facilitate comparison with findings from our first year in 2007, we pooled Sutter and Steamboat Slough into a single migration route, but survival through the Delta can be estimated separately for fish that enter Sutter Slough and fish that enter Steamboat Slough:

$$S_{\mathrm{B}} = \Psi_{\mathrm{B11}}S_{\mathrm{B1}} + \Psi_{\mathrm{B21}}S_{\mathrm{B2}}$$

where S_{B} is survival through the Delta for fish that enter either Sutter or Steamboat Slough, S_{B1} and S_{B2} are survival through the Delta for fish that enter Sutter Slough and Steamboat Slough, and where S_{B1} and S_{B2} are estimated as:

$$S_{\mathrm{B1}} = S_{\mathrm{A2}}\left(\phi_{\mathrm{B11,B12}}S_{\mathrm{B12}}S_{\mathrm{B13}} + \phi_{\mathrm{B11,B22}}S_{\mathrm{B22}}S_{\mathrm{B23}}\right)\left(\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}\right),$$

and $$S_{\mathrm{B2}} = S_{\mathrm{A2}}S_{\mathrm{B21}}S_{\mathrm{B22}}S_{\mathrm{B23}}\left(\phi_{\mathrm{A7,A8}}S_{\mathrm{A8}} + \phi_{\mathrm{A7,E1}}S_{\mathrm{E1,D5}}S_{\mathrm{D5}}S_{\mathrm{D6}}S_{\mathrm{D7}}\right).$$

For fish entering Sutter Slough, note that the first bracketed term in S_{B1} accounts for survival of fish taking either Miner Slough ($S_{\mathrm{B12}}S_{\mathrm{B13}}$) or Steamboat Slough ($S_{\mathrm{B22}}S_{\mathrm{B23}}$) weighted by the joint probability of surviving and taking each of these routes ($\phi_{\mathrm{B11,B12}}$ and $\phi_{\mathrm{B11,B22}}$).

We used an approach similar to Newman and Brandes (2010) to quantify survival through each migration route relative to survival of fish that migrate within the Sacramento River:

$$\theta_h = \frac{S_h}{S_{\mathrm{A}}} \qquad h \neq \mathrm{A}$$

We measured survival through each route relative to route A because the Sacramento River is considered the primary migration route. For Georgiana Slough, θ_{D} is analogous to θ estimated by Newman and Brandes (2010), who estimated the ratio of recovery rates of coded wire tagged fish released into Georgiana Slough and the Sacramento River near A_4. Survival through the Delta for route h is equal to Route A when $\theta_h = 1$, and survival through route h is less (greater) than Route A when θ_h is less (greater) than one. I interpreted survival through route h as significantly different than Route A at $\alpha = 0.05$ when $\theta_h = 1$ fell outside the 95% profile likelihood confidence interval of $\hat{\theta}_h$.

To aid in interpreting differences in survival through the Delta among routes and between releases, I examined variation in reach-specific survival rates. Survival probabilities estimate the proportion of fish that survive through a given reach, but direct comparison of survival probabilities among reaches can be hampered by variation in the length of each reach. In our study, reach length varied from just a few kilometers to over 20 km. Therefore, we scaled survival probabilities relative to reach length by calculating survival per unit distance:

$$s_{hi} = \sqrt[x_{hi}]{S_{hi}} \tag{4.1}$$

where s_{hi} is the per-kilometer probability of surviving from telemetry station h_i to the next downstream station, x_{hi} is the distance (km) from telemetry station h_i to the next downstream telemetry station, and S_{hi} is the probability of surviving over x_{hi} kilometers. For reaches where more than one exit location is possible (reaches beginning at B_{11}, A_7, and D_4), I used the average distance to each of the exit points. The length of some reaches is ill-defined because fish may take multiple, unmonitored routes (e.g., the interior Delta between D_4 and D_5). For these reaches, reach length was calculated as the shortest distance between upstream and downstream telemetry stations (usually the main channel). If fish took longer routes which led to higher mortality, then survival probabilities (S_{hi}) scaled to the shortest possible migration route (s_{hi}) would appear low relative to other routes. Thus, this approach is of utility in identifying reaches of high mortality relative to the shortest possible pathway through a reach.

4.3 Results

4.3.1 River conditions and migration timing

River conditions differed for the two release groups and influenced their travel times through the Delta (Figure 4.3). For first release, tagged fish passed the two river junctions when discharge of the Sacramento River at Freeport was between 10,000 ft^3/s and 14,000 ft^3/s. The central 80% of this release group passed junction 2 (Stations A_4, C_1, and D_1; Figure 4.1) over a 5-day period between 7 December and 11 December. The Delta Cross Channel closed at 1138 hours on 14 December 2007 and remained closed for the balance of the study (Figure 4.3). In contrast, the second release group passed the two river junctions on the descending limb of a freshet, during which flows declined from about 19,000 ft^3/s to 14,000 ft^3/s. Under these flow conditions, the second release group passed junction 2 over a two-day period between 17 January and 19 January. Travel times from release to junction 2 were also shorter for the second release group, with a median travel time of 2.7 d for the first release compared to 1.5 d for the second release.

During their migration through the lower regions of the Delta, most of first release group experienced relatively low and stable discharge accompanied by declining water exports, whereas migration of the second release group coincided with a second freshet during which discharge increased to about 40,000 ft^3/s and exports remained stable (Figure 4.3). As a consequence, most of the first release group passed Chipps Island over a 29-d period (12 December to 10 January), but the second release group passed Chipps Island over only a 16-d period (24 January to 9 February). Although the median travel time from release to Chipps Island for the first release (9.7 d) was less than for the second release (12.9 d), the 90th percentile for the first release (35.9 d) was substantially longer than for the second release (23.9 d). These findings suggest that the main effect of the freshet during the second release was to compress the tail of the travel time distribution rather than shift its central tendency. For both releases, it was difficult to compare travel time among migration routes because ≤4 fish per route were detected at Chipps Island for all routes but the Sacramento River.

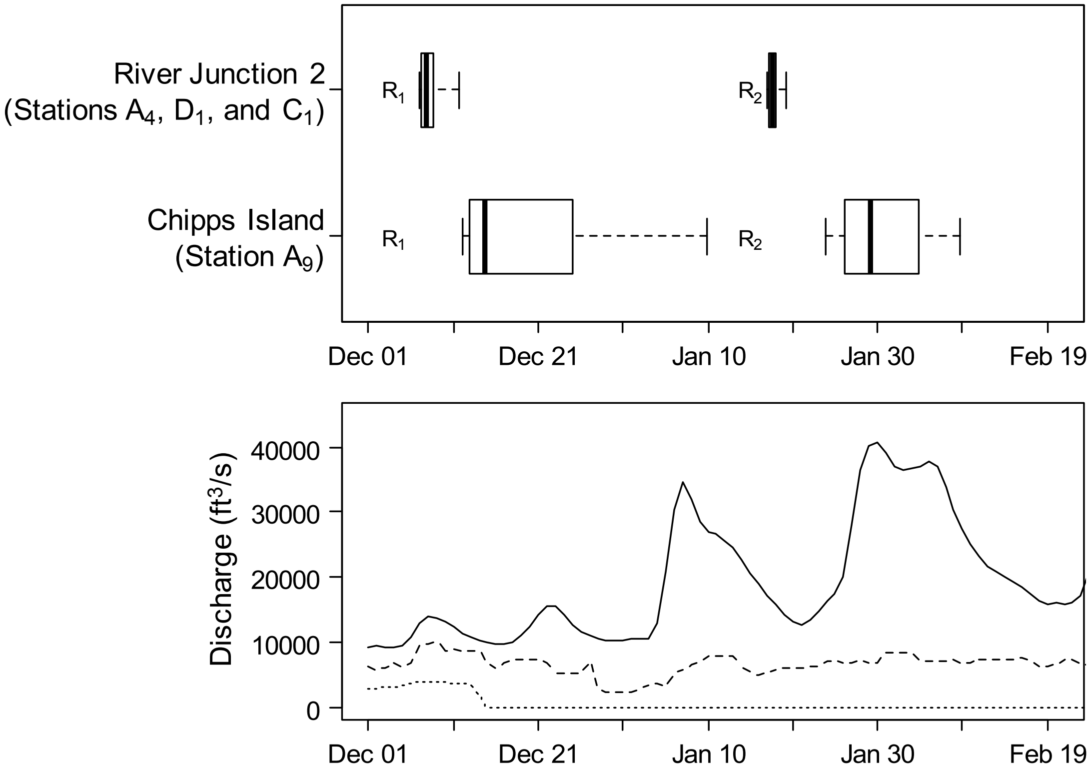

Figure 4.3. River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during winter 2007/2008. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River (telemetry stations A4, C1, and D1) and at Chipps Island, the terminus of the Delta (telemetry station A9). The two release dates are shown as R_1 = 4 December 2006 for a release size of 149 tagged fish and R_2 = 15 January 2007 for a release size of 130 fish. Whiskers represent the 10th and 90th percentiles, the box encompasses the 25th to 75th percentiles, and the line bisecting the box is the median arrival date. River discharge (solid line) is tidally filtered, daily discharge of the Sacramento River at Freeport (near telemetry station A2), Delta Cross Channel discharge (dotted line) is the tidally filtered daily discharge, and water exports (dashed line) are the total daily discharge of water exported from the Delta at the pumping projects.

4.3.2 Route-specific survival through the Delta

Comparison of parameters between release sites (Sacramento and Georgiana Slough) suggested no difference in survival or detection probabilities, allowing me to set parameters equal between release sites to improve precision of survival estimates. For both releases, likelihood ratio tests were not significant (for December, $\chi^2_9 = 12.4$, $P = 0.192$; for January, $\chi^2_9 = 14.8$, $P = 0.097$), so the reduced model was used to estimate route-specific survival and S_{Delta}. I found little difference between releases in survival through the Delta. The probability of surviving through the Delta was 0.174 for the December release and 0.195 for the January release (Table 4.2). For the December release, fish remaining in the Sacramento River exhibited higher survival than all other routes ($\hat{S}_{\text{A}} = 0.283$), whereas fish migrating through the interior Delta via the Delta Cross Channel and Georgiana Slough exhibited the lowest survival ($\hat{S}_{\text{C}} = 0.041$, $\hat{S}_{\text{D}} = 0.087$, Table 4.2 and Figure 4.4). In contrast, for the January release, fish migrating through Sutter and Steamboat sloughs exhibited similar survival ($\hat{S}_{\text{B}} = 0.245$) as fish migrating within the Sacramento River ($\hat{S}_{\text{A}} = 0.244$), whereas survival through the interior Delta via Georgiana Slough remained lower than the other migration routes ($\hat{S}_{\text{D}} = 0.086$). For both releases, separate estimates of route-specific survival for Sutter Slough and Steamboat Slough revealed fish entering Steamboat Slough exhibited survival that was about 9 percentage points higher than for fish that entered Sutter Slough (Table 4.2).

I detected significant differences between survival for the Sacramento River and survival for other migration routes. For the December release, the ratio of survival for each major migration route relative to the Sacramento River (i.e., θ_h) ranged from 0.14 for the Delta Cross Channel to 0.48 for Sutter and Steamboat Slough, showing that survival through other routes was less than half that of the Sacramento River. Since $\theta_h = 1$ fell outside the 95% confidence intervals of $\hat{\theta}_h$ for all major routes, these findings support the hypothesis that all routes had significantly lower survival than the Sacramento River (Table 4.3). Considering Sutter Slough and Steamboat Slough separately, only the estimate of θ_{B2} for Steamboat Slough

Table 4.2. Route-specific survival through the Sacramento–San Joaquin River Delta (S_h) and the probability of migrating through each route (Ψ_h) for acoustically tagged fall-run juvenile Chinook salmon released in December 2007 (R_1) and January 2008 (R_2). Also shown is population survival through the Delta (S_{Delta}), which is the average of route-specific survival weighted by the probability of migrating through each route.

Migration route	$\hat{S}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval	$\hat{\Psi}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval
R_1: December 2007				
A) Sacramento R.	0.283 (0.054)	0.187, 0.397	0.387 (0.044)	0.304, 0.475
B) Sutter & Steamboat S.	0.136 (0.039)	0.073, 0.225	0.345 (0.042)	0.267, 0.430
B_1) Sutter S.	0.107 (0.037)	0.050, 0.196	0.230 (0.037)	0.163, 0.308
B_2) Steamboat S.	0.193 (0.060)	0.095, 0.327	0.115 (0.028)	0.068, 0.178
C) Delta Cross Channel	0.041 (0.021)	0.013, 0.096	0.117 (0.029)	0.068, 0.182
D) Georgiana S.	0.087 (0.028)	0.043, 0.153	0.150 (0.033)	0.094, 0.221
S_{Delta} (All routes)	0.174 (0.031)	0.119, 0.242		
R_2: January 2008				
A) Sacramento R.	0.244 (0.048)	0.160, 0.346	0.490 (0.048)	0.397, 0.584
B) Sutter & Steamboat S.	0.245 (0.059)	0.143, 0.372	0.198 (0.037)	0.133, 0.278
B_1) Sutter S.	0.192 (0.070)	0.078, 0.343	0.086 (0.026)	0.044, 0.147
B_2) Steamboat S.	0.286 (0.070)	0.162, 0.430	0.112 (0.029)	0.033, 0.253
C) Delta Cross Channel	NA		0.000 (0.000)	
D) Georgiana S.	0.086 (0.023)	0.048, 0.140	0.311 (0.045)	0.229, 0.403
S_{Delta} (All routes)	0.195 (0.034)	0.135, 0.268		

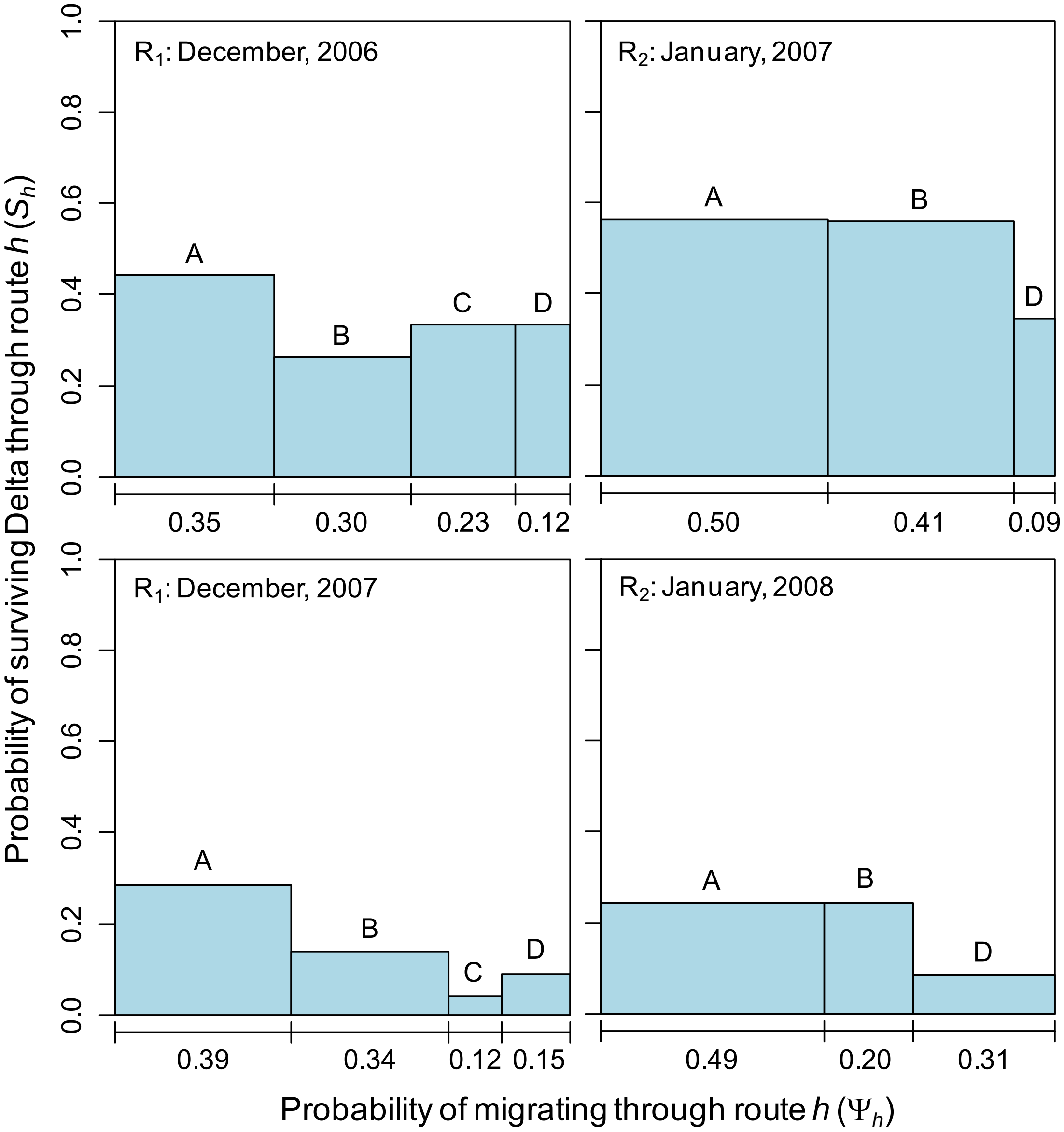

Figure 4.4. Probability of surviving migration through the Sacramento-San Joaquin River Delta (S_h) for each of four migration routes for tagged late-fall juvenile Chinook salmon emigrating from the Sacramento River. The width of each bar shows the fraction of fish migrating through each route (Ψ_h), and the total area under the bars yields S_{Delta}. The top panels show estimates from the winter of 2006/2007 (see Chapter 3), and the bottom panels show estimates from this study during the winter of 2007/2008. Labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively.

was not significantly different from one, likely due to small sample size and low precision for this secondary route. In contrast, in January, $\hat{\theta}_\text{B}$ = 1.005 whereas $\hat{\theta}_\text{D}$ = 0.352, showing that survival through the interior Delta (Route D) was only about one third that of other available routes. Survival for the interior Delta was significantly lower than for the Sacramento River, but survival for Sutter and Steamboat Slough (and each slough separately) was not significantly different than the Sacramento River (Table 4.3).

Table 4.3. The ratio (θ_h) of survival through route h (S_h) to survival through the Sacramento River (S_A) for acoustically tagged late fall-run juvenile Chinook salmon released in December 2007 and January 2008.

	R_1: December 2007		R_2: January 2008	
Migration route	$\hat{\theta}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval	$\hat{\theta}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval
B) Sutter & Sutter S.	0.481 (0.132)	0.265, 0.794	1.005 (0.215)	0.621, 1.480
B_1) Sutter S.	0.380 (0.127)	0.182, 0.689	0.787 (0.273)	0.330, 1.365
B_2) Steamboat S.	0.683 (0.205)	0.346, 1.153	1.172 (0.255)	0.698, 1.714
C) Delta Cross Channel	0.146 (0.077)	0.044, 0.363	NA	
D) Georgiana S.	0.307 (0.109)	0.145, 0.596	0.352 (0.110)	0.186, 0.642

4.3.3 Migration routing

For some migration routes, I found that the proportion of the population migrating through a given route deviated from the fraction of mean discharge in a route. As juvenile salmon migrated passed the first river junction, 34.5% of fish left the Sacramento River to the migrate through Steamboat and Sutter Slough (Ψ_B, Figure 4.4 and Table 4.2), about 10 percentage points higher than the fraction of total discharge entering this route (Figure 4.5). In contrast, for the January release, only 19.8% of fish entered Sutter and Steamboat Slough (Figure 4.4 and Table 4.2) despite 37% of river discharge entering this route (Figure 4.5). Route entrainment probabilities for each slough showed that the difference in $\hat{\Psi}_\text{B}$ between releases occurred at the entrance to Sutter Slough (Table 4.2). In December, twice the fraction of fish entered Sutter Slough ($\hat{\Psi}_{\text{B}11}$ = 0.230) as compared to Steamboat Slough ($\hat{\Psi}_{\text{B}21}$ = 0.115), whereas in January, the proportion entering Sutter Slough declined to 0.086 while the fraction entering Steamboat Slough remained unchanged at 0.112 (Table 4.2). As a consequence, 65% of fish remained in Sacramento River at the first river junction during the December release, whereas 80% remained in the Sacramento River for the January release (see Ψ_{A1} in Appendix Table 3.3). Thus, for the January release, a larger fraction of the population remained in the Sacramento River at the first junction, which increased exposure of the population to the second river junction where they could enter into the interior Delta.

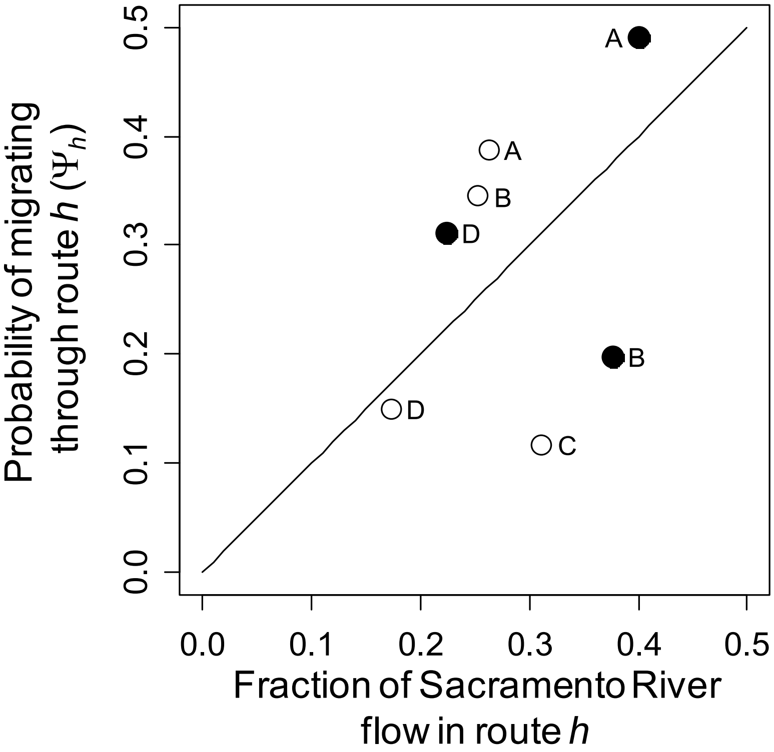

Figure 4.5. The probability of migrating through route *h* (Ψ_h) as a function of the proportion of total river flow in route *h* for tagged late-fall juvenile Chinook salmon released in December 2007 (open circles) and January 2008 (filled circles). Data labels A–D represent the Sacramento River, Steamboat and Sutter sloughs, the Delta Cross Channel, and Georgiana Slough, respectively. The fraction of river flow in each route was calculated as the proportion of tidally filtered daily discharge of each route relative to the total discharge of the Sacramento River at Freeport. The reference line shows where the fraction of fish migrating through each route is equal to the proportion of flow in each route (i.e., a 1:1 ratio).

For the December release, of fish that arrived at the second river junction where the Delta Cross Channel is located, 18% entered the Delta Cross Channel, 23% entered Georgiana Slough, and 59.2% remained in the Sacramento River (see Ψ_{C2}, Ψ_{D2}, and Ψ_{A2} in Appendix Table 3.3). In contrast, for the January release when the Delta Cross Channel was closed, 38.8% of fish arriving at the second river junction entered Georgiana Slough, with the remaining 61.2% migrating through the Sacramento River. Accounting for both river junctions, migration route probabilities for the December release indicated that 38.7% of the population migrated within the Sacramento River and 26.7% of the population entered the interior Delta. However, only 11.7% entered the interior Delta through the Delta Cross Channel even though 31% of the flow entered the Delta Cross Channel (Figures 4.4 and 4.5, Table 4.2). During January, nearly one third of the population was entrained into the interior Delta through Georgiana Slough (Figure 5, Table 2) despite the Delta Cross Channel being closed. Consequently, the fraction of the population entering the interior Delta was similar between release dates.

4.3.4 Relative contributions to S_{Delta}

Estimates of S_{Delta} were driven by 1) variation among routes in survival through the Delta ($\hat{S}_h$) and 2) the relative contribution of each route-specific survival to $\hat{S}_{\text{Delta}}$ as measured by migration route probabilities ($\hat{\Psi}_h$). For the December release, fish migrating within the Sacramento River exhibited the highest survival through the Delta ($\hat{S}_{\text{B}}$) relative to all other routes, but only 38.7% of the population migrated through this route ($\hat{\Psi}_{\text{B}}$), representing a relatively small contribution to $\hat{S}_{\text{Delta}}$ (Figure 4.4, Table 4.2). For the January release, 68.8% of the population ($\hat{\Psi}_{\text{A}} + \hat{\Psi}_{\text{B}}$) migrated through routes with the highest survival, since Sutter and Steamboat sloughs exhibited similar survival to the Sacramento River, but survival through the interior Delta was lower (Figure 4.4, Table 4.2). Because the fraction of the population entering the interior Delta was similar for both releases, lower survival through the interior Delta reduced population-level survival by a similar magnitude for both releases (Figure 4.4, Table 4.2).

4.3.5 Comparisons between 2007 and 2008

Some patterns in survival and migration route probabilities during 2008 differed considerably from 2007, whereas other patterns remained consistent. First, $\hat{S}_{\text{Delta}}$ for both releases in 2008 was lower than in 2007 (Table 3.1, Table 4.2, and Figure 4.4); $\hat{S}_{\text{Delta}}$ in 2007 was estimated at 0.351 and 0.543 for the December and January release groups compared to <0.20 for both releases in 2008. Although $\hat{S}_{\text{Delta}}$ was lower in 2008 relative to 2007, the pattern of survival probabilities among routes was similar between releases and years (Figure 4.4). In both years, all routes exhibited lower survival than the Sacramento River during the December release, but only fish entering the interior Delta exhibited lower survival than the Sacramento River for the January release (Figure 4.4). Larger sample size and the additional release site in Georgiana Slough during 2008 improved precision of route-specific survival compared to our 2007 study, allowing us to detect differences in survival among routes. We also found notable differences between years in route entrainment probabilities at the two primary river junctions. In 2007, migration route probabilities were similar to the fraction of flow in each route, but migration route probabilities deviated from this pattern in 2008. Consequently, in 2008 we found little difference between releases in the fraction of fish entering the interior Delta, whereas in 2007, the fraction of fish was lower during the January release when the Delta Cross Channel was closed (see Chapter 3).

4.3.6 Reach-specific patterns of survival and movement

I found high variation in per-km survival among reaches, ranging from as low as 0.867 km^{-1} to 1.0 km^{-1} for a few reaches where all fish survived. To put the magnitude of this survival in perspective, only 24% of fish will survive a 10-km reach at a rate of 0.867 km^{-1} (i.e., = $0.867^{10} = 0.247$) and only 6% will remain after 20 km. In contrast, at a rate of 0.99 km^{-1}, 90% of fish will survive 10 km and 82% will still be alive after 20 km. Reaches with the lowest survival rates occurred downstream of telemetry stations B_{13}, B_{23}, and A_6 (i.e., the Cache Slough to Rio Vista region, Figure 4.6). Two out of three of these reaches were among the four lowest survival probabilities observed in each release, highlighting a region of high local mortality relative to the length of these reaches. In contrast, other than survival probabilities that were fixed to one (Appendix Table 3.3), the highest per-km survival in both releases occurred in the first two reaches of the Sacramento River (downstream of A_2 and the Sacramento release site, A_1). These reaches were relatively long (~20 km each) and survival probabilities were >0.91 (see S_{A1} and S_{A2} in Appendix Table 3.3), leading to high survival relative to reach length.

Reach-specific survival was consistent with differences among routes in survival through the Delta. For the December release, 8 of the 11 reaches with the highest per-km survival were comprised of all 8 reaches in the Sacramento River (Route A, Figure 4.6). These reaches exhibited survival probabilities ≥ 0.96 km^{-1}. The remaining 11 reaches with the lowest per-km survival were comprised solely of the other three routes, with no particular route exhibiting consistently lower reach-specific survival rates. All of these reaches exhibited survival <0.96 km^{-1}. For the January release, the highest-ranking survival was still dominated by reaches within the Sacramento River (6 of the 11 highest per-km survival probabilities), but two reaches of the Sacramento River ranked in lowest 50 percent of survival rates (reaches beginning at A_6 and A_8).

Between releases, most reach-specific survival probabilities within the Sacramento River (Route A) and interior Delta (Route D) changed by less than 0.03 km^{-1} (Figure 4.7), and this finding agrees with the similarity in route-specific survival between releases for these routes (Figure 4.4). Furthermore, variation in survival between releases was low relative to the large variation in survival among reaches, especially for the Sacramento River (Figure 4.7). However, survival for all but one reach within Sutter and Steamboat sloughs increased substantially from December to January (Figure 4.7), which is consistent with the observed increase in survival through the Delta for this route. Thus, the observed difference in route-specific survival for Sutter and Steamboat sloughs was driven by coincident changes in survival rates for most reaches within this route and not by changes in survival within a specific reach.

One reach of particular management interest occurs downstream of D_4 in the interior Delta (see Figure 4.1). Although only about 17 km long by way of the San Joaquin River, this

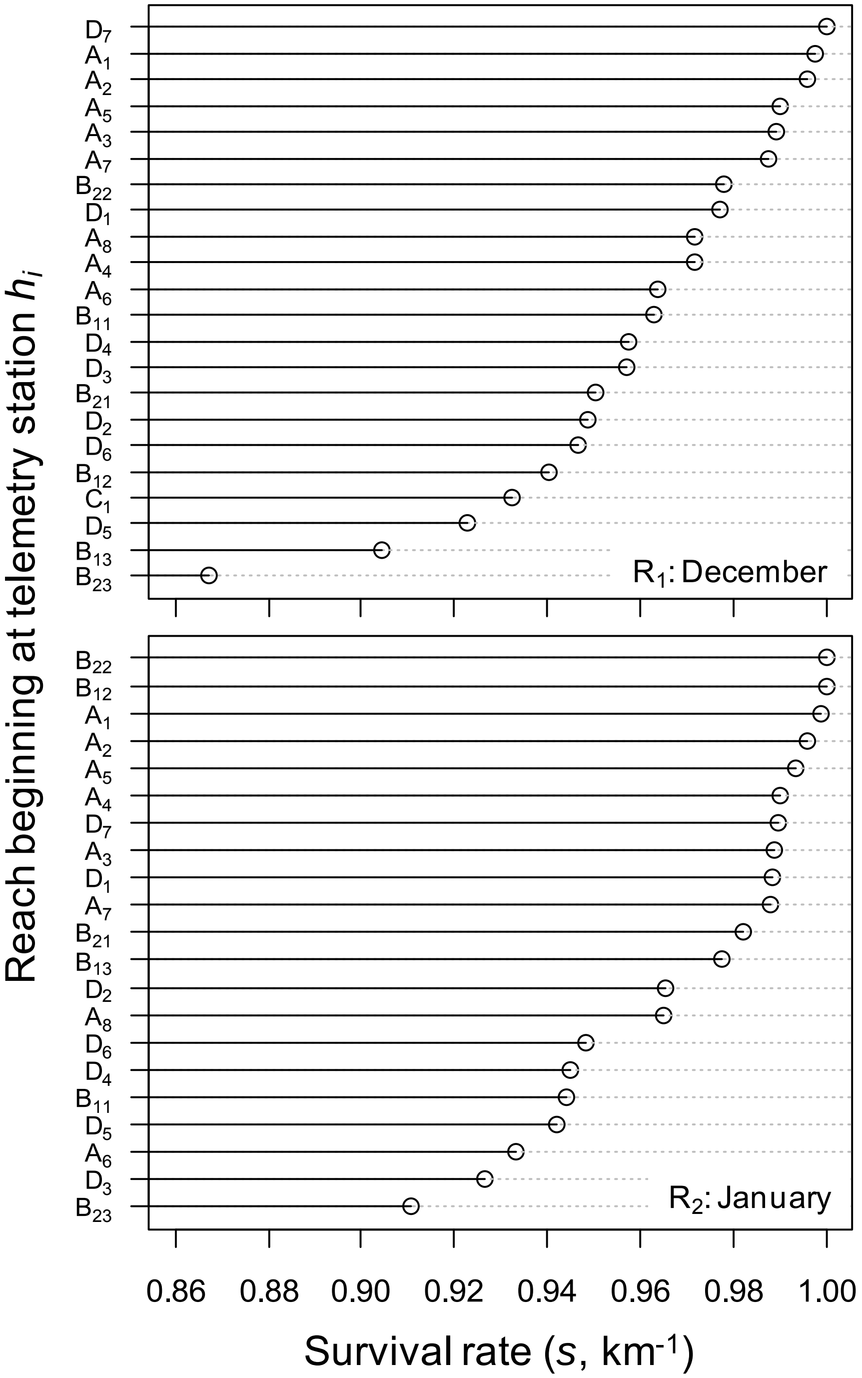

Figure 4.6. Reach-specific survival rates plotted in ascending order for tagged late fall Chinook salmon released in December 2007 (top) and January 2008 (bottom). Survival probabilities are scaled to the length of each reach from telemetry station h_i to the next downstream telemetry station (see Eqn. 4.1).

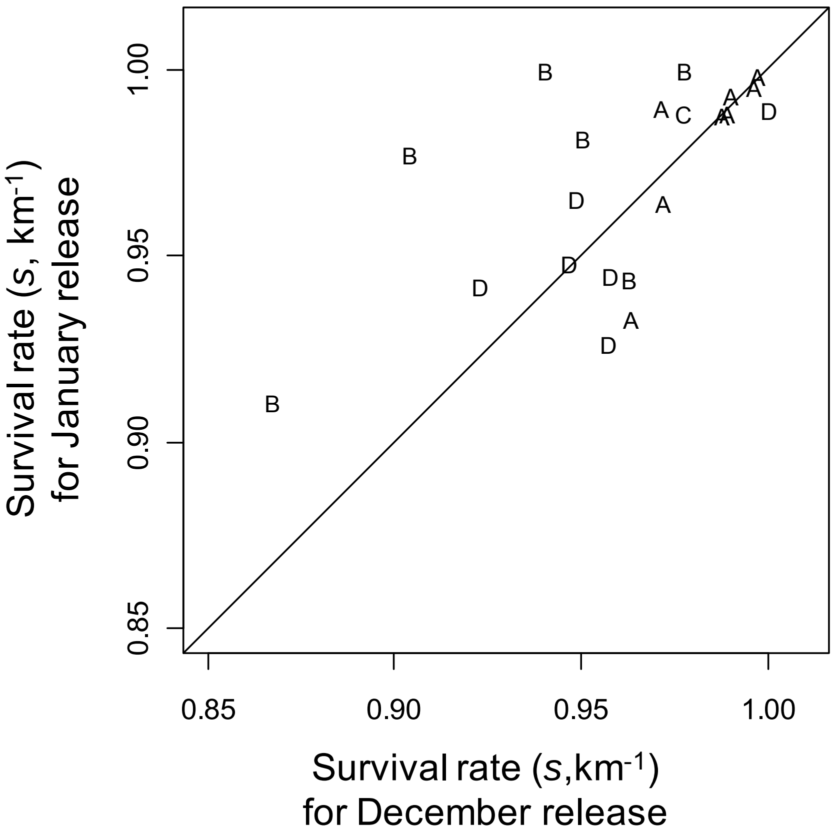

Figure 4.7. Reach-specific survival per km for the December 2007 release compared to the January 2008 release for acoustically tagged late fall Chinook salmon migrating through the Sacramento-San Joaquin River Delta. The reference line shows where survival rates are equal between releases. Letters correspond to reaches within A = Sacramento River, B = Sutter and Steamboat sloughs, and D = the interior Delta via Georgiana Slough.

reach encompasses a large network of channels and includes the pumping stations and fish salvage facilities in the southern Delta. This reach exhibited the lowest probability of survival of all reaches within the interior Delta, having observed survival probabilities of less than 50% (for R_1: $\hat{S}_{D4} = 0.484$, $\widehat{SE} = 0.071$; for R_2: $\hat{S}_{D4} = 0.395$, $\widehat{SE} = 0.080$; Appendix Table 3.3). However, when expressed as a function of reach length, other reaches within the interior Delta (Routes C and D) exhibited similar or lower survival rates than the reach downstream of D_4 (Figure 4.6). Direct mortality at the pumping stations appeared to contribute little to the estimate of S_{D4}. Both the State Water Project and Clifton Court Forebay were monitored by telemetry stations, but these stations could not be incorporated into the survival model because too few fish were detected at these locations to warrant parameter estimation. However, of the 76 fish passing D_4 that were never detected at or downstream of D_5 or E_1 (indicating probable mortality in this reach), only one fish was detected at the pumping stations. Overall, six tagged fish were detected at the pumping stations, and five of these were later detected at or downstream of D_5 or E_1 suggesting they had been salvaged at the fish facilities and transported to the lower Delta. Thus, mortality rates appear high in many reaches of the interior Delta relative the Sacramento River, not just the reach that includes a primary point source of known mortality.

Although I could not estimate route entrainment probabilities at other junctions in the Delta, I explicitly accounted for observed movement among routes by estimating joint survival-entrainment probabilities. At the junction of Sutter Slough with Miner and Steamboat Slough (the reach downstream of B_{11}; Figure 2), $\hat{\phi}_{\mathrm{B11,B22}}$ was about twice that of $\hat{\phi}_{\mathrm{B11,B12}}$ during both releases (Appendix Table 3.3). If survival was similar for the two reaches downstream of the junction, then these findings suggest that about two-thirds of fish entering Sutter Slough migrated down Steamboat Slough and one-third traveled through Miner Slough.

For both releases I observed fish passing in both directions through Three Mile Slough (E_1 in Figure 4.1). However, Three Mile slough appears to play a relatively minor role in movement dynamics through the Delta relative to contribution of the major migration routes. In the Sacramento River, fish moving from A_7 to A_8 contributed a substantially larger fraction of the total survival through this reach (for R_1: $\hat{\phi}_{\mathrm{A7,A8}} = 0.837$, $\widehat{\mathrm{SE}} = 0.074$; for R_2: $\hat{\phi}_{\mathrm{A7,A8}} = 0.781$, $\widehat{\mathrm{SE}} = 0.070$) compared to fish moving from A_7 to E_1 (for R_1: $\hat{\phi}_{\mathrm{A7,E1}} = 0.049$, $\widehat{\mathrm{SE}} = 0.034$; for R_2: $\hat{\phi}_{\mathrm{A7,E1}} = 0.109$, $\widehat{\mathrm{SE}} = 0.046$). In the San Joaquin River, fish moving from D_4 to E_1 contributed more to the total reach survival for the first release compared to the second release. For the first release, $\hat{\phi}_{\mathrm{D4,E1}} = 0.140$ ($\widehat{\mathrm{SE}} = 0.049$) and $\hat{\phi}_{\mathrm{D4,D5}} = 0.351$ ($\widehat{\mathrm{SE}} = 0.070$), whereas for the second release $\hat{\phi}_{\mathrm{D4,E1}} = 0.041$ ($\widehat{\mathrm{SE}} = 0.023$) and $\hat{\phi}_{\mathrm{D4,D5}} = 0.354$ ($\widehat{\mathrm{SE}} = 0.079$). Whether a higher fraction of fish in the San Joaquin River passed through Three Mile Slough (E_1) during the first release is difficult to ascertain because lower survival in the San Joaquin River downstream of its junction with Three-Mile Slough may also account for the observed difference.

4.4 Discussion

In 2007, $\hat{S}_{\text{Delta}}$ differed by nearly 20 percentage points between releases, and I attributed this observed difference to both a change in the proportion of fish entering the interior Delta and a change in survival within given migration routes (see Chapter 3). In contrast, for this study, I attribute lack of an observed difference in $\hat{S}_{\text{Delta}}$ between releases to 1) less variation between releases in survival for given migration routes, relative to 2007, 2) lower-than-expected entrainment into the Delta Cross Channel, 3) a decline in the proportion of fish entering Sutter and Steamboat sloughs in January, and 4) little difference in the proportion of fish entering the interior Delta between releases. In 2007, survival through the Delta for both the Sacramento River and Sutter and Steamboat slough increased substantially between December and January, partly driving the large observed difference in $\hat{S}_{\text{Delta}}$ between releases (Figure 4.4). However, during 2008 only Sutter and Steamboat sloughs exhibited a sizeable increase in survival from December to January. In 2008, although survival increased the proportion of fish entering Sutter and Steamboat sloughs declined from 0.34 to 0.20 from December to January. Had the proportion of fish entering Sutter and Steamboat sloughs remained unchanged, population-level survival would have received a larger boost from the increase in survival observed for this route. Given that survival for routes through the interior Delta were significantly lower than the Sacramento River during both releases, the fraction of fish entering the interior Delta dictated the magnitude of decrease in population-level survival due to fish using this migration route. Thus, the magnitude of decrease in population-level survival attributed to the interior Delta remained unchanged between releases because similar fractions of the population entered the interior Delta during both releases. However, because maximum survival for any given route during both releases was <0.30, population-level survival would remain low regardless of the fraction of fish entrained in the interior Delta.

That estimates of population-level survival were ≤0.20 for an 80-km section of river begs the question of whether the untagged population also experienced such low survival. To put the magnitude of these estimates in perspective, survival of hatchery-reared juvenile Chinook salmon over 600 km and through eight dams of the Snake and Columbia rivers ranged from 31%-59% (Williams et al. 2001). The absolute magnitude of survival relative to the distance traveled is clearly low compared to a similarly developed river system. However, factors such as source of the study fish and the effects of the transmitter could have reduced survival probabilities relative to untagged fish. Fish in this study were obtained directly from Coleman National Fish Hatchery, tagged, and then released about 40 km upstream of the first channel junction in the Delta. Initial "culling" of unfit hatchery fish obtained directly from a hatchery, a process suggested by Muir et al. (2001) and Newman (2003), could have lead to lower absolute survival compared to a population that had migrated in-river from natal tributaries or hatcheries to the Delta. If this process were pronounced in this study, I might have expected 1) low survival in the first reach following release, and 2) fish released at Sacramento to have higher survival probabilities through the interior Delta relative to fish that were released directly into the interior Delta at Georgiana Slough. In contrast, survival probabilities for the first reach of the Sacramento River were higher than all other reaches within this route (see S_{A1}, Appendix Table 3.3). Furthermore, the full model with different survival probabilities for each release site was not supported by the data. As for the effect of the transmitter, Hockersmith et al. (2003) found no difference in survival between radio tagged and PIT-tagged juvenile Chinook salmon over a similar distance as that studied here. Thus, I found little evidence to suggest that the low population-level survival through the Delta was a function of the source of fish or tagging methodology used for the study.

The strength of inferences from acoustic tag data to the untagged population depend on whether survival estimates are viewed from a relative or absolute point of view. Although I found no evidence that survival probabilities were lower than expected due to fish source or tagging method, I also have little basis with which to compare survival estimates from the study population to actively migrating populations of wild or hatchery origin in the Delta. However, regardless of the absolute magnitude of survival, differences among routes that influence survival should act similarly on all populations of salmon smolts migrating through the Delta. For example, both tagged and untagged fish migrating through the interior Delta likely experienced lower survival through the Delta relative to fish migrating within the Sacramento River. Therefore, the relative difference in survival among routes from our data should provide stronger inference to untagged populations than will inferences about the absolute magnitude of survival probabilities. From this perspective, although survival was low for all migration routes during 2008, survival for routes through the interior Delta was at most 35% that of survival for fish remaining in the Sacramento River (Table 4.3). Future studies that include fish obtained from Coleman National Fish Hatchery paired with releases of in-river, actively migrating hatchery or wild fish would help to interpret the absolute magnitude of survival probabilities from this study in the context of other populations of interest.

The primary working hypothesis of management actions related to the operation of the Delta Cross Channel is that closing the Delta Cross Channel will increase population-level survival by reducing the fraction of the population entering the interior Delta where survival is lower than alternative migration routes. Implicit in this hypothesis is that the fraction of fish entering the interior Delta is proportional to the fraction of flow entering the interior Delta. In contrast to previous findings, I found that the proportion of fish entering each migration route did not necessarily agree with the proportion of mean discharge entering a route. Furthermore, deviations from this “expected” relationship acted to decrease the proportion of fish entering the interior Delta during the December release, but increase it during the January release. Based on distribution of mean discharge, closing the Delta Cross Channel reduced the total fraction of flow entering the interior Delta from 48.4% during the December release to 22.5% during the January release. However, for the December release, the proportion of fish entering the Delta Cross Channel was only about one-third the proportion of flow entering this route, whereas the proportion of fish entering Georgiana Slough was similar to the proportion of flow (Figure 4.5). Thus, the proportion of fish entering the interior Delta was less than might otherwise be expected based only on the distribution of river flow during the December release. During the January release, only about 20% of fish entered Sutter and Steamboat Slough even though 37% of Sacramento River flow entered this route (Figure 4.5). Therefore, a higher fraction of fish remained in the Sacramento River relative to that expected based on the proportion of flow in this route, which in turn exposed a higher fraction of the population to entrainment into the interior Delta via Georgiana Slough. These findings show how variation in route entrainment probabilities at both major river junctions interacted to produce little observed difference between releases in the fraction of the population entering the Interior Delta, despite the Delta Cross Channel being open for the first release and closed for the second.

While dispersal of the population throughout the channel network of the Delta is likely driven in part by the distribution in mean river discharge among channels, my findings provide the first evidence that the distribution of fish entering each channel can deviate considerably from the distribution of flow entering each channel. Such deviation was expected by Burau et al. (2007), who identified a number of mechanisms likely to contribute to variation in route entrainment probabilities. First, flow distribution among the river channels at each junction varies with the tides on hourly time scales (Blake and Horn, 2003). Thus, diel patterns in migration behavior (Wilder and Ingram, 2006; Burau et al., 2007; Chapman et al., 2007) interacting with tidal fluctuations could produce route entrainment probabilities that deviate from that expected based on mean discharge. In addition, secondary circulation at river bends (Dinehart and Burau, 2005) combined with swimming behavior of juvenile salmon could concentrate the lateral distribution of migrating fish along the outside of river bends where they become more (or less) likely to be entrained into a given channel at a river junction (Burau et al., 2007). These fine-scale processes are an active area of research in the Delta (Burau et al., 2007) and should provide new insights into the mechanisms driving variability in route entrainment probabilities at river junctions.

While some aspects of migration and survival dynamics differed greatly between years, other patterns remained consistent. Although population-level survival in 2008 was lower than in 2007, the pattern of survival among routes was similar. During both releases, survival of fish migrating through the interior Delta was significantly less than for fish that remained in Sacramento River, which is consistent our findings in 2007 (Chapter 3) and with the findings of previous studies (Brandes and McLain, 2001; Newman and Rice, 2002; Newman, 2008; Brandes and Newman, 2010). This weight of evidence suggests that management actions that shift the distribution of the population from the interior Delta to the Sacramento River will improve population-level survival through the Delta. Similar to 2007, I also found that survival through the Delta for fish migrating in Sutter and Steamboat Sloughs was significantly lower than the Sacramento River during the December release, but was comparable to the Sacramento River during the January release. Higher total river discharge (Figure 4.3) in January combined with a higher fraction of that discharge entering Sutter and Steamboat sloughs (Figure 4.5) could have improved migration conditions and reduced predation rates during the January release. Reach-specific survival rates increased for nearly all reaches of Sutter and Steamboat Slough (Figure 4.7), which is consistent with an increase in discharge through these reaches.

Quantifying survival rates per unit distance allowed me to identify patterns in reach-specific survival that generally followed the pattern of route-specific survival probabilities. Most reaches within the Sacramento River exhibited the highest survival rates during both releases, while most reaches within the interior Delta exhibited survival rates lower than the Sacramento River (Figure 4.6). These findings suggest that particular reaches within a route did not drive the observed differences in survival among migration routes. For instance, the lowest survival probabilities for the interior Delta were observed for the longest reach and included the most complex channel network with the pumping stations (see S_{D4} in Appendix Table 3.3). Yet survival rates for this reach were comparable to other reaches within this route when expressed as a function of reach length. In addition, I observed locally high mortality in the Cache Slough region downstream of station B_{13}, B_{23}, and A_6 for both releases. Last, survival rates in Sutter and Steamboat sloughs increased in January for nearly all reaches within this route. These patterns of variation among reaches suggest that factors influencing survival are operating at a spatial scale larger than an individual reach.

Reach-specific survival rates expressed with respect to distance traveled changed little between releases relative to the variability observed among reaches, especially for the Sacramento River (Figure 4.8). These findings suggest that factors other than migration distance (e.g., travel time) may also influence mortality rates. In contrast, in the Columbia River, survival rates of juvenile Chinook salmon have been significantly related to migration distance, but only weakly correlated to travel time (Muir et al., 2001; Anderson et al., 2005). Anderson et al. (2005) offered a hypothesis explaining this apparently contradictory finding. When prey migrate through a “gauntlet” of predators, predator-prey encounter rates will be such that each prey encounters a predator at most once. Under these circumstances, predator-prey theory predicts that survival will be driven by distance traveled, but not by travel time. In contrast, when prey migration speeds are slow relative to predator swimming speeds such that multiple encounters are possible, then the situation reverses: the probability of survival becomes dependent on travel time. This hypothesis could partially explain the wide range in survival rates among reaches within the Sacramento River, but low variability between releases (Figure 4.7). Within our study area the Sacramento River transitions from river-driven discharge in the uppermost reaches to tidally driven discharge in the lower reaches. Coincident with this transition, fish movement patterns shift from downstream-only movements to both upstream and downstream movements in the lower reaches of the Delta. Thus, in lower reaches of the Delta fish may pass through a given reach more than once, which could increase predator encounter rates relative to the length of each reach.

This research continues to provide critical information to understand factors influencing migration and survival dynamics of juvenile Chinook salmon migration through the Delta. Improved precision of parameter estimates allowed me detect statistically significant differences in survival among migration routes. While some findings were similar to 2007, such as low survival through the Interior Delta relative to the Sacramento River, other findings deviated considerably between years. Survival through the Delta was less than 20% during 2008 (compared to 35%-54% in 2007), route-entrainment probabilities deviated from the fraction of mean river discharge entering each channel, and the proportion of the population entering the interior Delta was similar between releases despite closure of the Delta Cross Channel. Given the substantial variation in survival, route entrainment, and migration route probabilities observed among four releases and two years, I suspect that my analyses are just beginning to unmask the temporal and spatial variability in migration and survival dynamics in the Delta. Nonetheless, even with such variability, patterns in survival and movement dynamics are beginning to emerge. With the addition of migration data collected during the winter of 2008/2009, I plan to quantify factors that influence survival and migration route probabilities. Such information should provide insights into management actions that will improve survival of juvenile salmon populations migrating through the Sacramento-San Joaquin River Delta.

Chapter 5

INDIVIDUAL-, RELEASE-, AND ROUTE-SPECIFIC VARIATION IN SURVIVAL OF JUVENILE CHINOOK SALMON MIGRATING THROUGH THE SACRAMENTO–SAN JOAQUIN DELTA

5.1 Introduction

In previous chapters, I developed an analytical framework for quantifying survival of juvenile salmon migrating through the Sacramento-San Joaquin Delta. Key aspects of this framework include estimating survival of fish migrating through different pathways in the Delta and quantifying the fraction of the population using each migration route. Such an approach allowed me to explicitly quantify how survival through each migration route contributes to population-level survival. I applied this framework to acoustic tagging data from two migration seasons and found that survival of fish migrating through the Interior Delta was significantly lower than survival of fish remaining in the Sacramento River. While differences among routes remained similar between years, survival through all routes in 2008 was considerably lower than in 2007. In addition, I found that the distribution of fish among migration routes generally followed the distribution of river flow, but sizeable deviations from this relationship suggested that factors other than mean river flow also affect fish routing. The final two chapters of my dissertation focus on quantifying the mechanisms responsible for variability in survival and route entrainment probabilities. This chapter focuses on survival, while questions related to route entrainment probabilities are reserved for the next chapter.

Past studies examining the relation between environmental variables and survival in the Delta have identified Sacramento River flow, water temperature, tides, position of the Delta Cross Channel gates, salinity, and to a lesser extent, water exports as important factors affecting survival (Kjelson and Brandes, 1989; Newman and Rice, 2002; Newman, 2003, 2008, Newman and Brandes, 2010). These experiments have provided critical information to develop water management actions that aid in the recovery of endangered salmon. One limitation, however, is that the response variable has often been the ratio of recapture rates of coded-wire-tagged fish (CWT) between different release locations, which reduces to the ratio of survival probabilities under the assumption of equal capture probabilities. Ratios of recapture rates have then been modeled as a function of covariates (e.g., exports). When modeling ratios, it is impossible to disentangle the relation of the covariate with each of the underlying survival rates, and therefore, inference about the effect of the covariate on survival is indirect. In contrast, acoustic telemetry data allow for direct modeling of the survival probabilities for each migration route as a function of the relevant environmental variables. Since population-level survival is driven by the relative differences in survival among routes, explicitly modeling survival rates within migration routes is critical to understand how differences among routes arise. In this chapter, I capitalize on these advantages of acoustic tags to understand differences in survival among migration routes and factors affecting survival within routes.

This chapter unfolds as follows: First I use the multistate mark-recapture model presented in earlier chapters to estimate survival and migration route probabilities from acoustic tagged fish migrating through the Delta during winter 2008/2009 (hereafter, “2009”). This analysis proceeds much as in Chapters 3 and 4, but excludes most of the methods already presented in earlier chapters. I then examine patterns of variation in route-specific survival over all years (2007–2009). Last, to explain variability in survival, I undertake an analysis of this three-year data set along with additional acoustic tag data from a study conducted by UC Davis and NOAA fisheries. Since this chapter focuses on survival, I simplified the mark-recapture framework by excluding route entrainment probabilities, and I used a Cormack-Jolly-Seber mark-recapture model to examine effects of covariates. I incorporate both group-level covariates (migration route, study, release group, year) and individual covariates (river flow, fish size), then select among a set of alternative models to identify factors responsible for variation in survival.

5.2 Methods

5.2.1 Survival and migration route probabilities in 2009

I used a modified version of the multistate mark-recapture model presented in previous chapters to estimate survival and migration route probabilities for the 2009 migration year. Since statistical methods were presented extensively in previous chapters and experimental design remained largely unchanged, here I present only details of the 2009 study that differed from previous years. Other details of the 2009 study, such as model schematic and reach-specific parameter estimates, can be found in Appendix 4.

Release timing, release locations, and telemetry system design closely followed the design used in 2008. A number of telemetry stations used in 2008 were not implemented in 2009 (Figure 5.1), but since these stations divided reaches within routes, the model structure remained essentially unchanged from that presented in Chapter 4 (compare Figure 4.2 to Appendix Figure 4.1). Release timing and release locations were similar to 2008, with fish released at Sacramento and also in Georgiana Slough to increase sample sizes of fish migrating through the Interior Delta (Table 5.1). All fish were surgically implanted with VEMCO acoustic tags at Coleman National Fish Hatchery and transported to release sites where they were held in-river for 24 h prior to release. At each location, fish were released in early December and again in mid-January.

The first release group was intended to pass the Delta Cross Channel when the cross channel gates were open, and the second release group when the gates were closed; but a substantial fraction of the first release group passed the Delta Cross Channel after the gates had closed. Therefore, as presented in Chapter 3, I incorporated a parameter to estimate the probability of fish passing this river junction when the gates were open (ω_{open}). I then estimated route entrainment probabilities conditional on gate position (i.e., $\Psi_{hl,\text{open}}$ and $\Psi_{hl,\text{closed}}$). Route-specific survival was estimated for each release as described in Chapter 4. Thus, for the first release group, route-specific survival represents the average survival over conditions experienced by this release-group; that is, with the Delta Cross Channel gates both open and closed.

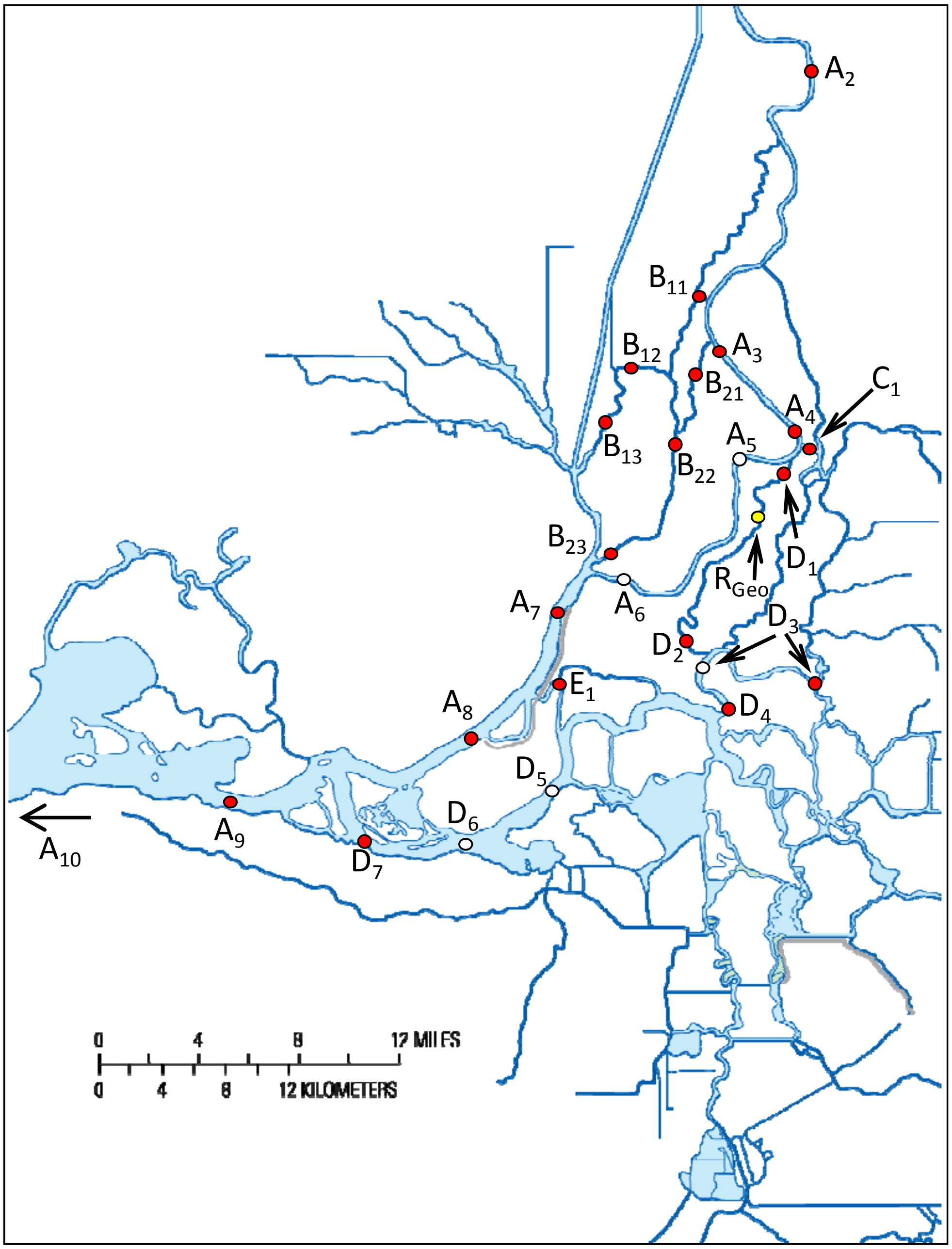

Figure 5.1. Location of telemetry stations used to estimate survival and migration route probabilities within four major migration routes of the Sacramento–San Joaquin River Delta during the winter of 2009. Red-filled circles labeled as h_i show the location of telemetry station i with route h. Locations denoted by unfilled circles show telemetry stations used in 2008 but not 2009. Station A_{10} pools all telemetry stations in San Francisco Bay downstream of A_9. The Sacramento release site was 19 river kilometers upriver of station A_2, and the Georgiana release site is noted as the yellow-filled circle labeled as R_{Geo}.

Table 5.1. Summary of release dates, release locations, and sample size of acoustically tagged late-fall Chinook salmon released into the Delta during the winter of 2009.

Release dates	Release number	Release location	Sample size
Nov 30 –Dec 4	1	Sacramento	192
Dec 2 –Dec 6	1	Georgiana Slough	100
Jan 13 – Jan 17	2	Sacramento	192
Jan 15 – Jan 19	2	Georgiana Slough	100

5.2.2 Multiyear analysis of route-specific survival

To quantify factors affecting survival over the three-year duration of this study, I incorporated covariates into a Cormack-Jolly-Seber (CJS) model that focused on a subset of the Delta (Cormack, 1964; Jolly, 1965; Seber, 1965). The CJS model was constructed to estimate survival to the exit of the Delta at Chipps Island from entry points into three major migration routes: 1) Sutter and Steamboat sloughs, 2) the Sacramento River, and 3) the interior Delta.

I examined a subset of the full multistate model for three reasons: First, the telemetry system differed in each year of study, resulting in year-specific multistate models that varied in their level of the spatial resolution. Second, my goal in this chapter was to examine factors affecting survival at the migration-route scale, rather than at the scale of reaches within routes. In Chapter 4, I found that changes in survival between releases occurred simultaneously for all reaches within a route (e.g., Sutter and Steamboat sloughs). This finding suggested that processes affecting survival acted at the migration-route scale rather than at the scale of reaches within routes. Last, I wanted to model survival as a function of individual covariates but imperfect detection probabilities for stations in the lower Delta made it impossible to use individual covariates due to missing covariate values for many fish. Rather, focusing the model on key entry points into migration routes where detection probabilities were nearly perfect allowed me to incorporate individual covariates without estimation and bias problems associated with missing covariate values (Catchpole et al., 2008).

Detections at key telemetry stations formed virtual "release" points where survival was modeled from the point of entry into each route. Virtual release points were formed from telemetry stations at the entry to Sutter and Steamboat sloughs (stations B_{11} and B_{21}), the

Sacramento River at its junction with the Delta Cross Channel and Georgiana Slough (station A_4), and the lower Mokulemne River where it enters the San Joaquin River (station D_4; Figure 5.1). Since detection probabilities at these locations were nearly perfect (See Appendix Tables 1.2, 3.3, and 4.3), conditioning the analysis on only detected fish resulted in little loss of information. Survival was then modeled for a single reach from each of these stations to Chipps Island. Reach length via the shortest possible pathway was 41.9 km for the interior Delta, 50.3 km for Sutter and Steamboat sloughs, and 51.9 km for the Sacramento River.

Reaches not included in this analysis are the Sacramento River from the release point at Sacramento to station A_4, the Delta Cross Channel from its junction with the Sacramento River to station D_4, and Georgiana Slough from the release location or from its junction with the Sacramento River to station D_4 (Figure 5.1). The upper reaches in the Sacramento River were excluded because telemetry stations were not implemented consistently in all years and survival in these reaches remained relatively high over all years of study (Appendix Tables 1.2, 3.3. and 4.3). The short reaches comprising Georgiana Slough, the Delta Cross Channel, and the North and South forks of the Mokelumne River were excluded so that survival of fish from both routes could be estimated simultaneously after they converge at the mouth of the Mokelumne River.

In addition to the USFWS study on which previous chapters are based, I also incorporated telemetry data from a CALFED-funded study (http://californiafishtracking.ucdavis.edu/, accessed December 2009). Telemetry data from both studies consisted of fish released during the winters of 2007, 2008, and 2009 from 11 release groups (Table 5.2). The CALFED and USFWS studies collaborated on tagging efforts, and the same personnel surgically implanted transmitters for both studies using methods described in Chapter 3. All juvenile salmon were monitored with same system of VEMCO telemetry stations. Although release sites varied among studies and years, all fish in the Sacramento River were released a minimum of 40 km upstream of entry points to migration routes used in the CJS model. By combining data from both studies, 932 fish were included in the analysis: 381 for the Sacramento River, 264 for Sutter and Steamboat sloughs, and 287 for the Interior Delta (Table 5.2).

Table 5.2. Route-specific sample sizes used in the CJS model for release groups of juvenile late-fall Chinook salmon implanted with acoustic tags during the winters of 2007 – 2009.

Study	Migration year	Release group	Release dates	Sacramento River	Steamboat and Sutter Slough	Interior Delta
USFWS	2007	1	Dec 5 – Dec 6	18	16	7
CALFED		2[*]	Jan 16–Feb 2	8	1	2
USFWS		3[*]	Jan 17 – Jan 18	33	29	2
USFWS	2008	4	Dec 4 – Dec 5	44	45	53
CALFED		5	Dec 7	22	12	8
USFWS		6	Jan 15 –Jan 16	52	23	73
CALFED		7	Jan 17	32	18	12
USFWS	2009	8	Nov 30 –Dec 4	56	48	48
CALFED		9	Dec 13	38	20	17
CALFED		10	Jan 11	19	15	6
USFWS		11	Jan 13 –Jan 17	59	37	59
All groups				381	264	287

[*] These release groups were pooled for analysis because sample sizes for release group 2 were inadequate for estimating route- and release-specific survival.

5.2.3 Incorporating covariates into the CJS model

The CJS model had two sampling occasions with four possible captures histories (111, 110, 101, and 100). The two occasions were formed from detections at station A_9 (Chipps Island) and station A_{10} (seaward of Chipps Island; Figure 5.1). I structured the negative log-likelihood of the CJS model following the approach of Skalski et al. (1993) where each individual's contribution to the likelihood is explicit:

$$\ln L\left(S_i, p_i, \lambda_i \mid \mathbf{Y}\right) = -\sum_{i=1}^{n} y_{i,111} \ln\left(S_i p_i \lambda_i\right) + y_{i,110} \ln\left(S_i p_i (1-\lambda_i)\right)$$

$$+ y_{i,101} \ln\left(S_i (1-p_i)\lambda_i\right) + y_{i,100} \ln\left(1 - S_i + S_i(1-p_i)(1-\lambda_i)\right). \tag{5.1}$$

Here, y_{ij} is an indicator variable resolving to 1 if the *i*th fish has the *j*th capture history, and zero otherwise, S_i is the probability of the *i*th fish surviving to Chipps Island from one of three starting points in the Delta, p_i is the detection probability of the *i*th fish at Chipps Island, and λ_i is the joint probability of the *i*th fish surviving and being detected at telemetry stations in San Francisco Bay. This model is overparameterized, and parameters for each individual are estimable only when constrained as a function of group-level or individual covariates.

I used the framework of generalized linear models (glm; McCullough and Nelder, 1989) to link a linear function of the CJS parameters, $g(\theta)$, to the covariates. I used a logit link function for all parameters:

$$g\left(\theta_i\right) = \ln\left(\frac{\theta_i}{1+\theta_i}\right) = \beta_0 + \beta_1 x_{i1} + \ldots + \beta_p x_{ip} = \boldsymbol{\beta}'\mathbf{x}_i \tag{5.2}$$

where $\theta_i = S_i$, p_i, or λ_i; β_0 is the intercept; and β_j is the slope parameter for $j = 1, \ldots, p$ covariates, x_{ij}. The covariates were introduced into the negative log-likelihood using the inverse logit function:

$$\theta_i = \frac{\exp\left(\boldsymbol{\beta}'\mathbf{x}_i\right)}{1+\exp\left(\boldsymbol{\beta}'\mathbf{x}_i\right)} \tag{5.3}$$

and the likelihood was iteratively minimized using optimization routines in the R statistical computing platform (R Development Core Team, 2008) to estimate the vector of β parameters. The variance-covariance matrix was estimated as the inverse of the observed Hessian matrix.

5.2.4 Defining group and individual covariates

I modeled survival through the Delta as function of both group-level and individual covariates. Individual covariates consisted of fork length and route-specific river discharge when individuals entered each route. Group-level covariates consisted of study (USFWS or CALFED), migration route, migration year, and mean river discharge for each release group and migration route.

I hypothesized that the 3-d period after fish entered a migration route was a critical period during which hydraulic conditions of the river could affect survival. Thus, individual covariates for river discharge were defined by mean discharge for the 3-d period after each fish entered the reach of interest. This time period was based on median travel times to the lower Sacramento River at Rio Vista (station A_7; Figure 5.1) from virtual release points in the Sacramento River (median = 2.4 d) and Sutter and Steamboat sloughs (median = 3.1 d). For the Interior Delta, I also focused on a 3-d period, hypothesizing that river conditions shortly after fish enter the San Joaquin River would influence their probability of moving towards the ocean or towards pumping stations in the southern Delta, which in turn, could affect survival.

For fish migrating through the Sacramento River, I modeled survival as a function of Sacramento River discharge just downstream of Georgiana Slough (Q_S, between stations A_4 and A_5 in Figure 5.1; also see Figure 6.1). Since the Delta Cross Channel diverts river flow upstream of this location, this gauging station measures flow remaining in the Sacramento River in response to operation of the cross channel gates. To capture the effect of tidal fluctuations on survival, I also considered the standard deviation of 15-min discharge over the 3-d period as a possible covariate. However, I found that the mean and standard deviation of discharge were highly correlated (r = -0.864, Figure 5.2). As inflow increases, tidal fluctuations are dampened; therefore, I used only mean discharge in the model because it quantifies both the effect of river inflow and the effect of inflow on tidal fluctuations.

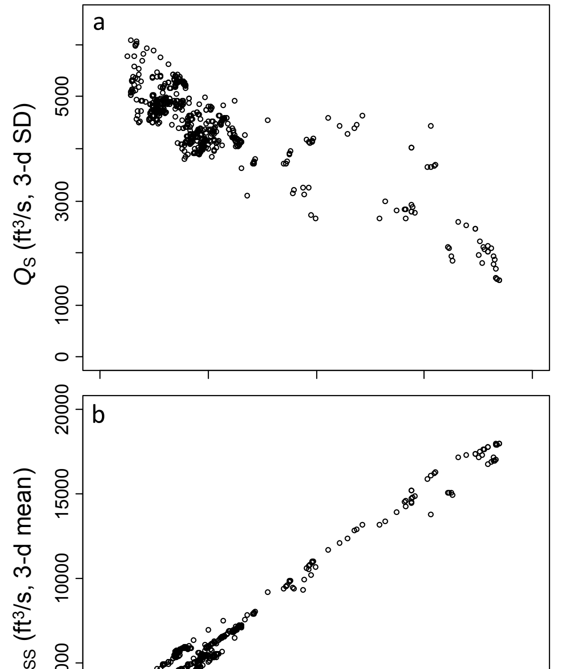

Figure 5.2. Relation between mean Sacramento River discharge measured downstream of Georgiana Slough (Q_S) with a) the standard deviation of Q_S, and b) the mean discharge entering Sutter and Steamboat sloughs (Q_{SS}). Means and standard deviations were calculated from 15-min flow data during the 3-d period following detection of tagged fish entering the Sacramento River and Sutter and Steamboat sloughs.

I also used Q_S for Sutter and Steamboat sloughs because 1) Q_S was highly correlated with discharge entering Sutter and Steamboat Slough ($r = 0.98$, Figure 5.2), 2) fish from both routes migrate through a common reach in the lower Sacramento River (Figure 5.1), and 3) using the same flow covariate allowed me to test whether the slope coefficients differed between migration routes. Specifically, the effect of Q_S on survival was modeled with the following structure (excluding the other covariates for clarity):

$$g(S) = \beta_1(I_\mathrm{Sac} + I_\mathrm{SS})Q_\mathrm{S} + \beta_2 I_\mathrm{SS} Q_\mathrm{S}$$

where I_Sac and I_SS are dummy variables resolving to one when fish enter the Sacramento River (Sac) or Sutter and Steamboat sloughs (SS), and zero otherwise. With both terms in the model, the first estimates the slope for the Sacramento River and the second estimates the difference in slopes between the Sacramento River and Sutter and Steamboat sloughs. Thus, the null hypotheses $\beta_2 = 0$ explicitly tests whether the effect of Q_S on survival differs between migration routes.

River flow and migration routing in the interior Delta is more complex than the other migration routes. Once fish exit the Mokelumne River and enter the San Joaquin River, their probability of surviving may depend on whether they move seaward or inland towards the pumping stations. The probability of fish moving towards the pumps likely depends on the balance of flows exiting the Mokelumne River and the San Joaquin River relative to water exports at the pumping stations. Thus, individual covariates for the interior Delta were defined as mean 3-d discharge of water exports at the pumping stations (Q_E), of the Mokelumne River where fish enter the San Joaquin River (Q_M, near station D_4), and of the San Joaquin River at Jersey Point (Q_J, near station D_5, Figure 5.1).

I formed group-level covariates for river flow by averaging the individual covariates over each release group and migration route. This approach is equivalent to a weighted average with weights proportional to the distribution of entry times to each reach. All covariates were standardized by subtracting the mean from each observation and then dividing by the standard deviation.

5.2.5 Model selection

I used a three-phase approach to determine factors affecting route-specific survival: I first identified the best-fit model for p and λ and used this model as a basis fitting covariates to survival. Second, I modeled group-level covariates using analysis of deviance (ANODEV). Last, I selected among models with individual covariates using likelihood-ratio tests (LRT) and Akaike's Information Criterion (AIC; Burnham and Anderson, 2002).

I used ANODEV because it explicitly accounts for overdispersion and replication at the route- and release group-level. Since the analysis consisted of only 10 release groups and 3 reaches, ANODEV "penalizes" for this low level of replication through the effects of the "source" and "error" degrees of freedom on the F test. Furthermore, the error mean deviance quantifies overdispersion (release-to-release variability unexplained by covariates in the model), ensuring that test statistics for model selection remain unbiased. Because likelihood ratio tests (LRT) account for only multinomial sampling variability, they too often reject the null hypothesis of no covariate effect in the presence of variability that is unrelated to the group covariates (Skalski et al., 1993). In contrast, I used LRT for the individual covariates because LRT remains unbiased for individual covariates in the presence extra variability unrelated to the covariate (Skalski et al., 1993).

The fully saturated model estimated a unique p and λ for each release group and unique survival probabilities for each release group and migration route. Using the glm framework, this model was parameterized by including a main effect of release group for p and λ; and release group, route, and a release:route interaction for S (where ':' denotes interaction) . Given this saturated model, I evaluated reduced models for p and λ that consisted of year-specific parameters and constant p and λ over all years. I first selected the best model for λ and then fit models for p under the best λ model. The best-fit λ and p models were selected on the basis of LRT and AIC.

At the group level, I fit a model with all covariates which included route, year, study, Q_S for the Sacramento River and Sutter and Steamboat sloughs, and Q_M, Q_J, and Q_E for the Interior Delta. I then constructed an ANODEV table analogous to ANOVA tables that partition the variance among different sources of error (Skalski et al., 1993). To select variables for inclusion in the model, I used stepwise selection, adding variables to the ANODEV table in order of the largest reduction in negative log-likelihood (NLL; Skalski et al., 1993). Interaction terms were always added to the model with their corresponding main effects. This approach results in a sequential ANODEV table where the *F* test for a given variable includes all other covariates previously added to the model.

For individual covariates, I added fork length (*L*) and flow variables to the saturated model for survival (i.e. to the model with route, release group, and route:release group). First, to test for differences in slopes among release groups, I considered interactions between release group and individual covariates. However, when simultaneously including all possible two-way interactions in the model, maximization of the likelihood became unstable and many parameters became inestimable, which was likely due to small sample size for some of the releases and routes (Table 5.2). Instead, prior to forming a full model, I added each covariate separately to the saturated model, crossed the covariate with release group, fixed inestimable slope parameters to zero, and then compared this model against the corresponding model lacking an interaction. None of the interactions were significant using LRT at $\alpha = 0.05$, so they were not included in the full model. Therefore, the full model with individual covariates estimated unique intercepts for each release group-route combination, but a common slope over all release groups.

Only the individual covariates were considered for model selection, keeping route, release, and route:release group in all models. The intent here was twofold: first, my goal was to explain within-release variation in survival over and above that accounted for by route and release group. Second, maintaining group-level structure ensured that group differences in survival were not wrongly attributed to the individual covariate. When covariate values do not overlap among groups, and group survival differs due to factors other than the covariate, LRT may falsely attribute a covariate effect to the group differences in survival (Hoffman and Skalski, 1995). However, Hoffman and Skalski (1995) showed that the LRT was unbiased when individual covariates were added to the fully saturated model. I used reverse elimination of covariates to identify the best-fit model, dropping terms one-at-a-time from the full model, eliminating the variable that least explained variation in survival (using LRT and AIC), re-fitting the reduced model, and then eliminating the next variable. Covariates were eliminated until no variable could be dropped without resulting in a significantly poorer fit based on a substantial increase in AIC and evaluation of LRT at $\alpha = 0.05$.

5.3 Results

5.3.1 Migration routing and survival in 2009

Sacramento River discharge was less than 10,000 ft^3/s for much of the study period, and travel times of the first release group were substantially longer than observed in previous years (Figures 5.3 and 5.6). For the December release group, the median travel time to junction 2 (Stations A_4, C_1, and D_1; Figure 5.1) was 13 days, and the central 80% of this release group took 25 days to pass the second river junction. The January release group exhibited much shorter travel times to river junction 2 (median = 4.1 days) and a more compressed distribution, despite flows remaining low (Figure 5.3). These findings suggest that the first release group may not have been actively migrating smolts at the time of release. Travel times of the first release group to the outlet of the Delta were substantially longer than the second release group and their arrival distributions overlapped. For the first release group, the median travel time to Chipps Island was 25 days, but arrival at Chipps Island was distributed over nearly two months. For the second release group, the median travel time was 10.9 days and arrival times between the 10th and 90th percentile were distributed over 32 days. All fish exited the Delta with the onset of a freshet in late February.

Migration route probabilities varied according to the position of the Delta Cross Channel gate. The first release group was supposed to pass the Delta Cross Channel while its gates were open, but long travel times caused 45% of fish to pass the Cross Channel when the gates were closed (See ω_{open}, Appendix Table 4.3). For this release group, fish that passed when the Delta Cross was open distributed in thirds among the Sacramento River, Sutter and Steamboat Slough, and interior Delta (via the Delta Cross Channel or Georgiana Slough; Table 5.3). For routes leading to the interior Delta, 22.4% of the population entered through the Delta Cross Channel, whereas 12.4% entered through Georgiana Slough (Table 5.3). In contrast, of the fish from the first release group that passed the Delta Cross Channel when the gates were closed, 46.6% remained in the Sacramento River and 21.2% entered the Interior

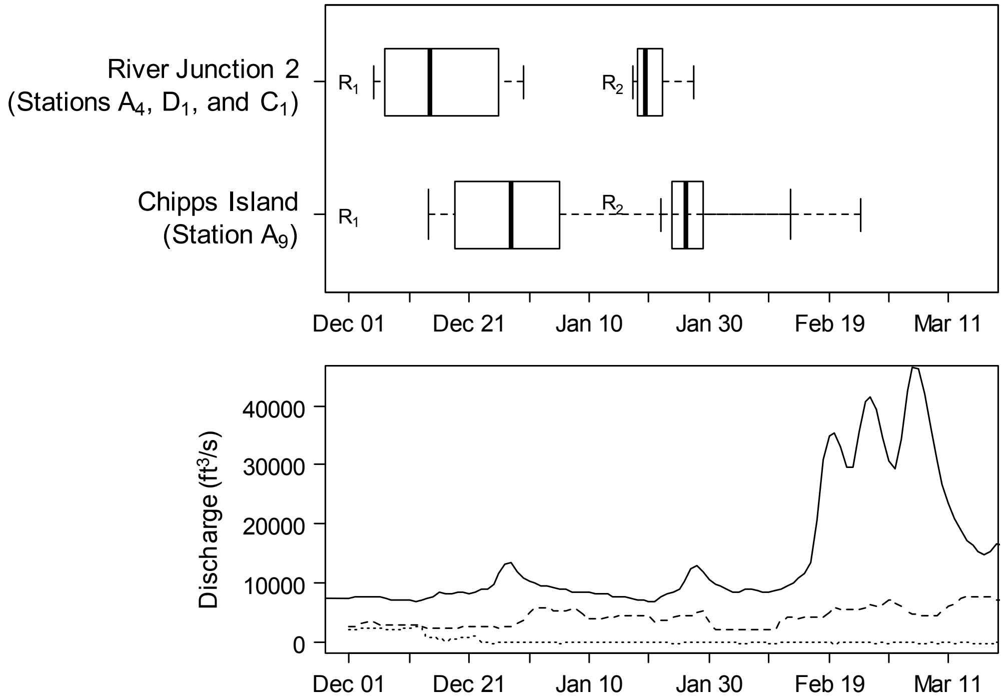

Figure 5.3. River discharge, water exports, and Delta Cross Channel discharge during the migration period of tagged juvenile Chinook salmon migrating through the Sacramento–San Joaquin River Delta during the winter of 2009. Box plots show the distribution of arrival dates at Junction 2 on the Sacramento River (telemetry stations A_4, C_1, and D_1) and at Chipps Island, the terminus of the Delta (telemetry station A_9). Release dates are shown as R_1 and R_2. Whiskers represent the 10th and 90th percentiles, the box encompasses the 25th to 75th percentiles, and the line bisecting the box is the median arrival date. For Chipps Island, whiskers have different widths to distinguish the overlap in arrival distributions. River discharge (solid line) is tidally filtered, daily discharge of the Sacramento River at Freeport (near telemetry station A2), Delta Cross Channel discharge (dotted line) is the tidally filtered daily discharge, and water exports (dashed line) are the total daily discharge of water exported from the Delta at the pumping projects.

Delta. Since the Delta Cross Channel was closed, migration route probabilities for the second release group were similar to those of the first release group that encountered a closed gate (Table 5.4). Closing the Delta Cross Channel increases discharge entering both the Sacramento River and Georgiana Slough. Coincident with this increase in flow, migration route probabilities for both releases indicate that the fraction of fish in both Georgiana Slough and the Sacramento River increased when the gate was closed. In Chapter 6, I expand on these findings to explicitly quantify entrainment probabilities as a function discharge entering each route.

Table 5.3. The probability of migrating through each route (Ψ_h) for acoustically tagged late fall-run juvenile Chinook salmon released in December 2008 as a function of gate position when fish passed the Delta Cross Channel.

	Cross Channel Open		Cross Channel Closed	
Migration route	$\hat{\Psi}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval	$\hat{\Psi}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval
A) Sacramento R.	0.331 (0.050)	0.238 , 0.431	0.466 (0.054)	0.360, 0.569
B) Sutter & Steamboat S.	0.321 (0.037)	0.251 , 0.397	0.321 (0.037)	0.251, 0.397
C) Delta Cross Channel	0.224 (0.045)	0.145 , 0.318	NA	
D) Georgiana S.	0.124 (0.036)	0.065 , 0.206	0.212 (0.049)	0.128, 0.315

Survival through the Delta was comparable between release groups even though the first release group had substantially longer travel times. Survival through the Delta was 0.386 for the first release group and 0.339 for the second release group (Table 5.4). Since half of the first release group encountered a closed Delta Cross Channel gate, migration route probabilities did not differ drastically between releases, resulting in similar contributions of route-specific survival to population-level survival. Among routes, fish migrating in the Sacramento River and Sutter and Steamboat sloughs exhibited the highest survival probabilities whereas fish migrating through the Delta Cross Channel and Georgiana Slough had lower survival (Table 5.4). For both releases, survival probabilities for the Sacramento River and Sutter and Steamboat sloughs ranged from 0.394 to 0.448. In contrast, survival probabilities ranged from 0.117 to 0.315 for fish migrating through the Interior Delta (Table 5.4).

The ratio of survival through each route relative to the Sacramento River (θ_h) indicated that fish entering the Interior Delta had significantly lower survival for two of the three survival probabilities. Fish entering the Delta Cross Channel exhibited significantly lower survival than the Sacramento River, as did fish entering Georgiana Slough from the second release group (Table 5.5). Although $\hat{\theta}_{\mathbf{D}} = 0.70$ indicated lower survival of fish entering Georgiana Slough for the first release group, the 95% confidence interval encompassed one. For Sutter and Steamboat sloughs combined, θ_B was not different from one during either release. However, considering these routes separately, fish from the first release group entering Sutter Slough exhibited significantly lower survival but fish entering Steamboat

Slough had significantly higher survival than the Sacramento River. For the second release group, fish within each of these routes experienced similar survival as fish remaining in the Sacramento River (Table 5.5).

Table 5.4. Route-specific survival through the Sacramento–San Joaquin River Delta (S_h) and the probability of migrating through each route (Ψ_h) for acoustically tagged late-fall juvenile Chinook salmon released in December 2008 (R_1) and January 2009 (R_2). Also shown is population survival through the Delta (S_{Delta}), which is the average of route-specific survival weighted by the probability of migrating through each route.

Migration route	$\hat{S}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval	$\hat{\Psi}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval
R_1: December 2008				
A) Sacramento R.	0.448 (0.053)	0.348, 0.553	0.392 (0.040)	0.354, 0.458
B) Sutter & Steamboat S.	0.394 (0.056)	0.296, 0.507	0.321 (0.037)	0.251, 0.397
B_1) Sutter S.	0.281 (0.061)	0.172, 0.407	0.217 (0.033)	0.157, 0.288
B_2) Steamboat S.	0.632 (0.059)	0.509, 0.741	0.104 (0.025)	0.062, 0.158
C) Delta Cross Channel	0.117 (0.048)	0.044, 0.228	0.224 (0.045)	0.145, 0.318
D) Georgiana S.	0.315 (0.054)	0.216, 0.426	0.164 (0.164)	0.112, 0.226
S_{Delta} (All routes)	0.386 (0.038)	0.315, 0.463		
R_2: January 2009				
A) Sacramento R.	0.398 (0.051)	0.308, 0.484	0.459 (0.043)	0.404, 0.498
B) Sutter & Steamboat S.	0.432 (0.067)	0.394, 0.514	0.253 (0.036)	0.188, 0.328
B_1) Sutter S.	0.426 (0.086)	0.271, 0.468	0.096 (0.024)	0.055, 0.151
B_2) Steamboat S.	0.436 (0.075)	0.372, 0.518	0.158 (0.030)	0.105, 0.222
C) Delta Cross Channel	NA		0.000 (0.000)	
D) Georgiana S.	0.163 (0.033)	0.146, 0.204	0.288 (0.040)	0.219, 0.361
S_{Delta} (All routes)	0.339 (0.035)	0.310, 0.379		

Table 5.5. The ratio (θ_h) of survival through route h (S_h) to survival through the Sacramento River (S_A) for acoustically tagged late fall-run juvenile Chinook salmon released in December 2008 and January 2009.

	R_1: December 2008		R_2: January 2009	
Migration route	$\hat{\theta}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval	$\hat{\theta}_h$ ($\widehat{\text{SE}}$)	95% Profile likelihood interval
B) Sutter & Sutter S.	0.879 (0.131)	0.644, 1.170	1.086 (0.199)	0.872, 1.251
B_1) Sutter S.	0.626 (0.139)	0.383, 0.925	1.070 (0.239)	0.832, 1.227
B_2) Steamboat S.	1.410 (0.144)	1.148, 1.728	1.096 (0.215)	0.977, 1.443
C) Delta Cross Channel	0.260 (0.109)	0.098, 0.527	NA	
D) Georgiana S.	0.703 (0.139)	0.466, 1.014	0.409 (0.094)	0.374, 0.449

5.3.2 Interannual patterns in route-specific survival

I observed substantial variation in the magnitude of within-route survival among years, yet stable patterns of survival across routes over all years. Among years, 2008 stands out as having the lowest survival at both the route scale and the Delta scale (Figure 5.4 and 5.5). Survival through the Delta was <0.20 for 2008, but > 0.33 for all other years and releases. In contrast, given that fish experienced the lowest flows in 2009 (Figure 5.6), estimates of S_{Delta} for 2009 were substantially higher than might be expected when compared relative to S_{Delta} for 2008 (Figure 5.4). Over all years, estimates of S_{Delta} exceeded 0.40 for only one release group (Dec. 2007), and only during 2007 did observed estimates of S_{Delta} differ between releases. Although rankings of route-specific survival vary somewhat across releases, one pattern remained constant: survival probabilities for the Sacramento River were always greater than survival for migration routes through the Interior Delta (via Georgiana Slough and the Delta Cross Channel; Figure 5.4). In addition, Sutter and Steamboat sloughs exhibited either similar survival to the Sacramento River (typically for January releases) or lower survival than the Sacramento River (typically for December releases). Except for the December release group in the 2007 migration year, observed survival estimates for Sutter and Steamboat Sloughs were greater than for routes leading to the Interior Delta. These findings clearly show that migration routes leading to the Interior Delta will reduce population survival proportional to the fraction of the population entering the interior Delta.

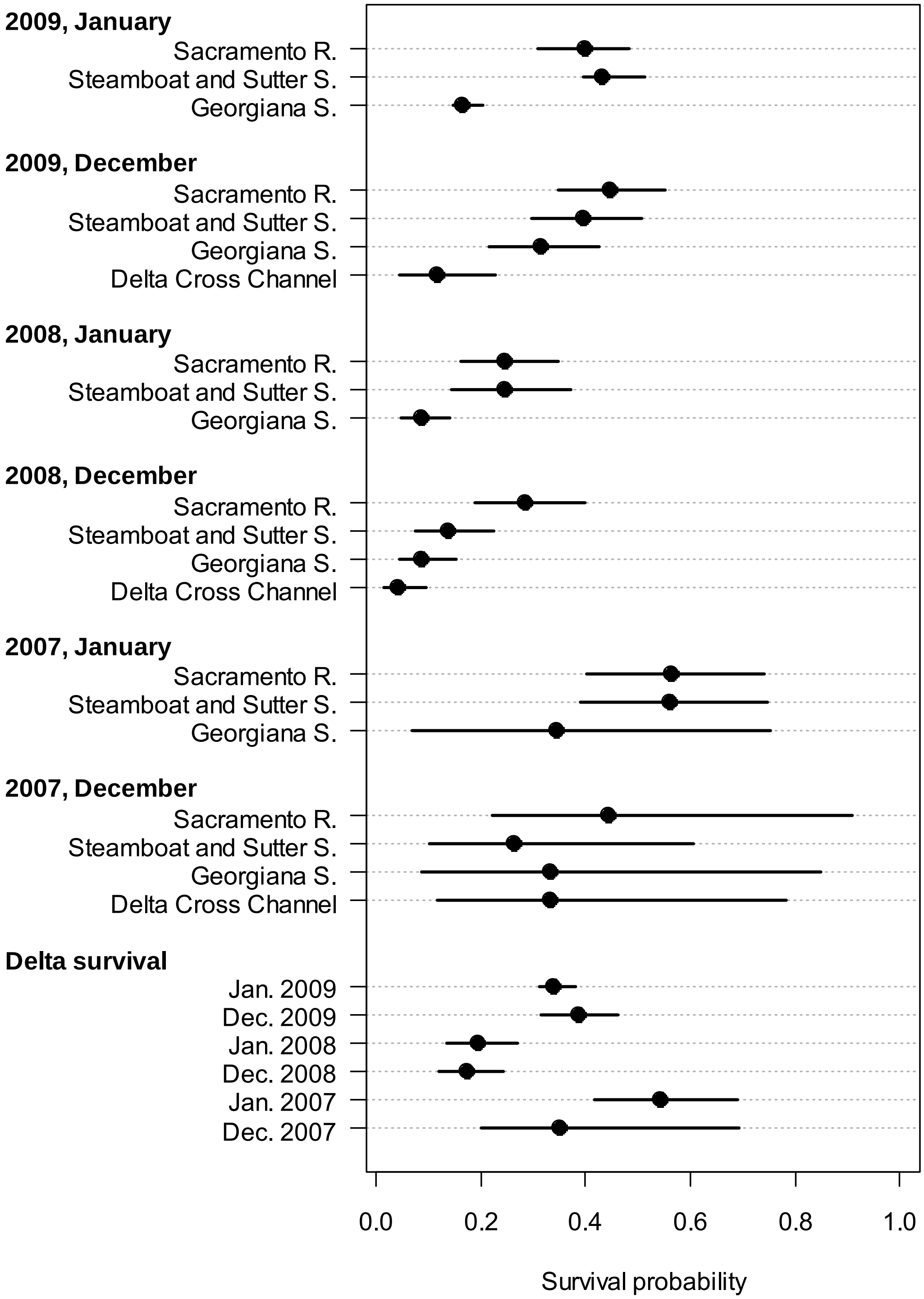

Figure 5.4. Summary of route-specific survival probabilities during migration years 2007–2009. Data points are organized by release group to facilitate comparison among routes within each release.

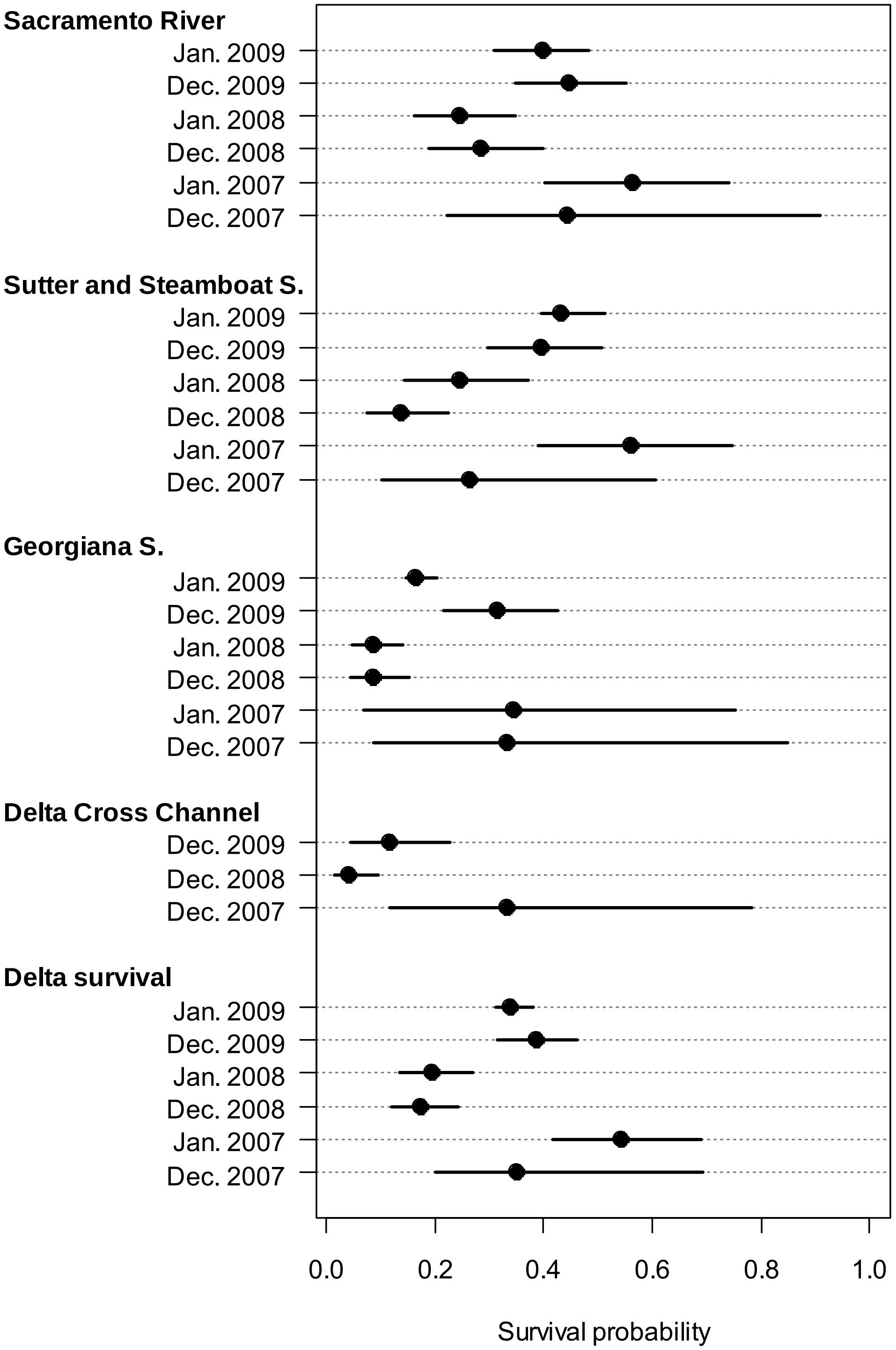

Figure 5.5. Summary of route-specific survival probabilities during migration years 2007–2009. Data points are organized by migration route to facilitate comparison among releases within each route.

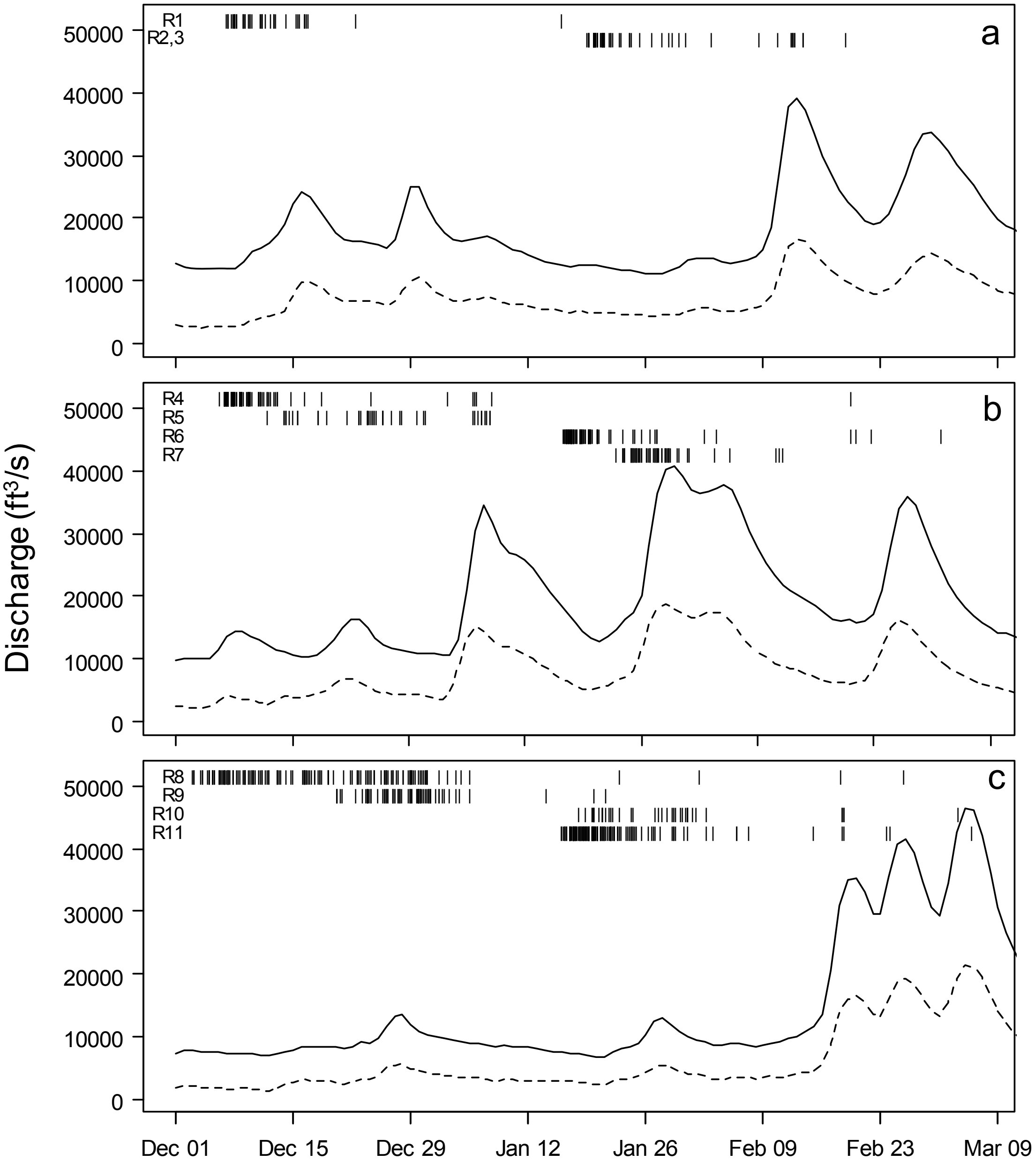

Figure 5.6. River conditions experienced by acoustic-tagged late-fall Chinook salmon smolts migrating through the Sacramento–San Joaquin River Delta during migration years a) 2007, b) 2008, and c) 2009. The solid line is mean daily discharge of the Sacramento River at Freeport and the dashed line is mean daily discharge of the Sacramento just downstream of Georgiana Slough. Tick marks show when tagged fish from each release group (R_1 – R_{11}) were detected at telemetry stations defining entry into migration routes used in the CJS survival model.

5.3.3 Factors affecting route-specific survival

For the CJS model, both λ and p varied among years, but not among releases within years. A model with a constant λ was not supported by AIC or LRT (Table 5.6). For constant p across years, the likelihood ratio test was significant at $\alpha = 0.05$, but not at $\alpha = 0.10$. However, since AIC increased with a 2-parameter decrease between models, I elected to use the year-specific p model for as the basis of model selection of group-level and individual-covariates (Table 5.6).

Table 5.6. Results of model selection to identify the best-fit CJS model for λ and p.

Parameter modeled	Model*	Number of parameters	AIC	NLL	LR	*P*
λ	S(rt*rel) p(rel) λ(rel)	49	1897.9	900.0		
	S(rt*rel) p(rel) λ(yr)	42	1889.2	902.6	5.3	0.63
	S(rt*rel) p(rel) λ(.)	40	1892.6	906.3	7.4	0.02
P	S(rt*rel) p(yr) λ(yr)	35	1879.1	904.6	5.8	0.57
	S(rt*rel) p(.) λ(yr)	33	1880.2	907.1	5.1	0.08

*Model notation is as follows: rel = release group, rt = route, and yr = migration year. An asterisk between variables indicates inclusion of both main effects and their interaction, and a period indicates an intercept-only model.

For group-level covariates, a nearly saturated model with route, year, study, and all possible interactions explained 85% of the discrepancy between the fully saturated and null models, whereas a model with only migration route and flow covariates explained 42%. These findings indicated that year and study shared common deviance with the flow covariates. The full covariate model explained 75.7% of the discrepancy in deviance between the saturated and null models, with year, study, and Q_S explaining most of this discrepancy (Table 5.7). I also found evidence of overdispersion as suggested by a mean error deviance of 1.5. Thus, even after accounting for the covariates, release-to-release variability was still greater than that expected by multinomial sampling variation. Year and study reduced the deviance more than any other variables and therefore appeared first in the ANODEV table (Table 5.7). Although route was not significant, it was entered next since the remaining flow variables were crossed with migration route indicator variables. Adding $(I_{Sac}+I_{SS})$:Q_S to the model explained significant deviance over that explained by route, year, and study, but none of the other flow variables were significant. Thus, the final model consisted of route, year, study, and $(I_{\mathrm{Sac}}+I_{\mathrm{SS}})\text{:}Q_{\mathrm{S}}$. The inclusion of year and study in the final model shows that river flow could not fully account for differences in survival among years or between studies.

Table 5.7. Analysis of deviance table for group covariates in the CJS model. Survival was modeled with year-specific p and λ. Indicator variables are I_{ID}, I_{Sac}, and I_{SS} for fish entering the interior Delta, Sacramento River, and Sutter and Steamboat Sloughs, respectively.

Source	Degrees of freedom	Deviance	Mean deviance	F	P-value
Total (saturated model)	29[*]	904.6			
Intercept (null model)	1	960.8			
Corrected total	28	112.4			
Covariate total	10	85.0	8.5	5.59	<0.001
Study	1	21.9	21.9	14.43	0.001
Year	2	33.9	16.9	11.15	<0.001
Route	2	4.5	2.2	1.47	0.255
$(I_{\mathrm{Sac}}+I_{\mathrm{SS}})\text{:}Q_{\mathrm{S}}$	1	18.1	18.1	11.94	0.003
$I_{\mathrm{ID}}\text{:}Q_{\mathrm{M}}$	1	4.8	4.8	3.15	0.092
$I_{\mathrm{ID}}\text{:}Q_{\mathrm{E}}$	1	1.1	1.1	0.70	0.414
$I_{\mathrm{SS}}\text{:}Q_{\mathrm{S}}$	1	0.7	0.7	0.45	0.512
$I_{\mathrm{ID}}\text{:}Q_{\mathrm{J}}$	1	0.1	0.1	0.07	0.800
Error	18	27.3	1.5		

[*] Release groups 2 and 3 were pooled as one group, and for this release group survival for the Interior Delta was fixed to 1 because all fish survived. For the saturated model, this led to 10 release groups, 3 routes, and 1 fixed parameter for a total of 10(3) - 1 = 29 degrees of freedom.

Individual covariates added six parameters to the saturated model but decreased AIC by 11 units, indicating that individual covariates explained considerable within-release variation in survival (Table 5.8). Model selection for individual covariates paralleled that for group-level covariates: flow variables for the interior Delta survival were not significant, nor was there a difference in slopes for Q_{S} between the Sacramento River and Sutter and Steamboat Sloughs (Table 5.8). However, when either fork length or $(I_{\mathrm{Sac}}+I_{\mathrm{SS}})\text{:}Q_{\mathrm{S}}$ were dropped from the model, model fit worsened considerably (Table 5.9). Thus, the best fit model with individual covariates consisted of release group, route, route:release group, $(I_{\mathrm{Sac}}+I_{\mathrm{SS}})\text{:}Q_{\mathrm{S}}$, and fork length. Despite the individual covariate model having 24 more parameters than the best-fit group covariate model, AIC for the individual covariate model (AIC = 1862.8) was 6.3

units less than for the group covariate model (AIC = 1869.1), indicating that individual covariates explained more variation in survival than group covariates alone.

Table 5.8. Results of model selection for the effect of individual covariates on survival. Survival was modeled with year-specific p and λ. Indicator variables are I_{ID}, I_{Sac}, and I_{SS} for fish entering the interior Delta, Sacramento River, and Sutter and Steamboat Sloughs, respectively.

Model or covariate dropped	Number of parameters	AIC	NLL	LR	*P*-value
Route*Release + all covariates	41	1869.2	893.6		
Route*Release – all covariates	35	1879.1	904.6	21.9	0.001
I_{ID}:Q_{J}	40	1867.2	893.6	0.0	1.000
I_{SS}:Q_{S}	39	1865.2	893.6	<0.1	0.888
I_{ID}:Q_{E}	38	1863.4	893.7	0.22	0.639
I_{ID}:Q_{M}	37	1862.8	894.4	1.41	0.235

Table 5.9. Likelihood ratio tests and AIC when each variable is dropped from the best fit model with individual covariates. Indicator variables are I_{ID}, I_{Sac}, and I_{SS} for fish entering the interior Delta, Sacramento River, and Sutter and Steamboat Sloughs, respectively.

Variable dropped	Number of parameters	NLL	Likelihood Ratio	AIC	ΔAIC	*P*-value
None (best fit)	37	894.4		1862.8	0.0	
Fork length	36	898.8	8.8	1869.6	6.8	0.003
(I_{Sac}+I_{SS}):Q_{S}	36	899.9	11.0	1871.8	9.0	0.001

5.3.4 Parameter estimates and predicted survival probabilities

Significant effects of study and year indicated that differences in survival among release groups could not be fully accounted for by my migration route and river flow (Table 5.10). A negative coefficient of -0.37 suggests that on average, release groups for the USFWS study exhibited lower survival than for the CALFED study. For example, predicted survival of the reference group (Sacramento R., 2009, CALFED study) is $\text{logit}^{-1}(0.71) = 0.67$ at the mean flow of 5127 ft^3/s, whereas for the USFWS, predicted survival is $\text{logit}^{-1}(0.71-0.37) = 0.58$. Among years, 2008 had a large negative coefficient, suggesting lower survival than in 2009. For example, relative to the reference group at the mean flow, predicted survival for 2007 and

2008 is $\text{logit}^{-1}(0.71-0.16) = 0.63$ and $\text{logit}^{-1}(0.71-1.19) = 0.38$. Among routes, the interior Delta had the largest negative coefficient despite being the shortest direct route to Chipps Island. Relative to the reference group, predicted survival for the interior Delta is $\text{logit}^{-1}(0.71-0.44) = 0.57$. These patterns of variation are consistent with my observations from the multistate model (Figures 5.4 and 5.5).

Although flow variables could not account for all variation among release groups, Sacramento River flow still explained significant variability in survival for the Sacramento River and Sutter and Steamboat sloughs. Positive slope estimates under both the group- and individual-covariate models show that survival is positively associated with Q_S (Tables 5.10 and 5.11). Under the group covariate model, most of the release groups experienced average flows <8000 ft^3/s, and two data points at higher discharge appear to be driving the relationship (both from release group 7; Figure 5.7). The individual covariate model strengthens the findings of the group covariate model because individuals from multiple releases experienced river discharge >8000 ft^3/s (Figure 5.6 and 5.8). For example, when release group 7 is excluded, Q_S remains statistically significant in the individual covariate model, suggesting that this release group was not driving the relationship. Under both models, predicted survival increases by about 40 percentage points over the observed range of discharge, although the slope is less steep under the individual covariate model (Figures 5.7 and 5.8).

The individual covariate model also revealed effects of fork length on survival and substantial among-release variation in survival. The slope estimate for fork length was positive, indicating that larger size was associated with higher survival (Table 5.11). The estimated slope for fork length was about half that of Q_S, and thus, a 1-SD change in fork length, when holding Q_S constant, results in a smaller change in survival than a 1-SD change in flow (when holding length constant; Table 5.8, Figure 5.8). For example, at the mean observed discharge, predicted survival increases by about 25 percentage points over the range in fork length, compared to a 40 percentage point change over the range in flow. Despite the relation of survival with fork length and Q_S, considerable release-to-release variation in survival remains. Mechanisms driving this variation remain unknown.

Table 5.10. Parameter estimates on the logit scale for group-level covariates best explaining survival and detection probabilities of the CJS model. Parameter estimates for categorical variables (Route, Year, and Study) are estimated as differences from a reference category set as the intercept.

Parameter modeled	Variable	Group description	$\hat{\beta}$ (SE)	95% Confidence interval (±1.96 SE)
S		Intercept (Sacramento R., CALFED, 2009)	0.71 (0.18)	0.35, 1.06
	Route	Sutter and Steamboat S.	-0.15 (0.18)	-0.49, 0.20
		Interior Delta	-0.44 (0.18)	-0.79, -0.09
	Year	2007	-0.16 (0.28)	-0.70, 0.39
		2008	-1.19 (0.19)	-1.56, -0.82
	Study	USFWS	-0.37 (0.20)	-0.77, 0.03
	$(I_{\mathrm{Sac}}+I_{\mathrm{SS}})Q_S$		0.74 (0.18)	0.38, 1.09
p	Year	Intercept (2009)	1.58 (0.20)	1.19, 1.96
		2007	-0.85 (0.38)	-1.60, -0.10
		2008	0.09 (0.34)	-0.58, 0.77
λ	Year	Intercept (2009)	1.75 (0.21)	1.34, 2.17
		2007	-0.95 (0.40)	-1.73, -0.18
		2008	-0.78 (0.30)	-1.37, -0.19

Table 5.11. Parameter estimates on the logit scale for individual-level covariates best explaining survival probabilities of the CJS model. Parameter estimates for categorical variables (Route and Release Group) are estimated as differences from a reference category set as the intercept. Parameter estimates for Release Group and Route:Release Group interaction terms can be found in Appendix Table 4.4.

Parameter modeled	Variable	Group description	$\hat{\beta}$ (SE)	95% Confidence interval (±1.96 SE)
S		Intercept (Sacramento R., Release group 5)	0.13 (0.50)	-0.84, 1.10
	Route	Sutter and Steamboat S.	-0.01 (0.81)	-1.60, 1.58
		Interior Delta	-0.58 (0.91)	-2.36, 1.20
	Fork length		0.26 (0.09)	0.09, 0.43
	$(I_{\mathrm{Sac}}+I_{\mathrm{SS}})Q_S$		0.52 (0.18)	0.17, 0.87
p	Year	Intercept (2009)	1.59 (0.20)	1.20, 1.98
		2007	-0.80 (0.37)	-1.53, -0.06
		2008	0.02 (0.35)	-0.67, 0.70
λ	Year	Intercept (2009)	1.77 (0.21)	1.35, 2.18
		2007	-0.90 (0.39)	-1.66, -0.13
		2008	-0.83 (0.30)	-1.43, -0.24

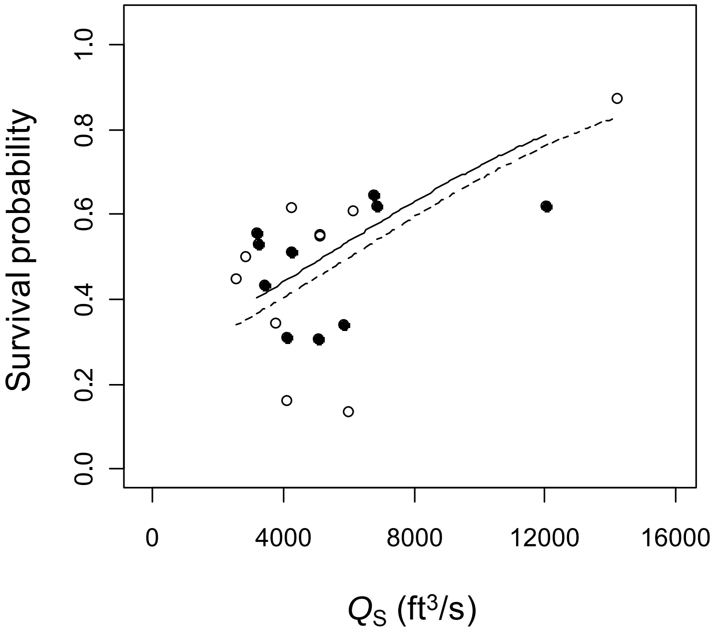

Figure 5.7. Predicted survival as a function of Q_S for the Sacramento River (solid line) and Sutter and Steamboat sloughs (dotted line) plotted against survival probabilities for the Sacramento River (filled circles) and Sutter and Steamboat sloughs (open circles). The fully saturated model was used to estimate route- and release group-specific survival probabilities. Predicted survival is plotted at the mean of group-specific intercepts estimated under the best-fit group covariate model.

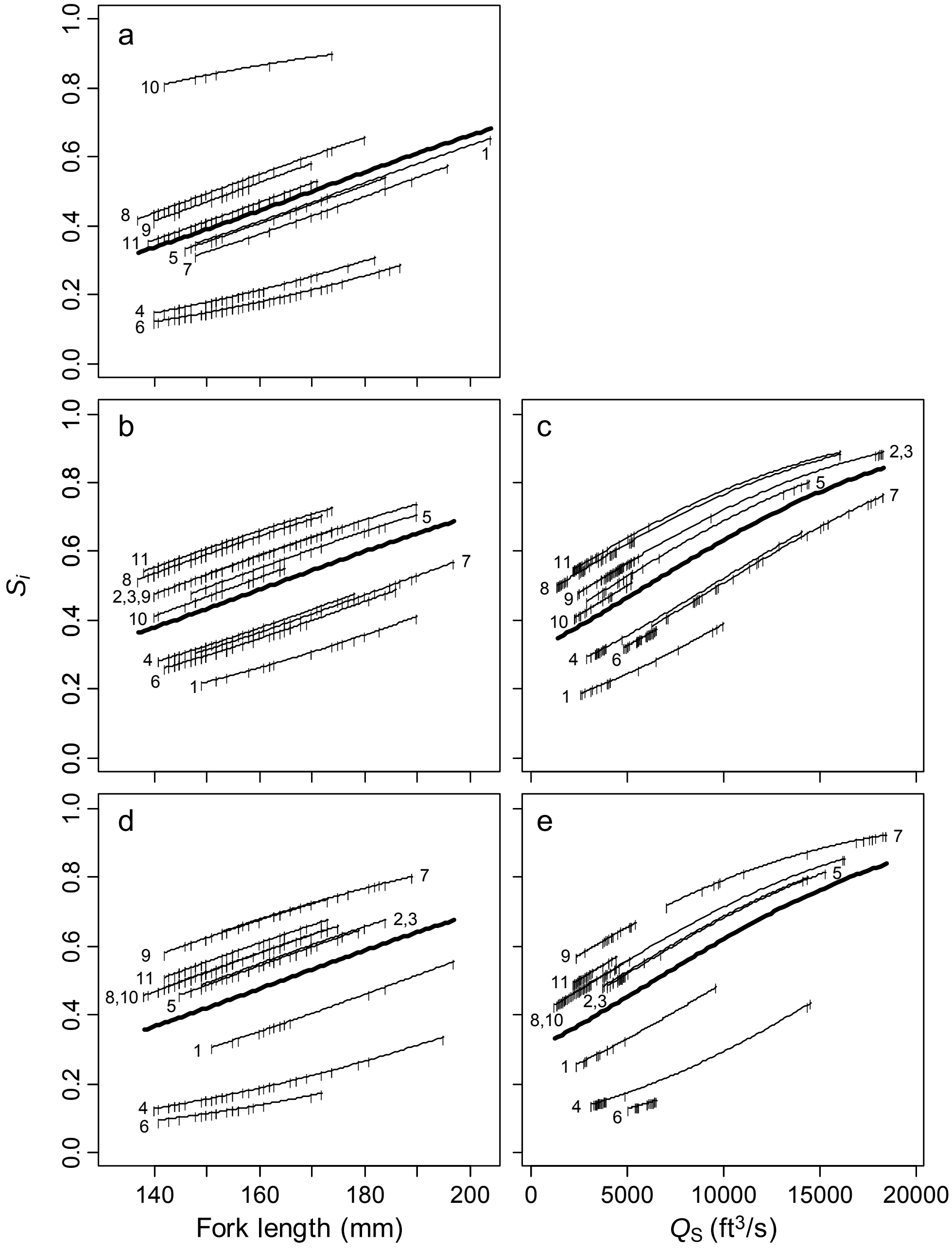

Figure 5.8. Predicted individual survival probabilities as a function of fork length (a, b, and d) and Q_S (c and e) for the interior Delta (a), the Sacramento River (b and c), and Sutter and Steamboat sloughs (d and e). Survival probabilities with respect to Q_S are calculated at the mean fork length (156.5 mm) and with respect to fork length are calculated at the mean discharge (5127 ft^3/s). Symbols show either observed fork lengths (a, b, and d) or observed flows when each fish entered a migration route (c and e). Each line is labeled by release group as defined in Table 5.2. The heavy line shows predicted survival plotted at the mean of release group-specific intercepts.

5.4 Discussion

Over the three-year duration of this study, I identified substantial variability in survival related to migration route, river flow, and fish size. Although considerable variability in survival remains unexplained, quantifying effects of river flow and migration route on survival helps to understand how water management actions might influence population-level survival. I observed stable patterns of variability in survival across migration routes, with migration routes leading to the interior Delta having lower survival than the Sacramento River or Sutter and Steamboat sloughs. Thus, water management actions affecting routing of fish through the Delta will influence population-level survival. My findings also suggest that decreases in discharge of the Sacramento River could reduce survival of fish migrating in the Sacramento River and Sutter and Steamboat sloughs. By combining both migration routing and survival in common framework, these relationships form the basis of dynamic models to simulate the effect of water management actions on population-level of survival.

The relation between Sacramento River flow and survival in Sacramento River and Sutter and Steamboat sloughs has important implications for management of water resources in the Delta. Climate change, upstream water withdrawals, and operation of the Delta Cross Channel alter river flow, and in turn, may affect survival of juvenile salmon. For example, at mean total inflows during this study (13642 ft^3/s at Freeport), flow of the Sacramento River downstream of the Delta Cross Channel increases from 2952 ft^3/s to 4791 ft^3/s upon closing the cross-channel gates (flows estimated from a regression model in Burau et al., 2007). My analysis suggests that survival would increase by about six percentage points due to this increase in discharge. Although relatively small, this change in survival must be considered simultaneously relative to survival in other routes and the fraction of fish using each migration. Closing the Delta Cross Channel reduces the fraction of fish entering the interior Delta where survival is low, and increases the fraction remaining in the Sacramento River where survival increases due to the increase in flow. Thus, water management actions that influence routing of fish as well as survival within routes can have a compounding effect on population survival.

Although smolt survival in two routes was positively associated with river flow, it is important to recognize that other variables correlated to river flow likely also affect survival. For example, tidal fluctuations may affect survival of juvenile salmon by influencing predator encounter rates. As river inflow increases, tidal fluctuations is discharge are dampened (Figure 5.2; also see Figure 6.8). In turn, the point at which the Sacramento River reverses direction on flood tides moves further downstream. These hydrodynamics govern the movements of juvenile salmon by advecting fish upstream on flood tides. Tidal excursions are large when river inflow is low, which increases the distance that fish are advected upstream. Fish pass stationary predators at most once when river discharge is unidirectional, but fish may experience multiple encounters with predators when they are advected upstream with the tides. Thus, although survival decreased with discharge, survival was also inversely related to tidal fluctuations. I suspect that the steepness of flow-survival relation is driven by both river inflow and by tidal fluctuations that affect predator encounter rates. Due to the correlation of river flow with other variables that might affect survival, caution should be exercised when using the flow-survival relation to predict survival in response to water management actions. For example, structural changes to the Delta that alter the relation between river flow and tidal dynamics (e.g., levee breaches) could change the relation between river discharge and survival.

Inability to identify a relation between flow and survival for the interior Delta is not unexpected given the small sample size relative to the spatial and hydrodynamic complexity of the interior Delta. Only 287 fish entered the interior Delta whereas 645 fish from both the Sacramento River and Sutter and Steamboat sloughs were used to estimate the relation between survival and Q_S. To detect a significant covariate effect, Hoffman and Skalski (1995) showed that 300 fish were needed to achieve 70% power ($\alpha = 0.05$) when the individual covariate caused survival to range between 0.5 and 1.0. Baseline survival and capture probabilities in their simulation was on the same order of magnitude observed here, but their study was comprised of three intervals (i.e., reaches), all of which informed the estimate of the slope. In our case, we modeled a single reach and had smaller sample size. Thus, even if an underlying relation existed, power to detect such a relation was likely low.

The interior Delta is a complex environment with multiple alternative migration routes, which also makes it difficult to link mean river flows to survival. Each migration pathway through the interior Delta differs in biotic and abiotic processes that could influence survival. Furthermore, hydrodynamics in the interior Delta are affected not only by river inflow and water exports, but also by tidal dynamics. The particular migration route used by fish migrating through the interior Delta is probably determined more by hourly-scale flow patterns when fish enter this region, rather than by daily scale mean flows as used in my analysis. In turn, the particular pathway used to migrate through the interior Delta could ultimately determine an individual's probability of surviving. Although the interplay between mean river inputs and exports may influence migration routing and survival, given the complexity of the interior Delta, substantially larger sample sizes over a wide range of conditions will likely be needed to detect such an effect. Newman and Brandes (2010) came to the same conclusion in an analysis of the export effects of survival of coded-wire-tagged juvenile salmon. Similar to my findings, they found that survival of fish through the Interior Delta was substantially lower than fish migrating through the Sacramento River. However, unexplained environmental variability was so large that an effect of exports on survival could not be detected.

Although a positive relation between survival and fish size in unsurprising, mechanisms driving this relation are less clear. Large juvenile salmon are better able to evade predators and preclude consumption by smaller predators (Sogard, 1997). However, a tag effect could also partially explain size-dependent survival. In this study, fish size was restricted above 140 mm to maintain tag-to-body mass ratios below 5%, a threshold beyond which growth and swimming performance of tagged juvenile salmon declines (Adams et al., 1998a, 1998b). Nonetheless, negative effects of the transmitter may persist: larger fish are better able to carry a tag of a given size. Thus, the magnitude with which size affects survival may be influenced by both predation and the effect of the tag. That is, smaller tagged fish may be less capable of evading predators than similarly sized untagged fish, whereas differences in survival between tagged and untagged fish may disappear as fish size increases. Such an interaction would increase the slope of the relation between fish size and survival relative to that expected for untagged fish. This potential interaction should be kept in mind when interpreting size-dependent survival observed in this study.

Among release groups, I identified systematic differences in survival among years and between studies. Mechanisms driving release-, year- and study-specific differences in survival remain unknown, but I present three potential hypotheses: 1) episodic events related to handling and release of tagged fish, 2) differences in expression of post-release mortality experienced by fish released at different locations, and 3) environmental factors that may have influenced survival but were not included in the model. First, the nature of mark-recapture studies requires that animals be handled, tagged, transported, and released; therefore, such studies are subject to unforeseen events that may subsequently compromise the survival of tagged animals. For example, release group 1 may have experienced handling mortality due to buckling of the net pen in which fish were held (P. Brandes, USFWS, personal communication), but the extent of this mortality is unknown.

A second possible mechanism explaining study-specific differences in survival is initial culling of unfit hatchery fish that occurs shortly after release. On average, fish released for the USFWS study exhibited lower survival, but were also released into the Sacramento River >176 km downstream of fish from the CALFED study. Since late-fall Chinook used in this study were obtained directly from a hatchery, all fish were naïve to the natural river environment and likely underwent some period of acclimation during which they could have been subject to higher mortality. If fish released further upriver experienced such mortality prior to arrival in Delta whereas fish released downriver had not yet fully expressed this mortality upon entering the Delta, then differences in route-specific survival might be expected. Such differential mortality among groups of fish released in different locations has been suspected in the both the Columbia River (Muir et al., 2001; Skalski et al., 2009b) and the Sacramento River (Newman, 2003). Although a plausible explanation, this hypothesis is not supported by observed survival estimates for 2009. Release locations in 2009 were the same as in 2008 yet survival estimates for between studies were similar (Figure 5.8).

A third explanation is that I failed to include critical variables that would explain the remaining variability among release groups not accounted for by migration route, river flow, or fish size. Since predation is a major source of juvenile salmon mortality in the Delta (Lindley and Mohr, 2003), mechanisms influencing predation rates could account for unexplained variability in survival. For example, turbidity can affect predation rates by affecting the reaction distance at which predators can detect prey (Gregory and Levings, 1998), and recapture ratios of juvenile salmon in the Delta have been positively associated with turbidity (Newman, 2003). In addition, since arrival timing at entry points to migration routes did not completely overlap among release groups, shifts in the spatial distribution of predators could cause differential mortality among release groups over and above that expected from river flow. High temperature has also been shown to negatively affect survival of juvenile salmon in the Delta (Baker, 1995; Newman and Rice, 2002; Newman, 2003), but fish migrating between December and February experience a much narrower range of temperatures (about 6 – 12 °C) than observed in these studies (e.g., mean temperature was 18.7°C in Newman's 2003 analysis). These hypotheses remain fruitful avenues of exploration to explain release-to-release variation in survival not explained by migration route, river flow, and fish size.

In a system complex as the Delta, management models are needed to understand how human- and natural-caused changes to the Delta influence dynamics of endangered fish populations. However, parameterizing such models with empirical data is difficult precisely due to the Delta's complexity. My analysis has taken an important step by providing a modeling framework and quantifying important mechanisms affecting survival. In this chapter, I found that survival differed among migration routes and was influenced by fish size and route-specific river flow. These relationships can be incorporated into the multistate framework to quantify population-level survival in response to survival in different migration routes. Although route-specific survival is clearly an important component of population survival, understanding the dynamics of migration routing is also critical. Therefore, in the next chapter, I focus on modeling entrainment probabilities as a function of tides, river flow, and gate operations. Given dynamic relationships for both migration routing and survival, managers can begin to understand how both components change simultaneously to drive survival of juvenile salmon emigrating through the Delta.

Chapter 6

EFFECT OF TIDES, RIVER FLOW, AND GATE OPERATIONS ON ENTRAINMENT OF JUVENILE SALMON INTO THE INTERIOR DELTA

6.1 Introduction

Understanding how juvenile salmon distribute among migration routes in the Sacramento-San Joaquin River Delta is critical to devise management strategies that improve survival through the Delta. Juvenile salmon that enter the interior Delta via the Delta Cross Channel and Georgiana Slough survive at a lower rate than fish migrating within the Sacramento River (Chapter 4; Perry et al. 2010; Newman and Brandes, 2010). Consequently, the Delta Cross Channel is prescriptively closed in mid-December each year under the rationale that fish distribute among migration routes in proportion to the discharge entering each route (Low et al., 2006). Closing the Delta Cross Channel reduces the fraction of mean Sacramento River inflow entering the interior Delta by about 30 percentage points. A coincident reduction in entrainment into the Interior Delta would increase population survival by shifting fish from low- to high-survival migration routes. However, the nature of the relationship between flow distribution and fish distribution is poorly quantified. The mean proportion of flow entering the interior Delta has been positively related to counts of juvenile Chinook salmon at pumping facilities, but these relations are driven by two influential observations (Low et al., 2006). Furthermore, recent analyses of acoustic telemetry data have shown that the proportion of fish entering each migration route can deviate considerably from the proportion of flow (Chapter 4). Identifying mechanisms that affect entrainment into the interior Delta will therefore provide a basis for quantifying how management actions affect survival of juvenile salmon.

At a given river junction, a number of factors influence whether a fish enters a particular river channel. Both the relative distribution of flow among river channels and the spatial distribution of fish migrating through a river junction will influence the probability of entering a given river channel. Intuitively, fish migrating through a river junction close to one shore will likely remain in the channel along that shore, whereas fish along the opposite shore will tend to enter the opposite channel. How fish are distributed in the channel cross-section relative to longitudinal division of flow vectors entering each channel will dictate the proportion of fish entering each channel relative to the proportion of flow. This conceptual model suggests that fish distribution relative to flow distribution will remain constant at a given set of river conditions for a given population of juvenile salmon. However, it is unclear whether the ratio of fish to flow, here defined as the entrainment efficiency of a given channel, will remain constant as total discharge varies.

Interactions between behavioral and physical processes affect the spatial distribution of fish, and in turn, the relationship between river discharge and entrainment efficiency. Secondary circulation at river bends is a phenomenon where surface velocity vectors are directed towards the outside of a river bend, dive toward the bottom, and then return toward the inside of the bend along the river bottom (Dinehart and Burau, 2005a). Surface-oriented behavior of juvenile salmon could interact with secondary circulation to concentrate juvenile salmon on the outside of river bends. Since the strength of secondary circulation increases with total discharge, entrainment efficiencies for channels on the outside of a river bend could increase with discharge, implying a relationship between fish and flow that is not strictly proportional. The vertical distribution of juvenile salmon may also vary on a diel basis (Beeman and Maule, 2006). At the junction of the Delta Cross Channel and Sacramento River, juvenile salmon are typically shallower at night than during the day (Blake and Horn, 2003, 2006). The consequence of these behavioral responses in terms of probability of entrainment into a given channel will depend on river conditions when fish arrive at a river junction.

River discharge at many junctions in the Delta varies not only on daily and seasonal time scales, but also on hourly time scales due to tidal forcing. At the junction of the Sacramento River, Delta Cross Channel, and Georgiana Slough, the Sacramento River often reverses direction and flows upstream on flood tides, with water entering Georgiana Slough and the Delta Cross Channel from both the upstream and downstream directions (Dinehart and Burau, 2005b; Blake and Horn, 2003, 2006). Clearly, if juvenile salmon arrive at the river junction when all water is flowing into the interior Delta, they will have a high probability of entering the interior Delta. Only a few hours later on the peak ebb tide, very little water flows into the Delta Cross Channel even though the gates are open. Fish arriving during this tidal stage will have a low probability of entering the Delta Cross Channel. Between these extremes, transition between tidal stages affect the cross-sectional distribution of fish in river junction (Blake and Horn, 2003, 2006), which in turn will influence entrainment probabilities. Hourly variation in entrainment probabilities integrate over each day of the juvenile salmon migration season, ultimately determining the fraction of the population entrained into the interior Delta. Linking the influence of hourly variation in entrainment probabilities on population-level entrainment into the interior Delta remains a formidable challenge in understanding the effects of management actions on juvenile salmon distribution.

The objective of this chapter is to understand how entrainment probabilities vary with hourly, diel, daily, and seasonal variation in river discharge at the junction of the Sacramento River with the Delta Cross Channel and Georgiana Slough. Ultimately, managers need models informed by reliable data to understand biological consequences of water management actions such as operation of the Delta Cross Channel. With this end in mind, I first develop a multinomial regression model to quantify entrainment probabilities of individual fish in response in flow variables. I then use this model to 1) examine variation in predicted entrainment probabilities at a range of temporal scales and 2) determine whether fish are likely to distribute in direct proportionality to the fraction of mean flow entering the interior Delta. Last, I illustrate how my model can be used to understand the effect of alternative management actions on entrainment of fish into the interior Delta by simulating entrainment probabilities under two scenarios of Delta Cross Channel gate operations.

6.2 Methods

I used a multinomial regression model to quantify the effect of hydraulic conditions of the river junction on the migration routes used by acoustically tagged fish. I used all acoustic telemetry data to date (winters of 2007-2009) where the migration of tagged fish was monitored at the junction of the Sacramento River with the Delta Cross Channel and Georgiana Slough. Gauging stations at this junction provide a nearly continuous record of river discharge entering each of these channels, providing the covariates for analysis. A multinomial model with individual covariates is an attractive framework for this problem: For each fish, the model estimates the probability that it will enter one of three river channels given the river conditions when it entered the junction.

6.2.1 Telemetry data

I used telemetry data on Late-fall Chinook salmon from three studies: 1) the U.S. Fish and Wildlife Service (referred to as "USFWS"; Perry et al., 2010), 2) NOAA Fisheries and University of California at Davis (referred to as "CALFED"; http://californiafishtracking.ucdavis.edu/, accessed December 2009), and 3) and the U. S. Geological Survey (referred to as "USGS"; Vogel, 2008; Table 6.1). For the first two studies, all fish were monitored by the same set of VEMCO telemetry equipment, as described in Chapters 3 and 4. The USGS study used telemetry equipment from HTI (Hydroacoustic Technologies Inc., Seattle, WA). For all studies, telemetry stations were situated just downstream of the entrance to the Delta Cross Channel and Georgiana Slough to detect fish as they left the Sacramento River and entered these routes (Figure 6.1). In the Sacramento River, telemetry stations were located from just upstream of the Delta Cross Channel to just downstream of Georgiana Slough (Figure 6.1). The location of telemetry stations varied among studies and years but all stations were ≤1 km from the entrance of the Delta Cross Channel or Georgiana Slough. Each telemetry station recorded the date and time when tagged fish passed by each telemetry station.

Telemetry data consisted of fish released during the winters of 2007, 2008, and 2009 in 13 different release groups (Table 6.1). All studies used late-fall Chinook salmon from Coleman National Fish Hatchery. All transmitters were surgically implanted and fish were released using methods similar to those described in Chapter 3. Although release sites varied among studies and years, all fish were released a minimum of 40 km upstream of the river junction (Figure 6.1). The fraction of each release group arriving at the river junction depended on upstream mortality rates and the proportion of fish entering Sutter and Steamboat sloughs, which diverges from the Sacramento River upstream of the Delta Cross Channel and Georgiana Slough. Overall, 714 fish were detected at the river junction, representing 38% of all fish released. About 29% of fish detected at the junction passed the Delta Cross Channel when its gates were open with the remainder passing the junction with the gates closed (Table 6.1).

Table 6.1 Sample sizes for release groups of juvenile late-fall Chinook salmon implanted with acoustic tags during the winters of 2007 – 2009. DCC = Delta Cross Channel.

Release group	Study	Year	Release dates	Number released	Number detected at junction	Number with DCC open	Fraction detected at night
1	USFWS	2006	Dec 5 – Dec 6	64	36	32	0.86
2	USGS		Dec 11– Dec 12	96	57	49	0.70
3	USFWS	2007	Jan 17 – Jan 18	80	39	0	0.85
4	USGS		Jan 12 –Jan 23	166	55	0	0.85
5	CALFED		Jan 16–Feb 2	200	11	0	0.55
6	USFWS		Dec 4 – Dec 5	149	76	73	0.79
7	CALFED		Dec 7	150	36	3	0.72
8	USFWS	2008	Jan 15 –Jan 16	130	85	0	0.72
9	CALFED		Jan 17	154	49	0	0.63
10	USFWS		Nov 30 –Dec 4	192	91	47	0.81
11	CALFED		Dec 13	149	57	1	0.82
12	CALFED	2009	Jan 11	151	30	0	0.70
13	USFWS		Jan 13 –Jan 17	192	92	0	0.64
All groups				1873	714	205	0.75

Telemetry data were organized into discrete detection events, and the fate of each fish was assigned to one of the three river channels based on the time series of detection events. The minimum criterion for a detection event consisted of two consecutive detections within 30-min period at a given telemetry station (Skalski et al., 2001; Pincock, 2008; Perry et al., 2010). Detections failing this criterion were considered inadequate for route assignment and excluded from analysis. A detection event ended with a time lapse of >1 h between detections at a given station, or when fish were detected at a different location. A migration route (S = Sacramento River, G = Georgiana Slough, and D = Delta Cross Channel) was assigned to each fish based on its final detection location in the time series of detection events at the river junction (Figure 6.1). The time of entrance to each channel was defined by the first detection of the final detection event upon entering a given river channel.

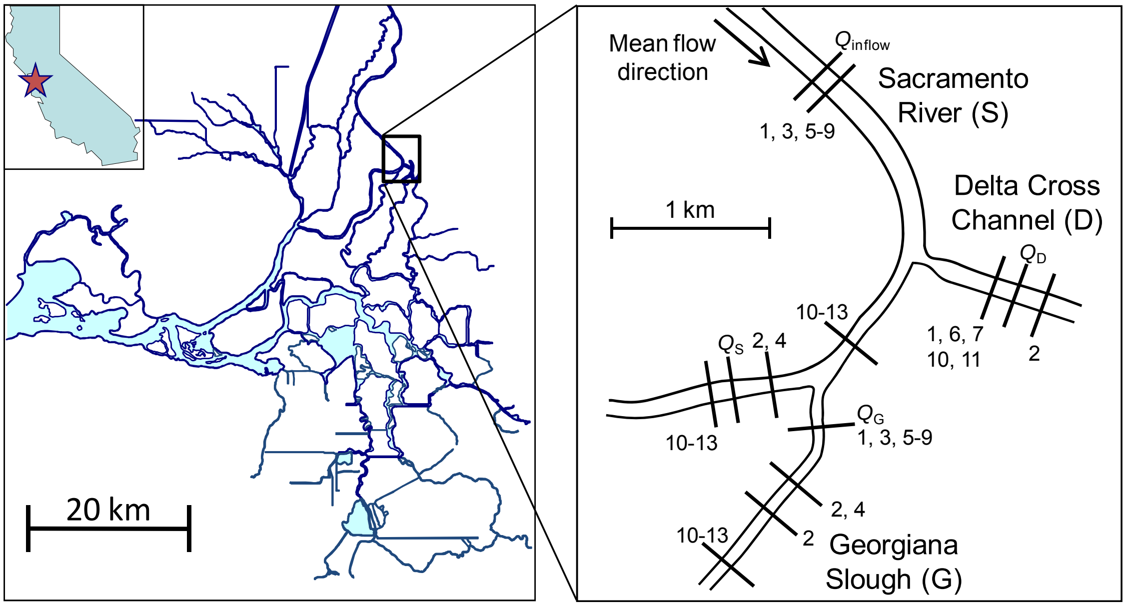

Figure 6.1. Map of the Sacramento–San Joaquin River Delta and the junction of the Sacramento River with the Delta Cross Channel and Georgiana Slough showing the location of telemetry stations and discharge gauging stations. Discharge gauging stations in each channel a labeled as *Q*. Telemetry stations are labeled by the particular release groups monitored at that location (see Table 6.1 for detail on release groups).

6.2.2 Model development

The three migration routes (S, G, D) used by each fish form a categorical response variable that is distributed as trinomial when the Delta Cross Channel gate is open and binomial when the gate is closed. The probability distribution for each individual can be expressed as

$$P\left(Y_{ij} = y_{ij}\right) = \pi_{i,\text{D}}^{y_{i,\text{D}}} \pi_{i,\text{G}}^{y_{i,\text{G}}} \pi_{i,\text{S}}^{y_{i,\text{S}}} \qquad \text{when the Delta Cross Channel is open}$$

and $$P\left(Y_{ij} = y_{ij}\right) = \pi_{i,\text{G}}^{y_{i,\text{G}}} \pi_{i,\text{S}}^{y_{i,\text{S}}} \qquad \text{when the Delta Cross Channel is closed,}$$

where $y_{ij} = 1$ when the *i*th fish enters the *j*th river channel and zero otherwise, and π_{ij} is the probability of the *i*th individual entering the *j*th river channel. The probability of entering the interior Delta, π_{ID}, is $\pi_{\text{D}} + \pi_{\text{G}} = 1 - \pi_{\text{S}}$. More generally, the distribution for each individual can be represented as

$$P\left(Y_{ij} = y_{ij}\right) = \pi_{i,\text{D}}^{y_{i,\text{D}} I_{i,\text{D}}} \pi_{i,\text{G}}^{y_{i,\text{G}}} \pi_{i,\text{S}}^{y_{i,\text{S}}} \qquad (6.1)$$

where $I_{i,\mathrm{D}}$ is an indicator variable resolving to one if the *i*th fish passes the river junction when the Delta Cross Channel gate is open and zero if it passes the junction when the gate is closed.

I also explored an alternative formulation of the distribution using conditional branching probabilities. With only downstream river flow, fish first past by the Delta Cross Channel but can enter Georgiana Slough only if they fail to enter the Delta Cross Channel. Under this rationale, the probability distribution when the Delta Cross Channel is open can be constructed as

$$P\left(Y_{ij}=y_{ij}\right)=\pi_{i,\mathrm{D}}^{y_{i,\mathrm{D}}}\left(\left(1-\pi_{i,\mathrm{D}}\right)\pi_{i,\mathrm{G|S}}\right)^{y_{i,\mathrm{G}}}\left(\left(1-\pi_{i,\mathrm{D}}\right)\left(1-\pi_{i,\mathrm{G|S}}\right)\right)^{1-y_{i,\mathrm{D}}-y_{i,\mathrm{G}}} \tag{6.2}$$

where $\pi_{i,\mathrm{G|S}}$ is the probability of an individual entering Georgiana Slough conditional on remaining in the Sacramento River at the Delta Cross Channel (Figure 6.1). I found that likelihood functions formed from either Eqns. 6.1 or 6.2 were maximized at the same value. Therefore, use of either parameterization is a matter of interpretation rather than goodness-of-fit. Since the river flows in both directions at this junction, fish can pass by both routes D and G, only to be advected upstream with the tides to ultimately enter either route. Therefore, I chose to use unconditional probabilities represented in Eqn. 6.1 because fish movement through this junction does not strictly adhere to a conditional branching process. Multi-route river junctions with unidirectional river flow may be better modeled with the conditional branching structure of Eqn. 6.2. Such a junction occurs where Sutter Slough and Steamboat Slough branch off the Sacramento River (see Figures 1.2 and 2.7).

My goal was to model entrainment probabilities (π_{ij}) as a function the hydraulic conditions of the river junction at the time the *i*th fish entered the *j*th migration route. I used a generalized linear model framework with a baseline-category logit function to link $g(\pi_{ij})$ to a linear combination of the explanatory variables

$$g\left(\pi_{ij}\right)=\ln\left(\frac{\pi_{ij}}{\pi_{iJ}}\right)=\beta_{j0}+\beta_{j1}x_{ij1}+\ldots+\beta_{jp}x_{ijp}=\boldsymbol{\beta}'_{j}\mathbf{x}_{ij} \tag{6.3}$$

where π_{ij} is measured relative to the baseline category π_{iJ}, β_{j0} is the intercept for the *j*th migration route, and β_{jk} are slope parameters for $k = 1, \ldots, p$ explanatory variables (x_{ijk}) for the *i*th individual and *j*th route. I used the Sacramento River route (J = S) as the baseline category against which to measure the probabilities of entering the Delta Cross Channel and Georgiana

Slough. I modeled each baseline logit function with its own set of explanatory variables, allowing a different set of variables to affect the probability of entrainment into each river channel. Entrainment probabilities are expressed directly as a function of the explanatory variables by taking the inverse of the baseline-category logits:

$$\pi_{ij} = \frac{\exp\left(\boldsymbol{\beta}_j' \mathbf{x}_{ij}\right)}{\sum_{h=1}^{J} \exp\left(\boldsymbol{\beta}_h' \mathbf{x}_{ih}\right)} \tag{6.4}$$

where $\boldsymbol{\beta}_J$ for the baseline category (J = S) is set to zero.

I estimated the regression parameters by maximizing the log likelihood function of the joint probability distribution over all individuals. The log-likelihood function for the data set of n fish is

$$\ln L\left(\boldsymbol{\pi} \mid \mathbf{Y}\right) = \ln\left(\prod_{i=1}^{n} \pi_{i,\mathrm{D}}^{y_{i,\mathrm{D}} I_{i,\mathrm{D}}} \pi_{i,\mathrm{G}}^{y_{i,\mathrm{G}}} \left(1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}\right)^{1 - y_{i,\mathrm{D}} I_{i,\mathrm{D}} - y_{i,\mathrm{G}}}\right)$$

$$= \sum_{i=1}^{n} y_{i,\mathrm{D}} I_{i,\mathrm{D}} \ln \pi_{i,\mathrm{D}} + y_{i,\mathrm{G}} \ln \pi_{i,\mathrm{G}} + \left(1 - y_{i,\mathrm{D}} I_{i,\mathrm{D}} - y_{i,\mathrm{G}}\right) \ln\left(1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}\right)$$

$$= \sum_{i=1}^{n} y_{i,\mathrm{D}} I_{i,\mathrm{D}} \ln \pi_{i,\mathrm{D}} + y_{i,\mathrm{G}} \ln \pi_{i,\mathrm{G}} + \ln\left(1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}\right) - y_{i,\mathrm{D}} I_{i,\mathrm{D}} \ln\left(1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}\right)$$
$$- y_{i,\mathrm{G}} \ln\left(1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}\right)$$

$$= \sum_{i=1}^{n} y_{i,\mathrm{D}} I_{i,\mathrm{D}} \ln\left(\frac{\pi_{i,\mathrm{D}}}{1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}}\right) + y_{i,\mathrm{G}} \ln\left(\frac{\pi_{i,\mathrm{G}}}{1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}}\right) + \ln\left(1 - I_{i,\mathrm{D}}\pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}\right) \tag{6.5}$$

Since the probabilities must sum to one, $\pi_{i,\mathrm{S}} = 1 - \pi_{i,\mathrm{D}} - \pi_{i,\mathrm{G}}$ for the baseline category. Eqn. 6.5 shows explicitly how the baseline category logits given in Eqn. 6.3 arise as the natural parameters of the multinomial distribution (Agresti, 2002).

To express the likelihood function in terms of the explanatory variables (x_{ijk}) and regression parameters (β), the baseline-category logits in the first two terms of Eqn. 6.5 are replaced with Eqn. 6.4, and π_{ij} in the last term is substituted with Eqn. 6.4, which reduces to:

$$\ln L\left(\boldsymbol{\pi} \mid \mathbf{Y}\right) = \sum_{i=1}^{n}\left[y_{i,\mathrm{D}} I_{i,\mathrm{D}} \left(\boldsymbol{\beta}_{\mathrm{D}}' \mathbf{x}_{i,\mathrm{D}}\right) + y_{i,\mathrm{G}} \left(\boldsymbol{\beta}_{\mathrm{G}}' \mathbf{x}_{i,\mathrm{G}}\right) + \ln\left(1 + I_{i,\mathrm{D}} \exp\left(\boldsymbol{\beta}_{\mathrm{D}}' \mathbf{x}_{i,\mathrm{D}}\right) + \exp\left(\boldsymbol{\beta}_{\mathrm{G}}' \mathbf{x}_{i,\mathrm{G}}\right)\right)\right].$$

The parameters were estimated using optimization routines in the R statistical computing platform (R Development Core Team, 2008) to minimize the negative log-likelihood function with respect to the parameters. The variance of the parameter estimates were estimated using the diagonal elements of the inverse of the Hessian matrix.

6.2.3 Explanatory variables

River discharge (Q_j), water velocity (V_j), and the proportion of total outflow (p_{Q_j}) entering each river channel were the primary variables used to explain variation in entrainment probabilities. USGS gauging stations are located just downstream of the entrance to these channels (Q_S, Q_D, and Q_G) and total discharge entering the junction is measured by a gauging station just upstream of the river junction (Q_inflow, Figure 6.1). These gauging stations record discharge and water velocity every 15 min, providing detailed information about the hydraulic conditions that tagged fish experienced when they migrated through the river junction.

Hydraulic conditions of the river junction were assigned to each fish based on the time of detection in each river channel. However, inconsistency in the location of telemetry stations among release groups (Figure 6.1, Table 6.1) introduced variability when basing covariate values on detection times at a given station. For example, because flow changes quickly with the tides, discharge of Georgiana Slough when a fish passes the telemetry station located near this flow gauge (Q_G in Figure 6.1) could differ substantially from the discharge when the same fish passes the telemetry station 1 km downstream of the flow gauge (Figure 6.1). To account for this variability, I referenced all detection times to a common spatial location in each channel by estimating the transit time of each fish from telemetry station to gauging station. Transit times were estimated from cross-sectional water velocities and distances between each telemetry station and gauging station. Thus, let Q_{ij} represent the discharge entering channel j when the ith fish is estimated to have passed a gauging station. The full model based on covariates from spatially-referenced detection times fit the data much better than did the same model with unreferenced times: Akaike's Information Criterion (AIC) = 800.8 and the minimum negative log-likelihood (NLL) = 384.4 for spatially referenced covariates compared to AIC = 876.8 and NLL = 422.4 for unreferenced covariates (lower values indicate better fit for both measures; Burnham and Anderson, 2002).

The effect of tidal fluctuations on hydraulic conditions of the river junction was captured by two variables. First, I calculated the rate of change in discharge of the Sacramento River as $\Delta Q_S(t) = Q_S(t{+}1) - Q_S(t)$ where t is measured in units of 15 minutes. This variable accounts for hydraulic conditions that may be quite different on a flood-to-ebb transition compared to an ebb-to-flood transition, even though total discharge may be similar during each transition. When ΔQ_S is negative, discharge is decreasing, which typically occurs during the transition from an ebb tide to a flood tide. In contrast, when ΔQ_S is positive, discharge is increasing, as typified by the transition from a flood to an ebb tide. Second, U is a dummy variable set to one when water is flowing upstream in the Sacramento River (i.e., $U = 1$ when $Q_S < 0$), and zero otherwise. Statistical significance of this variable indicates that water flowing upstream into the junction affects entrainment probabilities over and above the influence of Q_{ij}.

I included a number of other variables in the analysis unrelated to hydraulic conditions but that may also affect the probability of fish entering a given migration route. These variables included fork length (L, mean = 155.9 mm, range = 118 – 204 mm), time of day (a dummy variable where $D = 1$ for fish detected during day and $D = 0$ for night), and daily water temperature (T, mean = 9.4, range = 6.6 – 12.4 degrees) when fish passed through the river junction.

6.2.4 Model selection

To identify variables that affect entrainment probabilities, I formed an initial full model that included all possible explanatory variables and then eliminated variables that failed to improve model fit to the data. Each variable in $g(\pi_D)$ or $g(\pi_G)$ was dropped one-at-a-time from the full model, fit to the data, and a likelihood ratio test used to determine whether dropping the variable resulted in a significantly poorer fit of the model to the data. The variable with the largest P-value was eliminated from the model, a new "full" model was formed, and variables were again dropped one-at-a-time and fit to the data. This process was repeated until no further variables could be dropped from the model at $\alpha = 0.05$. Given a fully reduced model of main effects, I then formed all possible two-way interactions (i.e., products of variables) and used reverse elimination of interaction terms to arrive at a final model.

Due to the high correlation among Q_j, V_j, and p_{Q_j} variables, I formed three full models, one for each type of predictor variable. In addition, I excluded flow variables from the Delta Cross Channel (Q_{D}) and the upstream gauging station (Q_{inflow}) because they were highly correlated with those from downstream gauge on the Sacramento River (e.g., $r = -0.84$ between Q_{D} and Q_{S}) and caused variance inflation factors > 20. Variance inflation factors (VIFs) provide an index of multicollinearity by measuring the magnitude with which the variances of parameter estimates are inflated compared to when the explanatory variables are uncorrelated (Kutner et al., 2005). With these flow stations excluded, all variance inflation factors were < 5 (Kutner et al., 2005 recommend VIFs < 10). Using Q_j as an example, each full model had the following structure:

$$\ln\left(\frac{\pi_j}{\pi_{\mathrm{S}}}\right) = \beta_{j0} + \beta_{j1}Q_{\mathrm{S}} + \beta_{j2}Q_{\mathrm{G}} + \beta_{j3}\Delta Q_{\mathrm{S}} + \beta_{j4}U + \beta_{j5}T + \beta_{j6}D + \beta_{j7}L\,. \tag{6.6}$$

Because final models based on Q_j, V_j, and p_{Q_j} were not nested, I used Akaike's Information Criterion to compare these models (Burnham and Anderson, 2002).

All continuous explanatory variables were standardized by subtracting each observation from the mean and dividing by the standard deviation. Standardizing puts all variables on the same quantitative scale, facilitating comparison of parameters on different absolute scales. Parameter estimates based on standardized variables are interpreted as the magnitude of effect of each variable on entrainment probabilities for a one standard deviation change when holding the remaining variables constant.

6.2.5 Goodness of fit

I assessed model fit to the data using both quantitative and descriptive techniques. To check for systematic deviations of predicted from observed values, I grouped data into discrete classes, plotted mean observed versus predicted values, and performed approximate Pearson χ^2 tests. I also used the Hosmer-Lemeshow test, formed by 1) grouping the data set into 10 classes of equal sample size based on the ordered predicted probabilities, $\hat{\pi}_{ij}$; 2) calculating the $\hat{C}$ test statistic based on squared differences between observed and expected frequencies in each class; and 3) comparing $\hat{C}$ to a χ^2 distribution with 8 df (Hosmer and Lemeshow, 2000). Since the multinomial model produces two predicted probabilities ($\hat{\pi}_{i\mathrm{D}}$ and $\hat{\pi}_{i\mathrm{G}}$), I conducted the Hosmer-Lemeshow test for each. I used two grouping methods to visually inspect model fit to the data. First, data were discretized into 14 groups based on fixed cutpoints of the predicted probabilities. This approach leads to unequal sample size among groups but spans the range of predicted probabilities. I also compared mean predicted probabilities of each release group to the observed proportions in each group that entered each channel. This grouping approach tends to average over hydraulic conditions that might lead to very different predicted probabilities among individuals, but provides a natural classification for a group of fish that experienced the same set of average environmental conditions.

I calculated the area under the receiver operating curve (AUC) to quantify how well the model predicts the fates of fish (Hosmer and Lemeshow, 2000). The AUC is calculated as follows: if estimated probabilities of π_{ij} are greater than an arbitrary cutoff value of π_j, then the ith fish is assigned to route j. For a particular cutoff value, the actual route used by each fish is compared to the predicted route, and the false-positive and true-positive rate calculated. The receiver operating curve (ROC) plots the true-positive rate versus the false-positive rate for all possible cutoff values, and AUC is the area under this curve. An AUC of 0.5 indicates the model has no ability to predict the fish's migration route, whereas AUC = 1 indicates perfect classification ability. In practice, AUC between 0.7 and 0.8 is considered "acceptable" and between 0.8 and 0.9 is considered "excellent" (Hosmer and Lemeshow, 2000).

6.2.6 Variation in predicted entrainment probabilities

I used the best-fit model 1) to understand how entrainment probabilities vary over a range of time scales, 2) to evaluate the assumption that the daily fraction of fish is proportional to the mean daily fraction of flow entering the interior Delta, and 3) to examine the effect of river inputs and tides on the daily fraction of fish entering the interior Delta. Time-specific entrainment probabilities reveal the individual consequences of arriving at the junction at a particular time of day and tidal cycle. At the population level, however, the fraction of fish entering each route depends on 1) fluctuation in time-specific entrainment probabilities over each day and 2) the distribution of fish arrival times at the junction over the diel cycle.

For time-specific entrainment probabilities that vary among individuals, the expected number of fish entering migration route *j* on day *d*, n_{jd}, is

$$\mathrm{E}\left(n_{jd}\right) = \sum_{i=1}^{N_d} \pi_{ijd}$$

where N_d is the total number of fish migrating past the junction on day *d*. The expected fraction of fish entering route *j* is then

$$\frac{\mathrm{E}\left(n_{jd}\right)}{N_d} = \frac{1}{N_d} \sum_{i=1}^{N_d} \pi_{ijd} = \bar{\pi}_{jd}, \tag{6.7}$$

showing that the expected fraction is equivalent the mean entrainment probability on a given day. I used Eqn. 6.7 as the basis for extending individual probabilities to population-level entrainment.

First, I predicted entrainment probabilities using Eqn. 6.4 for the three-year time series of 15-min flow data at the river junction for the period December 1 to February 28. At the finest temporal scale I examined how π_{ij} varied over the tidal cycle under average conditions during the study. Next, I used the three-year time series to calculate $\bar{\pi}_{\mathrm{ID},d}$, the daily fraction of fish entering the interior Delta. Here, entrainment probabilities at the 15-min scale were averaged over each day, and also over day and night periods within each day. This approach assumes that fish arrive at the river junction uniformly over the diel cycle, and $\bar{\pi}_{\mathrm{ID},d}$ for day and night periods help understand how non-uniform arrival distributions affect population-level entrainment. Each day was defined to begin at sunrise (for sunrise, range = 0657-0728 hours; for sunset, range = 1640-1743 hours).

Entrainment efficiency on day *d*, $E_{\mathrm{ID},d}$, was calculated as

$$E_{\mathrm{ID},d} = \frac{\bar{\pi}_{\mathrm{ID},d}}{p_{\bar{Q}_{\mathrm{ID}},d}}$$

where $p_{\bar{Q}_{\mathrm{ID}},d}$ is the proportion of mean discharge on day *d* entering the interior Delta. Entrainment efficiencies <1 indicate lower mean probabilities of entering the interior Delta relative to the fraction of flow entering the interior Delta, whereas $E_{\mathrm{ID},d} > 1$ suggest more fish than the fraction of flow enter the interior Delta. Entrainment efficiencies remaining constant with respect to $p_{\bar{Q}_{\mathrm{ID}},d}$ indicate that the probability of entrainment into the interior Delta is directly proportional to the fraction of flow entering the interior Delta, with $E_{\mathrm{ID},d}$ measuring the constant of proportionality.

Last, I examined the contribution of river inputs and tides to variation in daily entrainment and water distribution. I compared $p_{\bar{Q}_{\mathrm{ID}},d}$ and $\bar{\pi}_{\mathrm{ID},d}$ to mean daily discharge entering the river junction ($\bar{Q}_{\mathrm{inflow},d}$). I calculated two measures to quantify the effect of tides on a given day, 1) the fraction of each day with upstream river flow into the junction (i.e., $Q_{\mathrm{S}} < 0$), and 2) the coefficient of variation in Q_{S}. The CV is the standard deviation of 15-min flows on each day divided by the daily mean flow of the Sacramento River downstream of the river junction. Since tidal fluctuations decrease as total river discharge increases, the CV measures the relative strength of tides at the river junction on a given day.

6.2.7 Simulating alternative gate operations

To illustrate the utility of an entrainment probability model for informing management decisions, I simulated entrainment probabilities under a management scenario where the Delta Cross Channel was open during the day but closed at night. The premise of this management action is that most of the water entering the interior Delta occurs during large daytime flood tides, whereas most of the tagged fish passed the river junction at night (see Table 6.1). Thus, the rationale is that closing the gates at night minimizes the risk of entrainment for most of the fish population, while opening the gates during the day still allows substantial water to be diverted to the interior Delta. Closed-at-night gate operations were implemented experimentally in 2009 and results are pending. However, given a model for predicting time-specific entrainment probabilities, an alternative approach is to simulate the effect closed-at-night gate operations.

I simulated closed-at-night gate operations for the period Nov 1 to Jan 31 based on current regulations for gate operations. Delta Cross Channel gates are mandated to be closed from Feb 1 to May 20 for fisheries protection (SWRCB, 1995). However, 45 days of discretionary gate closures for fishery protection are allowed between Nov 1 and Jan 31 (SWRCB, 1995). I focused simulations on this period when managers have considerable flexibility in operating the Delta Cross Channel.

I used the Delta Simulation Model II (DSM2) to simulate 15-min river flows at the river junction under a closed-at-night gate operation (CADWR, 2010). DSM2 is a model for simulating one-dimensional, unsteady, open-channel flow in the Delta in response to river inflows, tidal forcing, and water management actions. I used the most recent calibration of the model and the latest historical simulation. DSM2 was recently recalibrated for use in the Bay Delta Conservation Plan, and historical simulations of Delta hydrodynamics under this recalibration extend through the winter of 2007 (CH2MHILL, 2009). Since the historical simulation did not extend beyond 2007, I used simulated data for the period November 1, 2006 through January 31, 2007, which overlapped the first year that telemetry data were available.

I predicted entrainment probabilities under two scenarios: 1) the historical simulation, which matched inflows, tides, and gate operations during the period of interest, and 2) a closed-at-night simulation, which differed from the historical simulation only in the position of the Delta Cross Channel gates. Recall that under the historical conditions, the Delta Cross Channel gate was open prior to December 15 and closed thereafter (see Figure 3.3). In contrast, for the closed-at-night simulation, I opened the Delta Cross Channel gates at sunrise and closed the gates at sunset for the entire simulation period. Given flow data simulated under these scenarios, I then predicted entrainment probabilities for each 15-min observation using Eqn. 6.4.

I evaluated the two scenarios by 1) examining entrainment probabilities at a range of temporal scales, 2) comparing the distribution of daily entrainment probabilities, and 3) assessing the effect of diel activity patterns on daily entrainment probabilities. To evaluate the consequence of different diel activity patterns of fish, I assumed either a uniform arrival distribution, 85% of fish arriving at the junction during night, or 85% of fish arriving during the day. For predominant diurnal or nocturnal migration, the daily mean probability of entering the interior Delta was calculated as:

$$\bar{\pi}_{\text{ID},d} = A_{\text{Day}}\bar{\pi}_{\text{ID},d,\text{Day}} + \left(1 - A_{\text{Day}}\right)\bar{\pi}_{\text{ID},d,\text{Night}}$$

where A_{Day} is the probability of arriving at the junction during daylight hours, $\bar{\pi}_{\mathrm{ID},d,\mathrm{Day}}$ is the mean probability of entering the interior Delta during daylight hours on day d, and $\bar{\pi}_{\mathrm{ID},d,\mathrm{Night}}$ is the mean probability of entering the interior Delta during night.

6.3 Results

6.3.1 Model selection

Although the full model with discharge variables consisted of 16 parameters, many of these variables failed to improve model fit (Table 6.2), yielding a final model comprised of 7 parameters and 4 explanatory variables (Table 6.3). Water temperature, fork length, and time of day were eliminated entirely from the model because likelihood ratio tests showed that these factors did not significantly improve model fit. Upstream flow in the Sacramento River (U) and Q_{G} did not affect entrainment probabilities for the Delta Cross Channel, whereas ΔQ_{S} did not influence π_{G} (Table 6.1). None of the remaining variables could be eliminated without significantly increasing the negative log-likelihood (Table 6.3), and none of the two-way interactions among the remaining variables were significant (Table 6.2). Including water velocity instead of discharge did not change the structure of the final model (Appendix Table 5.1 and 5.2), and only marginally improved the fit of the model to the data (AIC = 786.8 for the best-fit V_j model; AIC = 787.6 for the best-fit Q_j model). Using the proportion of total outflow did not lead to a more parsimonious model (Appendix Table 5.3 and 5.4); ΔAIC = 9.5 when comparing the best-fit p_{Q_j} model (AIC = 797.1) with the best-fit Q_j model (Table 6.3). Therefore, I used the best fit model with discharge variables for subsequent analyses.

6.3.2 Goodness of fit

I found little evidence of systematic departures of predicted from observed values. The goodness-of-fit tests were not significant (for $g(\pi_{\mathrm{D}})$: $\hat{C} = 4.84$, $P = 0.775$; for $g(\pi_{\mathrm{G}})$: $\hat{C} = 5.19$, $P = 0.737$). Plots of mean observed versus predicted probabilities supported the statistical tests, showing no evidence of systematic deviations (Figure 6.2). These plots also revealed

Table 6.2. Results of reverse model selection for discharge variables (Q_j) showing the likelihood ratio test and associated statistics for the model with the given variable dropped relative to the preceding model with one additional variable.

Variable dropped	Linear predictor	Number of parameters	AIC	–Log-likelihood	Likelihood Ratio	P-value
None (full model)		16	800.8	384.4		
D (time of day)	$g(\pi_G)$	15	798.8	384.4	0.01	0.920
T (temperature)	$g(\pi_D)$	14	796.9	384.4	0.02	0.888
L (fork length)	$g(\pi_G)$	13	794.9	384.5	0.05	0.823
U (upstream flow)	$g(\pi_D)$	12	793.1	384.5	0.15	0.699
D (time of day)	$g(\pi_D)$	11	791.4	384.7	0.30	0.584
Q_G	$g(\pi_D)$	10	789.7	384.9	0.35	0.554
L (fork length)	$g(\pi_D)$	9	788.6	385.3	0.35	0.354
T (temperature)	$g(\pi_G)$	8	787.6	385.8	1.06	0.303
ΔQ_S	$g(\pi_G)$	7	787.6	386.8	1.98	0.159
None (all interactions)		11	790.3	384.2		
$Q_S \times U$	$g(\pi_G)$	10	788.3	384.4	0.03	0.863
$Q_S \times Q_G$	$g(\pi_G)$	9	786.9	384.5	0.57	0.450
$Q_G \times U$	$g(\pi_G)$	8	786.5	385.3	1.63	0.202
$Q_S \times \Delta Q_S$	$g(\pi_D)$	7	787.6	386.8	3.08	0.079

Table 6.3. Likelihood ratio tests when each variable is dropped from the best fit Q_j model.

Variable dropped	Number of parameters	Linear predictor	–Log-likelihood	Likelihood Ratio	AIC	P-value
None (best fit)	7		386.8		787.6	
Q_S	6	$g(\pi_G)$	417.6	61.5	847.1	<0.001
Q_G	6	$g(\pi_G)$	420.0	66.5	852.1	<0.001
U	6	$g(\pi_G)$	392.3	11.0	796.6	<0.001
Q_S	6	$g(\pi_D)$	449.0	124.5	910.1	<0.001
ΔQ_S	6	$g(\pi_D)$	391.8	10.0	795.6	0.002

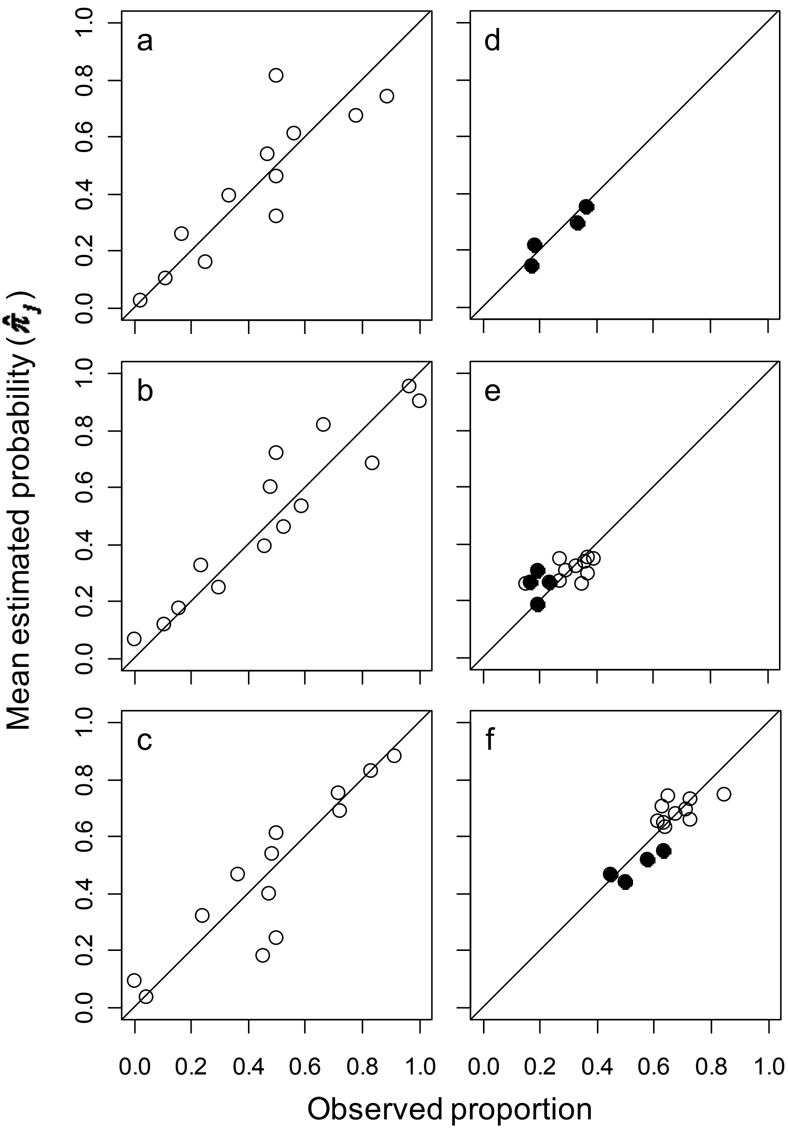

Figure 6.2. Observed proportions of fish entering the Delta Cross Channel (a and d), Georgiana Slough (b and e), and the Sacramento River (c and f) compared to the mean predicted probabilities entering each channel. For the left column (a-c), groups were formed by discretizing predicted probabilities into 14 intervals of equal-probability width. For the right column (d-f), means are calculated for each release group and Delta Cross Channel gate position (unfilled symbols = closed gate, filled symbols = open gate). For d-f, groups with ≤10 fish are not shown.

good agreement between predicted and observed values, regardless of how the data were grouped, with no large deviations between expected and observed values. I found that AUC = 0.785 for $\hat{\pi}_{i,\mathrm{G}}$, 0.873 for $\hat{\pi}_{i,\mathrm{D}}$, 0.841 for $\hat{\pi}_{i,\mathrm{S}}$, indicating that the model has excellent ability to predict the ultimate fates of fish. For example, $\hat{\pi}_{\mathrm{S}} > 0.7$ correctly predicts 80% of fish that actually remained in the Sacramento River, while 75% of fish that entered the interior Delta are also correctly classified (Appendix Figure 5.1). Taken together, the goodness-of-fit measures suggest little evidence of lack-of-fit, close agreement between predicted and observed values, and good ability to predict the likelihood of entering migration routes in response hydraulic dynamics.

6.3.3 Estimated parameters and entrainment probabilities

Under the best-fit model, Q_{S}, Q_{G}, and U significantly affected the probability of entering Georgiana Slough (π_{G}), whereas Q_{S} and ΔQ_{S} affected the probability of entering the Delta Cross Channel (π_{D}; Table 6.3). Parameter estimates indicate both the direction and magnitude of the effect of these variables on entrainment probabilities when holding the remaining variables constant (Table 6.4). For π_{G}, the slope parameter for Q_{S} is negative, indicating that increases in Q_{S} decreased the probability of entering Georgiana Slough (Figure 6.3b). In contrast, the positive slope estimate for Q_{G} indicates that π_{G} increased with Q_{G} (Figure 6.3f). Slope estimates for Q_{G} and Q_{S} are of similar magnitude, showing that a 1 SD change in either variable affected π_{G} by a similar magnitude, but in opposite directions. The positive parameter estimate for U indicates that water flowing upstream from the Sacramento River into the river junction increased the probability of entering Georgiana Slough (Figure 6.3n). For the Delta Cross Channel, decreases in both Q_{S} and ΔQ_{S} increased the probability of fish entering the Delta Cross Channel, but the slope estimate for Q_{S} is five times that for ΔQ_{S}, indicating that Q_{S} was the dominant factor driving entrainment probabilities into the Delta Cross Channel (Table 6.4, Figure 6.3c and 6.3k).

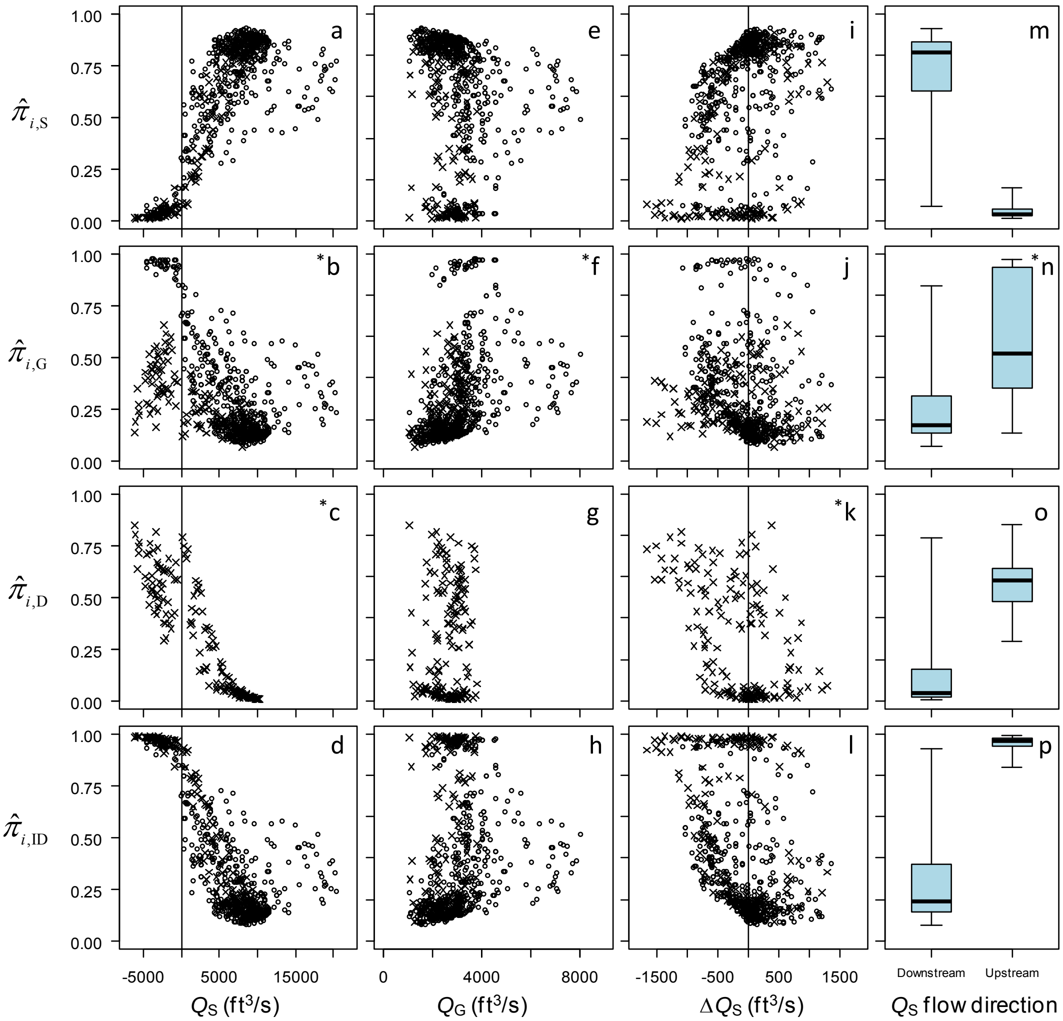

Figure 6.3. Plots of estimated entrainment probabilities ($\hat{\pi}_{ij}$) for route *j* and individual (*i*) as a function of flow variables in the best fit model. Panels with an asterisk indicate the driving relationships in the best fit model (see Tables 6.3 and 6.4). Box plots show the range, median, 25th, and 75th percentiles. Circles indicate fish that arrived at the river junction when the Delta Cross Channel was closed, and Xs indicate fish arriving when the Delta Cross Channel was open. Subscripts are as follows: S = Sacramento River, G = Georgiana Slough, D = Delta Cross Channel, and ID = Interior Delta.

Table 6.4 Maximum likelihood parameter estimates for the best fit model relating entrainment probability into Georgiana Slough (G) and the Delta Cross Channel (D) to hydraulic variables of the river junction.

Variable	Parameter	Estimate	Standard error
Intercept	β_{G0}	-0.900	0.106
Q_S	β_{G1}	-1.163	0.154
Q_G	β_{G2}	0.852	0.107
U	β_{G4}	1.595	0.512
Intercept	β_{D0}	-2.337	0.391
Q_S	β_{D1}	-2.694	0.337
ΔQ_S	β_{D3}	-0.474	0.158

6.3.4 Hourly variation in predicted entrainment probabilities

At mean river flows observed during our study (Table 6.5), flood tides caused the Sacramento River to reverse direction twice daily (Figure 6.4a and 6.5a). Under these conditions, discharge of the Sacramento River downstream of the junction (Q_S) varied substantially from -5,000 ft^3/s during the full flood tide to 10,000 ft^3/s during the full ebb tide only a few hours later (Figure 6.4a and 6.5a). Flow into the Delta Cross Channel was inversely related to the Sacramento River, increasing rapidly during the transition from ebb tide to flood tide as Q_S decreased (i.e., when $\Delta Q_S < 0$). Relative to Q_S and Q_D, discharge of Georgiana Slough exhibited much less variability regardless of whether the Delta Cross Channel gates were open or closed (Figure 6.4a and 6.5a).

Table 6.5. Summary of flow conditions experienced by juvenile salmon detected at the junction of the Sacramento River (Q_S, ΔQ_S) with the Delta Cross Channel (DCC, Q_D) and Georgiana Slough (Q_G). Discharge at Freeport is the mean daily discharge of the Sacramento River upstream of the Delta on dates fish were detected at the river junction.

Flow variable	Overall		DCC open	DCC closed
(ft^3/s)	Mean (SD)	Range	Mean (SD)	Mean (SD)
Q at Freeport	13,800 (6,483)	6,800 – 40,700	13,350 (3,999)	13,990 (7,243)
Q_{inflow}	10,350 (4,483)	-2,170 – 28,200	10,100 (3,219)	10,450 (4,900)
Q_S	6,254 (4,918)	-6,120 – 20,400	3,770 (5,112)	7,255 (4,468)
Q_G	3,044 (1,143)	1,070 – 8,073	2,663 (599)	3,198 (1,268)
Q_D	1,102 (2,246)	-1,370 – 9,140	3,838 (2,662)	0
ΔQ_S	-74 (476)	-1,659 – 1,360	-173 (556)	-33 (434)

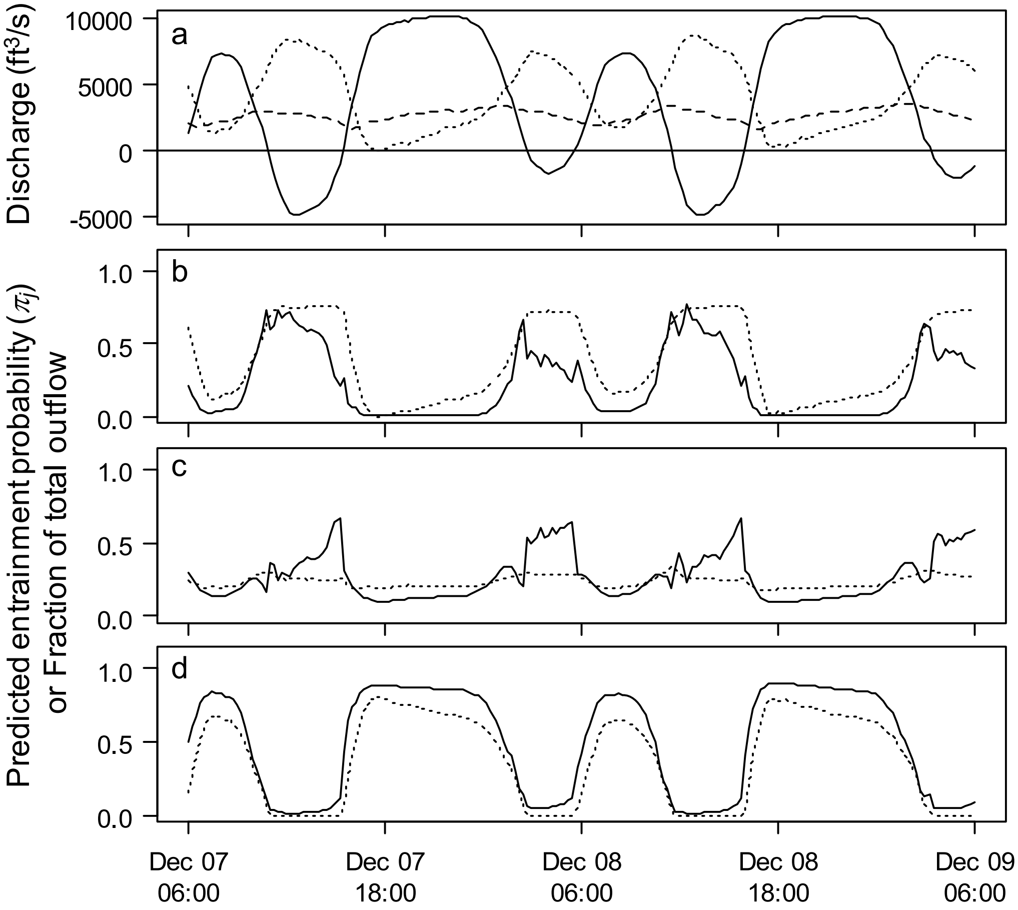

Figure 6.4. Predicted entrainment probability into route *j* as a function of river flow entering each channel for two days in December 2007 under average flow conditions with the Delta Cross Channel open. The top panel (a) shows river discharge just downstream of the river junction in the Sacramento River (Q_S, solid line), the Delta Cross Channel (Q_D, dotted line), and Georgiana Slough (Q_G, dashed line). Panels b-d show the predicted probability of entering each channel (π_j, solid line) and the fraction of total outflow entering each channel (p_{Q_j} , dotted line). Panel b = Delta Cross Channel, c = Georgiana Slough, and d = Sacramento River.

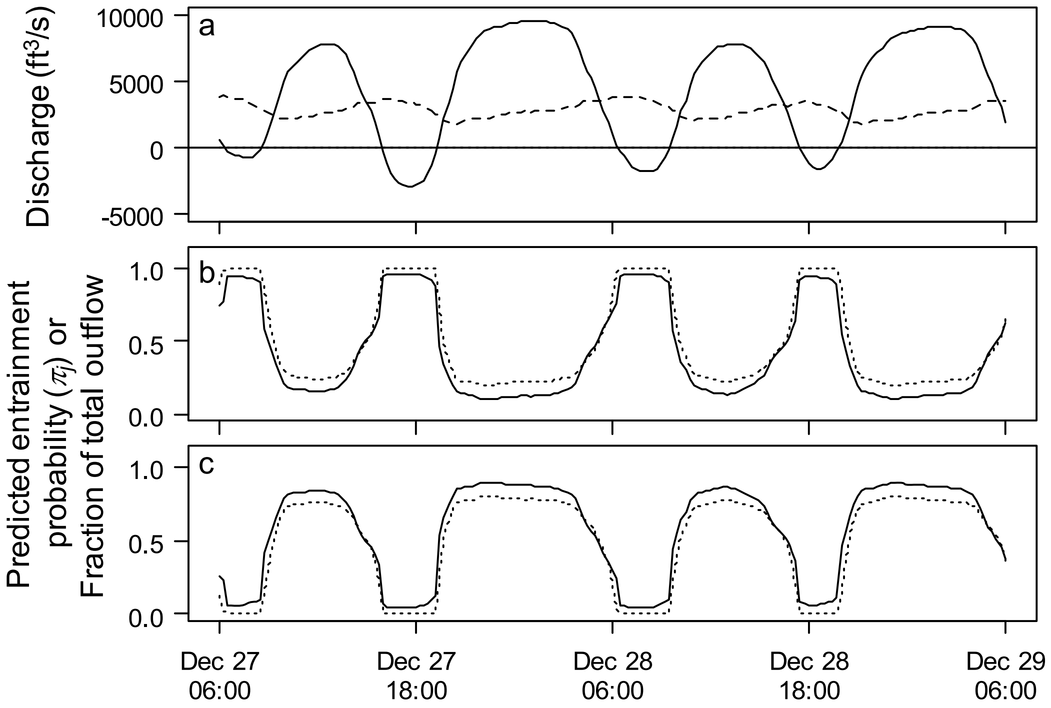

Figure 6.5. Predicted entrainment probability into route *j* as a function of river flow entering each channel for two days in December 2007 under average flow conditions with the Delta Cross Channel gate closed. The top panel (a) shows river discharge just downstream of the river junction in the Sacramento River (Q_S, solid line) and Georgiana Slough (Q_G, dashed line). Panels b-c show the predicted probability of entering each channel (π_j, solid line) and the fraction of total outflow entering each channel (p_{Q_j} , dotted line). Panel b = Georgiana Slough, and c = Sacramento River.

In response to fluctuating river flows driven by the tides, entrainment probabilities vary substantially throughout the day. For the Delta Cross Channel, π_D closely tracks Q_D and is inversely related to Q_S (Figure 6.4b). Thus, π_D is close to zero during the full ebb tide when flow of the Sacramento River is at its maximum and cross channel flow is minimal. As the tide transitions from ebb to flood, flow decreases in the Sacramento River and π_D increases to a maximum of about 75% just as Sacramento River reaches the full flood tide. The probability of entering the Delta Cross Channel is nearly always less than the fraction of total discharge entering the cross channel, except when Q_S declines from ebb to flood tide. During this tidal stage, π_D is similar to the fraction of Q_D. Following the peak of the flood tide, however, π_D begins to decline despite the proportion of flow entering the cross channel remaining relatively constant through the flood tide. This pattern is driven by the relative contributions of Q_S and ΔQ_S in the equation for π_D (Table 6.4). The negative slope for ΔQ_S increases π_D when Q_S declines during ebb-to-flood transitions, but decreases π_D when Q_S increases during flood-to-ebb transitions (Figure 6.4b).

Discharge of Georgiana Slough varies much less than Q_D or Q_S, yet the probability of entering Georgiana Slough varies substantially throughout the day (Figure 6.4c and 6.5b). When the Delta Cross Channel gate is open and Q_S is positive, π_G tends to track the fraction of discharge entering Georgiana Slough (Figure 6.4c). However, during flood tides that cause upstream flow in the Sacramento River, π_G increases substantially despite a constant fraction of discharge entering Georgiana Slough. In contrast, with the Delta Cross Channel closed, the fraction of discharge entering Georgiana Slough varies between 20% and 100% as Q_S cycles between negative and positive flow about a relatively constant Q_G (Figure 6.5b). Consequently, π_G closely tracks the fraction of flow entering Georgiana Slough, and ranges from approximately 0.10 during the full ebb tide to 0.95 during the flood tide. During flood tides with the Delta Cross Channel gates closed, the probability of entering Georgiana Slough is higher than when the gates are open (Figure 6.4c and 6.5b). This pattern also arises in the estimated entrainment probabilities where $\hat{\pi}_{i,G}$ tends to be higher with the gates closed compared to open for a given Q_S less than 5,000 ft^3/s (Figure 6.2b).

Since π_G increases when the Delta Cross Channel is closed, π_S follows as similar pattern regardless of the whether the cross channel gates are open or closed (Figure 6.4d and 6.5c). In general, π_S follows a step function, switching quickly from a high probability of remaining in the Sacramento River during an ebb tide to a very low probability during the flood tide (Figure 6.4d and 6.5c). During the full ebb tide, π_S remains at about 0.90 regardless of gate position. However, with the cross channel gate open during a flood tide, π_S is near zero, indicating that fish migrating through the river junction during this tidal stage will almost certainly enter either the Delta Cross Channel or Georgiana Slough (Figure 6.4d, also see Figure 6.2a and 6.2d). Although π_S remains low during flood tides when the gate is closed, fish still have 5-10% chance of remaining in the Sacramento River (Figure 6.4d).

6.3.5 Daily and diel variation in mean entrainment probabilities

At the daily scale, the mean probability of entering the interior Delta ($\bar{\pi}_{\mathrm{ID},d}$) tends to follow the seasonal trend in the fraction of discharge entering the interior Delta, but the difference between fish entrainment and water distribution varies over time (Figure 6.5b and Appendix Figures 5.2 and 5.3). For example, in December 2006 when the Delta Cross Channel was open, the fraction of mean flow entering the interior Delta is higher than $\bar{\pi}_{\mathrm{ID},d}$ (Figure 6.6b). However, when the Delta Cross Channel was closed, the fraction of flow entering the interior Delta declines much more than $\bar{\pi}_{\mathrm{ID},d}$ and remains less than $\bar{\pi}_{\mathrm{ID},d}$ for the remainder of the winter. The difference between total discharge entering the junction and the interior Delta increases as total discharge increases, which decreases the fraction of discharge, and in turn, the mean probability of entering the interior Delta (Figure 6.6a and 6.6b). Although $\bar{\pi}_{\mathrm{ID},d}$ generally tracks the fraction of flow entering the interior Delta, these findings suggest their relationship is not directly proportional.

I also found substantial differences between mean entrainment probabilities for day and night, with daytime entrainment probabilities cycling over a two-week period according to the spring-neap tidal cycle (Figure 6.6c and Appendix Figures 5.2 and 5.3). Semidiurnal tides

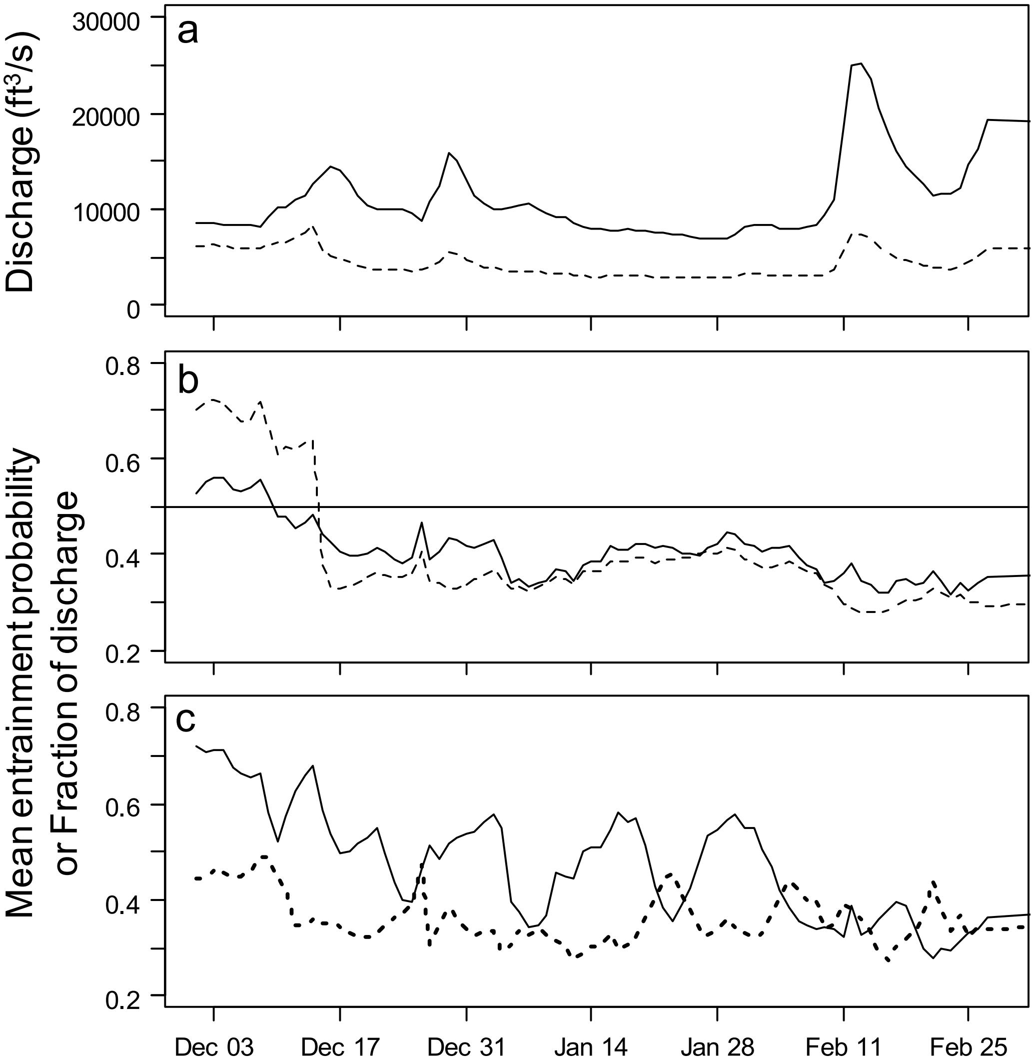

Figure 6.6. Mean daily river flow (a) and mean predicted probability of entrainment into the interior Delta (b and c) during winter 2006/2007. The top panel (a) shows mean daily discharge entering the river junction ($Q_{\text{inflow,}}$ solid line) and mean daily discharge entering the interior Delta through both the Delta Cross Channel and Georgiana Slough (dotted line). Panel b shows the mean daily probability of entering the interior Delta ($\bar{\pi}_{\text{ID},d}$, solid line) and the fraction of mean daily discharge entering the interior Delta ($p_{\bar{Q}_{\text{ID},d}}$, dashed line). Panel c shows the mean entrainment probability for day (solid line) and night (heavy dotted line) diel periods. The Delta Cross Channel was open prior to December 15, 2006 and closed thereafter.

at this river junction are characterized by two tidal cycles each day, one with a large tidal range and one with a smaller tidal range (tidal range is the difference in water elevation between peak flood tide and the next ebb tide). On large ebb tides, the probability of remaining in the Sacramento River remains high for a long period of time (e.g., 7 h for the nighttime floods in Figure 6.4d) relative to the following ebb tide when π_S is high for only brief periods (e.g., about 2 h for the daytime floods in Figure 6.4d). When the large ebb tide followed by the small flood tide occurs mostly at night, fish arriving at night, on average, have a high probability of remaining in the Sacramento River (conversely, a low probability of entering the interior Delta). However, the very next tide during the day is typically comprised of a small ebb tide and a large flood tide. Thus, when integrated over the daytime period, the average probability of entering the interior Delta is much higher for a fish that arrives at the river junction during the day (Figure 6.6). As tides shift by about an hour each day, the alternating high-low floods and ebbs switch between day and night, inducing cycles in the mean probability of entering the interior Delta during day and night. These findings indicate that seasonal migration timing combined with diel activity patterns of fish could substantially influence the fraction of the population entrained into the interior Delta. However, at higher total discharge, tidal cycles have less influence on hourly discharge and entrainment probabilities, and thus mean day and night entrainment probabilities are similar (e.g., late February in Figure 6.6c).

6.3.6 Expected relation between entrainment probability and flow distribution

Mean daily entrainment probabilities are positively related to the fraction of flow entering the interior Delta (Figure 6.7b). However, entrainment probabilities are not directly proportional to the fraction of river flow entering the interior Delta, nor is there a 1:1 relation between the entrainment probability and the fraction of flow. First, a slope of 0.47 indicates that, on average, a unit decrease in the fraction of discharge entering the interior Delta reduces the mean daily entrainment probability by only 0.47 units (Figure 6.7b). For instance, reducing the proportion of flow into the interior Delta by 30 percentage points (e.g., from 65% to 35%) is expected to reduce the mean entrainment probability by only about 15 percentage points. Second, mean entrainment probabilities are not directly proportional to the fraction of flow

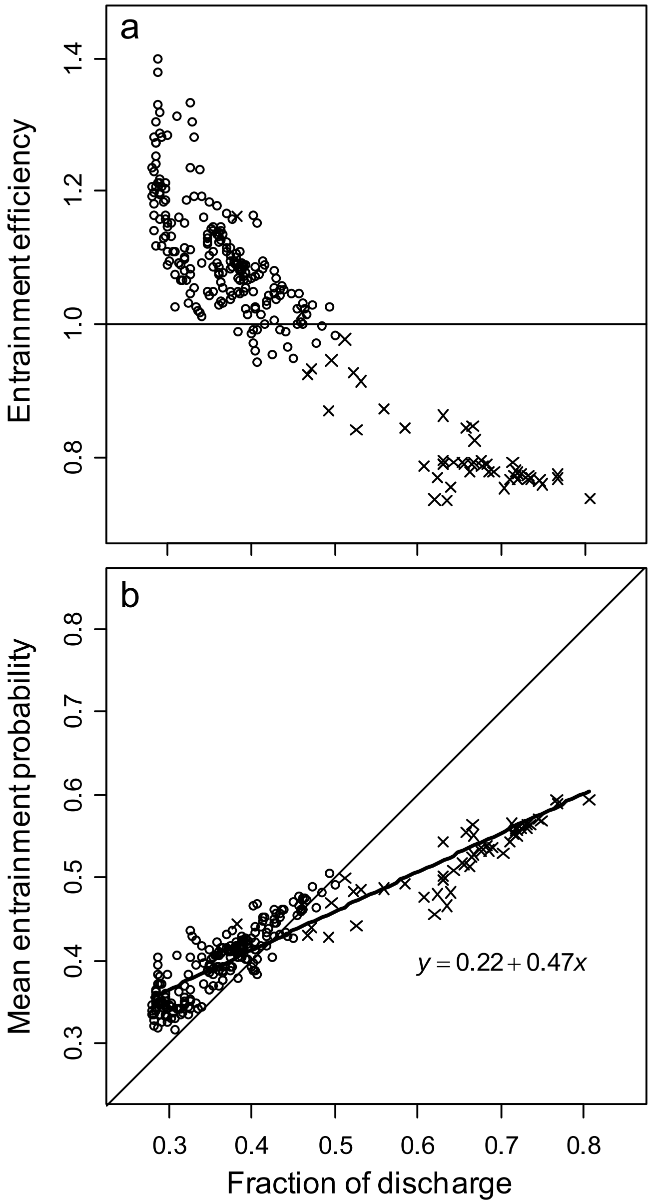

Figure 6.7. Entrainment efficiency (a; $E_{\mathrm{ID}} = \bar{\pi}_{\mathrm{ID}} / p_{\bar{Q}_{\mathrm{ID}}}$) and mean daily probability of entering the interior Delta (b; $\bar{\pi}_{\mathrm{ID}}$) as a function the proportion of mean inflow entering the interior Delta ($p_{\bar{Q}_{\mathrm{ID}}}$) for the period Dec 1 – Feb 28 during the winters of 2007 to 2009. Circles are days when the Delta Cross Channel was closed, and Xs are days when the Delta Cross Channel was open during some part of that day. The horizontal line at $E_{\mathrm{ID}} = 1$ in the top panel and the 45° line in the bottom panel show where the mean entrainment probability is equal to the fraction of flow entering the interior Delta.

since entrainment efficiency is not constant with respect to the fraction of flow (Figure 6.6a). Entrainment efficiency is greater than one when the fraction of flow entering the interior Delta is low, but decreases below one as the fraction of discharge entering the interior Delta increases. Thus, opening the Delta Cross Channel will increase the fraction of fish entering the interior Delta, but by considerably less than the increase in the fraction of flow.

6.3.7 Contribution of river inputs and tides

Both river flows and gate position affect the strength of the tides at the river junction (Figure 6.8), and in turn, the fraction of river flow entering the interior Delta. With increasing inflow to the junction, tidal forces are dampened (Figure 6.8b) and the fraction of each day with upstream flow declines (Figure 6.8a). For example, with the gates closed, reverse flows comprise 40% of the day at the lowest observed inflows, but the Sacramento River ceases to reverse direction at inflows exceeding about 12,000 ft^3/s (Figure 6.8a). At given inflows <15,000 ft^3/s, an open cross channel gate increases both $CV(Q_S)$ and the fraction of time with upstream river flow at Q_S (Figure 6.8). The fraction of mean daily discharge entering the interior Delta increases with the strength of the tides (Figure 6.9d) because much of the water entering the interior Delta occurs during flood tides (Figure 6.4 and 6.5). However, as river inflows increase, the fraction of discharge entering the interior Delta approaches an asymptote at just less than 30% (Figure 6.9b), the point at which tidal strength approaches zero (Figure 6.8b and 6.9d). With the gates open, the fraction of flow entering the interior Delta remains about 30 percentage points higher than with the gates closed (Figure 6.9c). These hydraulic relationships play a critical role in the likelihood that fish will be entrained into the interior Delta.

River inputs, tidal forces, and the position of the Delta Cross Channel gate influence the entrainment probability into the interior Delta. Mean daily entrainment probabilities follow the same pattern as the fraction of flow, initially decreasing as total discharge increases (Figure 6.9a). This pattern arises due to the effect of tides: Entrainment probabilities are highest when tides are strong (Figure 6.9c), which occurs at low inflows (Figure 6.8). Daily entrainment probabilities are highest at low inflow because the Sacramento River reverses direction for a substantial fraction of the day (Figure 6.8a), and under these conditions $\pi_{i,\mathrm{ID}}$ is at its maximum

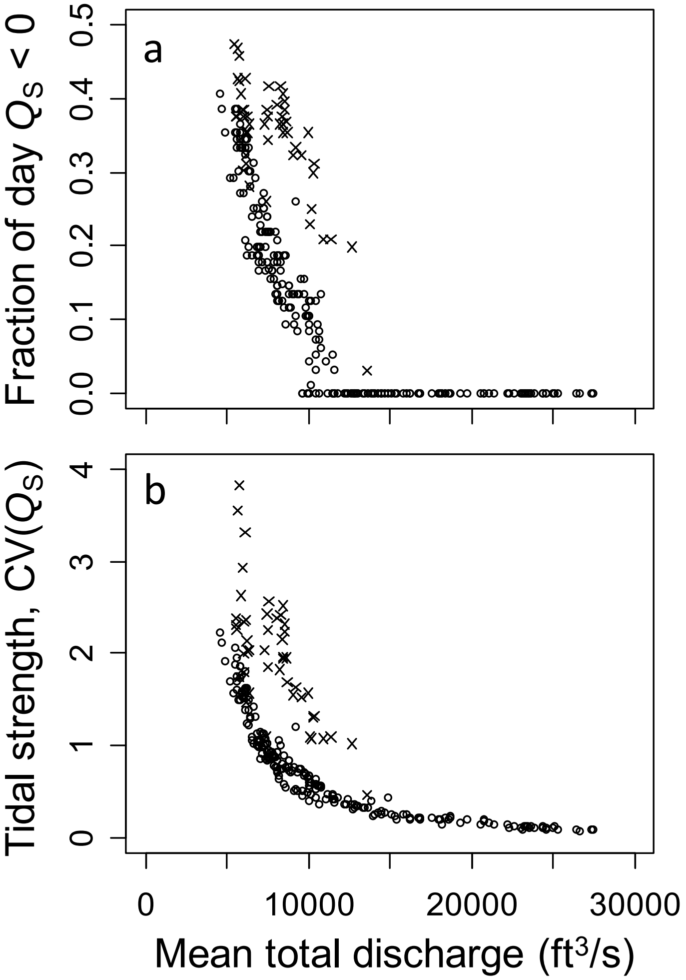

Figure 6.8. The proportion of each day with upstream flow into the junction (a) and tidal strength (b; coefficient of variation in Q_S) as a function of mean daily river discharge entering the junction ($\bar{Q}_{\mathrm{inflow},d}$). Circles are days when the Delta Cross Channel was closed, and Xs are days when the Delta Cross Channel was open during some part of that day. Three data points with 4 > CV(Q_S) < 6 are not shown.

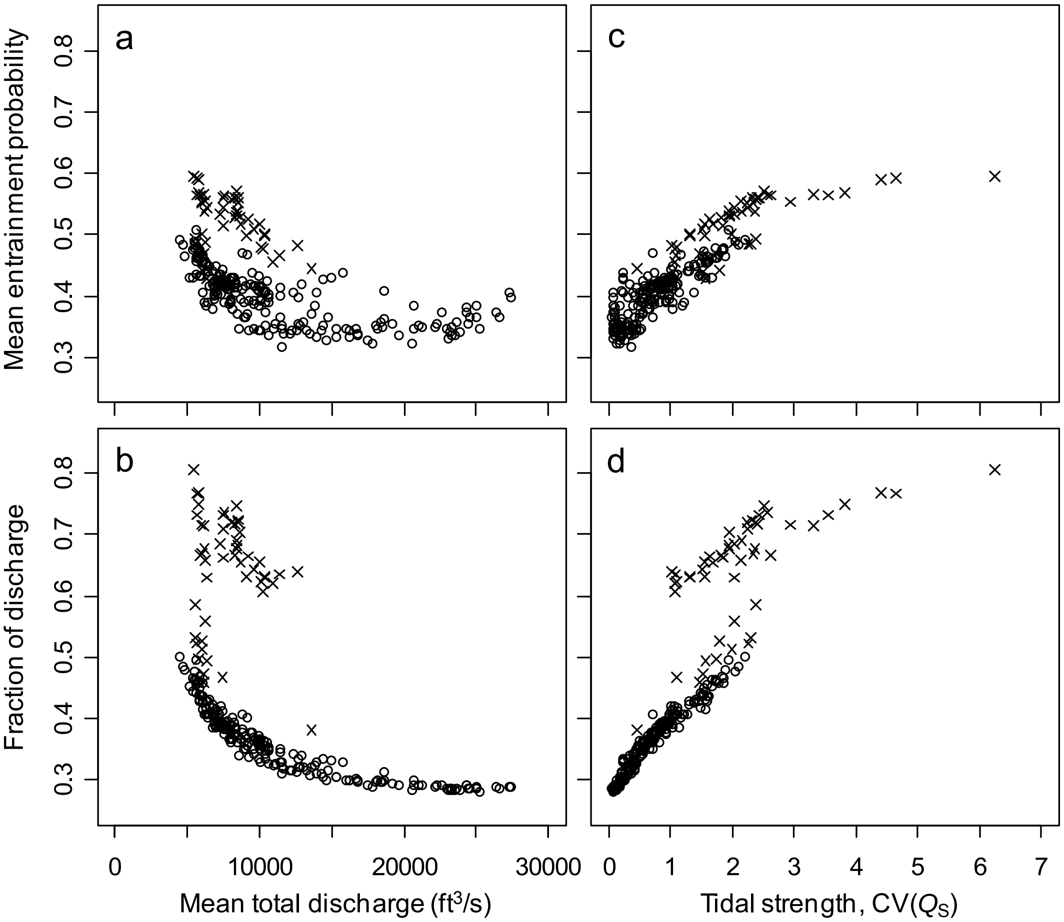

Figure 6.9. Mean daily probability of entering the interior Delta (a and c; $\bar{\pi}_{\mathrm{ID}}$) and the proportion of mean inflow entering the interior Delta (b and d; $p_{\bar{Q}_{\mathrm{ID}}}$) as a function of mean daily discharge entering the river junction (a and b; $\bar{Q}_{\mathrm{inflow},d}$) and tidal strength (c and d; coefficient of variation in Q_{S}) for the period Dec 1 – Feb 28 during the winters of 2007–2009. Circles are days when the Delta Cross Channel was closed, and Xs are days when the Delta Cross Channel was open during some part of that day. In the bottom panels (b and d), variability in $p_{\bar{Q}_{\mathrm{ID}}}$ with the Delta Cross Channel open at low discharge is due to experimental gate operations in 2009 when the cross channel was open during the day but closed at night.

(Figure 6.3d). Mean daily entrainment probabilities approach a minimum at inflows of about 12,000 ft^3/s (Figure 6.9a), the point at which the Sacramento River ceases to reverse direction (Figure 6.8a).

The difference in entrainment probability between cross channel gates open and closed (at a given total discharge) is only about 15 percentage points, half the difference in the fraction of flow between gates open and closed (Figure 6.9a and 6.9b). This finding illustrates the effect of the slope (0.47) in the relation between entrainment probability and fraction of discharge shown in Figure 6.6.

6.3.8 Simulating alternative gate operations

Closing the Delta Cross Channel at night had a large influence on the fraction of discharge entering the interior Delta, but much less effect on daily entrainment probabilities for the interior Delta (Figure 6.10 and 6.11). Prior to December 15, the period when the Delta Cross Channel is historically open, the closed-at-night operation reduces the interior Delta flow proportion by 15 percentage points (Figure 6.10a and 6.11a). In contrast, daily entrainment probabilities decrease on average by 5, 7, and 1.5 percentage points for uniform, 85% night, and 85% day arrival distributions at the junction (Figure 6.10b-6.10d). After December 15 when the gate is historically closed, switching to the closed-at-night operation increases the interior Delta flow proportion by 11 percentage points (Figure 6.10a and 6.11b). In this case, daily entrainment probabilities increase, on average, by 3, 1.3, and 6 percentage points for the uniform, 85% night, and 85% day arrival distributions at the junction (Figure 6.10b-6.10d). Thus, when switching from a fully closed gate position, opening the gates during the day has little effect on entrainment if most migration occurs at night, but a larger increase when migration occurs mostly during the day. Regardless of diel activity pattern, however, the change in daily entrainment probabilities is considerably less than the change in the fraction of discharge.

Hourly time series of route-specific entrainment probabilities reveal why gate operations affect flow proportions more than population-level entrainment. The probability of remaining in the Sacramento River (π_S) changes little in response to changes in gate position (Figure 6.12 and 6.13). For example, when the Delta Cross Channel is open, switching to

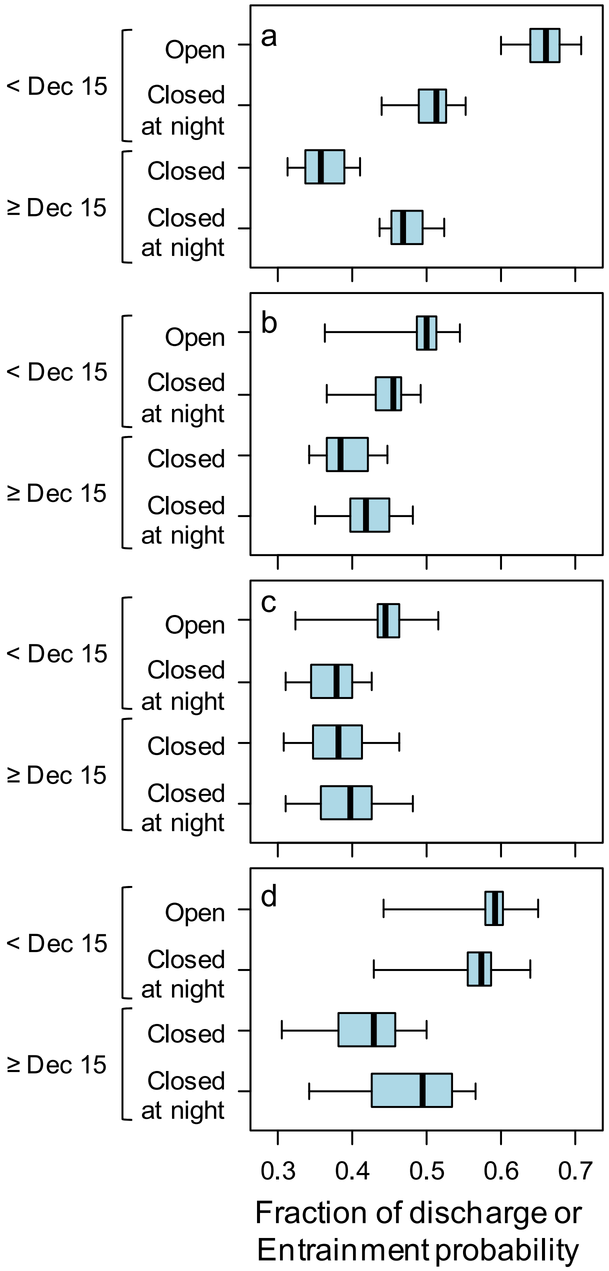

Figure 6.10. Distribution of the daily proportion of discharge entering the interior Delta (a) and predicted daily entrainment probabilities for the interior Delta (b-d) assuming b) a uniform diel arrival distribution at the junction, c) 85% of fish arriving at night, and d) 85% of fish arriving during the day. Entrainment probabilities were predicted from simulating flow data for the period November 1, 2006 – January 31, 2007 under two scenarios: 1) the historical gate operations where the Delta Cross Channel was open until December 15 and closed thereafter, and 2) operations where the gate was closed at night but open during the day for the entire simulation period.

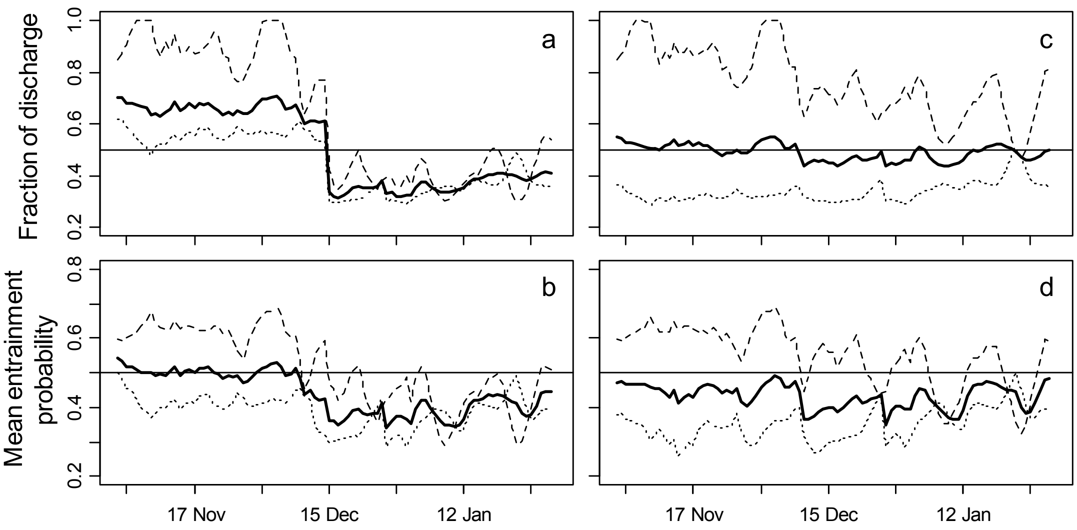

Figure 6.11. Daily fraction of discharge (a and c) and mean probability of entrainment (b and d) into the interior Delta under two simulated flow scenarios. Simulations were conducted for the period November 1, 2006 – January 31, 2007 under the historical gate operations where the Delta Cross Channel was open until December 15 and closed thereafter (a and b), and closed-at-night operations where the gate was closed at night but open during the day for the entire simulation period (c and d). The top panels (a and c) show the fraction of junction inflow entering the interior Delta for each day (solid line) and for day and night periods within each day (dashed and dotted lines). The bottom panels (b and d) show mean daily entrainment probabilities assuming uniform diel arrival at the junction (solid line), 85% of fish arriving during day (dotted line), and 85% of fish arriving at night (dashed line).

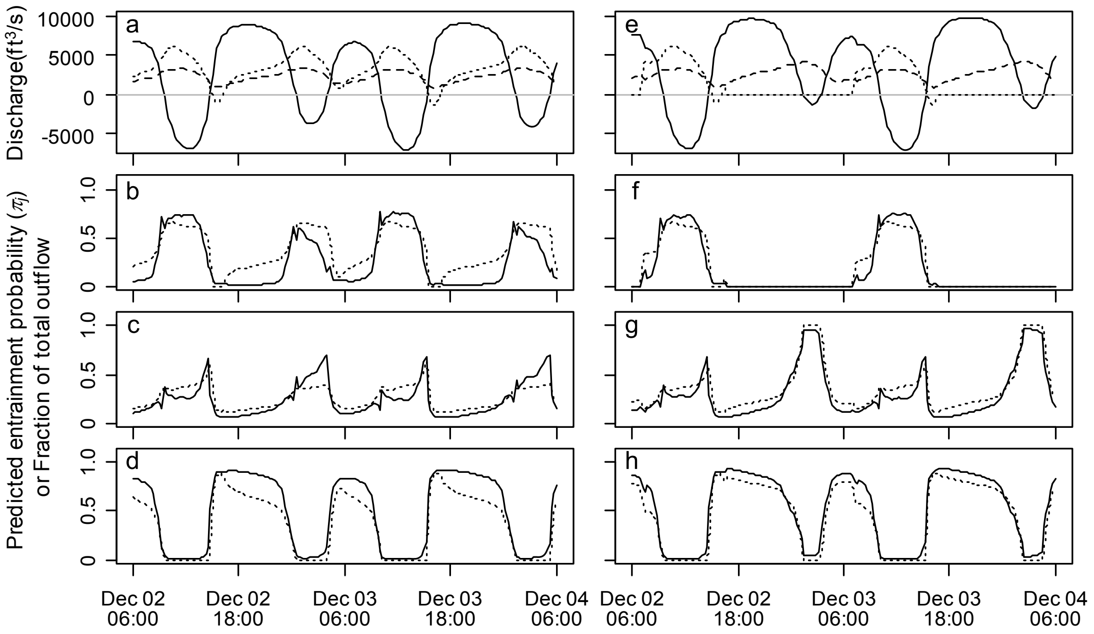

Figure 6.12. Predicted entrainment probability into route *j* as a function of simulated river flows entering each channel for two days in December 2006. Panels a-d = historical gate operations where the Delta Cross Channel was open until December 15, and e-h = closed-at-night operations where the gate was closed at night but open during the day for the entire simulation period. The top panels (a and e) show river discharge just downstream of the river junction in the Sacramento River (Q_S, solid line), Georgiana Slough (Q_G, dashed line), and the Delta Cross Channel (Q_D, dotted line). Lower panels (b-d and f-h) show the predicted probability of entering each route (π_j, solid line) and the fraction of total outflow entering each route (p_{Q_j} , dotted line). Panels b and f = the Delta Cross Channel, c and g = Georgiana Slough, and d and h = Sacramento River.

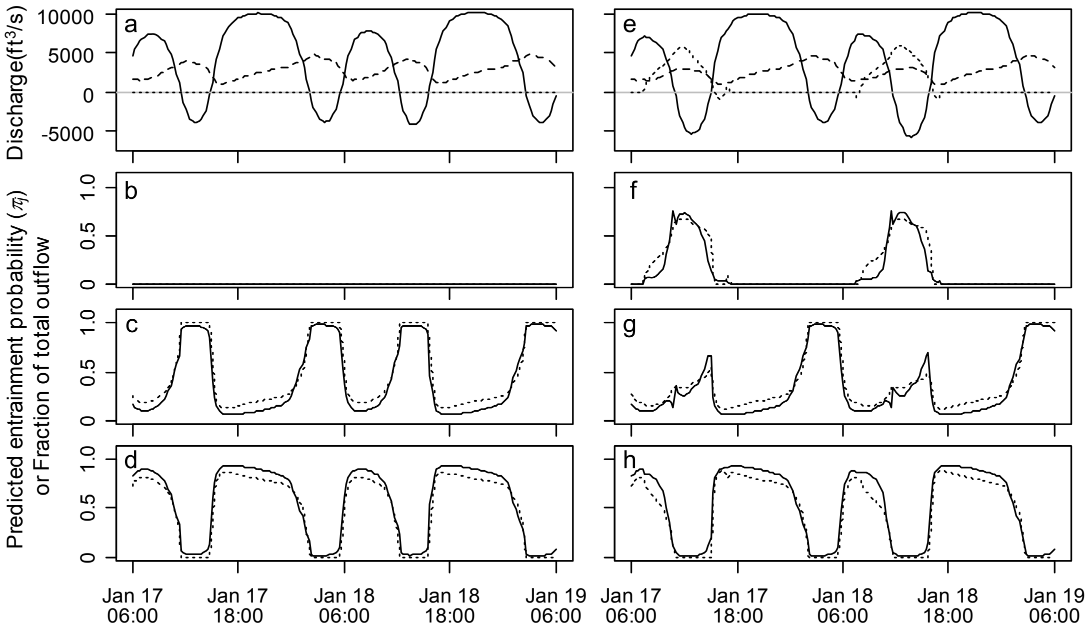

Figure 6.13. Predicted entrainment probability into route *j* as a function of simulated river flows entering each channel for two days in January 2007. Panels a-d = the historical gate operations where the Delta Cross Channel was closed after December 15, and e-h = closed-at-night operations where the gate was closed at night but open during the day for the entire simulation period. The top panels (a and e) show river discharge just downstream of the river junction in the Sacramento River (Q_S, solid line), Georgiana Slough (Q_G, dashed line), and the Delta Cross Channel (Q_D, dotted line). Lower panels (b-d and f-h) show the predicted probability of entering each route (π_j, solid line) and the fraction of total outflow entering each route (p_{Q_j} , dotted line). Panels b and f = the Delta Cross Channel, c and g = Georgiana Slough, and d and h = Sacramento River.

closed-at-night operations prevents fish from entering the cross channel but substantially increases their chances of entering Georgiana Slough during the flood tide (Figure 6.12). Thus, the only noticeable change in π_S is that it remains high for slightly longer during each ebb tide. When integrated over the 24-h period, daily entrainment into the interior delta decreases, but less than is expected based solely on changes in flow distribution. These findings illustrate how my model can be used to understand the effect of management actions on routing of fish in the Delta.

6.4 Discussion

Recovering endangered salmon populations in the Sacramento River requires a detailed understanding of how water management actions affect life history events that determine population dynamics. For a juvenile salmon migrating through the Delta, entering one of many migration routes is an important event that may determine its eventual fate. Entrainment events occur at small spatial and temporal scales at numerous river junctions, but how these events unfold over time determine population-level distribution among migration routes. At the individual level, I found that the probability of entering a given route varies on hourly timescales with the tides. At the population level, the fraction of fish entering a route varies on diel and fortnightly scales due to the spring-neap cycle, and on daily and seasonal scales due to river inflows and gate operations. These findings form the basis for understanding how water management actions affect entrainment into the interior Delta. As shown by simulating closed-at-night gate operations, my model can be used for predicting how fish distribute among routes in response to water management actions. Such management tools are critical for understanding the response of endangered salmon populations to water management actions in the Delta.

My findings show that flood tides causing the Sacramento River to reverse direction substantially increase the probability of entering both Georgiana Slough and the Delta Cross Channel. Parameter estimates indicate that entrainment probabilities into both the Delta Cross Channel and Georgiana Slough are at a maximum when 1) Q_S is at a minimum (increases both π_G and π_D), 2) the ebb tide transitions to a flood tide (increases π_D), 3) Q_G is at a maximum (increases π_G), and 4) discharge at Q_S is negative (increases π_G; Figure 6.4 and 6.5, Table 6.3). These conditions coincide and persist for the longest period of time during flood tides when mean river discharge entering the junction is low (Figure 6.8). As a consequence, daily entrainment into the interior Delta is highest at the lowest mean daily river discharge (Figure 6.9). As mean river discharge increases, tidal fluctuations are dampened and the river ceases to reverse direction on flood tides, causing daily entrainment probabilities to decrease as total inflow to the junction increases. These processes suggest that reduced inflows to the Delta will increase the frequency and duration of negative-flow flood tides at this river junction, increasing the fraction of juvenile salmon populations entrained into the interior Delta. In the future, inflows to the Delta may decrease through climate change or through water management actions that reduce discharge of the Sacramento River.

Overall, predicted daily entrainment into the interior Delta varied from about 30% to 60%. This range is driven by operation of the Delta Cross Channel and the interaction between river inflows and tides (Figure 6.9). Given the current physical setting of the Delta, reducing entrainment from the highest to lowest levels requires 1) closing the Delta Cross Channel gate and 2) maintaining mean daily inflows to the junction above 12,000 ft^3/s. Closing the gate is expected to reduce entrainment into the interior Delta by 10-15 percentage points. With the gates closed, entrainment probabilities decline an additional 15-20 percentage points from about 0.5 at the lowest inflow to 0.3 at about 12,000 ft^3/s. Increasing river inflow reduces tidal forces until about 12,000 ft^3/s, in turn reducing mean daily entrainment probabilities. At higher inflows, entrainment probabilities remain relatively constant, suggesting a shift from tidally dominated dynamics at hourly scales to inflow-dominated dynamics at daily scales. A third approach to reduce entrainment probabilities involves structural changes to the Delta that alter the relation between inflows and tides at this river junction. For example, wetland restoration at key locations in the Delta could absorb tidal forces, reducing upstream propagation of tides in the Sacramento River. Such actions would lower the inflow threshold at which tides begin to increase entrainment into the interior Delta by shifting the curves in Figure 6.8 to the left.

My analysis shows that low river inflows affect entrainment probabilities as much as operation of the Delta Cross Channel. This is an important finding because low inflows may have a compounding effect on population-level survival if survival through the interior Delta is negatively related to inflow. Under constant survival within routes, population-level survival (i.e., S_{Delta}) decreases with increasing entrainment into the interior Delta because survival in the interior Delta is lower than survival in the Sacramento River (Perry et al., 2010; Newman and Brandes, 2010; Chapter 4). However, if survival through the interior Delta decreases with inflow, then population-level survival may decline quickly because entrainment into the interior Delta increases while survival in the interior Delta is declining. Although the relation between inflow and survival through the interior Delta has yet to be firmly established (Newman and Brandes, 2010), my study highlights how river flow, route-specific survival, and entrainment into the interior Delta can act synergistically to affect population-level survival.

Understanding the relation between fish and flow distribution is important for quantifying both the economic and biological costs of water management actions. I found that predicted entrainment into the interior Delta was positively related but disproportional to discharge entering the interior Delta. Furthermore, entrainment efficiency was inversely related to the fraction of discharge entering the interior Delta, declining from 1.4 at low flow proportions when the Delta Cross Channel was closed, to 0.7 at high flow proportions with the Delta Cross Channel open (Figure 6.7). Thus, assuming a 1:1 relation between fish and flow considerably overestimates the fraction of fish entrained when the Delta Cross Channel is open. Nonetheless, reducing the interior Delta flow proportion reduces fish entrainment, but at a rate less than the change in flow. Specifically, the fraction of fish changes by only about half the change in the fraction of flow entering the interior Delta. Thus, each unit change in the fraction of fish entrained “costs” two units of fractional discharge. Understanding this relationship will allow managers to better quantify tradeoffs between the benefits of reducing fish entrainment relative to the costs of reduced water pumping associated with closure of the Delta Cross Channel.

Interaction between tides and diel migration behavior substantially affects the fraction of fish entrained into the interior Delta, especially during low inflows to the junction. During the winter migration period, flood tides during the day tend to be larger than at night, causing higher mean entrainment probabilities during the day. Consequently, relative to uniform diel migration, preferential diurnal migration will increase the fraction of fish entrained into the interior Delta, whereas nocturnal migration reduces entrainment. This finding was illustrated in my simulations of alternative gate operations: regardless of gate operations, mean entrainment probabilities were highest when 85% of fish migrated during the day, lowest when 85% of fish migrated at night, and intermediate when fish migrated uniformly over the diel cycle (Figure 6.10 and 6.11).

Increasing river inflow reduces tidal fluctuations at the river junction and in turn, reduces differences between day and night entrainment probabilities. Thus, day and night entrainment probabilities are similar when river flow exceeds the threshold at which at tidal strength approaches zero (about 12,000 ft^3/s). This pattern is illustrated in Figure 6.6 where day and night entrainment probabilities differed considerably during low flow in January, but were similar during February when inflow increased. Diel activity patterns affect population-level entrainment when river flow is low and tidal strength high, but will have little influence on entrainment at higher inflows when tidal strength is low. Given the relatively low flows observed during this three-year study, understanding diel activity patterns of migrating juvenile salmon is critical for quantifying entrainment into the interior Delta and identifying management actions that minimize entrainment.

In general, factors driving diel movement patterns in the Delta are poorly understood but will probably vary with season, environment, life stage, and life history strategy of juvenile salmon. In my study, the proportion of fish detected at night averaged 75% even though night comprised about 60% of the 24-h period. More importantly, nighttime arrival varied from 55% to 86% among release groups, ranging from diel arrival proportional to the availability of daylight hours to substantial nocturnal migration (Table 6.1). Such variation is not surprising given that diel activity patterns can switch from day to night in response to interactions between predation risk, physiological state, and environmental cues (Metcalfe et al. 1998, 1999). For example, an increase in nighttime activity with decreasing temperature is hypothesized as a behavioral response to lower metabolic requirements, reducing the need for juvenile salmon to feed during the day when predation risk is high. In my study, some preference for nocturnal migration is expected given that the study occurred during winter at water temperatures ranging from 6-12 °C. At higher temperatures, evidence suggests that juvenile salmon in the Delta may migrate preferentially during the day (Wilder and Ingram, 2006).

The primary strength of my model is its ability to estimate time-specific probabilities of entering each migration route in response to tidally varying flows. This property allows management actions to be simulated at hourly scales, but also permits assessment of different diel activity patterns. Diel activity of a given population can vary considerably, such as observed in this study. Furthermore, species, life stages, and rearing types (e.g., hatchery versus wild) that migrate simultaneously may exhibit different diel activity patterns. By simulating a range of diel activity patterns, management actions robust to uncertainty in diel activity can be identified. Simulations of closed-at-night gate operations provided one example of how my model could be used to optimize water management actions by maximizing water diversion and minimizing fish entrainment. Additional applications include simulating the effect of changes in mean river inputs and changes in tidal dynamics (e.g., through wetland restoration or levee breaches); both of which are critical factors affecting entrainment into the interior Delta.

It is important to recognize that population distribution among migration routes will depend on entrainment probabilities at a number of critical river junctions. First, many juvenile salmon never encounter the Delta Cross Channel or Georgiana Slough because 20-40% of the population enters Sutter and Steamboat Slough, the first major river junction in the Delta that juvenile salmon must negotiate (Perry et al., 2010; Chapter 4). Second, downstream of both river junctions, juvenile salmon may also enter the interior Delta through Three Mile Slough or at the confluence of the Sacramento and San Joaquin rivers near the terminus of the Delta. Future efforts to quantify channel-specific entrainment probabilities as a function of flow at other river junctions will help to predict Delta-wide movement of the population in response water management actions.

Prior to this study, fisheries managers had little mechanistic information to guide water management actions intent on minimizing entrainment into the interior Delta. Uncertainty about driving mechanisms forces fisheries managers to act in a precautionary manner, implementing actions least likely to harm endangered populations at the expense of consumptive water use. Furthermore, lack of understanding key mechanisms limits development of solutions that both minimize biological consequences, but also minimize costs to water users. Operation of the Delta Cross Channel is an obvious action that managers can control. Less obvious but equally important is the effect of river inflow on entrainment into the interior Delta. I quantified how these mechanisms affect route entrainment probabilities and developed a model that managers can use to assess the effect of a wide range of water management actions. This study takes an important step towards providing tools to understand how future water management in the Delta might influence migration and survival dynamics of juvenile salmon.

Chapter 7

SUMMARY AND CONCLUSIONS

Historically, California's Central Valley was among the most productive salmon-bearing watersheds in the continental United States. Today, the Sacramento-San Joaquin River Delta has the distinction as one of the most human-altered estuaries in the world. Yet such alteration has allowed water from the Delta to support 20 million Californians and the country's largest agricultural industry. Salmon and other endemic fish populations have suffered the consequence of this economic prosperity and are now but a wisp of their former magnitude. State and federal governments are wrestling with recovering endangered fishes while maintaining ecosystem services in the face of climate change and human population growth. My dissertation research takes place against this backdrop, but this general storyline has played out in many large rivers and estuaries across the nation.

Managers require detailed information about the response of endangered fish populations to alternative water management actions. Given the extreme spatial and hydrodynamic complexity of the Delta, unraveling migration and survival dynamics of juvenile salmon is a formidable challenge. Traditional capture-recapture techniques have limited utility in this setting, but acoustic telemetry allows the migration of individuals to be tracked at fine temporal and spatial scales to match the complexity of the Delta's channel network. Although acoustic telemetry provides a means for collecting reams of detailed data, lacking are statistical models to translate this data from mere descriptive assessments to population-level inferences. My dissertation takes a significant step towards coupling modern capture-recapture models with detailed information afforded by telemetry. The models presented in this dissertation illustrate the inferential power obtained when combining telemetry with statistical models to tackle complex problems in fisheries science.

At the outset of this research project, significant questions loomed not only about survival of juvenile salmon, but also about their movement patterns through the Delta. For the past 30 years, survival studies using coded wire tags provided an incomplete picture of population status. Annual survival indices indicated that mortality in some migration routes was lower than others. Without information about movement among routes, however, it was impossible to quantify the contribution of a particular migration route to survival of the population. This gap made it impossible to explicitly quantify the effects of management actions at the population level. My first goal, therefore, was to link survival in each migration route to population-level survival. In Chapter 2, I cast this problem as a spatially structured population model comprised of two sets of vital rates: 1) route-specific survival probabilities and 2) transition probabilities that governed movement among routes.

To estimate parameters of this spatially stratified model, I adapted the general class of models known as multistate mark-recapture models (Brownie et al., 1993; Lebreton and Pradel, 2002). I explicitly evaluated critical assumptions of the model in the context of using telemetry to sample individuals moving through space. I showed how the spatial location of telemetry stations could violate model assumptions, leading to biased estimates of transition probabilities. In addition, the dendritic, hierarchical structure of the Delta's channel network results in a constrained version of the general multistate model, which can cause confounding among parameters. I used formal statistical techniques and simulation to arrive at general principles for telemetry system design that both fulfills model assumptions and ensures estimability of parameters. My findings illustrate the direct link between developing a model containing parameters of interest, designing the telemetry system to estimate these parameters, and then testing the model to be sure parameters can be estimated from the data. Given the explosion in the use of remote detection systems for monitoring fish populations (Hewitt et al., 2010, McMichael et al., 2010), this work contributes directly towards understanding how to design both detection systems and statistical models capable of estimating parameters of interest.

In Chapters 3 and 4, I applied the multistate models to the first available telemetry data on Delta-scale movements of juvenile Chinook salmon. New insights were immediate. For the first time, managers could begin to understand how movement and survival at multiple spatial scales interact to affect population survival. At the finest spatial scale, transition probabilities quantified the chances of a fish being entrained into a particular channel at a given river junction. At the next scale, joint entrainment probabilities across multiple river junctions yielded the fraction of the population migrating through a particular pathway in the Delta. Understanding movement at both scales is critical to water management in the Delta. At the scale of a single junction, consequences of water management actions on fish entrainment can be directly quantified (e.g., operation of the Delta Cross Channel). At the scale of multiple junctions, the probability of migrating through a unique pathway quantifies the contribution of route-specific survival to population-level survival. For example, I showed that the survival in the Sacramento River was consistently higher than other migration routes, yet for some releases, less than half of the population migrated through the Delta via the Sacramento River. Without a spatially-structured model coupled with telemetry data to estimate the parameters, such insights would be impossible.

Matrix population models cast in the framework of a population viability analysis are a powerful approach to assess recovery of endangered species in response to alternative scenarios (Caswell, 2001; Morris and Doak, 2002). However, to understand how population growth rates are affected by a given management action on a particular life stage at a specific location, sufficient detail must be built into the model. Such detail often translates into numerous parameters for which few empirical estimates exist. By structuring the Delta as a series of spatially stratified transition matrices, I showed how the Delta can be fit neatly into the larger framework of a matrix population model for the complete salmon life cycle. Furthermore, the multistate mark-recapture model provides a natural framework for estimating the parameters of a matrix population model (Caswell and Fujiwara, 2004). Thus, my research has provided both the framework and the parameter estimates with which to quantify how management actions in the Delta affect not only juvenile survival, but population growth rates (e.g., see CALFED Science Review Panel, 2008). Linking spatial dynamics to a population model *and* estimating the parameters of such a model is a major strength of my work that has broad applicability to other systems.

My modeling approach stresses estimation of individual components of the population that can be reconstructed at different levels of organization to gain insights into population dynamics. Reach-specific survival probabilities and entrainment probabilities at a river junction form the basic building blocks of population-level survival. In and of themselves, these fundamental parameters yield insights into movement and survival dynamics at a local scale. In Chapter 4, for example, I found that reach-specific survival shifted simultaneously for all reaches within a route, shedding light on the spatial scale of variability in survival processes. More important, however, functions of the fundamental parameters provide insights at larger scales of organization. A key example is route-specific survival, the product of reach-specific survival probabilities tracing a particular migration pathway through the Delta. Ability to quantify survival between the same beginning and end points for fish traversing different pathways allows migration routes to be directly compared on the same spatial scale. Furthermore, with a unifying estimation framework, measures of uncertainty for both fundamental parameters and their functions can be readily obtained. Similar approaches are starting to be implemented and models being developed to deconstruct population survival into its component parts (Skalski et al., 2002; Buchanan, 2005). All rely on remote detection of tagged individuals, development of novel estimation models, and reconstruction of fundamental parameters into population-level parameters.

Given a three-year set of telemetry data, in Chapters 5 and 6 I began to tackle the dynamics of movement and survival in response to environmental factors. These analyses focused on individuals because the environment varied at temporal scales likely to impose substantial variation in the fates of individuals. Survival of individuals in two migration routes depended on hydraulic conditions (river flow and tidal strength) during the three days after fish entered a migration route. This finding is of direct use to managers that must quantify the effects of upstream water withdrawals on salmon populations. The Delta Cross Channel has long been the focus of intense scrutiny for both its importance to water users and its effect on juvenile salmon survival. Until my research, entrainment into the Delta Cross Channel was never quantified except for indirect measurements at the pumping facilities. I not only obtained release-specific point estimates of both junction- and population-level entrainment probabilities into the Delta Cross Channel, but I quantified how river flow, tides, and gate operations influenced daily entrainment probabilities into the interior Delta. I then showed how a dynamic model for entrainment probabilities could be used to understand the effect of water management actions on fish routing. This model can be applied immediately in Delta planning processes such as the Delta Bay Conservation Plan to understand how different water management actions affect migration routing in the Delta.

Although the dynamics of the Delta are complex, my findings are intuitive. Most fish are entrained into the interior Delta when all water flows into the interior Delta. Survival is low when fish migrate via a route in which more water can flow inland than towards the ocean. Survival increases when river flow speeds fish past hungry predators. Survival of big fish is greater than that of small fish. To some extent, each of these statements can be supported without data, based on common sense and first principles. Yet in the absence of data these statements stand as mere hypotheses to be challenged. The beauty of science lies in uncovering what should make sense; the central challenge, figuring out how to uncover it; the reward, finding out that indeed, the intuitive hypothesis is supported by the data. But collecting data is not enough. Telemetry techniques allow us to collect millions of detailed observations on individuals, but scientific insights remain hidden without mathematical models to extend individual observations to population-level inferences. My contribution to science is not my findings per se, but developing the mathematical frameworks that allow us to distill apparent complexity into a series of seemingly simple relationships. After all, it is the interaction of myriad simple relationships from which complexity arises. By breaking down systems into their component parts, developing models to relate the pieces to the whole, and applying modern technology to inform models with data, I have taken an important step towards unraveling the complexity of human and natural factors affecting survival of juvenile salmon in the Delta.

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Appendix 1

ADDITIONAL FIGURES AND TABLES FOR CHAPTER 3

Appendix Table 1.1. Counts of detection histories for the full model shown in Figure 3.2 for a release of $R_1 = 64$ fish on 5 December 2006 and $R_2 = 80$ fish on 17 January 2007. Counts for all other detection histories were zero and are not shown here. Each digit of the detection history indicates detection at telemetry stations within each of four migration routes (labeled A–D), with a “0” indicating a fish was not detected. Since some routes contained fewer telemetry stations than others, the “*“ notation acts as a place holder to maintain information about the *j*th telemetry station in the *j*th position of the detection history. In the fourth position of the detection history, the history for junction 2, a capital letter indicates a fish passed junction 2 when the Delta Cross Channel was open, and a lower-case letter indicates the Delta Cross Channel was closed when a fish passed junction 2.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
1BA**BBBB	1	1BA**BBBB	4
1BA**BB0B	2	1BA**0BBB	2
1BA**BBB0	2	1BA**00BB	1
1BA**B000	1	1BA**BB0B	4
1BA**0000	10	1BA**0B0B	1
1B0BB0BBB	1	1BA**BBB0	1
1B0BB0B0B	1	1BA**0BB0	2
1B0BBBBB0	1	1BA**BB00	3
1B0BBBB00	4	1BA**B000	1
1B0BBB000	3	1BA**0000	10
1B0BB0000	3	1BBbBBBBB	5
1B0B00000	1	1B0bBBBBB	1
1B0000000	5	1BBbB0BBB	3
100000000	7	10BbB0BBB	1
1B0bBBBBB	2	1BBbB00BB	1
1B0b00000	2	1BBbBBB0B	4
1B0C*C0BB	1	1BB0BBB0B	1
1B0C*C000	2	1BBbBBBB0	1
1B0C*0000	2	1BBbB0BB0	2
1B0c*0000	1	1BBbBBB00	1
1B0DDC00B	1	1BBbB0B00	1
1B0DD000B	1	1BBbBB000	2
1B0DDC0B0	1	1BBbB0000	10
1B0DD00B0	1	1BBb00000	1
1B0DDC000	2	1BB000000	1

Appendix Table 1.1 Continued.

1B0DD0000	5	1B0000000	3
1B0D00000	1	100000000	7
		1BBc***BB	1
		1BBc***B0	1
		1BBc***00	4
Total released (R_k)	64		80

Appendix Table 1.2. Parameter estimates for the mark-recapture shown in Figure 3.2 for releases of acoustically tagged late-fall juvenile Chinook salmon made in December, 2006 (R_1) and January, 2007 (R_2). Parameters not estimated are indicated by an "NA" in the estimate column, and parameters fixed at a constant value are noted by an "NA" in the profile likelihood column.

	R_1: December 2006		R_2: January, 2007	
Parameter	Estimate ($\widehat{\mathrm{SE}}$)	95% Profile likelihood interval	Estimate ($\widehat{\mathrm{SE}}$)	95% Profile likelihood interval
S_{B1}	0.389 (0.126)	0.176, 0.645	0.681 (0.093)	0.492, 0.850
S_{A1}	0.891 (0.039)	0.799, 0.951	0.913 (0.032)	0.838, 0.962
S_{A2}	0.947 (0.023)	0.890, 0.981	0.959 (0.024)	0.896, 0.990
S_{A3}	0.947 (0.023)	0.890, 0.981	0.976 (0.025)	0.895, 1.000
S_{A4}	0.833 (0.088)	0.623, 0.956	0.970 (0.030)	0.873, 0.998
S_{A5}	0.830 (0.110)	0.578, 1.000	0.725 (0.085)	0.549, 0.879
S_{A6}	0.750 (0.108)	0.511, 0.915	0.900 (0.059)	0.751, 0.983
S_{A7}	0.952 (0.237)	0.566, 1.000	0.953 (0.077)	0.794, 1.000
S_{D1}	0.648 (0.302)	0.193, 1.000	NA	
$S_{\mathrm{D2}}S_{\mathrm{D3}}$	0.571 (0.270)	0.166, 1.000	NA	
$S_{\mathrm{D1}}S_{\mathrm{D2}}S_{\mathrm{D3}}$	NA		0.368 (0.213)	0.071, 0.802
S_{C1}	0.917 (0.080)	0.681, 0.995	NA	
S_{C2}	0.707 (0.252)	0.322, 1.000	NA	
Ψ_{B1}	0.296 (0.062)	0.186, 0.426	0.414 (0.059)	0.303, 0.531
Ψ_{A1}	0.704 (0.062)	0.574, 0.814	0.586 (0.059)	0.469, 0.697
ω_{open}	0.861 (0.058)	0.725 , 0.948	0.000	NA
ω_{closed}	0.139 (0.058)	0.052 , 0.275	1.000	NA
$\Psi_{\mathrm{A2,open}}$	0.452 (0.089)	0.286 , 0.625	0.000	NA
$\Psi_{\mathrm{D2,open}}$	0.161 (0.066)	0.061 , 0.315	0.000	NA
$\Psi_{\mathrm{C2,open}}$	0.387 (0.087)	0.230 , 0.562	0.000	NA
$\Psi_{\mathrm{A2,closed}}$	0.800 (0.179)	0.372 , 0.987	0.850 (0.056)	0.719, 0.938
$\Psi_{\mathrm{D2,closed}}$	0.200 (0.179)	0.013 , 0.628	0.150 (0.056)	0.062, 0.281
P_{B1}	1.000	NA	1.000	NA
P_{A2}	1.000	NA	0.986 (0.014)	0.939, 0.999
P_{A3}	1.000	NA	0.975 (0.025)	0.895, 0.999
P_{A4}	1.000	NA	0.970 (0.030)	0.873, 0.998
P_{A5}	1.000	NA	1.000	NA
P_{A6}	0.857 (0.094)	0.621, 0.975	0.641 (0.077)	0.485, 0.779
P_{A7}	1.000	NA	0.941 (0.040)	0.829, 0.990
P_{A8}	0.500 (0.158)	0.218, 0.782	0.655 (0.088)	0.474, 0.810
P_{D1}	1.000	NA	1.000	NA
P_{D2}	0.600 (0.219)	0.199, 0.919	NA	
P_{D3}	1.000	NA	NA	
P_{C1}	1.000	NA	NA	
P_{C2}	1.000	NA	NA	
λ	0.500 (0.158)	0.218, 0.782	0.731 (0.087)	0.544, 0.874

Appendix 2

ASSESSING THE CONSEQUENCE OF ASSUMING $S_{A2} = S_{A3}$

Since a telemetry station at location A_3 was not implemented during 2008 nor for the December release in 2007, the parameters S_{A2}, S_{A3}, Ψ_{B11}, and Ψ_{B21} could not be uniquely estimated without imposing constraints on the parameters. Therefore, I estimated these parameters under the constraint that $S_{A2} = S_{A3}$. Although estimates from the January release in 2007 showed little difference between S_{A2} and S_{A3} (Appendix Table 1.2), station A_3 has not been monitored for three of the four releases thus far. If S_{A2} is not equal to S_{A3}, then associated estimates of route entrainment and survival probabilities will be biased. Here I evaluate the magnitude of bias introduced by assuming $S_{A2} = S_{A3}$, when in fact S_{A2} differs from S_{A3}.

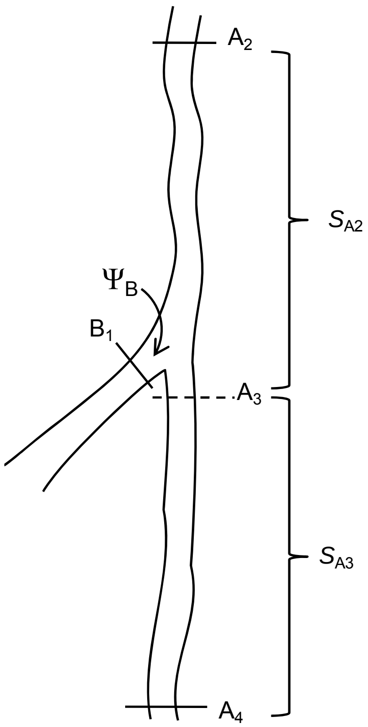
To illustrate the potential bias that might be incurred, I first simplified the problem by assuming a two-branch junction (Appendix Figure 2.1). I was interested not only in bias in Ψ_B, but also in bias that might occur in the product $S_{A2}S_{A3}$. This product appears in equations for route specific survival through the Delta for Routes A, C, and D (i.e., S_h). Thus, bias in this product is more relevant than bias in each of the reach-specific survival probabilities. Appendix Figure 2.1 shows a schematic of the problem with the underlying survival and route entrainment parameters. Without a telemetry station at location A_3, only two parameters can be estimated from information provided by telemetry stations at B_1 and A_4. The two estimable parameters are the joint probabilities of the underlying parameters between stations A_2 and B_1, and between A_2 and A_4:

$$\phi_{A2,\,B1} = S_{A2}\Psi_B \tag{A2.1}$$

$$\phi_{A2,\,A4} = S_{A2}S_{A3}\left(1-\Psi_B\right) \tag{A2.2}$$

Where $\phi_{A2,B1}$ is the joint probability of surviving the first reach and entering channel B, and $\phi_{A2,A4}$ is the joint probability of surviving the first reach, remaining in channel A, and surviving the second reach. As discussed in Chapter 2, these two parameters can always be estimated without bias from the data, as can the total survival from A_2 to either of the downstream exit points:

$$S_{\text{total}} = \phi_{\text{A2, B1}} + \phi_{\text{A2, A4}} \tag{A2.3}$$



Appendix Figure 2.1. Schematic of a two-branch river junction showing location of telemetry stations at A_2, B_2, and A_4. The dashed line notes lack of a telemetry station at A_3. Brackets show the probability of surviving between A_2 and A_3 and between A_3 and A_4. The probability of entering Channel B is Ψ_B, and the probability of remaining in Channel A is $1\text{-}\Psi_B$.

To quantify bias, I substituted Eqns. A2.1 and A2.2 into Eqn. A2.3, set $S_{A3} = S_{A2}$, and then solved Eqn. A2.3 for S_{A2} and Eqn. A2.1 for Ψ_B:

$$\tilde{S}_{\text{A2}} = \frac{\Psi_{\text{B}} - \sqrt{\Psi_{\text{B}}{}^{2} - 4S_{\text{total}}\left(\Psi_{\text{B}} - 1\right)}}{2\left(\Psi_{\text{B}} - 1\right)} \tag{A2.4}$$

$$\tilde{\Psi}_{\text{B}} = \frac{\phi_{\text{A2, B1}}}{\tilde{S}_{\text{A2}}} \tag{A2.5}$$

Here, $\tilde{S}_{A2}$ and $\tilde{\Psi}_B$ will be the biased estimates that result when assuming $S_{A2} = S_{A3}$ when in fact $S_{A2} \neq S_{A3}$; and S_{total} and $\phi_{A2,B1}$ are calculated using hypothesized true values of S_{A2}, S_{A3}, and Ψ_B.

Estimates of S_{total} from my data will be unbiased regardless of bias that might be present in estimates of S_{A2}, S_{A3}, or Ψ_B , and we used this fact to establish the maximum possible bias that could arise by assuming $S_{A2} = S_{A3}$. For example, for the first release in 2008, I estimated $\hat{\Psi}_B = 0.345$ and $\hat{S}_{A2} = \hat{S}_{A3} = 0.919$ (Appendix Table 3.3), resulting in $\hat{S}_{total} = 0.87$. Now suppose $\hat{\Psi}_B = \tilde{\Psi}_B = 0.345$ is the biased estimate of Ψ_B: What true values of Ψ_B, S_{A2}, and S_{A3} could have produced the observed estimate, $\tilde{\Psi}_B$? First, the true parameter values Ψ_B, S_{A2}, and S_{A3} are constrained such that $\hat{S}_{total} = 0.87$ (according to Eqn. A2.3) and $\tilde{\Psi}_B = 0.345$ (according to Eqn. A2.5). Also, given that $\hat{S}_{total} = 0.87$, S_{A2} and S_{A3} are further constrained such that all of the observed mortality could have occurred in either the first reach (i.e., $S_{A3} = 1$) or the second reach (i.e., $S_{A2} = 1$). Clearly, mortality will occur in both reaches, but I used these two scenarios to bound the extremes of bias that could possibly occur given that $\hat{S}_{total} = 0.87$ and $\tilde{\Psi}_B = 0.345$. Thus, maximum bias is calculated by setting $S_{A2} = 1$ (or $S_{A3} = 1$), and then finding the true values of S_{A3} (or S_{A2}) and Ψ_B that satisfy $S_{total} = 0.87$ and $\tilde{\Psi}_B = 0.345$. Should the maximum possible bias be low under these extreme scenarios, then I can infer that the realized bias would be even less.

Under these extreme scenarios, I found that maximum possible bias was quite low. For the December release, maximum absolute bias in Ψ_B was less than 0.028, and bias in $S_{A2}S_{A3}$ was less than 0.035 (Appendix Table 2.1). Maximum possible bias for the January release was even less (Appendix Table 2.1). These findings suggest that the realized bias in these parameters will be much less than the maximum possible bias, given that we know mortality occurs in both reaches, and that past evidence suggests little difference between S_{A2} and S_{A3} (see Appendix Table 3.3). Parameter stimates are robust to deviations from $S_{A2} = S_{A3}$ partly due to the relatively high total survival (S_{total}) observed in this reach. Since S_{total} constrains the range of possible true values of S_{A2} and S_{A3}, as S_{total} decreases S_{A2} and S_{A3} may take on a wider range of values between 0 and 1. Thus, as S_{total} decreases, the possible maximum bias will increase under the extreme scenarios of all mortality occurring in either one reach or another.

Although this sensitivity analysis shows that bias was likely minimal, the appropriate course of action is to ensure a telemetry station is implemented at A_3 in future years. Given the influence of Sutter and Steamboat sloughs on migration dynamics through the entire Delta, this river junction is too important to rest future research on such assumptions.

Appendix Table 2.1. Maximum possible bias induced by assuming $S_{A2} = S_{A3}$, when in fact, all mortality occurs in either the upstream reach or the downstream reach.

	True values				Estimates when assuming $S_{A2} = S_{A3}$		Bias	
Release	S_{A2}	S_{A3}	Ψ_B	S_{total}	$\tilde{S}_{A2}$	$\tilde{\Psi}_B$	$\Psi_B - \tilde{\Psi}_B$	$S_{A2}S_{A3} - \tilde{S}_{A2}^2$
R_1: December	0.870	1.000	0.364	0.870	0.918	0.345	-0.019	-0.025
	1.000	0.810	0.318	0.870	0.920	0.345	0.028	0.035
R_2: January	0.852	1.000	0.213	0.852	0.914	0.198	-0.014	-0.016
	1.000	0.819	0.182	0.852	0.915	0.198	0.017	0.017

Appendix 3

ADDITIONAL FIGURES AND TABLES FOR CHAPTER 4

Appendix Table 3.1. Counts of detection histories for the model shown in Figure 4.2 for a release of R_1 = 208 fish on 4 December 2007 and R_2 = 211 fish on 16 January 2008. Counts for all other detection histories were zero and are not shown here. Each digit of the detection history indicates detection at telemetry stations within each of four migration routes (labeled A–D) and Three Mile Slough (E). A "0" indicating either a fish was not detected or a telemetry station within that route was not implemented at that position in the capture history (since some routes had more telemetry stations than others). Detection histories beginning with "0 0 0 D" indicate fish released in Georgiana Slough whereas those beginning with "A" are fish released into the Sacramento River.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
0 0 0 D 0 0 0 0 0 0 0 0 0	11	0 0 0 D 0 0 0 0 0 0 0 0 0 0	5
0 0 0 D D 0 0 0 0 0 0 0 0	5	0 0 0 D D 0 0 0 0 0 0 0 0	4
0 0 0 D D D 0 0 0 0 0 0 0	7	0 0 0 D D D 0 0 0 0 0 0 0	21
0 0 0 D D D D 0 0 0 0 0 0	20	0 0 0 D D D D 0 0 0 0 0 0	32
0 0 0 D D D D D 0 0 0 0 0	6	0 0 0 D D D D D 0 0 0 0 0	4
0 0 0 D D D D E 0 0 0 0 0	3	0 0 0 D D D D E 0 0 0 0 0	1
0 0 0 D D D D D 0 D 0 0 0	2	0 0 0 D D D D 0 0 D 0 0 0	1
0 0 0 D D D D D 0 D D A 0	1	0 0 0 D D D D D 0 D 0 0 0	2
0 0 0 D D D D E A 0 0 A A	2	0 0 0 D D D D 0 0 D D 0 0	1
0 0 0 D D D D D 0 0 D A A	1	0 0 0 D D D D 0 0 0 0 A 0	1
0 0 0 D D D D D 0 D D A A	1	0 0 0 D D D D E A 0 0 0 A	1
A 0 0 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D D 0 D D 0 A	1
A A 0 0 0 0 0 0 0 0 0 0 0	18	0 0 0 D D D D 0 0 0 0 A A	1
A 0 B1 0 0 0 0 0 0 0 0 0 0	1	0 0 0 D D D D D 0 0 0 A A	1
A A B1 0 0 0 0 0 0 0 0 0 0	8	0 0 0 D D D D E A 0 0 A A	1
A A B2 0 0 0 0 0 0 0 0 0 0	3	0 0 0 D D D D D 0 D 0 A A	2
A A 0 A 0 0 0 0 0 0 0 0 0	7	0 0 0 D D D 0 D 0 0 D A A	1
A A B1 B1 0 0 0 0 0 0 0 0 0	4	0 0 0 D D D D D 0 0 D A A	1
A A B1 B2 0 0 0 0 0 0 0 0 0	1	A 0 0 0 0 0 0 0 0 0 0 0 0	6
A 0 B2 B2 0 0 0 0 0 0 0 0 0	1	A A 0 0 0 0 0 0 0 0 0 0 0	16
A A B2 B2 0 0 0 0 0 0 0 0 0	2	A A B1 0 0 0 0 0 0 0 0 0 0	4
A 0 0 C 0 0 0 0 0 0 0 0 0	1	A A B2 0 0 0 0 0 0 0 0 0 0	1
A A 0 C 0 0 0 0 0 0 0 0 0	9	A A 0 A 0 0 0 0 0 0 0 0 0	3
A A 0 D 0 0 0 0 0 0 0 0 0	6	A 0 0 D 0 0 0 0 0 0 0 0 0	2

Appendix Table 3.1. Continued.

A 0 0 A A 0 0 0 0 0 0 0 0	1	A A 0 D 0 0 0 0 0 0 0 0 0	4
A A 0 A A 0 0 0 0 0 0 0 0	5	A 0 0 A A 0 0 0 0 0 0 0 0	1
A A B1 B1 B1 0 0 0 0 0 0 0 0	7	A A 0 A A 0 0 0 0 0 0 0 0	6
A A B1 B2 B2 0 0 0 0 0 0 0 0	4	A 0 B1 B1 B1 0 0 0 0 0 0 0 0	1
A A B2 B2 B2 0 0 0 0 0 0 0 0	2	A 0 B2 B2 B2 0 0 0 0 0 0 0 0	1
A A 0 D D 0 0 0 0 0 0 0 0	1	A A B2 B2 B2 0 0 0 0 0 0 0 0	3
A A 0 0 A A 0 0 0 0 0 0 0	1	A A 0 D D 0 0 0 0 0 0 0 0	3
A A 0 A A A 0 0 0 0 0 0 0	4	A A 0 A A A 0 0 0 0 0 0 0	10
A A 0 D D D 0 0 0 0 0 0 0	1	A 0 0 D D D 0 0 0 0 0 0 0	1
A A 0 A A 0 A 0 0 0 0 0 0	1	A A 0 D D D 0 0 0 0 0 0 0	2
A A B1 B2 B2 0 A 0 0 0 0 0 0	1	A A B1 B2 B2 0 A 0 0 0 0 0 0	1
A A B2 B2 B2 0 A 0 0 0 0 0 0	1	A A B2 B2 B2 0 A 0 0 0 0 0 0	1
A A 0 A A A A 0 0 0 0 0 0	2	A 0 0 A A A A 0 0 0 0 0 0	1
A A 0 C 0 D D 0 0 0 0 0 0	3	A A 0 A A A A 0 0 0 0 0 0	2
A A 0 D D D D 0 0 0 0 0 0	3	A 0 0 D D D D 0 0 0 0 0 0	4
A A B2 B2 B2 0 0 A 0 0 0 0 0	1	A A 0 D D D D 0 0 0 0 0 0	12
A A 0 A A 0 A A 0 0 0 0 0	1	A A B1 B1 B1 0 0 A 0 0 0 0 0	1
A A B1 B1 B1 0 A A 0 0 0 0 0	1	A 0 B1 B2 B2 0 0 A 0 0 0 0 0	1
A A B2 B2 B2 0 A A 0 0 0 0 0	1	A A B2 B2 B2 0 0 A 0 0 0 0 0	1
A 0 0 A A A A A 0 0 0 0 0	1	A A 0 A A A 0 A 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 0 0	9	A A 0 A A 0 A A 0 0 0 0 0	1
A A 0 D D D D D 0 0 0 0 0	1	A A B1 B1 B1 0 A A 0 0 0 0 0	2
A A 0 D D D D E 0 0 0 0 0	1	A A B2 B2 B2 0 A A 0 0 0 0 0	3
A A 0 D D D D 0 0 D 0 0 0	1	A 0 0 A A A A A 0 0 0 0 0	1
A A 0 A A 0 0 A 0 0 0 A 0	1	A A 0 A A A A A 0 0 0 0 0	5
A A B1 B2 B2 0 A A 0 0 0 A 0	1	A A 0 D D D D D 0 0 0 0 0	2
A A B2 B2 B2 0 A A 0 0 0 A 0	1	A A 0 A A A A E 0 0 0 0 0	2
A A 0 A A A A A 0 0 0 A 0	2	A A 0 A A 0 A E 0 D 0 0 0	1
A A B1 0 B1 0 0 E D D D A 0	1	A A 0 A A A A 0 0 0 0 A 0	1
A A 0 0 A 0 A 0 0 0 0 0 A	1	A A 0 A A A A A 0 0 0 A 0	3
A A 0 D D D D D 0 D D 0 A	2	A A 0 A A A A E 0 D 0 A 0	1
A A 0 A A A A E D D D 0 A	1	A A 0 D D D D D 0 D D A 0	1
A A 0 A A A A 0 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 0 A	1
A A B2 B2 B2 0 0 A 0 0 0 A A	1	A 0 0 A A 0 A E 0 D 0 0 A	1
A A 0 A A A 0 A 0 0 0 A A	2	A A 0 D D D D 0 0 0 0 A A	1
A A 0 A A 0 A A 0 0 0 A A	1	A A 0 A A A 0 A 0 0 0 A A	1
A A B1 B1 B1 0 A A 0 0 0 A A	1	A A 0 A A 0 A A 0 0 0 A A	3
A A B2 B2 B2 0 A A 0 0 0 A A	2	A 0 B2 B2 B2 0 A A 0 0 0 A A	1
A A 0 A A A A A 0 0 0 A A	5	A A B2 B2 B2 0 A A 0 0 0 A A	2
A A 0 C 0 D D E A 0 0 A A	1	A 0 0 A A A A A 0 0 0 A A	1
A A 0 D D D D D 0 0 D A A	1	A A 0 A A A A A 0 0 0 A A	5
A A 0 D D D D D 0 D D A A	1	A A 0 D D D D 0 0 0 D A A	1
Total released (R_k)	208		211

Appendix Table 3.2. Parameter constraints applied under the full model for each release, representing the minimum estimable model with the maximum number of parameters. Parameters not shown below were estimable by iteratively maximizing the likelihood of the multinomial model. Constraints include parameters that had to be fixed to a constant value or set equal to other parameters because they could not be estimated from the data set of detection histories.

R_1: December 2007		R_2: January 2008	
Parameter	Constraint	Parameter	Constraint
S_{A3}	$= S_{A2}$	Ψ_{C2}	$= 0$
$S_{D7,\ Sac}$	$= 1$	$\phi_{D4,E1,Sac}$	$= 0$
$S_{E1,D5}$	$= 1$	S_{A3}	$= S_{A2}$
P_{A3}	$= 0$	S_{B12}	$= 1$
P_{A5}	$= 1$	S_{B22}	$= 1$
$P_{E1,Sac}$	$= 1$	S_{C1}	$= 0$
P_{B11}	$= 1$	$S_{D7,Sac}$	$= 1$
P_{B21}	$= 1$	$S_{E1,D5}$	$= \phi_{D4,D5,Geo}$
P_{B22}	$= 1$	$S_{E1,A8,Sac}$	$= 0$
P_{B13}	$= 1$	P_{A3}	$= 0$
P_{B23}	$= 1$	P_{A4}	$= 1$
P_{C1}	$= 1$	P_{A5}	$= 1$
P_{D1}	$= 1$	P_{B11}	$= 1$
$P_{D2,Sac}$	$= 1$	P_{B12}	$= 1$
$P_{D3,Sac}$	$= 1$	P_{B13}	$= 1$
$P_{D4,Sac}$	$= 1$	P_{B21}	$= 1$
$P_{D7,Sac}$	$= 1$	P_{B22}	$= 1$
$S_{D7,Geo}$	$= 1$	P_{B23}	$= 1$
$P_{D2,Geo}$	$= 1$	P_{C1}	$= 0$
$P_{D3,Geo}$	$= 1$	P_{D1}	$= 1$
$P_{D4,Geo}$	$= 1$	$P_{D2,Sac}$	$= 1$
$P_{D5,Geo}$	$= 1$	$P_{D3,Sac}$	$= 1$
$P_{D7,Geo}$	$= 1$	$P_{D4,Sac}$	$= 1$
$P_{A8,Geo}$	$= 1$	$P_{E1,Sac}$	$= 1$
$P_{A9,Geo}$	$= 1$	$P_{D2,Geo}$	$= 1$
$P_{E1,Geo}$	$= 1$	$P_{D3,Geo}$	$= 1$
$S_{A8,Geo}$	$= 1$	$P_{A8,Geo}$	$= 1$
		$P_{E1,Geo}$	$= 1$
		$S_{A8,Geo}$	$= 1$

Appendix Table 3.3. Parameter estimates under the reduced model for releases of acoustically tagged late-fall juvenile Chinook salmon in December, 2007 (R_1) and January, 2008 (R_2). Parameters not estimated are indicated by an "NA" in the estimate column, and parameters fixed at a constant value are noted by an "NA" in the profile likelihood column.

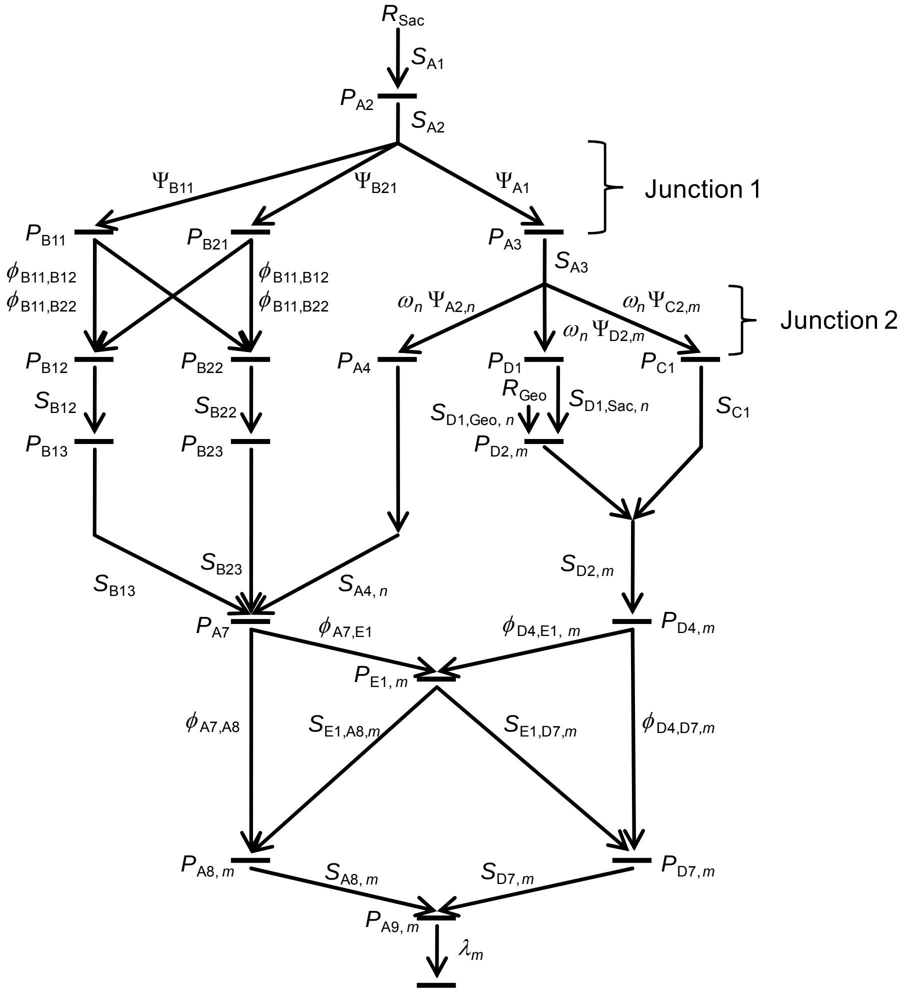
	R_1: December 2007		R_2: January 2008	
Parameter	Estimate ($\widehat{\text{SE}}$)	95% Profile likelihood interval	Estimate ($\widehat{\text{SE}}$)	95% Profile likelihood interval
S_{A1}	0.951 (0.019)	0.907, 0.981	0.975 (0.020)	0.927, 1.000
S_{A2}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A3}	0.919 (0.019)	0.877, 0.951	0.915 (0.020)	0.869, 0.949
S_{A4}	0.841 (0.055)	0.715, 0.928	0.942 (0.032)	0.857, 0.985
S_{A5}	0.874 (0.062)	0.734, 0.984	0.914 (0.061)	0.785, 1.000
S_{A6}	0.843 (0.075)	0.671, 0.963	0.728 (0.078)	0.563, 0.864
S_{A7}	0.886 (0.068)	0.733, 1.000	0.890 (0.058)	0.758, 1.000
S_{A8}	0.618 (0.090)	0.441, 0.789	0.548 (0.087)	0.380, 0.716
S_{B11}	0.715 (0.087)	0.534, 0.876	0.600 (0.155)	0.299, 0.855
S_{B12}	0.692 (0.128)	0.423, 0.893	1.000	NA
S_{B13}	0.308 (0.149)	0.087, 0.623	0.765 (0.221)	0.282, 1.000
S_{B21}	0.800 (0.103)	0.560, 0.946	0.923 (0.074)	0.702, 0.995
S_{B22}	0.790 (0.094)	0.576, 0.929	1.000	NA
S_{B23}	0.616 (0.130)	0.360, 0.841	0.728 (0.123)	0.464, 0.921
S_{C1}	0.286 (0.121)	0.099, 0.545	NA	
$S_{\text{D1,Sac}}$	0.667 (0.111)	0.437, 0.852	0.818 (0.067)	0.665, 0.923
$S_{\text{D1,Geo}}$	0.814 (0.051)	0.702, 0.898	0.938 (0.027)	0.872, 0.977
S_{D2}	0.900 (0.039)	0.808, 0.959	0.932 (0.025)	0.873, 0.970
S_{D3}	0.862 (0.045)	0.758, 0.934	0.772 (0.051)	0.672, 0.885
S_{D4}	0.491 (0.073)	0.352, 0.635	0.395 (0.080)	0.262, 0.604
S_{D5}	0.658 (0.129)	0.411, 0.946	0.733 (0.180)	0.415, 1.000
S_{D6}	0.700 (0.145)	0.393, 0.915	0.709 (0.181)	0.155, 1.000
S_{D7}	1.000	NA	0.866 (0.159)	0.463, 1.000
$S_{\text{E1,D5}}$	1.000	NA	0.750 (0.288)	0.245, 1.000
$S_{\text{E1,A8}}$	0.433 (0.189)	0.130, 0.780	0.683 (0.279)	0.165, 1.000
Ψ_{A1}	0.655 (0.042)	0.570, 0.733	0.802 (0.037)	0.722, 0.868
Ψ_{B11}	0.230 (0.037)	0.163, 0.308	0.086 (0.026)	0.044, 0.147
Ψ_{B21}	0.115 (0.028)	0.068, 0.178	0.112 (0.029)	0.063, 0.178
Ψ_{A2}	0.592 (0.056)	0.481, 0.696	0.612 (0.053)	0.506, 0.711
Ψ_{C2}	0.179 (0.043)	0.105, 0.273	0.000	NA
Ψ_{D2}	0.230 (0.048)	0.146, 0.331	0.388 (0.053)	0.289, 0.494
$\phi_{\text{B11,B12}}$	0.482 (0.096)	0.305, 0.674	0.400 (0.155)	0.146, 0.700
$\phi_{\text{B11,B22}}$	0.233 (0.077)	0.108, 0.403	0.200 (0.127)	0.036, 0.499
$\phi_{\text{A7,A8}}$	0.837 (0.074)	0.679, 0.978	0.781 (0.07)	0.634, 0.914

Appendix Table 3.3. Continued.

$\phi_{\mathrm{A7,E1}}$	0.049 (0.034)	0.008, 0.143	0.109 (0.046)	0.040, 0.220
$\phi_{\mathrm{D4,D5}}$	0.351 (0.070)	0.225, 0.497	0.354 (0.079)	0.225, 0.564
$\phi_{\mathrm{D4,E1}}$	0.140 (0.049)	0.063, 0.253	0.041 (0.023)	0.010, 0.102
P_{A2}	0.959 (0.018)	0.915, 0.985	0.852 (0.034)	0.777, 0.910
P_{A3}	0	NA	0.000	NA
P_{A4}	0.949 (0.035)	0.850, 0.991	1.000	NA
P_{A5}	1.000	NA	1.000	NA
P_{A6}	0.821 (0.072)	0.655, 0.932	0.781 (0.073)	0.620, 0.899
P_{A7}	0.829 (0.064)	0.683, 0.928	0.850 (0.057)	0.719, 0.937
$P_{\mathrm{A8,Sac}}$	0.905 (0.064)	0.734, 0.983	0.950 (0.049)	0.798, 0.997
$P_{\mathrm{A8,Geo}}$	1.000	NA	0.950 (0.049)	0.798, 0.997
$P_{\mathrm{A9,Sac}}$	0.812 (0.084)	0.618, 0.937	0.846 (0.071)	0.678, 0.949
$P_{\mathrm{A9,Geo}}$	1.000	NA	0.846 (0.071)	0.678, 0.949
P_{B11}	1.000	NA	1.000	NA
P_{B12}	0.900 (0.095)	0.628, 0.994	1.000	NA
P_{B21}	1.000	NA	1.000	NA
P_{B22}	1.000	NA	1.000	NA
P_{B13}	1.000	NA	1.000	NA
P_{B23}	1.000	NA	1.000	NA
P_{C1}	1.000	NA	NA	
P_{D1}	1.000	NA	1.000	NA
P_{D2}	1.000	NA	1.000	NA
P_{D3}	1.000	NA	1.000	NA
P_{D4}	1.000	NA	0.958 (0.041)	0.829, 0.998
P_{D5}	0.922 (0.075)	0.699, 0.995	0.500 (0.118)	0.133, 0.872
P_{D6}	0.778 (0.139)	0.458, 0.959	0.500 (0.134)	0.255, 0.745
P_{D7}	1.000	NA	0.385 (0.135)	0.046, 0.848
P_{E1}	1.000	NA	1.000	NA
λ	0.748 (0.082)	0.570, 0.883	0.759 (0.080)	0.585, 0.888

Appendix 4

ADDITIONAL FIGURES AND TABLES FOR CHAPTER 5



Appendix Figure 4.1. Schematic of the mark-recapture model used to estimate survival (S_{hi}), detection (P_{hi}), route entrainment (Ψ_{hl}), and joint survival-entrainment ($\phi_{hi,jk}$) probabilities of juvenile late-fall Chinook salmon migrating through the Sacramento–San Joaquin River Delta for releases made in December 2008 and January 2009. Release sites are denoted by R_m (m = Sac (Sacramento) and Geo (Georgiana Slough)), parameters subscripted by n are conditional on the position of the Delta Cross Channel gate, and m denote parameters which can be estimated separately for each release site.

Appendix Table 4.1. Counts of detection histories for the model shown in Figure 4.2 for a release of R_1 = 208 fish on 4 December 2007 and R_2 = 211 fish on 16 January 2008. Counts for all other detection histories were zero and are not shown here. Each digit of the detection history indicates detection at telemetry stations within each of four migration routes (labeled A–D) and Three Mile Slough (E). A “0” indicating either a fish was not detected or a telemetry station within that route was not implemented at that position in the capture history (since some routes had more telemetry stations than others). Detection histories beginning with “0 0 0 D” indicate fish released in Georgiana Slough whereas those beginning with “A” are fish released into the Sacramento River.

R_1: December 2006		R_2: January 2007	
Detection history	Frequency	Detection history	Frequency
0 0 0 D 0 0 0 0 0 0	67	0 0 0 D 0 0 0 0 0 0	42
0 0 0 D D 0 0 0 0 0	7	0 0 0 D D 0 0 0 0 0	19
0 0 0 D D 0 D 0 0 0	1	0 0 0 D D D 0 0 0 0	17
0 0 0 D D D 0 0 0 0	11	0 0 0 D D D 0 0 0 A	1
0 0 0 D D D 0 0 A A	1	0 0 0 D D D 0 0 A A	4
0 0 0 D D D D 0 0 0	2	0 0 0 D D D D 0 A 0	2
0 0 0 D D D D 0 0 A	4	0 0 0 D D D D 0 A A	11
0 0 0 D D D D 0 A A	4	0 0 0 D D D DE 0 0 0	1
0 0 0 D D D DE 0 0 0	1	0 0 0 D D D DE EA 0 0	1
0 0 0 D D D DE EA A A	2	0 0 0 D D D DE EA A A	2
A 0 0 0 0 0 0 0 0 0	21	A 0 0 0 0 0 0 0 0 0	23
A 0 A a 0 0 0 0 A A	1	A 0 A d D D 0 0 A A	1
A 0 A a 0 0 A 0 0 0	1	A 0 B2 0 0 0 0 0 0 0	1
A 0 A a 0 0 A 0 A A	1	A 0 B2 B2 0 0 0 0 0 0	1
A 0 A a 0 A 0 0 0 A	1	A A 0 0 0 0 0 0 0 0	23
A 0 A a 0 A 0 0 A 0	1	A A A 0 0 0 0 0 0 0	13
A 0 B1 0 B2 A AE 0 0 0	1	A A A a 0 0 0 0 0 0	24
A A 0 0 0 0 0 0 0 0	14	A A A a 0 0 0 0 0 A	3
A A 0 0 B2 A A 0 A 0	1	A A A a 0 0 0 0 A 0	1
A A 0 d D D 0 0 0 0	1	A A A a 0 0 0 0 A A	1
A A 0 B2 0 0 A 0 0 0	1	A A A a 0 0 A 0 0 A	2
A A A 0 0 0 0 0 0 0	8	A A A a 0 0 A 0 A A	10
A A A 0 0 0 A 0 0 0	1	A A A a 0 A 0 0 0 0	1
A A A A 0 0 0 0 0 0	11	A A A a 0 A 0 0 0 A	3
A A A A 0 0 A 0 A A	4	A A A a 0 A A 0 0 0	2
A A A A 0 A 0 0 0 0	3	A A A a 0 A A 0 A 0	1
A A A A 0 A A 0 0 0	2	A A A a 0 A A 0 A A	11
A A A A 0 A A 0 0 A	1	A A A d 0 0 0 0 0 0	13
A A A A 0 A A 0 A 0	2	A A A d D 0 0 0 0 0	4
A A A A 0 A A 0 A A	3	A A A d D D 0 0 0 0	12
A A A C 0 0 0 0 0 0	13	A A A d D D D 0 0 0	2
A A A C 0 D 0 0 0 0	2	A A A d D D D 0 A A	4
A A A C 0 D D 0 0 A	1	A A A d D D DE EA 0 0	1
A A A C 0 D D 0 A 0	1	A A B1 0 0 0 0 0 0 0	3

Appendix Table 4.1. Continued

A A A C 0 D D 0 A A	1
A A A D 0 0 0 0 0 0	1
A A A D D 0 0 0 0 0	1
A A A D D D 0 0 0 0	4
A A A D D D D 0 A A	3
A A A D D D DE 0 A A	1
A A A a 0 0 0 0 0 0	4
A A A a 0 0 0 0 A 0	2
A A A a 0 0 A 0 0 A	1
A A A a 0 0 A 0 A 0	1
A A A a 0 0 A 0 A A	1
A A A a 0 0 AE 0 0 0	1
A A A a 0 0 AE 0 A A	1
A A A a 0 A 0 0 0 0	3
A A A a 0 A 0 0 A A	3
A A A a 0 A A 0 0 0	2
A A A a 0 A A 0 A 0	1
A A A a 0 A A 0 A A	5
A A A d 0 0 0 0 0 0	1
A A A d D 0 0 0 0 0	2
A A A d D 0 D 0 A A	1
A A A d D D 0 0 0 0	3
A A A d D D 0 0 A A	1
A A A d D D D 0 A A	4
A A A d D D DE EA 0 0	1
A A B1 0 0 0 0 0 0 0	12
A A B1 0 B1 A A 0 A A	1
A A B1 B1 0 0 0 0 0 0	2
A A B1 B1 B1 0 0 0 0 0	5
A A B1 B1 B1 0 A 0 0 0	1
A A B1 B1 B1 0 AE ED A A	1
A A B1 B1 B1 A A 0 0 A	1
A A B1 B1 B1 A A 0 A A	2
A A B1 B1 B1 A AE 0 A 0	1
A A B1 B2 0 A A 0 A A	1
A A B1 B2 B2 A A 0 0 0	3
A A B1 B2 B2 A A 0 A 0	1
A A B1 B2 B2 A A 0 A A	1
A A B2 B2 0 0 0 0 0 0	1
A A B2 B2 0 A A 0 0 A	1
A A B2 B2 B2 0 0 0 A A	2
A A B2 B2 B2 0 A 0 0 A	1
A A B2 B2 B2 A 0 0 0 0	1
A A B2 B2 B2 A 0 0 A A	1
A A B1 B1 0 0 0 0 0 0	1
A A B1 B1 B1 0 0 0 0 0	1
A A B1 B1 B1 0 A 0 0 A	1
A A B1 B1 B1 A 0 0 0 A	1
A A B1 B1 B1 A 0 0 A A	1
A A B1 B1 B1 A A 0 A A	2
A A B1 B2 0 0 0 0 0 0	1
A A B1 B2 B2 0 A 0 A A	1
A A B1 B2 B2 A 0 0 0 0	1
A A B1 B2 B2 A A 0 A A	1
A A B2 0 0 0 0 0 0 0	3
A A B2 B1 0 0 0 0 0 0	1
A A B2 B1 B1 0 0 0 A A	1
A A B2 B1 B1 A 0 0 0 0	1
A A B2 B1 B1 A A 0 A A	1
A A B2 B2 0 0 0 0 0 0	2
A A B2 B2 B2 0 0 0 0 0	2
A A B2 B2 B2 0 A 0 A A	2
A A B2 B2 B2 A 0 0 0 A	2
A A B2 B2 B2 A 0 0 A A	1
A A B2 B2 B2 A A 0 0 0	1
A A B2 B2 B2 A A 0 A 0	2
A A B2 B2 B2 A A 0 A A	2

Appendix Table 4.1. Continued

A A B2 B2 B2 A A 0 A 0	1	
A A B2 B2 B2 A A 0 A A	6	
A A B2 B2 B2 A AE ED 0 0	1	
Total released (R_k)	292	292

Appendix Table 4.2. Parameter constraints applied under the full model for each release, representing the minimum estimable model with the maximum number of parameters. Parameters not shown below were estimable by iteratively maximizing the likelihood of the multinomial model. Constraints include parameters that had to be fixed to a constant value or set equal to other parameters because they could not be estimated from the data set of detection histories.

R_1: December 2007		R_2: January 2008	
Parameter	Constraint	Parameter	Constraint
$\phi_{\mathrm{B21,B12}}$	$= 0$	Ψ_{C2}	$= 0$
$\phi_{\mathrm{B21,B22}}$	$= 1$	$\Psi_{\mathrm{A2,open}}$	$= 0$
S_{B23}	$=1$	ω_{open}	$= 0$
$S_{\mathrm{D1,open}}$	$= S_{\mathrm{D1,closed}}$	$S_{\mathrm{D1,open}}$	$= 0$
$P_{\mathrm{E1,Sac}}$	$= 1$	$S_{\mathrm{A4,open}}$	$= 0$
$P_{\mathrm{E1,Geo}}$	$= 1$	S_{C1}	$= 0$
P_{B21}	$= P_{\mathrm{B11}}$	$S_{\mathrm{E1,D7}}$	$= 0$
P_{B13}	$= 1$	$\phi_{\mathrm{A7,E1}}$	$= 0$
P_{C1}	$= 1$	P_{A3}	$= 0$
P_{D1}	$= 1$	P_{A4}	$= 1$
$P_{\mathrm{D2,Sac}}$	$= 1$	P_{B11}	$= 1$
$P_{\mathrm{D2,Geo}}$	$= 1$	P_{B12}	$= 1$
		P_{B13}	$= 1$
		P_{B21}	$= 1$
		P_{B22}	$= 1$
		P_{B23}	$= 1$
		P_{C1}	$= 0$
		P_{D1}	$= 1$
		$P_{\mathrm{D2,Sac}}$	$= 1$
		$P_{\mathrm{D3,Sac}}$	$= 1$
		$P_{\mathrm{D4,Sac}}$	$= 1$
		$P_{\mathrm{E1,Sac}}$	$= 1$
		$P_{\mathrm{D2,Geo}}$	$= 1$
		$P_{\mathrm{D4,Geo}}$	$= 1$
		$P_{\mathrm{A8,Geo}}$	$= 1$
		$P_{\mathrm{E1,Geo}}$	$= 1$

Appendix Table 4.3. Parameter estimates under the reduced model for releases of acoustically tagged late-fall juvenile Chinook salmon in December, 2008 (R_1) and January, 2009 (R_2). For both release dates, survival in the interior Delta was set equal between release sites (Sacramento, Georgiana Slough) based on lack of significance of likelihood ratios tests. Parameters not estimated are indicated by an "NA" in the estimate column, and parameters fixed at a constant value are noted by an "NA" in the profile likelihood column.

	R_1: December 2008		R_2: January 2009	
Parameter	Estimate ($\widehat{\text{SE}}$)	95% Profile likelihood interval	Estimate ($\widehat{\text{SE}}$)	95% Profile likelihood interval
S_{A1}	0.894 (0.023)	0.844, 0.933	0.883 (0.024)	0.832, 0.924
S_{A2}	0.920 (0.022)	0.870, 0.957	0.861 (0.027)	0.804, 0.908
S_{A3}	0.928 (0.026)	0.867, 0.970	0.881 (0.031)	0.811, 0.933
$S_{\text{A4, open}}$	0.600 (0.101)	0.401, 0.785	NA	
$S_{\text{A4, closed}}$	0.901 (0.066)	0.744, 1.005	0.616 (0.068)	0.482, 0.746
S_{A7}	0.924 (0.049)	0.815, 1.016	0.944 (0.053)	0.812, 1.030
S_{A8}	0.791 (0.062)	0.658, 0.900	0.902 (0.050)	0.783, 0.979
S_{B11}	0.413 (0.086)	0.256, 0.586	0.674 (0.155)	0.390, 0.980
S_{B12}	0.846 (0.100)	0.596, 0.964	0.818 (0.116)	0.537, 0.967
S_{B13}	0.606 (0.148)	0.321, 0.860	0.923 (0.111)	0.616, 1.063
S_{B21}	1.000	NA	0.826 (0.079)	0.641, 0.942
S_{B22}	0.962 (0.042)	0.829, 1.006	0.789 (0.094)	0.576, 0.929
S_{B23}	1.000	NA	0.900 (0.093)	0.665, 1.037
S_{C1}	0.286 (0.109)	0.113, 0.522	NA	
$S_{\text{D1,Sac}}$	0.917 (0.056)	0.764, 0.986	0.649 (0.078)	0.489, 0.789
$S_{\text{D1,Geo}}$	0.330 (0.047)	0.243, 0.426	0.580 (0.049)	0.482, 0.674
S_{D2}	0.844 (0.057)	0.722, 0.952	0.720 (0.050)	0.617, 0.809
S_{D4}	0.576 (0.074)	0.431, 0.716	0.518 (0.067)	0.389, 0.648
S_{D7}	0.862 (0.080)	0.676, 0.983	0.919 (0.071)	0.731, 1.014
$S_{\text{E1,D7}}$	0.686 (0.198)	0.289, 0.968	0.000	NA
$S_{\text{E1,A8}}$	0.847 (0.190)	0.393, 1.065	0.800 (0.179)	0.372, 0.987
ω_{open}	0.550 (0.05)	0.451, 0.646		
Ψ_{A1}	0.679 (0.037)	0.603, 0.749	0.747 (0.036)	0.672, 0.812
Ψ_{B11}	0.217 (0.033)	0.157, 0.288	0.096 (0.024)	0.055, 0.151
Ψ_{B21}	0.104 (0.025)	0.062, 0.158	0.158 (0.030)	0.105, 0.222
$\Psi_{\text{A2,open}}$	0.488 (0.068)	0.357, 0.619	0.000	NA
$\Psi_{\text{A2,closed}}$	0.687 (0.069)	0.543, 0.810	0.615 (0.050)	0.515, 0.708
Ψ_{C2}	0.329 (0.064)	0.214, 0.460	0.000	NA
$\Psi_{\text{D2,open}}$	0.183 (0.052)	0.096, 0.299	0.000	NA
$\Psi_{\text{D2,closed}}$	0.313 (0.069)	0.190, 0.455	0.385 (0.050)	0.292, 0.485
$\phi_{\text{B21,B12}}$	0.000	NA	0.174 (0.079)	0.058, 0.359
$\phi_{\text{B21,B22}}$	1.000	NA	0.652 (0.099)	0.449, 0.823

Appendix Table 4.3. Continued.

$\phi_{B11,B12}$	0.413 (0.086)	0.256, 0.586	0.500 (0.134)	0.255, 0.745
$\phi_{B11,B22}$	0.223 (0.073)	0.104, 0.384	0.286 (0.121)	0.099, 0.545
$\phi_{A7,A8}$	0.843 (0.057)	0.724, 0.950	0.944 (0.053)	0.812, 1.030
$\phi_{A7,E1}$	0.081 (0.032)	0.033, 0.158	0.000	NA
$\phi_{D4,D7}$	0.479 (0.074)	0.339, 0.624	0.433 (0.066)	0.309, 0.566
$\phi_{D4,E1}$	0.097 (0.041)	0.037, 0.198	0.085 (0.036)	0.031, 0.173
P_{A2}	0.962 (0.015)	0.924, 0.974	0.979 (0.012)	0.948, 1.000
P_{A3}	0.990 (0.010)	0.956, 0.999	1.000	NA
P_{A4}	0.976 (0.024)	0.899, 0.999	1.000	NA
P_{A7}	0.689 (0.056)	0.573, 0.790	0.585 (0.068)	0.451, 0.711
$P_{A8,Sac}$	0.765 (0.059)	0.637, 0.866	0.716 (0.064)	0.582, 0.829
$P_{A8,Geo}$	0.765 (0.059)	0.637, 0.866	1.000	NA
$P_{A9,Sac}$	0.825 (0.048)	0.720, 0.905	0.761 (0.060)	0.633, 0.864
$P_{A9,Geo}$	0.825 (0.048)	0.720, 0.905	0.947 (0.052)	0.787, 1.000
P_{B11}	0.947 (0.036)	0.846, 0.991	1.000	NA
P_{B12}	0.917 (0.080)	0.681, 0.995	1.000	NA
P_{B21}	0.947 (0.036)	0.846, 0.991	1.000	NA
P_{B22}	0.915 (0.057)	0.761, 0.985	1.000	NA
P_{B13}	1.000	NA	1.000	NA
P_{B23}	0.865 (0.072)	0.687, 0.962	1.000	NA
P_{C1}	1.000	NA	NA	
P_{D1}	1.000	NA	1.000	NA
P_{D2}	1.000	NA	1.000	NA
$P_{D4,Geo}$	0.931 (0.047)	0.802, 0.978	1.000	NA
$P_{D4,Sac}$	0.931 (0.047)	0.802, 0.978	1.000	NA
$P_{D7,Geo}$	0.833 (0.076)	0.654, 0.945	0.707 (0.110)	0.475, 0.883
$P_{D7,Sac}$	0.833 (0.076)	0.654, 0.945	0.836 (0.149)	0.462, 1.000
P_{E1}	1.000	NA	1.000	NA
λ	0.813 (0.049)	0.706, 0.895	0.901 (0.038)	0.810, 0.959

Appendix Table 4.4. Parameter estimates on the logit scale for the effect Release Group and Route:Release Group on survival for the best-fit individual covariate model.

Coefficient	$\hat{\beta}$ (SE)	95% Confidence interval (±1.96 SE)
Release 1	-1.24 (0.75)	-2.71, 0.23
Release 2,3	0.15 (0.63)	-1.08, 1.39
Release 4	-0.71 (0.61)	-1.90, 0.49
Release 6	-0.84 (0.58)	-1.98, 0.30
Release 7	-0.76 (0.69)	-2.10, 0.58
Release 8	0.39 (0.59)	-0.76, 1.54
Release 9	0.15 (0.61)	-1.04, 1.34
Release 10	-0.11 (0.70)	-1.48, 1.26
Release 11	0.46 (0.58)	-0.68, 1.60
I_{SS}:Release 1	0.43 (1.14)	-1.81, 2.67
I_{SS}:Release 2,3	-0.18 (0.98)	-2.11, 1.75
I_{SS}:Release 4	-0.96 (0.98)	-2.87, 0.96
I_{SS}:Release 6	-1.19 (1.07)	-3.28, 0.90
I_{SS}:Release 7	1.31 (1.40)	-1.44, 4.06
I_{SS}:Release 8	-0.27 (0.91)	-2.04, 1.51
I_{SS}:Release 9	0.39 (1.00)	-1.57, 2.34
I_{SS}:Release 10	0.24 (1.09)	-1.90, 2.37
I_{SS}:Release 11	-0.21 (0.92)	-2.01, 1.59
I_{ID}:Release 1	1.27 (1.35)	-1.39, 3.92
I_{ID}:Release 4	-0.22 (1.04)	-2.26, 1.82
I_{ID}:Release 6	-0.31 (1.01)	-2.29, 1.67
I_{ID}:Release 7	0.63 (1.20)	-1.72, 2.98
I_{ID}:Release 8	0.19 (1.00)	-1.78, 2.15
I_{ID}:Release 9	0.33 (1.09)	-1.81, 2.47
I_{ID}:Release 10	2.35 (1.60)	-0.77, 5.48
I_{ID}:Release 11	-0.21 (0.99)	-2.16, 1.74

Appendix 5

ADDITIONAL FIGURES AND TABLES FOR CHAPTER 6

Appendix Table 5.1. Results of reverse model selection for water velocity variables (V_j) showing the likelihood ratio test and associated statistics for the model with the given variable dropped relative to the preceding model with one additional variable.

Variable dropped	Linear predictor	Number of parameters	AIC	–Log-likelihood	Likelihood Ratio	*P*-value
None (full model)		16	800.8	384.4		
D (time of day)	$g(\pi_G)$	15	798.8	384.4	0.00	1.000
T (temperature)	$g(\pi_D)$	14	796.8	384.4	0.02	0.890
L (fork length)	$g(\pi_G)$	13	794.8	384.4	0.04	0.841
D (time of day)	$g(\pi_D)$	12	793.1	384.5	0.17	0.680
U (upstream flow)	$g(\pi_D)$	11	791.4	384.7	0.42	0.517
V_G	$g(\pi_D)$	10	790.0	385.0	0.58	0.446
T (temperature)	$g(\pi_G)$	9	788.8	385.3	0.86	0.354
ΔV_S	$g(\pi_G)$	8	787.7	385.8	0.83	0.362
L (fork length)	$g(\pi_D)$	7	786.8	386.4	1.15	0.284
None (all interactions)*		10	787.6	383.8		
$V_G \times U$	$g(\pi_G)$	9	786.1	384.1	0.49	0.484
$V_S \times V_G$	$g(\pi_G)$	8	785.9	385.0	1.79	0.181
$Q_S \times \Delta Q_S$	$g(\pi_D)$	7	786.8	386.4	2.91	0.088

* The interaction $V_S \times U$ was excluded from $g(\pi_G)$ due to high variance inflation factors caused by this term.

Appendix Table 5.2. Likelihood ratio tests when each variable is dropped from the best fit V_j model.

Variable dropped	Number of parameters	Linear predictor	–Log-likelihood	Likelihood Ratio	AIC	P-value
None (best fit)	7		386.4		786.1	
Q_S	6	$g(\pi_G)$	415.1	57.4	842.2	<0.001
Q_G	6	$g(\pi_G)$	418.9	65.0	849.9	<0.001
U	6	$g(\pi_G)$	392.3	11.8	796.7	<0.001
Q_S	6	$g(\pi_D)$	447.5	122.1	906.9	<0.001
ΔQ_S	6	$g(\pi_D)$	392.7	12.6	797.4	<0.001

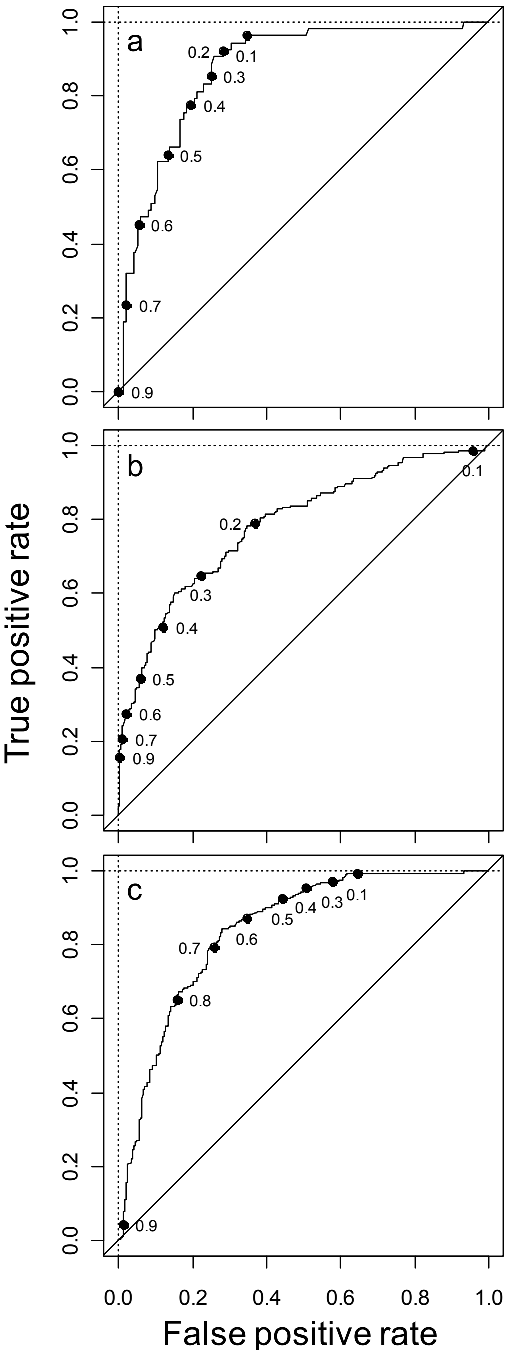
Appendix Table 5.3. Results of reverse model selection for discharge proportion variables (p_{Q_j}) showing the likelihood ratio test and associated statistics for the model with the given variable dropped relative to the preceding model with one additional variable.

Variable dropped*	Linear predictor	Number of parameters	AIC	–Log-likelihood	Likelihood Ratio	*P*-value
None (full model)		15	809.4	389.7		
T (temperature)	$g(\pi_{\text{D}})$	14	807.5	389.7	0.01	0.920
L (fork length)	$g(\pi_{\text{D}})$	13	805.5	389.7	0.03	0.863
T (temperature)	$g(\pi_{\text{G}})$	12	803.7	389.8	0.16	0.690
D (time of day)	$g(\pi_{\text{G}})$	11	801.8	389.9	0.20	0.655
L (fork length)	$g(\pi_{\text{G}})$	10	800.4	390.2	0.56	0.454
D (time of day)	$g(\pi_{\text{D}})$	9	799.1	390.6	0.71	0.399
ΔQ_{S}	$g(\pi_{\text{D}})$	8	798.0	391.0	0.91	0.340
$p_{Q_{\text{S}}}$	$g(\pi_{\text{D}})$	7	797.1	391.6	1.08	0.299
None (all interactions)		10	801.1	390.6		
$\Delta Q_{\text{S}} \times p_{Q_{\text{G}}}$	$g(\pi_{\text{G}})$	9	799.3	390.7	0.22	0.639
$\Delta Q_{\text{S}} \times U$	$g(\pi_{\text{G}})$	8	797.1	391.6	1.25	0.264
$U \times p_{Q_{\text{G}}}$	$g(\pi_{\text{G}})$	7	786.8	386.4	2.91	0.088

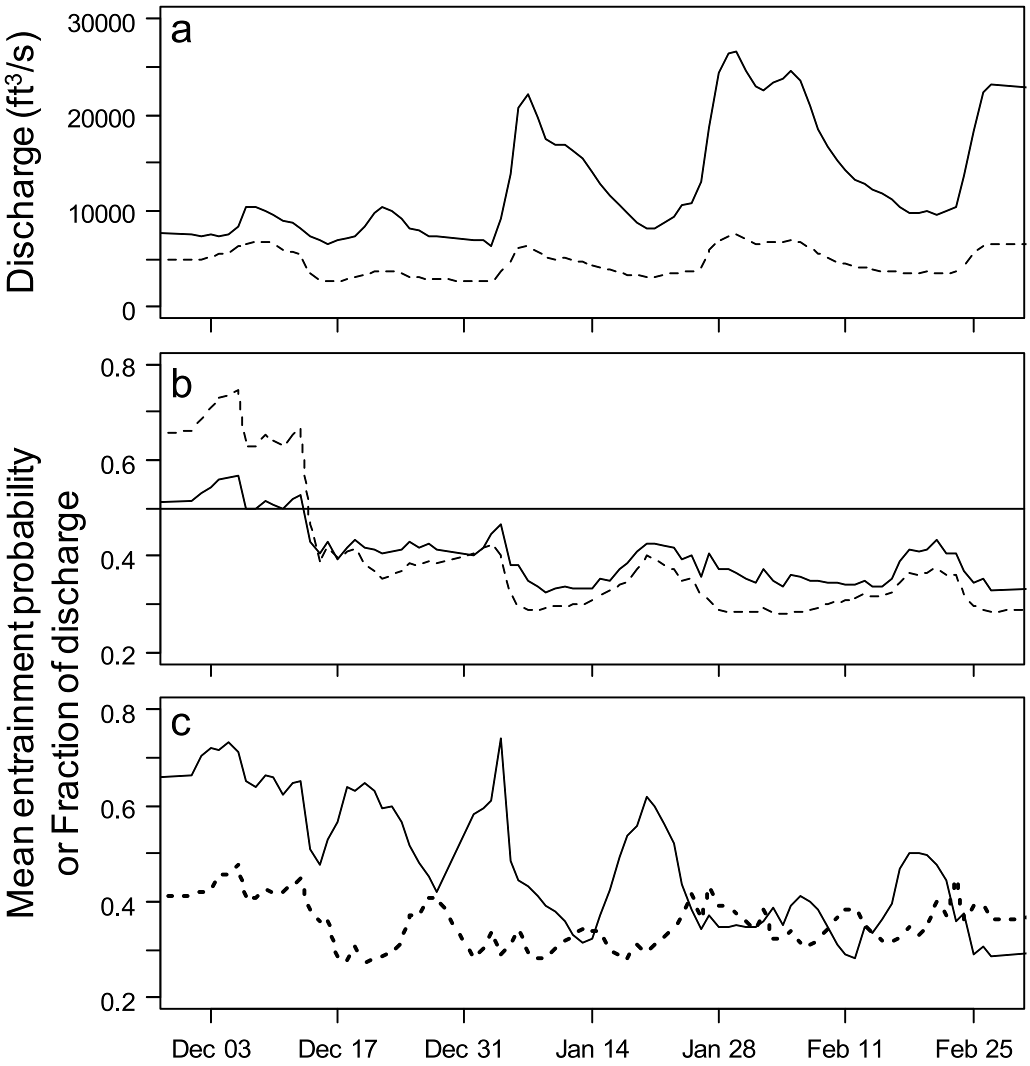
* The terms U and $p_{Q_{\text{S}}} \times p_{Q_{\text{G}}}$ was excluded $g(\pi_{\text{D}})$ due to high variance inflation factors caused by these terms.

Appendix Table 5.4. Likelihood ratio tests when each variable is dropped from the best fit p_{Q_j} model.

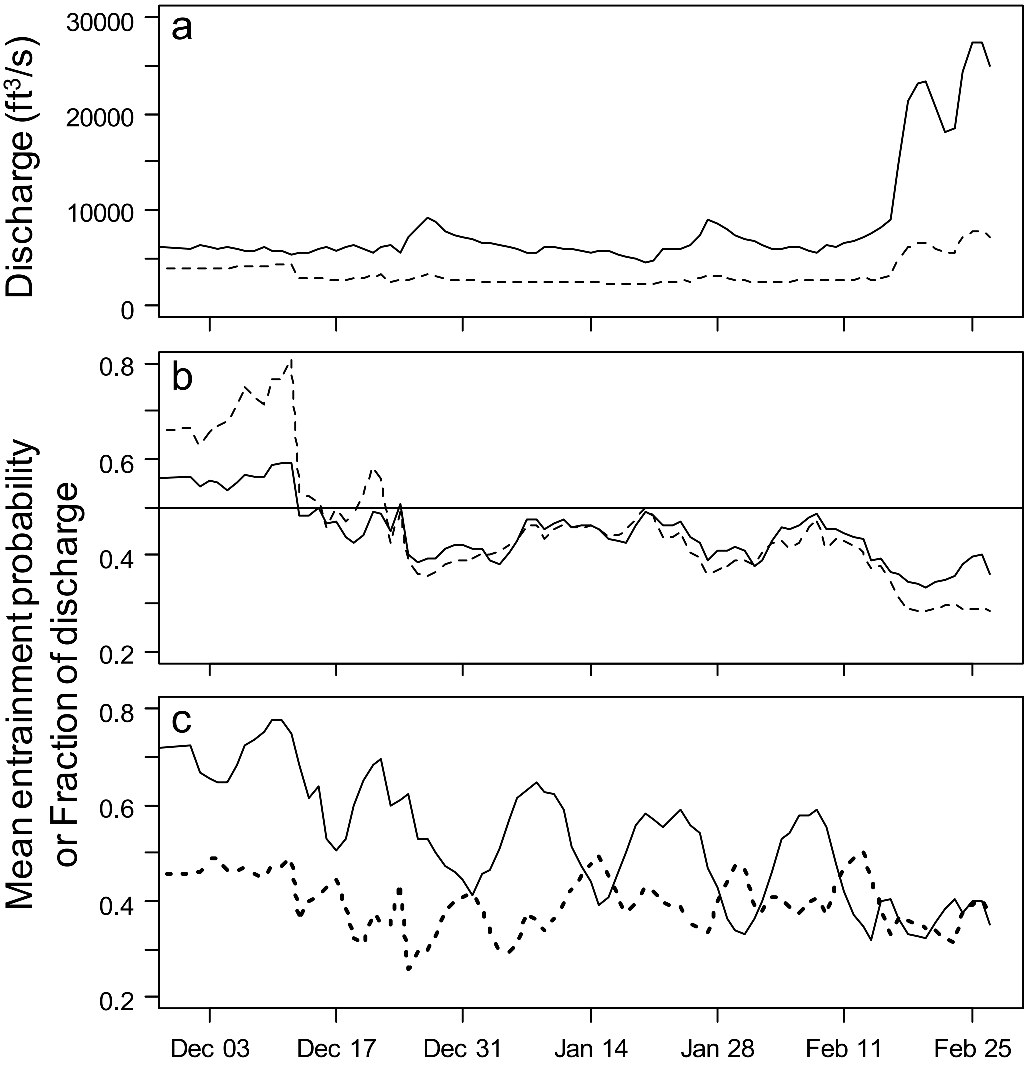
Variable dropped	Number of parameters	Linear predictor	–Log-likelihood	Likelihood Ratio	AIC	P-value
None (best fit)	7		391.6		797.1	
$p_{Q_{\text{S}}}$	6	$g(\pi_{\text{G}})$	419.9	56.7	851.8	<0.001
ΔQ_{S}	6	$g(\pi_{\text{G}})$	414.2	45.2	840.3	<0.001
U	6	$g(\pi_{\text{G}})$	396.0	8.9	804.0	0.003
$p_{Q_{\text{S}}}$	6	$g(\pi_{\text{D}})$	404.8	26.6	821.7	<0.001
$p_{Q_{\text{G}}}$	6	$g(\pi_{\text{D}})$	394.6	6.1	801.3	0.013



Appendix Figure 5.1. Reciever operating curve (ROC) showing the true and false positive rates for classifying fish to a) the Delta Cross Channel, b) Georgiana Slough, and c) the Sacramento River based on cutoff values of π_j ranging from zero to one (shown as labeled points). The 45° reference line shows the performance of a model with no ability to predict whether fish enter a particular route.



Appendix Figure 5.2. Mean daily river flow (a) and mean predicted probability of entrainment into the interior Delta (b and c) during winter 2007/2008. The top panel (a) shows mean daily discharge entering the river junction (Q_{inflow}, solid line) and mean daily discharge entering the interior Delta through both the Delta Cross Channel and Georgiana Slough (dotted line). Panel b shows the mean daily probability of entering the interior Delta ($\bar{\pi}_{\text{ID},d}$, solid line) and the fraction of mean daily discharge entering the interior Delta ($p_{\bar{Q}_{\text{ID},d}}$, dashed line). Panel c shows the mean entrainment probability for day (solid line) and night (heavy dotted line) diel periods. The Delta Cross Channel was open prior to December 15, 2007 and closed thereafter.



Appendix Figure 5.3. Mean daily river flow (a) and mean predicted probability of entrainment into the interior Delta (b and c) during winter 2008/2009. The top panel (a) shows mean daily discharge entering the river junction ($Q_{\text{inflow,}}$ solid line) and mean daily discharge entering the interior Delta through both the Delta Cross Channel and Georgiana Slough (dotted line). Panel b shows the mean daily probability of entering the interior Delta ($\bar{\pi}_{\text{ID},d}$, solid line) and the fraction of mean daily discharge entering the interior Delta ($p_{\bar{Q}_{\text{ID},d}}$, dashed line). Panel c shows the mean entrainment probability for day (solid line) and night (heavy dotted line) diel periods. Operation of the Delta Cross Channel followed a variable schedule but closed after December 22, 2008.

VITA

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Interannual variation of reach specific migratory success for Sacramento River hatchery yearling late-fall run Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss)*

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Abstract The release of hatchery reared salmonid smolts is a common management tool aimed at enhancing depleted wild stocks and maintaining fisheries throughout Northern California and the Pacific Northwest. In the Sacramento River watershed, smolts must migrate through the river, delta and estuary in order to successfully reach the Pacific Ocean. Migration success (success defined as apparent survival from one monitor location to another) may vary between species, year and habitat. We released 500 late-fall run Chinook salmon and 500 steelhead smolts in 2009 and 2010 in the Sacramento River (river kilometer 207). Each smolt was implanted with a coded ultrasonic tag, which was detected by an array of over 300 underwater receiver stations deployed throughout the system. Less than 25 % of fish migrated successfully to the Pacific Ocean in both years. We found that reach specific success was greater in the Delta in 2009 (>60 %) than in 2010 (<33 %), whereas this pattern was reversed in the Bay (<57 % in 2009, >75 % in 2010). Identifying the location, timing and causes of smolt mortality can lead to improved management of the resource.

Keywords Steelhead trout · Chinook salmon · Telemetry · Sacramento River · Migratory success · San Francisco Estuary

Introduction

Understanding the survival patterns of outmigrating salmonid smolts is a key issue for fisheries management, especially where hatcheries are used to artificially propagate and release smolts to supplement natural populations. The Sacramento River watershed in the California Central Valley (CV) is a particularly complex drainage system which includes a multitude of habitats – the more natural run-riffle-pool structure of the upper river, a channelized lower river, the heavily modified and intricate Sacramento-San Joaquin Delta, and the San Francisco Bay Estuary. Within the estuary, there are tidal marshes, tidally influenced river channels, shoals, shipping channels and marinas that are subject to dredging, and natural and modified shore areas. Several species of anadromous fish are native to

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this system, including four runs of Chinook salmon (*Oncorhynchus tshawytscha*) and the anadromous form of rainbow trout – the steelhead (*O. mykiss*). As they migrate through each of these different habitats, smolts are exposed to different natural and anthropogenic sources of mortality. Studies of reach-specific mortality may help to identify and mitigate major threats to the outmigrating smolts.

Native salmon and steelhead stocks are in decline throughout California (Huntington et al. 1996). CV Chinook salmon stocks have been conservatively estimated to have peaked at 1–2 million active spawners (Yoshiyama et al. 1998, 2000). However, all runs in the CV have shown population declines, and late-fall run Chinook are federally listed as a "species of concern" (NMFS 2004) after numbers of returning fish declined drastically in the early 1990s (Moyle 2002). Central Valley steelhead were listed as "threatened" under the Endangered Species Act in 1998. Naturally reproducing steelhead and rainbow trout that support anadromy in the Sacramento River Watershed have been relegated to populations that spawn in the upper Sacramento, Feather, Yuba, Mokelumne, Calaveras, and Stanislaus rivers, and Butte, Deer, and Mill Creek (McEwan 2001).

Late-fall run Chinook salmon mainly display a stream-type juvenile life strategy – they may reside in the river for 7–13 months before migrating out to the ocean at a size of 150–170 mm fork length, where they remain along the coast of California until they return to spawn as 4–5 year olds (Moyle 2002).

Central Valley steelhead are classified as winter-run, with adults returning to fresh water during winter pulse flow events, even though some fish enter freshwater as early as the summer and peak as late as September to October (Moyle 2002). Most juveniles rear in cool, clear, fast moving portions of rivers and tributaries for up to 2 years, before migrating to the ocean in spring (McEwan 2001). Others may residualize remaining in freshwater for their entire lives (Quinn 2005).

One of the main management responses to declining salmon stocks has been to implement large scale hatchery release programs in most river basins along the Pacific coast of the USA, a practice that is not without controversy (e.g. see Meffe 1992; Brannon et al. 2004; Myers et al. 2004). Hatchery programs for salmonids in California began in the 1870 s, with the objective of increasing populations that were declining due to overfishing, the placement of dams and the resulting habitat loss (Moyle 2002). Hatchery programs increase growth rates and size at release to enhance smolt to adult survival (Mahnken et al. 1982; Dickhoff et al. 1995). Currently, approximately 37 million fish (mostly Chinook, steelhead and Coho) are released by hatcheries in California each year (Kostow 2009).

Several studies have addressed the mortality of outmigrating hatchery-reared salmonid smolts on the Pacific coast of the USA (e.g. Welch et al. 2008; Melnychuk et al. 2010). Early studies in the Sacramento River focused on mass tagging of smolts with coded wire tags, release at specific locations, and recapture further downstream (Kjelson et al. 1981; Brandes and McLain 2001). More recently, Newman and Brandes (2010) used a similar approach to study the survival of outmigrating Chinook salmon through the Sacramento-San Joaquin Delta in relation to water pumping facilities. In recent years, ultrasonic telemetry has been used to study the survival and migratory pathways of salmonid smolts through river systems. This involves the placement of small internal tags within smolts that emit a unique ultrasonic code detected by an array of passive receivers placed along and across the river. Examples of such systems include the Pacific Shelf Ocean Tracking (POST) array (e.g. see Welch et al. 2008, 2009; Melnychuk 2009; Melnychuk et al. 2010), and the California Fish Tracking Consortium (CFTC) (e.g. Perry et al. 2010; Chapman et al. 2012; Sandstrom et al. 2012; Ammann et al. 2011).

The CFTC maintains ultrasonic receiver stations at locations from Redding (river km 559) down to the Golden Gate (river km 0) and including an offshore linear array at Point Reyes, 57.84 km to the north of San Francisco. Cross-river arrays have been placed at key sites to maximize the detection probability of fish passing through specific river reaches. Single-lined arrays are at Benicia, Carquinez, Richmond and Bay Bridges, and a double-lined array is maintained at the Golden Gate. A suite of receivers was deployed in the Delta in order to study the route selection of migrating smolts (Perry et al. 2010).

Here, we describe the reach-specific success of outmigrating hatchery-reared steelhead and late-fall run Chinook salmon smolts carrying these coded tags in 2009 and 2010, based on their detection by automated tag-detecting monitors from their release site near Sacramento to the Golden Gate Bridge – the entrance to the Pacific Ocean. Apparent survival and detection probabilities were estimated using Program Mark (White and Burnham 1999). We hypothesize several factors regarding survival estimates: (a) that smolts with higher condition factors will have higher apparent survival than those with lower condition factors, (b) fishes traveling through the east Delta will have lower survival when compared to fishes not selecting this route, due to a longer overall migration distance and possible entrainment in the pumping facilities in the Delta, (c) intraspecies apparent survival by reach across the 2 years of the study will be similar, and (d) Chinook will have higher overall apparent survival, as steelhead may residualize in fresh water.

Methods and materials

Surgical procedure

In 2009 and 2010 500 late-fall run Chinook salmon and 500 steelhead trout smolts were obtained from Coleman National Fish Hatchery (CNFH), located in Anderson, CA. The fish were transported from CNFH to the UC Davis campus and held for approximately 5 weeks prior to tagging and fed rations of feed at 1 % of their body weight per day. The fish were starved 48 h prior to the tagging procedure. The fish were anaesthetized with a dose of 90 mg/L tricaine methanesulphonate (MS222) in accordance with a UC Davis Animal Care Protocol (#15486). Once anesthetized, each individual was removed from the solution, photographed, and the fork length, weight and condition were recorded. Any fish whose tag to body weight ratio was greater than 5 % was not tagged and returned to the tanks. A 5 % tag to body weight ratio was a conservative cutoff based on previous research conducted by Lacroix and McCurdy (2004) and Martinelli et al. (1998) who reported tag burdens of 8 and 6 % respectively. Fish were then placed ventral-side up on a surgery cradle and kept sedated by flushing a lower concentration of 30 mg/L MS222 over the gills. A 10 mm incision was made beside the mid-ventral line, ending 3 mm anterior to the pelvic girdle. A sterilized, cylindrical ultrasonic tag was inserted into the peritoneal cavity of the fish and positioned so as to lay just under the incision. The incision was then closed using two simple interrupted sutures (Supramid, 3–0 extra nylon cable). Mean surgery time was 129(± 36 SD) seconds.

All fish were placed into a 284 L tank to recover from the anesthetic before being moved outside to larger holding tanks, where they were kept under observation before release. No mortalities or tag shedding were observed during this period.

The tags (Vemco V7-4 L) used on the steelhead were 22.5 mm length, 7 mm diameter, weighed 1.84 g in air, and had a power rating of 136 dB (1 μP @ 1 m). They had a 30–90 s random delay, and a battery life of 138 days. The tags (Vemco V7-2 L) used on the Chinook smolts were 20 mm long, 7 mm in diameter, weighed 1.6 g in air, and had a power rating of 136 dB (1 μP @ 1 m). They had a 15–45 s random delay, and a battery life of 52 days. The steelhead smolts, which are larger than the Chinook smolts at the time of release from the hatchery, were implanted with the V7-4 L tags. The V7-4Ls were programmed with a longer delay, so that we could take advantage of the longer battery life of the tag, because we anticipated a longer outmigration time for these fish.

Release site and procedure

The smolts were released at Elkhorn Boat Landing in Sacramento, CA 36.6227°N, 121.6248°W, approximately 18 km upstream from the first receiver they would be expected to encounter at the I80/50 junction (Fig. 1). Fish were released after dark, in batches of 500 (250 steelhead and 250 late-fall Chinook), on February 27th and March 6th 2009, and January 30th and February 5th 2010. Two fish transport tanks, one for each species, were used for transport to the release site at Elkhorn Boat Landing on the river above Sacramento. Oxygen was pumped from tanks mounted on the truck through hoses to oxygen diffusers placed in the bottom of each tank. Dissolved oxygen and temperature were monitored throughout transport. Upon arrival at the release site, we compared the temperatures in the tank and the river. When water temperature differed by greater than 1°C the fish were acclimated by bringing the tank temperature up to within 1°C of the river temperature in increments of 1°C every 45 min. The fish were released once the temperatures were within 1°C of each other.

Receivers and array maintenance

An array of underwater passive ultrasonic receiver stations (VR2/VR2W, VEMCO Ltd. Halifax, Canada)

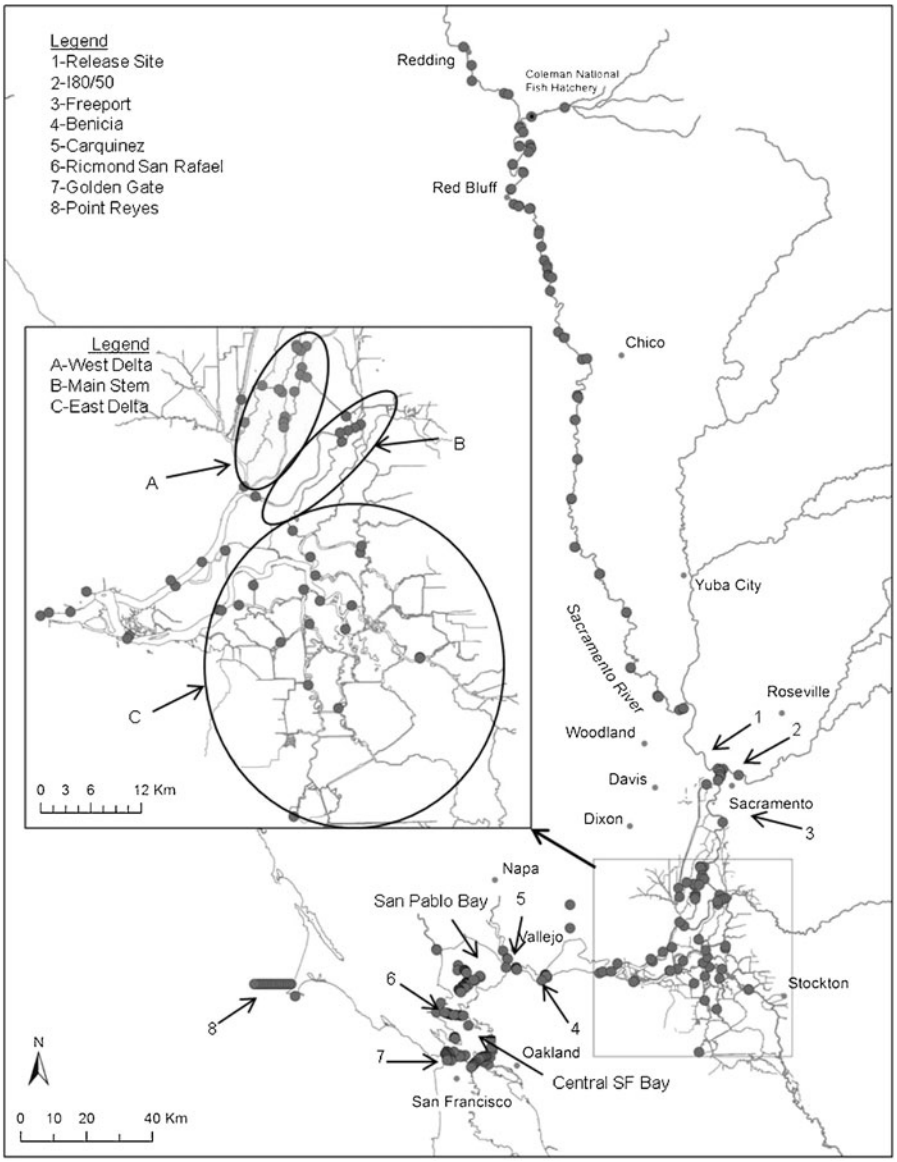


Fig. 1 Map of study area. Inset is the Delta with three routes highlighted. Numbers indicate locations of various checkpoints used in study, and letters indicate the different routes. Circles on the map indicate the location of tag detecting monitors maintained by the California Fish Tracking Consortium, including the monitors used in this study

was deployed throughout the Sacramento River system. Along the river and delta, the receivers were mostly deployed on weighted moorings (9–41 kg mass), attached to steel cables running from onshore manmade or natural structures. Cross section arrays at major bridges (Benicia, Carquinez, Richmond and Bay Bridge) involved direct attachment of receivers to weighted steel cables at bridge abutments. Other receivers were deployed on acoustic releases for ease of recovery in deepwater and mid-channel locations (such as the Golden Gate, or arrays in San Pablo Bay) where no structure was available for mooring the receivers. Receivers were interrogated and maintained every 3–4 months. Receiver locations that define the reaches and their corresponding river kilometers (rkm) can be found in Table 1. The files of tag detections were entered into the CFTC shared database, maintained by the National Marine Fisheries Service.

We carried out a range test to determine the ideal spacing of receivers within cross section arrays. A range test tag, similar in characteristics to the tags used in the fish, except that the pulse interval was fixed, was placed on a mooring with a receiver. This was followed by a line of receivers each spaced 30 m apart to a distance of 330 m, followed by a final receiver at 410 m from the tag. After 24 h we

Table 1 Reaches used to create encounter histories by name, river km, and reach length

Location	River km	Reach length (km)
Elk Landing	207.7	
I-80/50	189.0	18.77
Freeport	168.5	20.46
Benicia Bridge	51.69	116.8
Carquinez Bridge	41.47	10.22
Richmond Bridge	14.72	26.76
Golden Gate East Line	1.717	13.0
Golden Gate West Line	0.798	0.919
Point Reyes	−57.84	58.64

recovered the array and calculated the detection probability of the range test tag with increasing distance. Range tests were conducted in three locations that were representative of the different environments expected to be encountered in our study area. Range testing was conducted at Knights Landing, the San Francisco Bay, and Comanche Reservoir. We found that the tag had a detection probability of a value of 0.75 at a distance of 75 m from a receiver, in a less than ideal acoustic environment. Therefore, a conservative spacing of 150 m was used between receivers at cross section arrays.

In order to gain information on the amount of water the fish encountered as they migrated through our array, we obtained river discharge (in cubic feet per second, which were then converted to cubic meters per second) at Freeport from the California Data Exchange Center (http://cdec.water.ca.gov/cgi-progs/staSearch).

Routes

We subdivided the Delta into the major routes which fish might select, based on Perry et al. (2010), but excluded the Delta Cross Channel (DCC) as this remained closed throughout the migration of our fish during both years. The estuary was subdivided into several regions, each bordered by receivers or receiver arrays at bridges. At the head of the estuary, the Sacramento and San Joaquin rivers flow into Suisun Bay (upstream of location 4 Fig. 1). This is largely brackish and is separated from San Pablo Bay by the Carquinez Strait (the area between locations 4 and 5 Fig. 1), an area between the Benicia and Carquinez Bridges. South of the Richmond-San Rafael Bridge (Location 6 in Fig. 1) lies the Central Bay, bordered on the west by the Golden Gate Bridge (Location 7 in Fig. 1), and to the south by the Bay Bridge and the South Bay (Fig. 1).

Successful migration

Successful migration through a particular reach by an individual fish was defined by that individual being detected at the end cross-section array of that reach or at any receiver located downstream from that array. For example, a fish was assumed to have successfully migrated through San Pablo Bay if it was detected at Richmond Bridge or below. Successful migration to the ocean was defined as those fish detected at the Golden Gate plus those detected at Point Reyes which were not detected at the Golden Gate. Values for the Golden Gate were corrected to include those fish detected at the Point Reyes array. However the results may be underestimations of the overall success rate, given that once fish arrive at the ocean they may potentially take a wide number of routes.

Data analysis

The body condition factor (K) was calculated by incorporating the weights and fork lengths (Figs. 2 and 3) of the fish recorded during the surgeries into the equation developed by Fulton (1902):

$$K = \left(10^5 \times W\right)/L^3$$

Where W is the mass of the fish (measured in grams) and L is the fork length of the fish (measured in mm). The value of K is then used an index for body condition, with higher K values indicating a better body condition. We compared fork lengths and K factor between species and years using a Kruskal-Wallis One Way Analysis of Variance on Ranks.

We divided the Delta into routes (see Fig. 1) similar to those described by Perry et al. (2010). We estimated the number of fish moving through each route by analysis of the detection sequence in the Delta array. For each route, we compared the numbers and proportions (with 95 % confidence intervals) of fish that successfully migrated through successive river reaches to the Golden Gate. A Pearson's Chi-Squared test was

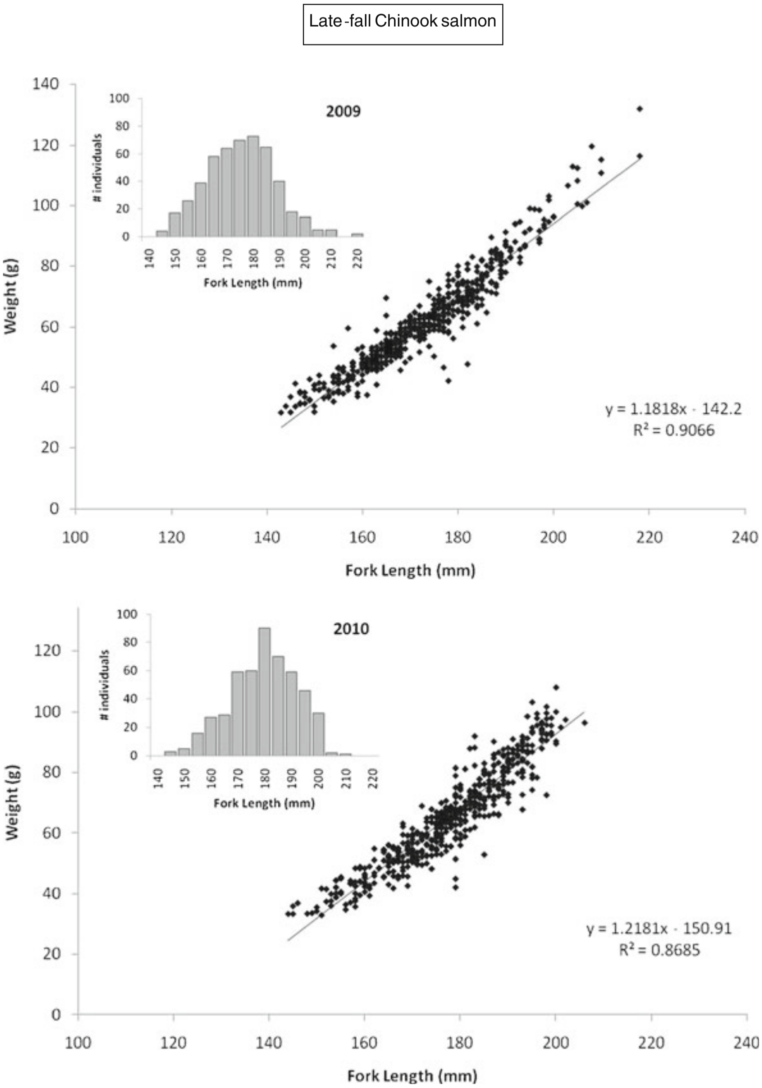


Fig. 2 Size structure for juvenile late-fall run Chinook salmon in 2009 (top) and 2010 (bottom). Fork Length in mm along the x-axis and weight in grams along the y-axis. The inset histogram shows the length distributions

run to compare survival by species and year across reaches.

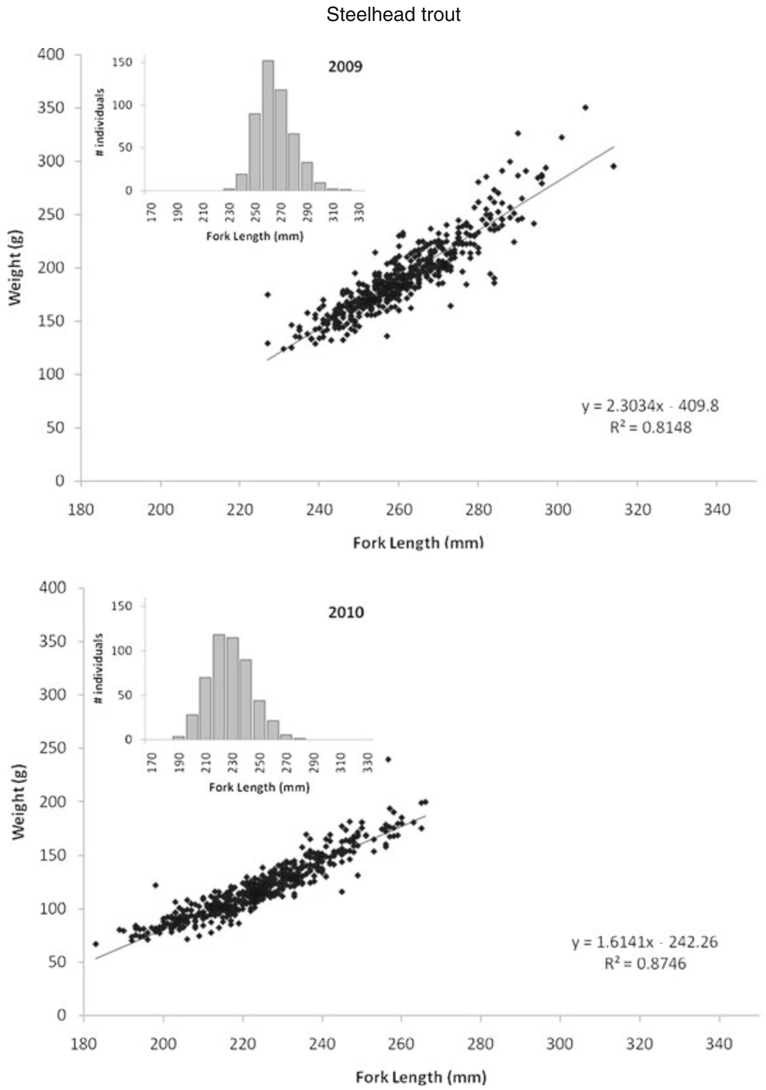
Encounter histories were created for each fish based on the detection data from our array of monitors. The fish were then placed into one of 12 groups based on release timing, route selected through the Delta, and the year in which the fish was released. All of the data were incorporated into several models in Program Mark (White and Burnham 1999) in order to estimate apparent survival and detection probabilities. The candidate models were then ranked using Akaike's Information Criterion (AIC), and the top performing models were used to report the results of this study (Akaike 1973). The same models were run with data from both steelhead and late-fall run Chinook.

Results

Size and body condition

The size range of Chinook salmon was similar in both years. The fork lengths varied between 140 and 220 mm, although a Kruskal-Wallis One Way Analysis of Variance on Ranks revealed that the median length of 178 mm was significantly greater ($P<0.001$) in 2010 than the median length of 174 mm in 2009. Steelhead were larger than Chinook, but there was a greater difference in fork length range between years ($P<0.001$). The median length in 2009 was 260 mm, whereas in 2010, median length was 223 mm (Figs. 2 and 3). The

Fig. 3 Size structure for juvenile steelhead trout in 2009 (top) and 2010 (bottom). Fork Length in mm along the x-axis and weight in grams along the y-axis. The inset histogram shows the length distributions



mean condition factor was slightly greater in the 2009 fish for both species. However, there was no significant difference in condition factor within years between fish which successfully migrated to the Golden Gate and those which did not (Fig. 4). The relatively low K values for the fish used in this study were expected, and are indicative of the smoltification process. MacFarlane and Norton (2002) reported mean condition factors for juvenile Chinook salmon sampled at different points within the estuary ranging from 1.0 to 1.1. Campos and Massa (2010) reported mean condition factors for juvenile steelhead captured in rotary screw traps ranging from 0.9 to 1.1. These data are similar to our calculations for condition factor (Fig. 4).

Release site conditions

2009 smolts were released from Elkhorn Landing (river km 207.7) when the flows registered 1,125 $m^3\ s^{-1}$ and 961 $m^3\ s^{-1}$ and in-river temperatures were 12.3°C and 11.3°C respectively. In 2010, the first release coincided with a flow of 1,454 $m^3\ s^{-1}$ and a temperature of 9.7°C, while the second release occurred at 836 $m^3 s^{-1}$ and temperature of 10.9°C (Fig. 5), resulting in a much larger range of observed discharge.

Route selection

More than half of the fish migrating through the delta remained in the main stem Sacramento. A total of

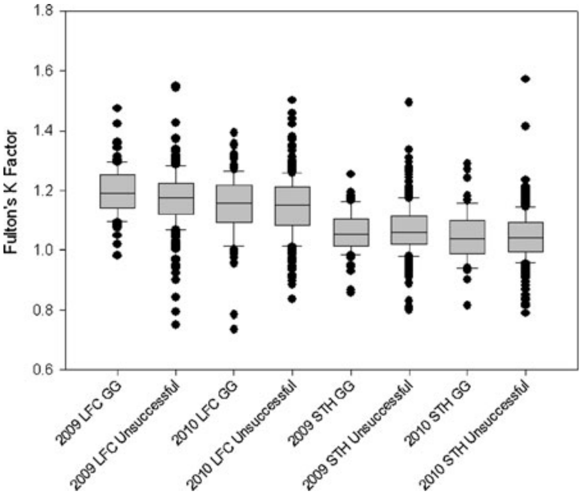


Fig. 4 Box plot comparing Fulton's condition factor of fish that successfully migrated to the Golden Gate Bridge to those that were unsuccessful. Late-fall Chinook (LFC) Steelhead (STH)

63.6 % (n=281) of Chinook that traveled far enough to encounter a junction that required a route selection, remained in the mainstem in 2009 and 54 % (n=234) remained in the mainstem in 2010. A total of 59.9 % (n=187) of the steelhead passed through the mainstem in 2009, while 52.4 % (n=109) passed through the same reach in 2010. Of these smolts, a greater percentage of Chinook, 26 %, and steelhead, 33 %, reached the Golden Gate in 2010, compared with 20 % and 25 % for both species, respectively in 2009. A similar percentage of each species were entrained into the East Delta each year, each of which displayed lower (9–19 %) success to the Golden Gate than for the other routes. Those fish which migrated through the West Delta had the highest survival rates of 30 % to the Golden Gate, with the exception of the 2009 batch of steelhead that had only a 10 % survival rate (Table 2).

Reach specific success

Chinook numbers declined only slightly (500 to 487 in 2009 and 500 to 471 in 2010) between the release site and Freeport (the start of the Delta). This is in stark

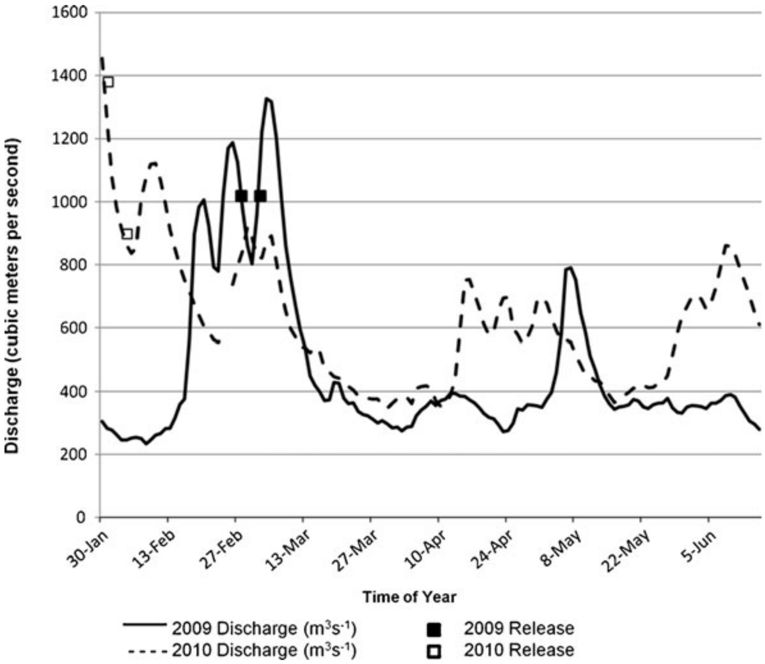


Fig. 5 Discharge by date as recorded at the CDEC station located at Freeport on the Sacramento River. Discharge is recorded in cubic meters per second. Dates of releases are indicated with squares

Table 2 Number and proportion of fish that used each route though the Delta, and their success to the Golden Gate Bridge

		Chinook		Steelhead	
		2009	2010	2009	2010
West Delta	# of fish	93	137	72	60
	Prop utilizing route	0.21	0.316	0.231	0.288
	# to Golden Gate	28	42	7	18
	Prop. Success to ocean	0.30	0.31	0.10	0.30
East Delta	# of fish	68	62	53	59
	Prop utilizing route	0.154	0.143	0.17	0.188
	# to Golden Gate	6	10	10	6
	Prop. Success to ocean	0.09	0.16	0.19	0.10
Mainstem	# of fish	281	234	187	109
	Prop utilizing route	0.636	0.54	0.599	0.524
	# to Golden Gate	55	61	46	36
	Prop. Success to ocean	0.20	0.26	0.25	0.33
Total fish in delta		442	433	312	208

contrast with steelhead, where over 20 % of the fish released each year were never detected. These fish probably did not migrate as far as the first receiver, I80/50, 20 km downstream from the release site - in 2009 only 357 of the 500 steelhead released were detected at Freeport or below, and in 2010 only 310 fish were detected here or below.

In the reach between Freeport and Benicia, both species exhibited similar rates of apparent survival. In 2009, the survival in the aforementioned reach was nearly identical at 66.7 % for steelhead and 63.0 % for Chinook ($p=0.3098$). In 2010, in the same reach survival across species was similar (35.8 % for steelhead and 43.5 % for Chinook), however and intraspecies comparison of survival differed significantly between years ($p=0.0169$).

Survival in the reach between Benicia and Carquinez differed little between species and years, and indicated little mortality for both species in this reach, although it is important to note that this was the shortest reach in the study site. In the Carquinez Straits success for Chinook ranged from 86.6 % (2009) to 94.6 % (2010), and 89.9 % (2009) to 90.1 % (2010) for steelhead. Success continued to decline as fish migrated through San Pablo Bay and Central San Francisco Bay. The Richmond to the Golden Gate Bridge reach had the lowest reach specific success for both species in 2009. In that reach, the final one before entry into the Pacific Ocean, success ranged from 56.5 % (2009) to 78.1 % (2010) for Chinook, and 45.6 % (2009) to 75.0 % (2010) for steelhead (Table 3).

Although overall migratory success to the Golden Gate was similar between 2009 and 2010, reach specific success was very different between years. Intraspecies success to the ocean (fish detected at either the Golden Gate or the Pt. Reyes array) was similar across years, 19.2 % ($n=96$) of Chinook salmon smolts in 2009, and 23.6 % ($n=118$) in 2010; and 14.6 % ($n=73$) of steelhead in 2009 and 13.8 % ($n=69$) in 2010. Successful migration through the Delta declined for both species from 2009 to 2010. However, in contrast with 2009, in 2010 many of the surviving fish then proceeded to the Golden Gate, with very few losses throughout the bay. In 2010 the Freeport to Benicia reach (Delta) had the lowest migratory success rates for both species, whereas in 2009 the reach with the lowest migratory success rates for both species was Richmond to the Golden Gate. Between Carquinez and the Golden Gate (the bay) apparent mortality of late-fall run Chinook in 2009 exceeded that in 2010 and apparent mortality of steelhead in 2009 also exceeded that of the 2010 fish. The overall pattern observed in the data was an apparent flip-flop of regions of higher mortality, with the bay appearing to be more perilous to migratory juvenile salmonids in 2009 and the Delta more perilous in 2010.

Reach specific survival estimates and detection probabilities

Fifteen candidate models were developed and then ranked according to their AIC for Chinook salmon

Table 3 Success of Steelhead and Chinook for both 2009 and 2010, based on raw detections. Elkhorn Landing was the release site

	Success to Site 2009	From Release Site % 2009	Reach Specific % 2009	Success to Site 2010	From Release Site % 2010	Reach Specific % 2010
Steelhead						
Elkhorn landing	500			500		
I80/50	378	75.6	75.6	339	67.8	67.8
Freeport	357	71.4	94.4	310	62.0	91.4
Benicia	238	47.6	66.7	111	22.2	35.8
Carquinez	214	42.8	89.9	100	20.0	90.1
Richmond	160	32.0	74.8	92	18.4	92.0
Golden Gate	73	14.6	45.6	69	13.8	75.0
Chinook						
Elkhorn landing	500			500		
I80/50	488	97.6	97.6	482	96.4	96.4
Freeport	487	97.4	99.8	471	94.2	97.7
Benicia	307	61.4	63.0	205	41.0	43.5
Carquinez	266	53.2	86.6	194	38.8	94.6
Richmond	170	34	63.9	151	30.2	77.8
Golden Gate	96	19.2	56.5	118	23.6	78.1

(Table 4) and steelhead trout (Table 5). Steelhead survival estimates calculated in the top candidate model suggest that survival was higher through the Delta in 2009, than in 2010. Additionally, survival through the bay was lower in 2009 than it was in 2010 for Steelhead. This same pattern was seen for Chinook in the best model. Detection probabilities were consistently higher in 2010. This is likely due to the addition of monitors on the Carquinez and Richmond San Rafael Bridges. Complete survival estimates can be found for the top-ranked model for steelhead (Table 6) and for Chinook (Table 7).

While survival estimates varied depending on the year and release group the overall trend suggests that Chinook have a better chance of surviving the Freeport to Benicia route if they took the mainstem Sacramento route or West Delta route, as opposed to the East Delta. In 2009, steelhead taking the West and East Delta route had similar survival estimates, while the mainstem fish had better survival in this reach. However, steelhead in 2010 had much better survival in the West Delta and mainstem Sacramento than they did in the East Delta.

Discussion

We found that in both 2009 and 2010, migratory success from the release site at Elkhorn Landing, near Sacramento, to the Golden Gate (a distance of 207 km) was less than 25 % for both late-fall Chinook salmon and steelhead. However, migratory success varied considerably between reaches and between years. Success for both species in the Delta was above 60 % in 2009, yet dropped to below 45 % in 2010. Conversely, successful migration through San Francisco Bay was only around 50 % in 2009, yet increased to over 75 % in 2010. This apparent reversal in the relative success rates (which might be assumed to reflect mortality) may be counterintuitive, given that flows were higher in 2010, and increased flows are often associated with increased survival (Sims and Ossiander 1981). Survival of salmonid smolts in the Delta is positively correlated (r=0.95) with volume of flow and that the survival rate changed greatly as the flow changed. The survival was nearly 100 % when the flows were above 708 $m^3\ s^{-1}$ (25 000 cfs), but less than 20 % when the flows were near 283 $m^3\ s^{-1}$ (10 000 cfs) (Fischer et al. 1991). The paradox we observed may have resulted from indirect effects of climate and

Table 4 Candidate models and their ranks, according to AIC for late-fall Chinook

Results for Late-fall Chinook

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(t*Year*Route*Release) p(t*Year)}	4787.41	0	1	1	52	697.29
{Phi(t*Year*Route) p(t*Year)}	4843.41	56.00	0	0	34	790.73
{Phi(t*Year*Route*Release) p(t)}	4951.64	164.23	0	0	47	871.98
{Phi(t*Year*Release) p(t)}	4956.73	169.32	0	0	39	893.71
{Phi(t*Year*Route) p(t)}	4976.26	188.85	0	0	27	937.97
{Phi(t*region*year*route*release) p(t)}	4989.15	201.74	0	0	39	926.13
{Phi(t*Year) p(t)}	4995.82	208.41	0	0	23	965.72
{Phi(t*region*year*route) p(t)}	5019.03	231.62	0	0	23	988.93
{Phi(t*region*Year) p(t)}	5038.63	251.22	0	0	19	1016.69
{Phi(t*Release) p(t)}	5068.56	281.15	0	0	23	1038.46
{Phi(t*Route) p(t)}	5076.64	289.23	0	0	17	1058.77
Phi(t*Region*Route*Release) p(t)}	5087.96	300.55	0	0	23	1057.86
{Phi(t) p(t)}	5100.90	313.49	0	0	15	1087.08
{Phi(t*region*route) p(t)}	5118.21	330.80	0	0	15	1104.39
{Phi(t*region) p(t)}	5142.47	355.06	0	0	13	1132.70

flow– the 2010 releases occurred in March, 1 month later than in 2009. Additionally, during the 2010 out-migration period, the western coast of North America was experiencing El Niño conditions. A brief look at sea surface temperatures at the San Francisco Bar (http://www.ndbc.noaa.gov/station_history.php?station=46237) during the time in which the salmonids were migrating showed that the mean temperature was only slightly higher in 2010 (12.07±1.37°C SD in 2009, 12.43±0.84°C in 2010). This subtle difference

Table 5 Candidate models and their ranks, according to AIC steelhead trout

Results for Steelhead

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
{Phi(t*Year*Route) p(t*Year)}	3399.09	0	0.78	1	35	693.21
{Phi(t*Year*Release*Route) p(t*Year)}	3401.67	2.57	0.22	0.28	53	657.53
{Phi(t*Year*Route) p(t)}	3486.36	87.27	0	0	27	797.18
{Phi(t*Year) p(t)}	3488.95	89.86	0	0	23	808.04
{Phi(t*Year*Release) p(t)}	3492.19	93.10	0	0	39	777.89
{Phi(t*Year*Release*Route) p(t)}	3492.94	93.85	0	0	47	761.66
{Phi(t*Region*Year) p(t)}	3501.35	102.26	0	0	19	828.68
{Phi(t*Region*Route*Year*Release) p(t)}	3520.67	121.58	0	0	40	804.26
{Phi(t*Region*Route*Year) p(t)}	3524.74	125.65	0	0	24	841.77
{Phi(t*Release) p(t)}	3534.71	135.62	0	0	23	853.81
{Phi(t*Route) p(t)}	3537.76	138.67	0	0	17	869.19
{Phi(t) p(t)}	3542.84	143.75	0	0	15	878.36
{Phi(t*Region*Route) p(t)}	3551.75	152.66	0	0	15	887.27
{Phi(t*Region) p(t)}	3558.87	159.78	0	0	14	896.44
{Phi(t*Region*Route*Release) p(t)}	3565.76	166.67	0	0	24	882.79

Table 6 Survival estimates and detection probabilities from the best fit model for Chinook. Estimates for the Pt. Reyes reach are confounded, as there are no downstream monitors

Survival Estimates and Detection Probabilities for Chinook Salmon

Label	Estimate	SE	LCI	UCI
Phi Elkhorn to 180/50 Release 1 2009	1	4E-07	0.999999	1.00001
Phi 180/50 to Freeport Release 1 2009	1	3E-07	0.999999	1.00001
Phi Freeport to Benicia (MS) Release 1 2009	0.562987	0.048372	0.467032	0.654448
Phi Freeport to Benicia (WD) Release 1 2009	0.602543	0.068723	0.463472	0.726814
Phi Freeport to Benicia (ED) Release 1 2009	0.313323	0.073488	0.189372	0.47124
Phi Benicia to Carquinez Release 1 2009	0.895141	0.07521	0.639657	0.97622
Phi Carquinez to RSR bridge Release 1 2009	0.616018	0.084521	0.443327	0.763693
Phi RSR Bridge to GG East Release 1 2009	0.614797	0.095187	0.42061	0.778219
Phi GG East to GG West Release 1 2009	1	1.7E-06	0.999997	1.000003
Phi GG West to Pt. Reyes Release 1 2009	0.428481	0	0.428481	0.428481
Phi Elkhorn to 180/50 Release 2 2009	0.811651	0.035321	0.732612	0.871426
Phi 180/50 to Freeport Release 2 2009	1	2.3E-06	0.999995	1.000005
Phi Freeport to Benicia (MS) Release 2 2009	1	3E-07	1	1.000001
Phi Freeport to Benicia (WD) Release 2 2009	1	1.6E-06	0.999997	1.000003
Phi Freeport to Benicia (ED) Release 2 2009	0.699152	0.143073	0.37991	0.898116
Phi Benicia to Carquinez Release 2 2009	0.932502	0.063067	0.659682	0.989946
Phi Carquinez to RSR Bridge Release 2 2009	0.706509	0.079746	0.531134	0.836482
Phi RSR Bridge to GG East Release 2 2009	0.613944	0.086653	0.43717	0.765037
Phi GG East to GG West Release 2 2009	0.867951	0.124447	0.438998	0.98221
Phi GG West to Pt. Reyes Release 2 2009	0.980661	0	0.980661	0.980661
PhiElkhom to 180/50 Release 1 2010	0.687292	0.098508	0.472312	0.843677
Phi 180/50 to Freeport Release 1 2010	0.80474	0.118992	0.482992	0.947868
Phi Freeport to Benici (MS) Release 1 2010	0.849305	0.075682	0.638797	0.947258
Phi Freeport to Benici (WD) Release 1 2010	0.884648	0.063421	0.69404	0.962864
Phi Freeport to Benici (ED) Release 1 2010	0.477967	0.198467	0.161488	0.813182
Phi Benicia to Carquinez Release 1 2010	0.977109	0.041347	0.532603	0.999375
Phi Carquinez to RSR Bridge to GG West Release 1 2010	0.820426	0.056508	0.682974	0.906447
Phi RSR Bridge to GG East Release 1 2010	0.721483	0.055879	0.600318	0.817106
Phi GG East to GG West Release 1 2010	0.983648	10.21562	0	1
Phi GG West to Pt. Reyes Release 1 2010	0.959401	0	0.959401	0.959401
Phi Elkhorn to 180/50 Release 2 2010	1	1E-07	1	1
Phi 180/50 to Freeport Release 2 2010	1	0	1	1
Phi Freeport to Benicia (MS) Release 2 2010	0.513124	0.043704	0.427913	0.597579
Phi Freeport to Benicia (WD) Release 2 2010	0.365738	0.07088	0.240594	0.512081
Phi Freeport to Benicia (ED) Release 2 2010	0.300614	0.075987	0.174689	0.466054
Phi Benici to Carquinez Release 2 2010	1	2E07	1	1
Phi Carquinez to RSR Bridge Release 2 2010	0.729562	0.053734	0.612683	0.821449
Phi RSR Bridge to GG East Release 2 2010	0.6632125	0.063679	0.529599	0.774861
Phi GG East to GG West Release 2 2010	0.899202	9.338738	0	1
Phi GG West to Pt. Reyes Release 2 2010	0.999597	0	0.999597	0.999597
p 180/50 2009	0.017337	0.006499	0.008284	0.035923
p Freeport 2009	0.071824	0.012875	0.05033	0.101517

Table 6 (continued)

Survival Estimates and Detection Probabilities for Chinook Salmon

Label	Estimate	SE	LCI	UCI
p Benicia 2009	0.747211	0.029945	0.684184	0.801313
p Carquinez 2009	0.562963	0.042691	0.478291	0.644118
p RSR Bridge 2009	0.539326	0.052836	0.435565	0.639787
p GG East 2009	0.467008	0.057215	0.358314	0.578927
pGG West 2009	0.659505	0.071862	0.508465	0.783862
p Pt. Reyes 2009	0.328311	0	0.328311	0.328311
p 180/50 2010	0.101157	0.016714	0.072782	0.138938
p Freeport 2010	0.36211	0.02704	0.310954	0.416593
p Benicia 2010	0.902881	0.022344	0.84944	0.938722
p Carquinez 2010	0.645083	0.036705	0.570347	0.713352
p RSR Bridge 2010	0.805825	0.038976	0.718065	0.871169
p GG East 2010	0.806122	0.039935	0.715896	0.872787
p GG West 2010	0.994592	10.32927	0	1
p Pt. Reyes	0	0	0	0

may be one of several factors that influenced the location and abundance of salmon smolt predators, such as striped bass, which are more abundant in the ocean and estuaries during El Niño years (Moyle 2002). In the future, acoustic telemetry studies that pair the tagging of striped bass (and other predators of juvenile salmonids) and subsequent analysis of the relationship of movement patterns between species, would help to elucidate the extent of these predator/prey interactions.

In both 2009 and 2010 we observed a much higher initial loss for steelhead than for Chinook (Table 3). There may be several explanations for this. Some steelhead, unlike Chinook, will residualize and remain in freshwater for their entire lives (Moyle 2002). In addition, tag retention studies conducted on hatchery fish of both species indicate that there are differences in tag shedding. Sandstrom et al. (2012) concluded that after 60 days, steelhead tagged with dummy tags equivalent to a Vemco V7-2 L (which is 2.5 mm shorter in length then V7-4Ls used on the steelhead in this study) ultrasonic transmitters shed their tags 8 % of the time. In contrast, Ammann et al. (2011) concluded that after 120 days 100 % of Chinook tagged with V7-2Ls (the same tags used on the Chinook in this study) retained their tags, so that tag shedding is unlikely to be a source of error in our migratory success estimates for Chinook. Another possible bias is that steelhead may be more affected by the stress involved in transport, release, and acclimation to the new environment – over 100 steelhead each year were not detected anywhere downstream after release, compared with only several Chinook. While success within species was similar across years, successful migration to the ocean was higher in both years for Chinook salmon than steelhead, although this may not necessarily reflect different survival rates. In, addition to the potential for tag shedding, the random delay on the steelhead tags was nominally twice that of the Chinook, so fish being transported out of the Golden Gate at peak tidal flows are more likely to traverse the detection range of the array between pulses without being detected. Future comparative studies addressing transport stress across Pacific salmonid species could be useful to salmonid researchers. Additionally, residualized steelhead, malfunctioning tags, and fish that shed their tags may appear as a mortality when analyzing movement data. Developing a model used to adjust survival rates of acoustically tagged salmonids in a manner that adjusts for falsely assumed mortalities is another way that we intend to advance our analyses.

Previous studies of outmigrating salmon smolts in the Sacramento-San Joaquin drainage indicate that survival was affected by the route that the fish chose (Newman and Brandes 2010) and that the probability

Table 7 Survival estimates and detection probabilities from the best fit model for steelhead. Estimates for the Pt. Reyes reach are confounded, as there are no downstream monitors

Survival Estimates and Detection Probabilities for Steelhead Trout

Label	Estimate	SE	LCI	UCI
Phi Elkhom to 180/50 2009	0.828629	0.037245	0.743048	0.889929
Phi 180/50 to Freeport 2009	1	1E-07	1	1
Phi Freeport to Benicia (MS) 2009	0.898	0.045987	0.766946	0.959271
Phi Freeport to Benicia (WD) 2009	0.738349	0.093568	0.522014	0.879393
Phi Freeport to Benicia (ED) 2009	0.791391	0.092839	0.557527	0.919497
Phi Benicia to Carquinez 2009	0.882348	0.063369	0.693898	0.961258
Phi Carquinez to RSR Bridge 2009	0.856703	0.101689	0.541064	0.968069
Phi RSR bridge to GG East 2009	0.531836	0.091866	0.355341	0.700709
Phi GG East to GG West 2009	1	5.98E-05	0.999883	1.000117
Phi GG West to Pt. Reyes 2009	0.261186	21.37851	0	1
Phi Elkhorn to 180/50 2010	0.725212	0.054341	0.607304	0.818309
Phi 180/50 to Freeport 2010	0.91465	0.090799	0.523001	0.990543
Phi Freeport to Benicia (MS) 2010	0.7403	0.083363	0.549256	0.869596
Phi Freeport to Benicia (WD) 2010	0.66825	0.098578	0.457291	0.828042
Phi Freeport to Benicia (ED) 2010	0.40753	0.102376	0.230545	0.612271
Phi Benicia to Carquinez 2010	0.966342	0.029029	0.833125	0.99398
Phi Carquinez to RSR Bridge 2010	0.932232	0.037539	0.811051	0.97782
Phi RSR Bridge to GG East 2010	0.716216	0.056568	0.593938	0.813251
Phi GG East to GG West 2010	0.843623	0	0.843623	0.843623
Phi GG West to Pt. Reyes 2010	2.13E-05	0	2.13E-05	2.13E-05
p 180/50 2009	0.154719	0.023203	0.114479	0.205818
p Freeport 2009	0.379063	0.033249	0.316394	0.446046
p Benicia 2009	0.699348	0.037071	0.622137	0.766698
p Carquinez	0.486956	0.04661	0.39703	0.577734
p RSR Bridge 2009	0.507939	0.062986	0.386469	0.628478
p GG East 2009	0.329725	0.064366	0.217506	0.465406
p GG West 2009	0.545752	0.085351	0.379592	0.70231
p Pt. Reyes 2009	0.261186	21.3785	0	1
p 180/50 2010	0.384504	0.046149	0.298872	0.477945
p Freeport	0.384143	0.050636	0.290799	0.48688
p Benicia 2010	0.941177	0.025521	0.866351	0.975304
p Carquinez 2010	0.687499	0.051822	0.578272	0.779236
p RSR Bridge 2010	0.946429	0.030089	0.846641	0.98262
p GG East 2010	0.755102	0.061432	0.61654	0.855342
p GG West 2010	0.996784	0	0.996784	0.996784
p Pt. Reyes 2010	2.13E-05	0	2.13E-05	2.13E-05

of selecting a particular migratory route is positively correlated with the fraction of total river discharge that flows through that route (Perry et al. 2010). Entrainment in the interior delta (East Delta) is negatively correlated with survival (Newman and Brandes 2010; Perry et al. 2010) Perry et al. (2010) found that 8.8 % of fish were entrained into the interior delta when the DCC was closed, whereas 35.2 % were entrained when it was open. In our study, which took place while the DCC was closed, we found that the proportion of fish migrating through the interior delta was consistently higher for both species, 14.3–15 % for Chinook and 17.0–18.8 % for steelhead. It has been suggested that fish entrained in the East Delta have lower survival rates than other routes (Perry et al. 2010), although it is important to note that Perry defined "survival" as migration to Chipps Island. This was consistent with our results - throughout the duration of our study, fish migrating through the East Delta had lower overall survival than fish choosing either the West Delta or the mainstem Sacramento River, with the exception of West Delta steelhead in 2009 (Fig. 6). Several factors may have interacted to produce conditions that were unfavorable for steelhead, including water temperatures, increased suspended sediment loads in the water, and spatio-temporal distribution of steelhead smolt predators.

Survival is negatively related to total distance traveled during migration to the ocean (Muir et al. 2001; Smith et al. 2002). Because of the convoluted configuration of the East Delta smolts choosing this migratory pathway undoubtedly have a longer route to the ocean, and encounter obstacles not seen by fish choosing other routes (e.g. Central Valley Project and State Water Project pumping facilities). The pumping facilities have taken many precautionary measures to reduce fish loss; however the predator assemblages in the forebays, the physical stress of going through the salvage process, and the subsequent transport and re-release into the river may be too much for the smolts to overcome. Previous studies of juvenile fall run Chinook suggest survival is negatively associated with water exports (Kjelson et al. 1981; Brandes and McLain 2001; Newman and Rice 2002; Newman 2003). Additionally, the Operations Criteria and Plan (OCAP) Biological Assessment (BA) (USBR 2008) contains regressions of monthly steelhead salvage at the Central Valley Project and State Water Project pumping facilities, which shows a significant relationship between number of steelhead salvaged and the amount of water exported during the months of January through May, the same time that our tagged fish where in the Sacramento River Watershed. Our study suggests that entrainment in the east delta was negatively correlated with success to the ocean.

These results highlight the need to improve our understanding of the dynamics of smolt outmigration through the Sacramento River watershed, and the factors that affect their migratory behaviors. Future studies pairing the tagging of piscivorous fish and juvenile

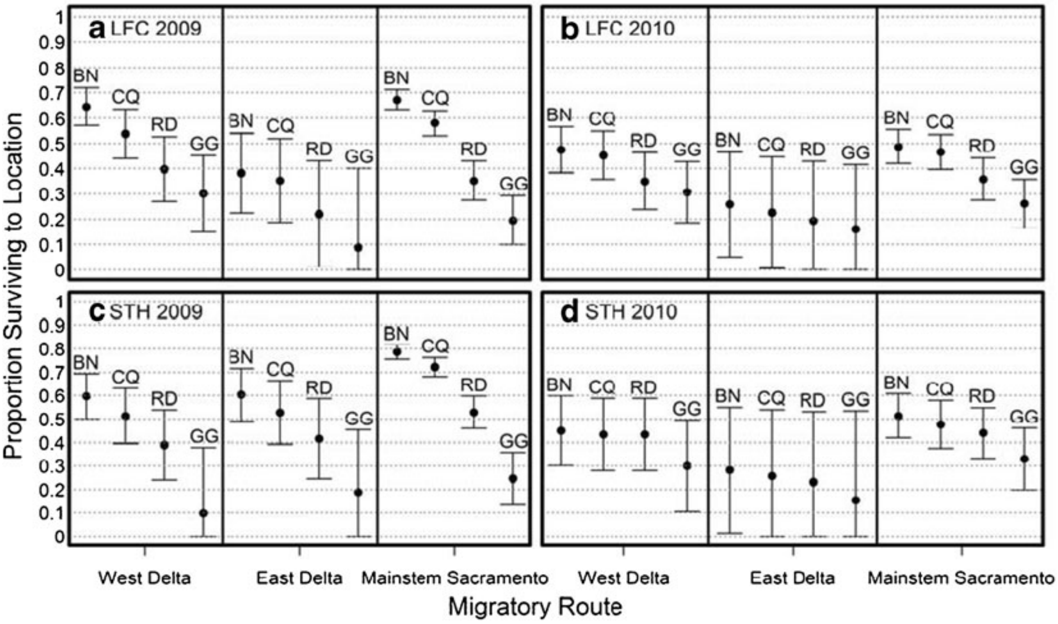


Fig. 6 Proportion of fish from each group successfully migrating to different reaches in the San Francisco Bay based on route selection through the Delta. Figure is divided by species, year, and route. The bars on the graph indicated 95 % confidence intervals in regards to our estimates of successful migration. The following abbreviations were used for location code: Benicia Bridge (BN), Carquinez Bridge (CQ), Richmond Bridge (RD), and the Golden Gate (GG). The following abbreviations were used to identify the species of reference: Late-fall Chinook salmon (LFC) and steelhead trout (STH)

salmonids in order to elucidate the intricacies of the spatio-temporal movements of predators in relation to prey availability are needed. Comprehensive studies designed to highlight the interactions of flow, temperature, turbidity, climate change, diel movements, pumping operations in the Delta, and predator abundance and interactions would fill in gaps in our knowledge of juvenile salmonid migration.

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Predictors of Chinook salmon extirpation in California's Central Valley

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Abstract Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), populations have declined rapidly along the western coast of North America since the year 2000, possibly because of factors such as habitat loss, altered hydrology and barriers to migration. However, few analyses have rigorously examined which of these factors actually explain historical patterns of extirpation. Data were compiled on flow regimes, habitat loss and migration barriers for 27 streams that historically supported autumn run salmon and 22 streams that supported spring runs. The probability of extirpation in streams supporting autumn run was predicted solely by migration barriers. All other factors were $>10^5$ times less likely to explain existing variation. By contrast, models for spring run salmon suggest that habitat loss and altered flow regimes were also predictors of extirpation. These results suggest that regional extirpation of Chinook salmon has been driven by multiple forms of environmental change, and restoration efforts must address a multitude of bottlenecks that now impact spring and autumn run populations.

KEYWORDS: dam, habitat loss, hydrology, Sacramento, San Joaquin.

Introduction

Pacific salmon (*Oncorhynchus* spp.) is an important economic, recreational and cultural resource throughout its geographical range. Although total production of some species has increased during the 20th century (Schindler *et al.* 2008), populations in many regions have experienced major declines and an estimated 29% of all salmon populations have been extirpated from the Pacific Northwest and California (Gustafson *et al.* 2007). Loss of local populations has reduced the range of life-history characteristics and genetic diversity of species, which could limit the ability of salmon to adapt to climate change and, ultimately, limit the long-term viability of some species (Moyle 1994; Crozier *et al.* 2008). Populations at greatest risk tend to occur in interior as opposed to coastal regions (Gustafson *et al.* 2007). Additionally, the biological consequences of extirpation are high for populations that occur at the extremes of the species range distribution because these populations often have unique biological adaptations, such as tolerance of extreme temperatures, that

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disproportionately contribute to the genetic diversity of the species relative to populations in the middle of the species' range (Allendorf *et al.* 1997). The Central Valley of California is an interior region that supports the southernmost spawning populations of Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Thus, conservation of these populations has been deemed a high priority to maintain the genetic and life-history diversity of Chinook salmon that is essential to the long-term persistence of the species (Ruckelshaus *et al.* 2002).

A recovery plan has been implemented for Central Valley salmon (USFWS 2001) that includes Chinook salmon. However, the goal of doubling natural production has not been reached, and instead, many populations continue to decline. Part of the problem is that many recovery plans lack basic information on the nature of threats, complicating attempts to prioritise restoration strategies (Lawler *et al.* 2002). A common problem in salmon recovery plans is that data available for assessment and decision-making by policy makers are often qualitative, consisting of professional opinion- or semi-quantitative, consisting of extrapolated or inferred data integrated with empirical measurements (Ruckelshaus *et al.* 2002). Although threats to Central Valley salmon are well known (Moyle 1994), attempts to quantify the relative importance of these threats and rank potential restoration strategies have been largely lacking. Thus, Boersma *et al.* (2001) suggested that explicit science designed to prioritise risk and address specific questions is needed to improve the recovery process for threatened and endangered species.

An information theoretical approach was used to evaluate quantitatively the weight of evidence for three hypotheses that are commonly proposed as explanations for the extirpation of Chinook salmon in the Central Valley of California. The first hypothesis is that migration barriers best explain extirpation where streams above barriers no longer support salmon and below barriers, salmon continue to persist. The second hypothesis is that habitat loss – in terms of length of river kilometres still accessible to salmon – best explains extirpation. The mechanism underpinning this hypothesis is that smaller habitats support fewer individuals that, in turn, increase the chance that demographic or environmental stochasticity will result in extirpation. The third hypothesis is that flow regimes have been altered such that they no longer support salmon. The mechanism underpinning this hypothesis is that post-regulation flow regimes have created conditions that reduce survival such as stranding of juveniles and dewatering redds (Ugedal *et al.* 2008), and reduced or eliminated access to favourable habitats such as floodplains (Sommer *et al.* 2001). Thus, streams where salmon persist have different flow regimes than streams where salmon have been extirpated.

Quantitative evaluations of these hypotheses were conducted for both spring run and autumn run Chinook salmon. These two runs were historically the most widely distributed in the Central Valley of California and represent distinct life-history types. Life-history characteristics have been shown to influence strongly extirpation probabilities for other at risk fish species (Olden *et al.* 2006). Autumn run salmon enter freshwater streams during a period from late summer through autumn and spawn soon after reaching suitable habitat. In winter and early spring, juveniles emerge from the benthic habitat, where eggs are laid and alevins are hatched and rear in fresh water for weeks to several months before starting their migration to marine waters (ocean-type life-history). Spring run salmon enter freshwater systems from spring to early summer and inhabit pools throughout the summer before completing maturation and spawning in early autumn. Juveniles may follow an ocean-type life-history similar to autumn run or they may spend a full year in fresh water before migrating out of the system the following spring (stream type life-history).

Methods

Study system

The Central Valley of California extends approximately 600 km from the Cascade Mountains in the north to the Tehachapi Mountains in the south. The eastern border of the valley is the Sierra Nevada Mountains and the Coast Range forms the western boundary. The Sacramento and San Joaquin rivers are the two principal river basins draining an area of approximately 69 930 and 82 900 km^2, respectively. The Sacramento River drains the northern portion of the valley and runs north to south, whereas the San Joaquin River drains portions of the southern valley and runs south to north. Both rivers terminate in the San Francisco Estuary in an area known as the Sacramento-San Joaquin Delta. The principal tributaries of the Sacramento enter from the east and drain the western slope of the Sierras and portions of the southern Cascades. Tributaries draining the Coast Range are less substantial but several support Chinook salmon populations. Major tributaries of the San Joaquin also drain the western slope of the Sierras. Unlike the Sacramento basin, tributaries entering the

San Joaquin from the Coast Range are generally intermittent and are unlikely to have ever supported salmon populations (Yoshiyama *et al.* 2001).

Aquatic habitats in the Central Valley have a long history of modification associated with human activities. Extensive gold mining in the mid 19th century severely degraded many rivers through the addition of large volumes of fine sediments, mercury pollution and construction of barriers to salmon migration. Historical accounts suggest that these activities had a large impact on salmon populations, although they have seldom been quantified (Yoshiyama *et al.* 2001). During the 20th century, a large number of dams and diversions were constructed on Central Valley streams to support agricultural and urban development. Most of these dams are total barriers to salmon migration preventing access to productive spawning and rearing habitats. Additionally, dam operations have altered the natural flow regimes of downstream reaches that remain accessible to Chinook salmon.

Data used to address hypotheses

Evaluation of the three hypotheses presented in the introduction required that several types of data to be available for a stream: (1) records of the presence of salmon prior to the era of anthropogenic alteration (historical data) and modern day (period following completion of most major dams) presence or absence; (2) height of potential barriers to salmon passage; (3) estimates of the amount of river kilometres lost because of impassable barriers; and (4) flow data for a period sufficient to characterise reliably the hydrological dynamics of the stream. Historical and current distributions of Central Valley Chinook salmon and estimates of habitat loss (% river kilometres) were obtained from Yoshiyama *et al.* (2001) and National Marine Fisheries Service (1999). The historical data were compiled from a variety of sources including early agency reports, newspaper articles, accounts of settlers and interviews with biologists. Modern day distributions primarily consist of agency reports and published papers. Yoshiyama *et al.* (2001) and NMFS (1999) provide details on the various data sources.

Salmon were recorded as extirpated if historical records indicated that a stream was used by salmon during at least one life-stage, but modern day assessments indicate they are absent. Salmon was recorded as extant if at least one life-stage continues to use the stream (Fig. 1). Habitat loss was estimated as the percent of river kilometres lost in each stream calculated from the stream mouth to the estimated upstream distribution limit. The height of potential barriers was obtained from the California Department of Water

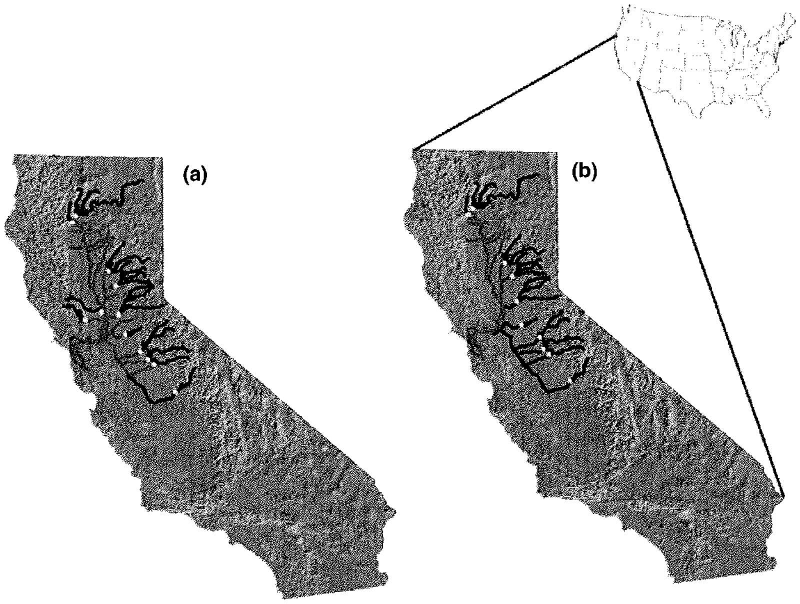

Figure 1. Maps depicting all streams that conformed to data requirements for analysis of autumn run (a) and spring run (b) Chinook salmon extirpations. Streams in red continue to support autumn run salmon. Streams in black historically supported salmon but have been extirpated. Yellow circles indicate the location of dams within the historic range of salmon that are total barriers to migration. When multiple streams were located above a dam, only the north fork was included in statistical models.

Resources Division of Safety of Dams. Barriers greater than 2.4 m that did not contain fish passage facilities were assumed to be too high for salmon to pass [which is roughly the height that Chinook salmon can jump (Bjornn & Reiser 1991)] and thus were barriers to upstream migration.

Data on flow regimes were obtained from the US Geological Survey (USGS) that operates a network of flow gauges throughout the Central Valley. Thus, for a stream to be included in the data set, it had to be gauged by the USGS. Most gauges were located downstream of dams near the modern distributional limits. When rivers contained more than one gauge, the gauge nearest to the distribution limit was selected. A 30-year period of record (1973–2003) of daily stream flow was selected to represent the modern flow regime. Flow regimes can change considerably in a 30-year time period. Nevertheless, records comprising several decades are required to estimate accurately the probabilities of infrequent events such as floods and extreme low-flows that may be important to the persistence of salmon. The analyses were only dated back to 30 years because the period after 1973 represents a time when all major dams were completed in the Central Valley, and nearly all land had become dominated by agriculture. The records were ended at 2003 because this was the last year for which flow data were cross checked and validated by the USGS when the analyses were performed.

A suite of 12 flow regime descriptors was calculated from mean daily flow records to represent the four broad categories of flow variability identified by Poff and Ward (1989) as influencing lotic taxa at regional scales: basin descriptors, overall flow variability, pattern of the flood regime and extent of extreme low-flows (Table 1). These 12 flow descriptors were previously used to categorise the life-history characteristics of stream and river species that occupy different flow regimes in North America (Poff & Ward 1989; Puckridge *et al.* 1998). As such, the 12 descriptions were used to describe the impact of flow regimes on everything from algae to invertebrates to fish. Many of the hydrological variables were correlated with one another, thus the variables were reduced into orthogonal axes of variation using principal components analysis (PCA using CANOCO Version 4, Microcomputer Power). Separate analyses were performed for the spring and autumn run streams. All subsequent analyses used PCA scores on the first two axes (which explained 78–83% of all the variation in hydrology among streams) in place of individual variables. These axes had biological interpretations that are described in the next paragraph.

Table 1. Flow regime descriptors used in principal components analysis. Descriptors were calculated from 30 years of mean daily flow data (1973–2003) obtained from U.S. Geological Survey flow gauges

Variable name	Definition
Basin descriptors	
Area	Drainage area (km^2)above the stream gauge
MAF	Mean annual flow from 1973 to 2003
SS	Size scalar–MAF/area
Flow variability	
Co/month	Colwell's predictability index for mean monthly flow
CV/month	Coefficient of variation of mean monthly flow
Flow/month	Log-transformed mean flow in each month
Pattern of the flood regime	
Co/flood	Colwell's predictability index for floods
FI	Flood interval – mean number of days between floods
TSR	Total slope rising – average slope of the rising limb of floods
Season/flood	Season with the greatest mean number of floods
Extent of low flows	
LFI	Low-flow interval – average number of days between low-flow periods
Season/low	Season with the greatest mean number of low-flow events

To augment the interpretation of select hydrological patterns, the modification of historical flow regimes by dams was characterised for five rivers where there were sufficient pre- and post-dam data available. Only five rivers had mean daily flow records for a 30-year period prior to dam construction in addition to a 30-year period after dam construction. The influences of dam construction and initial operation on flow data were avoided by excluding 8 years of data immediately prior to and immediately following the year of dam completion from the 30-year period.

Two data sets were constructed for the two most widely distributed Chinook salmon runs – spring and autumn. There were sufficient data to include a total of 27 streams in the autumn run data set and 22 streams in the spring run data set (Fig. 1). Some streams for which data were available were excluded from analysis because of a lack of independence. This occurred when more than one fork of a river was upstream of a total barrier to migration. When this occurred, only the north fork was selected simply as a consistent means for inclusion in the data set.

Data analysis

A series of logistic regression models was constructed to test the three hypotheses proposed to explain the probability of Chinook salmon being extirpated from Central Valley Rivers. For all models, the response variable was salmon status (1 = extant, 0 = extirpated). Predictor variables included: location of the stream relative to a barrier (1 = downstream, 0 = upstream), percent of river km lost, sample scores on principal component axes 1 and 2 that describe the major axes of hydrological variation. Separate model sets were constructed for the autumn and spring run. All models were constructed in SAS (Version 9.1.3, SAS Institute Inc., Cary, NC, USA).

Best approximating models were selected for spring and autumn run data sets using an information theoretic approach. Akaike's Information Criterion corrected for small sample size (AIC_c) was calculated for each candidate model. The difference in AIC_c values between the best model and competing models (ΔAIC_c) was used to calculate AIC_c weights and evidence ratios. Model weights are interpreted as the probability that a particular model is the best fit to the data relative to all other models being considered. Evidence ratios indicate the level of support for two or more competing models based on AIC_c weights. Thus, using AIC_c weights and evidence ratios, it was possible to evaluate the relative weight of evidence for or against each of the three hypothesised causes of Chinook salmon extirpation.

It was not possible to conduct a rigorous statistical analysis to test whether the probability of Chinook salmon extirpation could be linked to specific hydrological changes imposed by the construction of a dam because of the small number of rivers that had both pre- and post-dam flow records. Nevertheless, pre- and post-dam flow records were used to make several qualitative comparisons that, despite the lack of any direct statistical test, can be used to raise new hypotheses about why changes in hydrology may have influenced salmon at different life stages.

Results

Autumn run

Autumn run Chinook were extirpated from seven streams but persist in 20 streams. All streams where Chinook salmon were extirpated were upstream of structures that are barriers to salmon migration (Fig. 1a). Models that predicted expiration of autumn run salmon included habitat loss and migration barriers as parameters (AIC_c weights ≥0.48 and evidence ratios ≤ 1.08), whereas all other models were poor predictors (model weights <0.01 and evidence ratios >1 000 000) (Table 2). The model that included habitat loss was well supported because 100% habitat loss predicted extirpation as well as the location of a stream relative to a migration barrier. It is not at all a surprise that migration barriers can explain salmon extirpation. What was surprising from the analysis was complete lack of support for any other explanation or hypothesis for extirpation of the autumn run.

Table 2. Best approximating models for autumn run Chinook salmon. Models are arranged from best to worst based on evidence ratios. AIC weights are the relative likelihoods of a model given the data, and evidence ratios are the relative likelihood of each model vs the best model

Model	Variables in model	AIC_c	ΔAIC_c	AIC_c weight	Evidence ratio
2	Lost km	4.89	0.00	0.52	1.00
1	Barrier	5.04	0.15	0.48	1.08
4	PC1	33.31	28.42	0.00	1 482 221.23
3	PC1, PC2	33.87	28.98	0.00	1 959 679.47
5	PC2	33.98	29.09	0.00	2 068 951.16

Despite the poor performance of hydrological-based models to predict Chinook salmon extirpation, PCA explained 78% of the total variation in 12 hydrological variables among the 27 streams. Axis 1 determined 56% of the variation and differentiated streams with long intervals between floods and extreme low-flows, greater flood predictability and greater flows in summer and autumn from streams with greater monthly flow variability and spring flooding. Axis 2 (22% of variance explained) differentiated large streams with greater mean annual flow and flow predictability among months from smaller streams with steep flood profiles and greater flows during winter. Although there was variation in flow regimes among streams captured by PCA, these differences were insignificant relative to the presence of barriers in predicting Chinook salmon extirpations.

Spring run

Spring run Chinook salmon were extirpated from 12 streams and continued to persist in 10 streams (Fig. 1b). Model selection indicated that both migration barriers ($AIC_cW = 0.64$, ER = 1.00) and habitat loss ($AIC_cW = 0.25$, ER = 2.55) were well supported as predictors of extirpation (Table 3).By contrast to the autumn run, one of the hydrology models (predictor = PC1) had a sufficient level of support in the

Table 3. Best approximating models for spring run Chinook salmon. Models are arranged from best to worst based on evidence ratios. AIC weights are the relative likelihoods of a model given the data, and evidence ratios are the relative likelihood of each model vs the best model

Model	Variables in model	AIC_c	ΔAIC_c	AIC_c weight	Evidence ratio
1	Barrier	24.90	0.00	0.64	1.00
2	Lost km	26.78	1.88	0.25	2.55
4	PC1	29.09	4.19	0.08	8.10
3	PC1, PC2	31.86	6.96	0.02	32.31
5	PC2	33.36	8.46	0.01	68.44

Table 4. Best approximating models for spring run Chinook salmon in rivers located below migration barriers. Models are arranged from best to worst based on evidence ratios. AIC weights are the relative likelihoods of a model given the data, and evidence ratios are the relative likelihood of each model vs the best model

Model	Variables in model	AIC_c	ΔAIC_c	AIC_c weight	Evidence ratio
3	PC2	21.59	0.00	0.59	1.00
4	PC1, PC2	22.16	0.57	0.44	1.33
2	PC1	23.29	1.70	0.25	2.34
1	Lost km	24.19	2.60	0.16	3.67

analyses to prevent its exclusion as a viable hypothesis ($AIC_cW = 0.08$, $ER = 8.10$). The spring run PCA determined 79% of the total variation among streams and described the same relationships as the autumn run PCA. Thus, compared with autumn run Chinook salmon, the probability of spring run extirpation was less clear with models supporting migration barriers, habitat loss and possibly changes in stream hydrology as potential contributors to extirpation.

The potential role of hydrology in predicting extirpation was explored with a model selection exercise that excluded streams upstream of migration barriers. A third PCA was performed that included only the streams downstream of a barrier. A total of 16 streams were included in this analysis. Chinook salmon were extirpated from six of these streams and persisted in 10. Models that included hydrology were stronger predictors of extirpation than was habitat loss ($AIC_cW \geq 0.25$, $ER \leq 2.34$); but habitat loss remained a competing predictor (Table 4). The best approximating model included PC 2 as the predictor variable, and all streams with positive scores on PC 2 continued to support spring run salmon populations (Fig. 2). Streams with positive scores on Axis 2 had steeper flood profiles, greater flows in late autumn and early winter and longer intervals between extreme low-flow periods. Streams with negative sample scores were larger and had greater flows during summer and early autumn. The difference in the strength of models that use hydrology to predict extirpations of spring run Chinook salmon below barriers suggests that autumn and spring run salmon may respond differently to changes in hydrology and habitat loss following the construction of dams.

The analysis of post-dam hydrological changes suggested that dams may be reducing stream flows

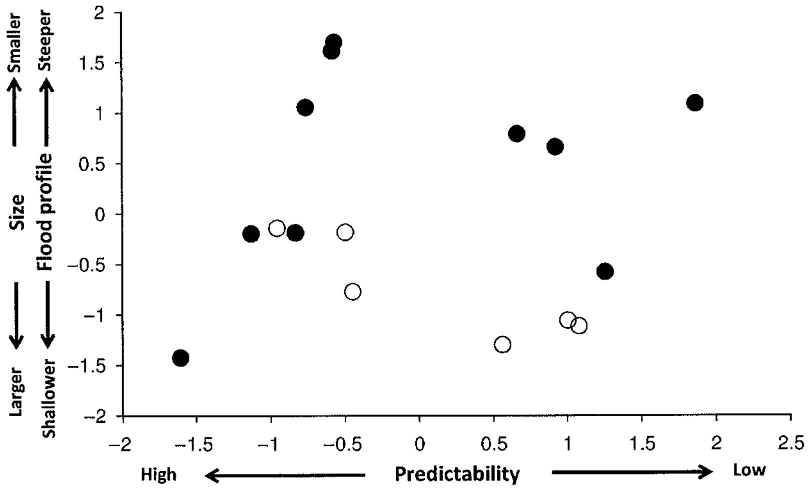

Figure 2. Bi-plot of sample scores on principal components PC1 (abscissa) and PC2 (ordinate). All streams used in the analysis historically supported spring run Chinook salmon and are located below barriers to migration. Closed circles represent streams where Chinook salmon persist, and open circles represent streams where they have been extirpated. Variables that loaded strongly on axis one included Colwell's predictability index for floods and monthly flow, drought interval and the coefficient of variation for monthly flow. Variables that loaded strongly on axis 2 included mean annual flow, drainage area and the slope of the rising limb of flood events.

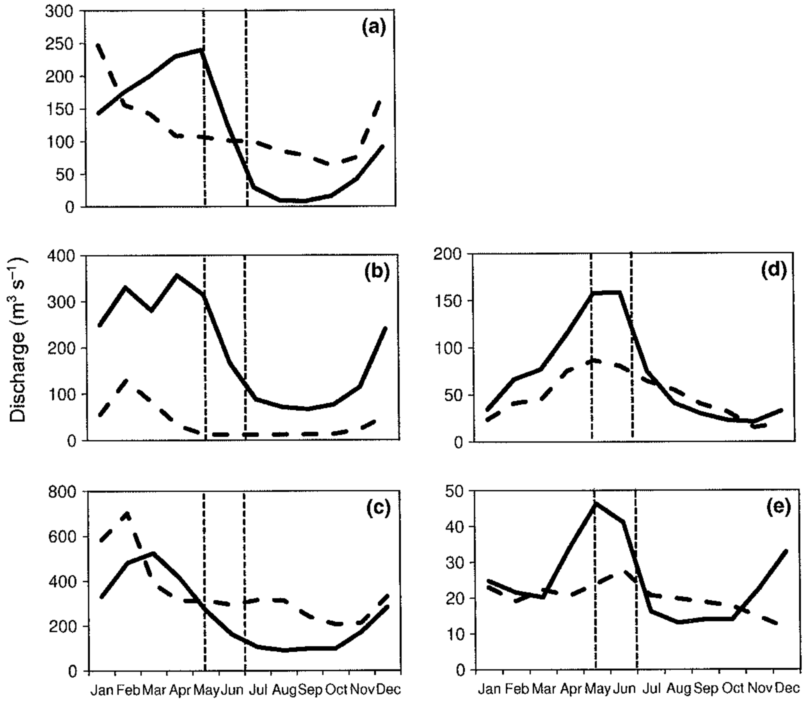

Figure 3. Pre- and post-dam hydrographs for five Central Valley rivers. Solid lines are mean monthly discharge values for 30 years prior to dam construction. Dashed lines are mean monthly discharge values for 30 years after dam construction. Vertical dashed lines indicate the peak period of spring run migration. Note that the discharge scales (y-axis) differ between the graphs, that the peak migration period corresponds to the peak or declining limb of floods in the pre-dam hydrograph and that these discharge pulses have been attenuated or shifted outside of the migration period in the post-dam hydrographs. Rivers: a, American River; b, Feather River; c, Sacramento River; d, San Joaquin River and e, Mokelumne River.

during a critical period when spring run Chinook salmon are trying to migrate upstream and that this change may be contributing to extirpation. Monthly stream flow data before and after dam construction were available for only five Central Valley streams (Fig. 3). Two streams were located in the San Joaquin basin (Mokelumne River and San Joaquin River) and three were located in the Sacramento basin (Sacramento River, Feather River and American River). Of the five streams, only the Feather and Sacramento continue to support spring run salmon, but the Feather River run is strongly supported by hatchery production (Lindley *et al.* 2004). All five streams support autumn run salmon, but the San Joaquin is currently used only as a migration route to spawning tributaries.

Plots of mean monthly flows suggested that dams imposed major changes in the hydrograph of all five streams. A similar pattern of alteration was observed in four of the five rivers where water is held back during winter and spring months resulting in an attenuated flood pulse, and released during summer and autumn producing higher flows than prior to dam construction (Fig. 3). In the Feather River, flows were reduced during all seasons (Fig. 3). Attenuation of annual flow pulses may have impacted the persistence of spring run populations because migration of spring run salmon coincides with periods of peak flows or during the declining limb of high-flow periods in the pre-dam hydrographs (Fig. 3). The Sacramento was the only river with greater flows during the spring migration period and spring run fish continue to persist in this river. Flows during the summer holding period were greater in the three streams where spring run salmon have been extirpated, as well as the Sacramento, and lower in the Feather where they persist. Effects of flow regulation during the autumn spawning period were mixed, but autumn run fish continue to spawn successfully during this period except in the San Joaquin.

Discussion

Data were compiled on historical and modern Chinook salmon distributions, habitat loss, barriers to migration and flow regime to test the weight of evidence for three hypotheses that are commonly posed to explain the loss of Chinook salmon in the Central Valley. The persistence of autumn run Chinook salmon was predicted by their location relative to migration barriers. The negative effect of barriers on upstream populations of migratory fishes is well known; thus, it is not surprising that dams have the potential to explain extirpation of these, or other migratory fishes (Gehrke *et al.* 2002; Morita & Yamamoto 2002). What was surprising is that there was no evidence that other hypothesis considered had the potential to explain Chinook salmon extirpation for the autumn run. The hypothesis that altered hydrological regimes led to extirpation had no ability to explain patterns in the data (> 1 000 000 times less likely than barriers), and this was true despite there being wide variation in hydrological conditions among streams and that pre- and post-dam comparisons revealed substantial changes in hydrology. The lack of any detectable effect of hydrology on autumn run salmon is, perhaps, surprising given that this factor is frequently cited as a major contributor to the loss of Chinook salmon in the Central Valley of California, and re-creation of historical hydrological conditions is a focus of many recovery efforts (United States Fish and Wildlife Service 2001).

Migration barriers and habitat loss were competing predictors of spring run salmon extirpation, and flow regime was a strong predictor among rivers that remain accessible. Thus, the best predictors of extirpation depended on the population of rivers used in the analysis. Spring run Chinook salmon historically used higher elevation habitats (> 150 m) where temperatures remain cool during the summer holding period (Yoshiyama *et al.* 2001; Lindley *et al.* 2004). Most of this habitat in the Central Valley has been lost through construction of impassable dams. Restriction of spring run salmon to lower elevation habitats used by autumn run salmon also may reduce genetic distinctiveness as has been inferred from studies of the Feather River Chinook populations (Lindley *et al.* 2004). The greater influence of habitat loss on spring run salmon extirpation probabilities may be accounted for by this difference in habitat use and needs to be considered when formulating recovery strategies.

Hydrological regime was also a strong predictor of spring run salmon extirpation below migration barriers, with extant runs found in smaller streams that retained a steep flood profile. Spring run salmon enter fresh water from spring through early summer during high flow periods and hold in the river over summer before spawning in autumn. By contrast, autumn run salmon spawn soon after entering fresh water in late summer and autumn. The longer period in fresh water may expose spring run salmon to risks that are not experienced by autumn run Chinook salmon (Williams 2006). However, the analyses suggested that greater flow during the summer months was associated with streams where spring run Chinook salmon had been extirpated. Additionally, three streams where spring run salmon were extirpated had greater summer flows in the post-dam period. The period of spring run migration appeared to be an important component of the hydrological regime. Streams where spring run salmon persist were associated with steeper flood profiles and the peak of spring run salmon migration occurs during peak flows or on the declining limb of pre-dam hydrographs. Post-dam hydrographs revealed a common pattern among the few regulated rivers in the Central Valley where sufficient historical data are available; that pattern suggested that high flows in spring are stored in reservoirs and released during summer for diversion downstream. High flows provide an important spawning cue for some species (Zeug & Winemiller 2007; Bailly *et al.* 2008) and the loss of this aspect of the flow regime may have contributed to the extirpation of spring run salmon. Only the Sacramento River had greater flows during the migration period post-regulation, and spring run salmon continue to persist in this system.

Limits to inference

The analyses presented have focused somewhat narrowly on the presence or absence of salmon in streams. Limitations in data quality and availability prevented the use of measures of abundance or population growth rate of Chinook salmon as dependent variables. This leaves open the possibility that some factors considered could still be leading to declines of Chinook salmon, even if the species is not yet locally extirpated. This is potentially important because although barriers cause rapid extirpation of upstream populations, downstream populations may experience long periods of decline prior to extirpation (Kareiva *et al.* 2000). Schick and Lindley (2007) found that barrier-related extirpation of certain spring run salmon populations in the Central Valley had a disproportionate effect on the remaining populations because of source-sink dynamics. Additionally, the large number of Chinook salmon produced by hatcheries in the Sacramento-San Joaquin system may prevent extirpation through the straying of returning adults. Genetic data from spawning populations in the Central Valley indicate little differentiation between hatchery and natural spawning Chinook salmon and low heterogeneity among individuals collected from different rivers suggesting extensive straying of hatchery fish (Williamson & May 2005). Barnett-Johnson *et al.*

(2007) found that large numbers of Sacramento and San Joaquin salmon taken in the ocean fishery were of hatchery rather than wild origin (84–96%). If similar percentages of returning adults are of hatchery origin, natural populations in the rivers that remain accessible may not be self-sustaining.

The information theoretic approach was limited in that it only evaluated the weight of evidence among the given hypotheses; thus, the possibility that other hypotheses not evaluated here could prove to be a better fit to the data cannot be eliminated. Hypotheses such as competition with and predation by non-native species, changing stream temperature regimes, availability of appropriate spawning and rearing substrate and a myriad of others have also been proposed to explain patterns of Chinook salmon loss. While data regarding these hypotheses were not available at the scale of the current analysis, one of the advantages of the information theoretic approach is that as data become available, it is straight-forwarded to pit explanatory variables against one another and decide which is the better potential explanation. As analyses are improved, it is worth noting that some hypotheses may only be the proximate causes of extirpation while several of the ultimate causes (barriers, habitat loss and altered flow regimes) were captured by the analysis. For example, barriers have constrained spring run to reaches that may not provide the appropriate temperatures during the summer holding period (Williams 2006). Additionally, dams prevent the movement of spawning gravel from upstream areas and attenuate flood pulses that are essential for the geomorphological development of rearing habitat for juveniles. Despite the limitations of the current approach, the evidence suggests that dams increase the probability for extirpation of Chinook salmon by blocking migration routes (autumn run), constraining the amount of habitat available (spring run) and altering the natural flow regimes (spring run).

Implications for management

Attempts to increase production of Chinook salmon populations in the Central Valley focus entirely on rivers downstream of large dams (United States Fish and Wildlife Service 2001) and there are currently no plans to address passage upstream of these projects (CDWR 2005), although this strategy has been proposed for some rivers (USFWS 1995). Most river restoration projects in the Central Valley are small relative to the scale at which river habitats have been altered, and increases in salmon populations resulting from these efforts may be difficult to detect (Kondolf *et al.* 2008). Large-scale projects such as dam removal may be more effective to recover Chinook salmon populations, but effectiveness is often not the primary criteria used to select what restoration projects will be implemented (Kondolf *et al.* 2008).

Although there is controversy regarding the effectiveness of fish passage above dams and even dam removal as a viable strategy to prevent the extirpation of Chinook salmon (Kareiva *et al.* 2000; Welch *et al.* 2008), dams have strong direct and indirect effects on the growth rate of Chinook salmon populations downstream and increase the probability of future extirpations (McClure *et al.* 2003; Hoekstra *et al.* 2007).These analyses suggest that management of flow regimes downstream of barrier dams could be an important component of conservation efforts to prevent the loss of spring run or to increase the success of recolonisation. Regardless, the evidence that barriers have been one of, if not the, primary driver of Chinook salmon extirpations in the Central Valley seems indisputable.

Chinook populations are at risk of extirpation throughout their range, and populations in interior basins such as the Central Valley are at greater risk than most coastal populations (Gustafson *et al.* 2007). Additionally, the Central Valley represents the southern-most spawning populations of Chinook salmon, and several populations are at high risk of extinction with high biological consequences to the species if they are lost (Allendorf *et al.* 1997). Despite the critical status of Central Valley Chinook, this study is among the first quantitative assessments of the hypothesised drivers of extirpation at a regional scale. A lack of quantitative evaluation is a common problem in salmon management where expert opinion and inferred or extrapolated data are substituted for quantitative measurement and analysis (Ruckelshaus *et al.* 2002). The number of potential hypotheses to explain extirpation of Chinook salmon is large, but data are lacking for most. One advantage of information theoretic methods is that as more data become available, other hypotheses can be quantitatively evaluated against those presented here (Burnham & Anderson 2002). Although some results may appear intuitive, they quantify the importance of addressing large barrier dams that have isolated a large proportion of salmon habitat in the Central Valley; an issue that has yet to be addressed in recovery strategies.

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Application of a Life Cycle Simulation Model to Evaluate Impacts of Water Management and Conservation Actions on an Endangered Population of Chinook Salmon

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Abstract Fisheries and water resource managers are challenged to maintain stable or increasing populations of Chinook salmon in the face of increasing demand on the water resources and habitats that salmon depend on to complete their life cycle. Alternative management plans are often selected using professional opinion or piecemeal observations in place of integrated quantitative information that could reduce uncertainty in the effects of management plans on population dynamics. We developed a stochastic life cycle simulation model for an endangered population of winter-run Chinook salmon in the Sacramento River, California, USA with the goal of providing managers a tool for more effective decision making and demonstrating the utility of life cycle models for resource management. Sensitivity analysis revealed that the input parameters that influenced variation in salmon escapement were dependent on which age class was examined and their interactions with other inputs (egg mortality, Delta survival, ocean survival). Certain parameters (river migration survival, harvest) that were hypothesized to be important drivers of population dynamics were not identified in sensitivity analysis; however, there was a large amount of uncertainty in the value of these inputs and their error distributions. Thus, the model also was useful in identifying future research directions. Simulation of variation in environmental inputs indicated that escapement was significantly influenced by a 10% change in temperature whereas larger changes in other inputs would be required to influence escapement. The model presented provides an effective demonstration of the utility of life cycle simulation models for decision making and provides fisheries and water managers in the Sacramento system with a quantitative tool to compare the impact of different resource use scenarios.

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Keywords California · Delta · Life cycle model · Sacramento River · Simulation · Winter run Chinook salmon

1 Introduction

Understanding what drives interannual variability in Chinook salmon (*Oncorhynchus tshawytscha*) populations is of considerable interest to resource managers because of the large number of salmon stocks that are currently listed as threatened or endangered [1, 14]. Declines in the number of salmon returning to spawn have triggered recovery plans intended to stabilize or increase population sizes. The success of these plans has varied considerably and many populations remain at risk [15]. The factors responsible for declines in Chinook salmon populations are generally known yet, the relative importance of each factor and the scale at which it operates is often unknown, which complicates attempts to effectively apply management actions to recover Chinook salmon stocks [7, 31, 37].

Both scientists and managers have increasingly recognized the utility of life cycle models for evaluating salmon population responses to management actions [28], and a recent review of salmon recovery efforts in California's Central Valley recommended their use [12]. Although there have been many studies and monitoring efforts focused on the ecology of salmon at the individual and population level, many of these data relate only to a single life stage, habitat type, or environmental variable. This has made it difficult to integrate these data into a traditional statistical framework to estimate interannual population dynamics or to identify specific bottlenecks to population recovery. Life cycle models utilize available time-series data as well as values taken from laboratory studies or other sources to parameterize model relationships, thereby utilizing the greatest amount of data available to dynamically simulate responses of populations across multiple life stages to changes in environmental variables or combinations of environmental variables at specified times and locations. Thus, these models are powerful tools that can be used by managers to plan and evaluate recovery actions for Chinook salmon. Here, we present a life cycle simulation model for an endangered winter-run Chinook salmon population in the Sacramento River, California, USA (Fig. 1).

Sacramento River Chinook salmon stocks have experienced severe declines over the last century resulting in extirpation of some populations [14] and a moratorium on commercial and sport harvest in recent years to protect extant populations. Winter run in the Sacramento River was listed as endangered under the Federal Endangered Species Act in 1994 [9]. Historically, winter run utilized high elevation stream habitats in the Upper Sacramento River and tributaries for holding, spawning, and rearing [36]. However, extensive dam construction in the early twentieth century restricted winter run to a single reach of the lower Sacramento River below Keswick Dam [35]. After leaving the spawning and rearing habitat, juvenile winter run migrate down the Sacramento River, through the Sacramento–San Joaquin Delta (hereafter referred to as the Delta) and spend from 2 to 4 years in the ocean before returning to their natal spawning grounds.

As pressure on Sacramento River water resources continues to increase from domestic and agricultural users, resource managers are in need of quantitative tools to compare the relative impact of future water use activities on the winter-run population and to select relevant life stages and environmental variables to focus on for recovery actions. Our goals for this study were to describe a stochastic life cycle simulation model for winter run in the Sacramento River: the Interactive Object-Oriented Simulation Model (IOS). Specifically, we: (1) present the structural and functional relationships of the IOS model, (2) conduct a sensitivity analysis that describes uncertainty in estimates of model parameters, and uncertainty due to inherent stochasticity of the population, and (3) examine the response of the model to variability in the four environmental drivers for which sufficient data were available including: temperature that affects egg and fry survival during early development, flow that affects survival and migration travel time during freshwater migration, water exports that affect survival in certain migration pathways, and ocean productivity that affects survival in the ocean.

2 Methods

2.1 Model Description and Structure

The IOS model uses a systems dynamics modeling framework, a technique that is used for framing and understanding the behavior of complex systems over time [6, 10]. System dynamics models are made up of stocks (e.g., number of fish) and flows (e.g., sources of mortality) which are informed by mathematical equations [10]. IOS was implemented in the software GoldSim, which enables the simulation of complex processes through creation of simple object relationships, while incorporating Monte Carlo stochastic methods [27]. Terms used in the model description are defined in Table 1.

The IOS model is composed of six model stages that are arranged sequentially to account for the entire life cycle of winter run, from eggs to returning spawners (Fig. 2). In sequential order, the IOS model stages are: (1) *spawning*, that models the number and temporal distribution of eggs deposited in the gravel at the spawning grounds; (2) *early development*, that models the impact of temperature on maturation timing and mortality of eggs at the spawning grounds; (3) *fry rearing*, that models the relationship between temperature and mortality of salmon fry during the river rearing period; (4) *river migration*, that estimates mortality of migrating salmon smolts in the Sacramento River between the spawning and rearing grounds and the Delta; (5) *delta passage*, that models the impact of flow, route selection, and water exports on the survival of salmon smolts migrating through the Delta to San Francisco Bay; and (6) *ocean survival*, that estimates the impact of natural mortality and ocean harvest to predict survival and spawning returns (escapement) by age. Below is a detailed description of each model stage.

Spawning For the first four simulation years, the model is seeded with a fixed number of female spawners. In subsequent years, the number of spawners is determined by the model's probabilistic simulation of survival to this life stage. To ensure that developing fish experience the correct environmental conditions during each year, spawn timing mimics the observed arrival of salmon on the spawning grounds as determined by 8 years of carcass surveys (2002–2009) conducted by the United States Fish and Wildlife Service (USFWS). Winter run die after spawning which allows the size of the spawning population to be estimated from the number of carcasses observed. In each year, one of the eight spawning distributions is chosen at random. Eggs deposited on a particular date are treated as cohorts which experience temperature and flow on a daily time step during this stage. The daily number of spawners is calculated by multiplying the daily proportion of the total carcasses observed during the USFWS surveys by the total Jolly–Seber estimate of spawners [24].

$$S_d = C_d S_{JS} \tag{1}$$

where, S_d is the daily number of spawners, C_d is the daily proportion of total carcasses, and S_{JS} is the total Jolly–Seber

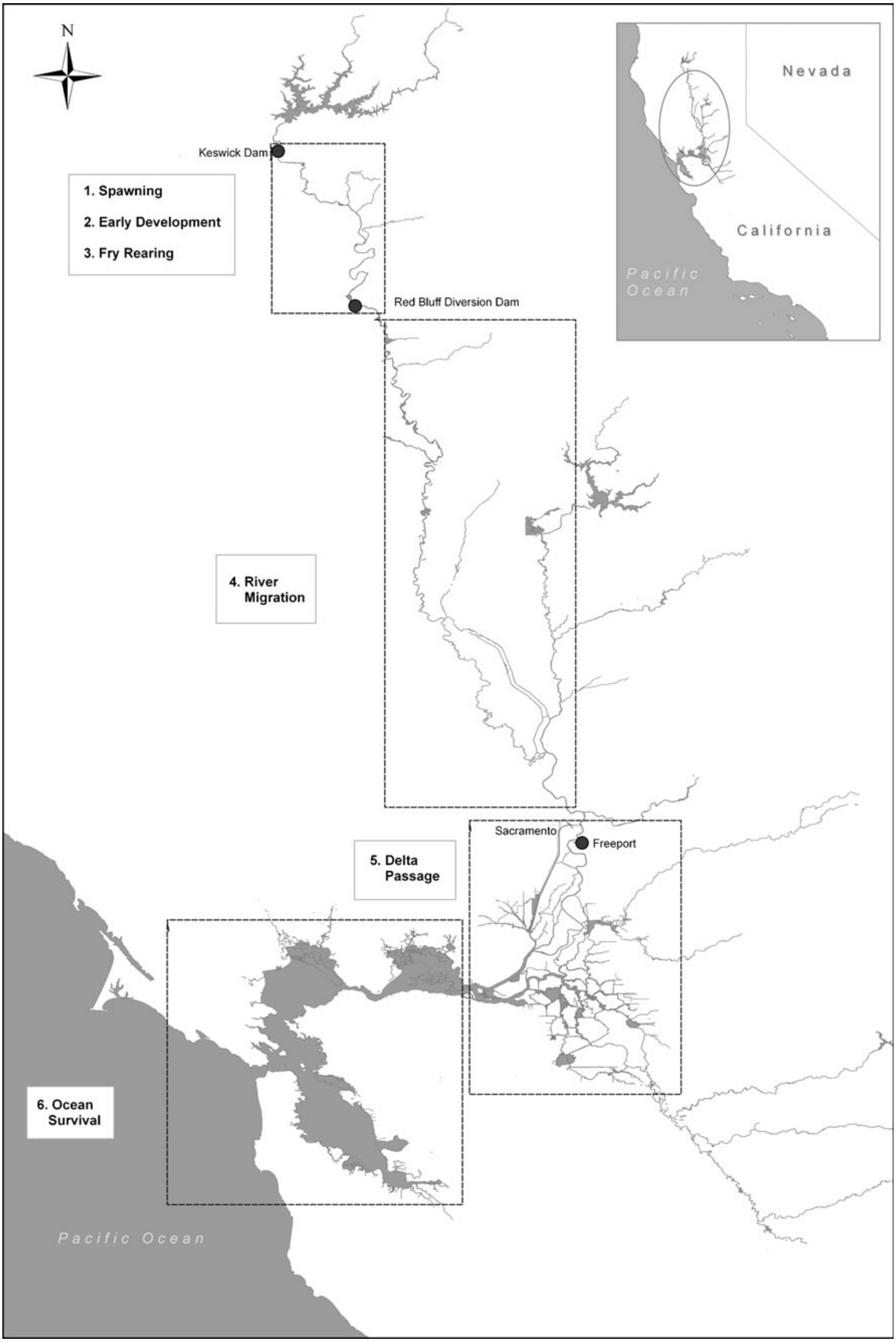

Fig. 1 Map of the Sacramento River and the Sacramento–San Joaquin Delta, including approximate areas defined by each model-stage

Table 1 Glossary of terms used to describe model functions, data sources, and relevant locations in the study area

Term	Definition
CDFG	California Department of Fish and Game
Delta	A freshwater tidal estuary formed by the Sacramento and San Joaquin Rivers that salmon juveniles must pass through on their way to the Pacific Ocean
Escapement	The total number of Chinook salmon that leave the ocean and return to the Sacramento River to spawn. This number includes 2-, 3-, and 4-year-old fish
Fry	Salmon life stage that occurs from the period of emergence from spawning gravels until the start of physiological changes in preparation for migration
Jolly_Seber estimate	A statistical method of estimating the size of a population using mark and recapture data
Screwtrap	A passive sampling devise that traps juvenile salmon as they migrate downstream
Smolt	Salmon life stage characterized by physiological changes in preparation for migration and ocean entry
Spawner	Salmon that leaves the ocean and returns to the Sacramento River to spawn. This can occur at age 2, 3 or 4. All fish die after spawning
USFWS	United States Fish and Wildlife Service
Winter-run Chinook salmon	A genetically distinct population of Chinook salmon that completes the freshwater portion of their life cycle in the Sacramento River. This population has been listed as endangered under the federal Endangered Species Act
Junction Geo/DCC	The combined junction of the Sacramento River, Georgiana Slough and the Delta Cross Channel. Both Georgiana Slough and the Delta Cross channel lead into the Interior Delta reach
Junction SS	The junction between two potential migration routes, the Sacramento River and Sutter/Steamboat Slough
Interior Delta	A reach that fish entering through Junction Geo/DCC must pass through on their way to the ocean. This reach is a network of tidal channels and a relationship between water exports and survival is present in this reach
Reach Geo/DCC	The combined reach of Georgiana Slough and the Delta Cross Channel
Reach Sac 1	The Sacramento River between the start of the Delta at Freeport and the junction with Steamboat/Sutter Slough
Reach Sac2	The Sacramento River between the reach Sac1 and the Junction of Georgiana Slough and the Delta Cross Channel
Reach Sac3	The Sacramento River between Sac2 and the confluence of Steamboat/Sutter Slough and the Sacramento River. A flow–survival relationship is present in this reach
Reach Sac4	The Sacramento River between the confluence of the Sacramento River and Sutter/Steamboat Slough and the end of the Delta Passage model stage
Reach SS	The combined reach of Sutter and Steamboat Slough. A flow–survival relationship is present in this reach.

estimate of spawners. In order to better match the timing of carcass observations to the deposition of eggs, the date of egg deposition is shifted 14 days before the carcasses were observed (Kevin Niemela, personal communication).

To obtain an estimate of juvenile production, a Ricker stock-recruitment curve [26] was fit between the number of fry produced each year (R) and the number of spawners (S) as estimated by the California Department of Fish and Game screw trap sampling (juveniles) and USFWS carcass surveys (spawners) for years (1996–1999, 2002–2007):

$$R = \alpha S e^{-\beta S} + \varepsilon \qquad (2)$$

where, R is the estimate of juvenile recruitment, α is a parameter that describes recruitment rate, and β is a parameter that measures the level of density dependence. The density-dependent parameter (β) did not differ significantly from zero (95% CI=-6.3×10^{-6}–5.5×10^{-6}). Therefore, β was removed from the equation and a linear version of the relationship was estimated. The number of spawners explained 86% of the variation in fry production ($F_{1,9}$= 268, $p<0.001$) in the data, so the value of α was taken from the regression:

$$R = 1043 \bullet S \qquad (3)$$

This linear relationship is used to predict values for mean fry production along with the confidence intervals for the predicted values. These values are then used to define a normal probability distribution, which is randomly sampled each year to determine the annual fry production. Although the Ricker model accounts for mortality during egg incubation, the data used to fit the Ricker model were from a limited time period (1996–1999, 2002–2007) when water

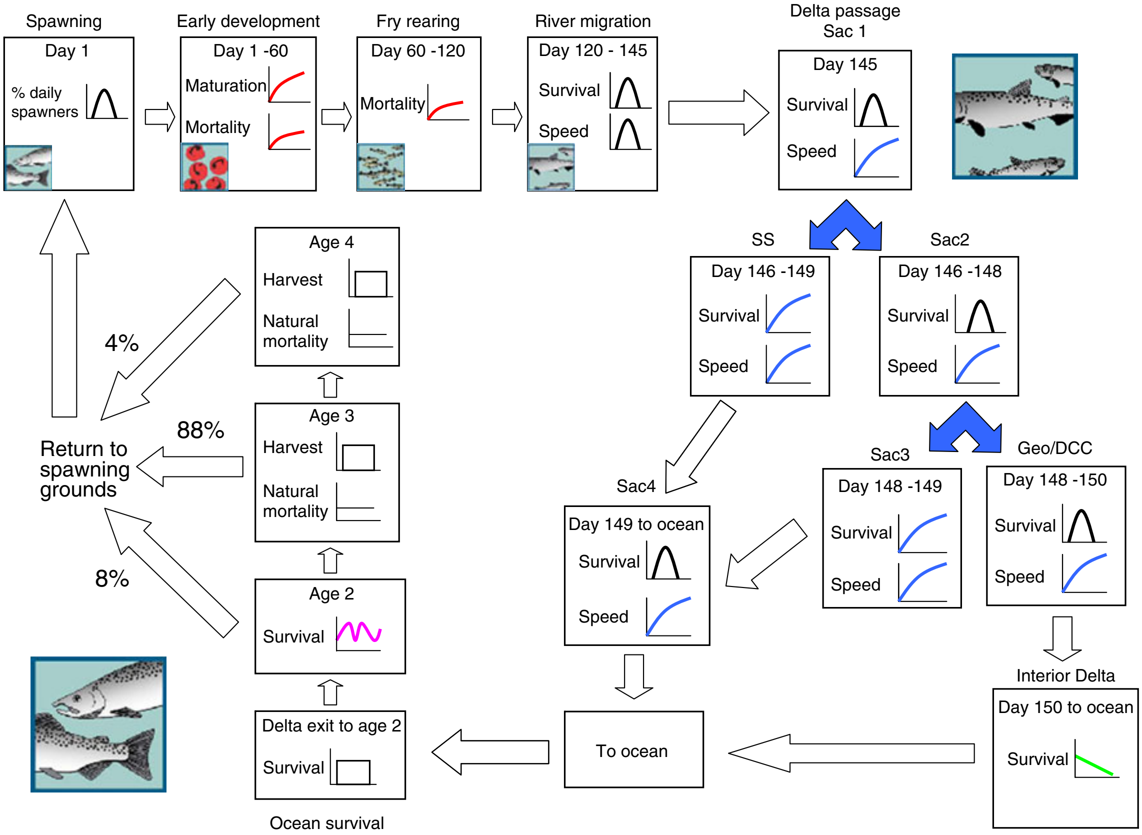

Fig. 2 Conceptual diagram of IOS model stages and environmental influences on functional relationships at each stage. *Colors* indicate the environmental driver influencing each relationship where *red* temperature, *blue* flow, *green* water exports, and *pink* ocean productivity. Relationships in *black* indicate that values are drawn from a normal distribution, a uniform distribution, or are constants

temperatures during egg incubation were too cool (<14°C) to cause significant temperature-related egg mortality [32]. Thus, additional mortality was imposed in the model when temperatures exceeded those experienced during the years used to construct the Ricker model.

Early Development Data from three laboratory studies was used to estimate the relationship between temperature, egg mortality, and development time [4, 19, 32]. Using data from these experiments, a relationship was constructed between maturation time and water temperature. First, we converted *maturation time* (days) to a daily *maturation rate* (1/day):

$$\text{daily maturation rate} = \text{maturation time}^{-1} \tag{4}$$

A significant linear relationship between maturation rate and water temperature was detected using linear regression ($F_{1,15}$=2,188, p<0.001):

$$\text{daily maturation rate} = 0.00058 \bullet \text{Temp} - 0.018 \tag{5}$$

Each day, the mean maturation rate of the incubating eggs is predicted from the daily temperature using the above linear function; the predicted mean maturation rate along with the confidence intervals of the predicted values are used to define a normal probability distribution, which is then randomly sampled to determine the daily maturation rate. A cohort of eggs accumulates a percentage of total maturation each day from the above equation until 100% maturation is reached.

Data from the USFWS [32] was used to inform the relationship between temperature and mortality of developing winter-run eggs. This study utilized a small number of treatments (three temperature treatments) and although studies from other regions could have been used, we chose to use data specific to winter run. Salmon populations are adapted to local temperature regimes and use of data from outside of the Sacramento River may not conform with the requirements of winter run. The functional form of the temperature–mortality relationship was similar to data from other regions suggesting that USFWS data on winter run was sufficient to parameterize the model-predicted mortality over the entire incubation period was converted to a daily mortality rate to apply temperature effects in the model. This conversion was used to calculate daily mortality using the methods described in [3]:

$$\text{mortality} = 1 - (1 - \text{total mortality})^{(1/\text{development time})} \tag{6}$$

where, *total mortality* is the predicted mortality over the entire incubation period observed for a particular water temperature and *development time* was the time to develop from fertilization to emergence.

The following exponential relationship was fitted between observed *daily mortality* and observed water temperatures [32]:

$$\text{daily mortality} = 1.38\bullet 10^{-15} e^{(0.503\bullet \text{Temp})} \quad (7)$$

Each day, the mean mortality rate of the incubating eggs is predicted from the daily temperature measured at Bend Bridge on the Sacramento River using the above exponential function. The predicted mean mortality rate along with the confidence intervals of the predicted values is used to define a normal probability distribution, which is then randomly sampled to determine the daily egg mortality rate.

Fry Rearing Data from USFWS [32] was used to model fry mortality during rearing as a function of water temperature. The following exponential relationship was fitted between observed *daily mortality* and observed water temperatures [32]:

$$\text{daily mortality} = 3.92\bullet 10^{-12} e^{(0.349\bullet \text{Temp})} \quad (8)$$

Each day, the mean proportional mortality of the rearing fish is predicted from the daily temperature using the above exponential relationship; the predicted mean mortality along with the confidence intervals of the predicted values are used to define a normal probability distribution, which is then randomly sampled to determine daily mortality. Temperature mortality is applied to rearing fry for 60 days that is the approximate time required for fry to transition into smolts [32] and enter the next stage.

River Migration In this model stage, survival of smolts from the spawning and rearing grounds to the Delta (City of Freeport on the Sacramento River) is a normally distributed random variable with a mean of 23.5% and a standard error of 1.7%. Mortality in this stage is applied only once and occurs on the same day that a cohort of smolts enters the model stage rather than being applied daily as in the *Early Development* stage because there was no data to support a relationship with flow or temperature. Smolts are delayed from entering the next model stage to account for travel time. Mean travel time (20 days) is used along with the standard error (3.6 days) to define a normal probability distribution, which is randomly sampled to determine the total travel time of migrating smolts. Survival and travel time means and standard deviations were acquired from an acoustic study of late-fall run Chinook smolt migration in the Sacramento River [18].

Delta Passage Smolt migration is evaluated based on four major functional relationships: (1) route selection by smolts at river junctions, that is a function of the proportion of flow entering each route; (2) reach specific and flow-survival relationships, where survival in two reaches is a function of flow and a normally distributed variable in all other reaches; (3) flow–migration speed, which is a function of reach specific flow; and (4) export mortality, which is caused by entrainment into State and Federal water pumping facilities. Daily cohorts of smolts enter the first reach of the Delta on a day of the year determined by timing in the previous model stages. In reaches with a flow–survival relationship, mean flow on the day smolts enter the reach is used to calculate a survival value and a migration speed for that reach. The survival value is applied once to all smolts that entered the reach on that date. Then, smolts are delayed from entering the next reach by a number of days determined by the calculated migration rate and the length of the reach. In reaches without a flow–survival relationship, survival values are drawn from a normal probability distribution and migration speed is calculated as a function of flow on the day of entry into the reach. When smolts reach a junction, a daily cohort will split according to the relationships described below, based on the flow on the day smolts reach the junction.

Fish route selection at junctions is based on acoustic tagging studies in the Delta by Perry et al. [23]. At the junction of the Sacramento River and Steamboat/Sutter Slough (Junction SS, Table 1), smolts consistently entered downstream reaches in proportion to the flow being diverted. For the Sacramento River–Geo/DCC junction (Junction Geo/DCC, Table 1), there was a linear, nonproportional relationship between flow and fish movement:

$$y = 0.22 + 0.47x \quad (9)$$

where, y is the proportion of fish diverted into Geo/DCC and x is the proportion of flow diverted into Geo/DCC.

Reach-specific survival and associated error estimates also were obtained from Delta acoustic tagging studies [23] where mean reach survival is used with reach-specific standard deviation to define a normal probability distribution sampled daily to determine the survival rate. There was a significant relationship between survival and flow for two Delta reaches (SS and Sac3; [23]) and we used a logit survival function to predict mean reach survival (S) from reach flow (*flow*):

$$S = \frac{e^{(\beta_0+\beta_1 \text{flow})}}{1 + e^{(\beta_0+\beta_1 \text{flow})}} \quad (10)$$

where, β_0 (SS=−0.175, Sac3=−0.121) is the reach coefficient and β_1 (0.52) is the flow coefficient. All the benefits of increased flow are accounted for the in relationships we have applied for reaches SS and Sac3.

Daily downstream smolt movement occurs as function of reach-specific length and migration speed as developed from acoustic tagging results. We used flow and migration speeds reported by Vogel [33] to create a best-fit logarithmic relationship:

$$y = 16.59\ln(x) - 76.79 \qquad (11)$$

where, y is migration speed (kilometer per day^1) and x is flow (cubic meter per second). Due to assumed strong tidal influences in reach Sac4, migration speed in this reach is independent of flow; set at 22.6 km·day^{-1}, the average speed of acoustic tagged smolts [33]. Migration speed variance from acoustic study data is used along with mean migration speed to define a normal probability distribution that is sampled from each day to determine the daily migration speed in each reach.

Fish that enter the DCC/Georgiana Slough junction enter the interior delta that is a complex network of tidal freshwater channels where smolts are exposed to natural mortality as well as entrainment in large water diversions. To apply water export-related effects, we used the export–mortality relationship described by Newman and Brandes [22]:

$$S = -0.000024 \bullet \text{exports} + 0.625 \qquad (12)$$

where, S is mean survival and the slope (−0.000024) is from the relationship between survival and Delta exports in cubic meter per second. The intercept was adjusted from 0.58 to 0.625 so the regression line passes the point (184, 0.47), where 184 is the mean export level (cubic meter per second) and 0.47 is the mean survival rate observed during the acoustic studies we used to estimate survival in the Interior Delta. In effect, we used the slope of the relationship between survival and exports estimated by Newman and Brandes [22] as a scalar on the survival rates observed from acoustic tagging studies. Mean survival is then used along with the standard deviation to inform a normal probability distribution that is sampled from each day to determine Interior Delta survival.

As each cohort of smolts exits the final reaches of the Delta, they accumulate until all cohorts from that year have exited the Delta. After all smolts have arrived, they enter the *Ocean Survival* stage as a single cohort and the model begins applying mortality on an annual time step.

Ocean Survival This model stage utilizes equations for smolt-to-age-2 mortality, winter mortality, ocean harvest, and spawning returns to predict yearly survival and escapement numbers (i.e., individuals exiting the ocean to spawn). Ocean Survival model stage elements are listed in Table 2 and discussed below.

Relying on ocean harvest, mortality, and returning spawner data from Grover et al. [13], we applied a uniformly distributed random variable between 96% and 98% mortality for winter run from ocean entry to age 2 and we developed functional relationships to predict ocean survival and returning spawners for age 2 (8% return), age 3 (88% return), and age 4 (4% return), assuming that 100% of individuals which survive to age 4 return for spawning. Ocean survival to age 2 is given by:

$$A_2 = A_i(1 - M_2)(1 - M_w)(1 - H_2)(1 - S_{r2}) \bullet W \qquad (13)$$

survival to age 3 is given by:

$$A_3 = A_2(1 - M_w)(1 - H_3)(1 - S_{r3}) \qquad (14)$$

and survival to age 4 is given by:

$$A_4 = A_3(1 - M_w)(1 - H_4) \qquad (15)$$

where, A_i is abundance at ocean entry (from the Delta Passage model stage), $A_{2,3,4}$ are abundances at ages 2–4, $H_{2,3,4}$ are harvest percentages at ages 3–4 represented by uniform distributions bounded by historical harvest levels, M_2 is smolt-to-age-2 mortality, M_w is winter mortality for ages 2–4, and $S_{\text{r2,r3}}$ are returning spawner percentages at ages 2 and 3. Age 2 survival is multiplied by a scalar W that corresponds to the value of Wells' Index of ocean productivity. This metric was shown to significantly influence growth and maturation of age 2 fish [34]. The value of Wells' Index is a normally distributed random variable that is resampled each year. In our analysis, we used the following values from Grover et al. [13]: H_2=0%, H_3=0–39%, H_4=0–74%, M_2=94–98%, M_w=20%, S_{r2}=8%, and S_{r3}=96%.

The number of adult fish in the ocean that will return to the spawning grounds is determined on day 334 of each year according to the percentages described above. Returning fish are assumed to be 65% female and are assigned a prespawn mortality of 5% to determine the final number of female returning spawners [30].

2.2 Environmental Input Data

Daily flows and temperatures experienced by salmon (Table 3) are determined by selection of a water year type in the Sacramento River as classified by the California Department of Water Resources (critical, dry, below normal, above normal, and wet). The probability of each type of water year being selected is represented by a discrete distribution based on the previous 100 years of data. With the exception of flow into the State Water Project (SWP) and Central Valley Project (CVP) pumping plants, flow is modeled using daily (tidally averaged) flow output from the hydrology module of the Delta Simulation Model II (DSM2-HYDRO; http://baydeltaoffice.water.ca.gov/modeling/deltamodeling/). Export flow into the CVP and SWP pumping plants is modeled using monthly flow output from the hydrologic simulation tool CALSIM II

Table 2 Functional relationships in the IOS model during each model stage and environmental variables associated with each relationship

Model Stage	Parameter	Environmental variable	Function
Spawning	Daily proportion of total spawners	None	Equation 1
Early development	Daily egg mortality	Temperature	Equation 7
	Egg-to-fry development time	Temperature	Equation 5
Fry rearing	Daily fry-to-smolt survival	Temperature	Equation 8
River migration	Downstream survival	None	Normally distributed random variable
Delta passage	Reach-Sac1 survival	None	Normally distributed random variable
	Reach-Sutter/Steamboat	Flow	Equation 10
	Reach-Sac2	None	Normally distributed random variable
	Reach-Sac3	Flow	Equation 10
	Reach-Sac4	None	Normally distributed random variable
	Reach-Geo-DCC	None	Normally distributed random variable
	Interior Delta	Water exports	Equation 12
	Junction-Sac2-Sutter/ Steamboat	Flow	Proportional to flow in each reach
	Junction-Sac3-Delta Cross Channel	Flow	Equation 9
	Migration duration	Flow	Equation 11
	Migration duration (Sac4)	None	Constant
Ocean survival	Smolt-age 2 survival	None	Uniform random variable
	Age 2 ocean survival	Well's Index of ocean productivity	Equation 13
	Age 3 ocean survival	None	Equation 14
	Age 4 ocean survival	None	Equation 15
	Age 3 harvest	None	Uniform random variable
	Age 4 harvest	None	Uniform random variable

that are "disaggregated" into mean daily flows based on historical patterns. Mean flow and temperature was averaged each day over the entire period of record for each of the five water year types to create a single flow and temperature regime for each water year type. Daily temperature in the Sacramento River at Bend Bridge from 1989 to 2010 was obtained from the California Data Exchange Center (http://cdec.water.ca.gov/).

2.3 Sensitivity Analysis

Sobol' indices were used to evaluate the sensitivity of model output to input parameters. Sobol' indices are a variance-based global sensitivity method that produces main indices (effects independent of other input parameters) and total indices (effects accounting for first-order interactions with

Table 3 Environmental variables used to inform functional relationships in the IOS model

Location	Variable	Model stage	Source
Sacramento River at Bend Bridge	Temperature	Early Development	CDEC
Sacramento River at Hood	Flow	Delta migration	DSM2
Sutter-Steamboat Slough	Flow	Delta migration	DSM2
Delta Cross Channel	Flow	Delta migration	DSM2
Georgiana Slough	Flow	Delta migration	DSM2
Sacramento River at Rio Vista	Flow	Delta migration	DSM2
Interior Delta	Exports	Delta migration	CALSIM2
Ocean	Ocean productivity	Ocean survival	Wells et al. 2007

other input parameters). This method does not require a linear relationship between model output and input parameters and thus is superior to other global methods, such as multiple regression, when relationships are nonlinear or nonmonotonic [5, 8, 29].

For the sensitivity analysis, 1,000 bootstrap resamples were used to calculate 95% confidence intervals for Sobol' main and total effects. The number of female spawners returning (escapement) was used as the response variable and model inputs included as independent variables for each age class are listed in Table 4. Each group of returning spawners is composed of three age classes (age 2, 3, and 4) that experiences a different set of environmental conditions during their life. Thus, sensitivity analyses were conducted separately for each year class. Certain parameters were not included in all sensitivity analyses because they did not apply to all year classes. For example, age 2 fish are not exposed to harvest.

Latin Hypercube sampling was used to generate 1,000 Monte Carlo iterations of the IOS model for use in calculation of the Sobol' indices. For each iteration, the first 4 years of the model was seeded with 5,000 returning spawners and allowed to run for 5 years. The fifth year of output data was used for the sensitivity analysis because this is the first year that the number of returning spawners is a function of model parameters. Fish returning to the spawning grounds are mix of 2-, 3-, and 4-year-old fish that account for 8%, 88%, and 4% of the total, respectively. Input parameters were considered sensitive if their confidence interval did not include zero and were then ranked based on their absolute values. Sobol' indices were calculated using the package "sensitivity" within the R statistical program [25].

To explore how uncertainty in parameter estimates influenced model output, we conducted five additional sets of 1,000 Monte Carlo simulations where the variation around the mean of selected parameters was increased by 10%, 20%, 30%, 40%, and 50%. The parameters we chose to examine were those that could potentially be addressed by management actions including: egg mortality, fry-to-smolt survival, river migration survival, Delta survival, age 3 harvest, and age 4 harvest. Coefficients of variation were calculated for each set of simulations to examine how the sensitivity of model output changed with increased uncertainty in input parameters estimates.

2.4 Influence of Environmental Parameters

To understand the influence of environmental parameters on model output, we examined the response of escapement to variation in the four environmental parameters: flow, exports, temperature, and ocean productivity. For each parameter, we performed three sets of 100 Monte Carlo simulations. All simulations ran for four winter-run generations (16 years) and included a baseline condition, a 10% increase in the parameter and a 10% decrease in the parameter. A one-way analysis of variance and a Tukey's multiple comparisons test was then used to determine which treatments resulted in escapement estimates that were significantly different from baseline conditions. All statistical tests were performed with the R statistical program [25].

3 Results and Discussion

3.1 Sensitivity Analysis

Sobol' sensitivity indices suggested that escapement was sensitive to different input parameters depending on the age class examined (Table 4). For age 2 fish, main indices indicated

Table 4 Sobol' sensitivity indices (standard deviation in parentheses) for each age class of returning spawners based on 1,000 Monte Carlo iterations

Input parameter	Age 2		Age 3		Age 4	
	Main	Total	Main	Total	Main	Total
Water year	0.300[a] (0.083)	0.306[a] (0.079)	0.181[a] (0.091)	0.150 (0.091)	0.073 (0.067)	0.012 (0.065)
Egg mortality	0.030 (0.016)	−0.006 (0.016)	0.222[a] (0.081)	−0.021 (0.081)	0.102[a] (0.044)	−0.072 (0.044)
Fry-to-smolt survival	0.039 (0.020)	−0.009 (0.020)	0.166 (0.090)	0.091 (0.092)	0.079[a] (0.017)	−0.071 (0.017)
River migration survival	0.007 (0.034)	0.135[a] (0.034)	0.164 (0.084)	0.062 (0.085)	0.079 (0.018)	−0.07 (0.018)
Delta survival	0.010[a] (0.002)	−0.009 (0.002)	0.404[a] (0.180)	0.643[a] (0.177)	0.313[a] (0.134)	−0.009 (0.132)
Smolt to age 2 survival	0.734[a] (0.118)	0.454[a] (0.113)	0.015 (0.016)	−0.006 (0.016)	0.057[a] (0.017)	−0.052 (0.017)
Ocean productivity	0.003 (0.009)	0.009 (0.009)	0.034[a] (0.015)	−0.034 (0.015)	0.061[a] (0.030)	−0.048 (0.029)
Age 3 harvest	N/A	N/A	0.029[a] (0.001)	−0.028 (0.001)	1.48[a] (0.306)	0.188 (0.293)
Age 4 harvest	N/A	N/A	N/A	N/A	0.055[a] (0.003)	−0.054 (0.003)

[a] Index value was statistically significant at α=0.05

escapement was sensitive to smolt-to-age-2 survival, water year type, and Delta survival (Table 4). Main and total indices were similar for water year whereas the main index value for smolt-to-age-2 survival was considerably larger than the total value (Table 4). Additionally, age 2 escapement was sensitive to river migration survival when interactions were accounted for in the total index. This suggests that there were strong interactions between certain input parameters for fish returning to the spawning grounds at age 2 and confirmed that Sobol' sensitivity measures were the best choice for this sensitivity analysis, as interactions are difficult to deal with using other global analysis techniques [5]. The main index for Delta survival was significant yet the total index value was negative. Negative numbers are possible for Sobol' indices [2] and we considered negative values to indicate zero sensitivity [8]. Main indices for age 3 escapement suggested that model output for this age class was sensitive to many of the input parameters examined (Table 4). However, total index values indicated there were strong interactions between inputs, and age 3 escapement was only sensitive to Delta survival after accounting for these interactions. Similarly, main indices for age 4 escapement indicated that output was sensitive to many parameters (Table 4) whereas after accounting for interactions in the total index, none of the input parameters significantly influenced model output.

Although there were differences among age classes in the sensitivity of input parameters, each age is not represented equally among returning spawners. Thus, sensitivity should be viewed in terms of the contribution of each age class and the relationship among age classes. Age 3 fish comprised the largest proportion of returning spawners (88%) thus, inputs driving variability in this age class should have the largest effect on total escapement. Delta survival, water year, and egg mortality were significant drivers of variability in age 3 escapement, however, water year and egg mortality were not significant after accounting for interactions. The Delta passage portion of the model has flow–survival relationships in two reaches, thus, it is not surprising that there are interactions between water year type and Delta survival. Similarly, temperatures were higher in critical and dry water years and there was an exponential relationship between temperature and egg mortality.

Age 2 and age 4 fish accounted for 8% and 4% of total escapement, respectively. Age 4 escapement was most sensitive to harvest of age 3 fish. This is an intuitive result as harvest at age 3 has a direct influence on the number of fish that survive to age 4. Age 2 escapement was most sensitive to smolt-to-age-2 mortality and this relationship remained strong after accounting for interactions with other inputs (Table 4). This is a critical period of the salmon life cycle when fish are transitioning from freshwater to saltwater habitats and a large portion of total mortality occurs during this time [16]. Water year also was an important driver of variability in age 2 escapement with significant main and total effects where as Delta survival was not significant when interactions were accounted for. This is likely a result of interactions with water year as discussed above for age 3 fish.

As variability in input parameters was increased, escapement ranged from 2,806±984 fish (mean and standard deviation) in the baseline treatment to 2,337±904 fish in the 50% treatment suggesting that model output was robust to parameter uncertainty (Fig. 3). Coefficients of variation differed among input variables yet, CVs for individual input parameters did not vary much among treatments (Fig. 3). Ages 3 and 4 harvest had the greatest CVs of any variable (0.55–0.60) and both of these parameters were represented by a uniform distribution due to limitations in the data available to inform the relationship. The use of uniform distributions to represent parameter uncertainty has been identified as a limitation in other sensitivity analyses [11]. Harvest may have a profound effect on salmon population dynamics [17, 28] and the IOS model could be improved by further research on harvest of winter run that would reduce uncertainty in the true levels of harvest. All other input parameters were represented by normal distributions and CVs were less than 0.30 (Fig. 3).

There is a tendency to identify sensitive parameters as most important to model output. However, Fullerton et al.

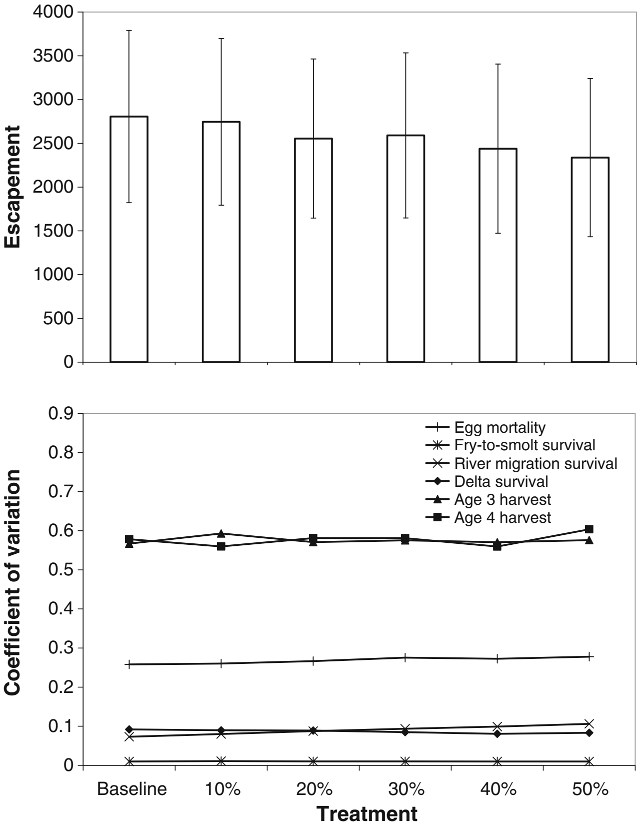

Fig. 3 Mean salmon escapement values (*top panel*) and coefficients of variation for input parameters (*bottom*) when variability of each input was increased by 10%, 20%, 30%, 40%, and 50%. All calculations are based on 1,000 Monte Carlo iterations

[11] recognized the importance of distinguishing between sensitivity and ecological relevance. For example, several of the relationships in the IOS model are based on limited data that influence the estimate of input parameters and the form of uncertainty distributions associated with those estimates. For example, river migration survival has been hypothesized to be influenced by flow [21], yet survival during the *river migration* stage is not influenced by flow in our model because the values we used to inform the relationship were taken from a field study conducted over three low-flow years [18]. Thus, the data available do not cover the range of potential conditions that may be experienced by out migrating salmon. A similar situation exists for other relationships such as smolt-to-age-2 mortality that is hypothesized to be an important determinant of year class strength but is difficult to estimate in the field and is thus represented by a uniform distribution. This is in contrast to laboratory studies of temperature–mortality relationships applied in the *early development* and *fry rearing* model stages where one of the goals was to examine biological responses over a range of environmental conditions. One of the strengths of the IOS model is that it can be used to identify where knowledge gaps exist and the model is flexible enough to allow the integration of new data and functional relationships as they become available.

3.2 Influence of Environmental Variables

Escapement was significantly affected by both the 10% increase and 10% decrease in temperature ($F_{2,297}$=346, $p<$ 0.001). However, the increase in temperature had a much greater effect producing a 95.7% reduction in escapement whereas the decrease in temperature yielded a 11% increase in escapement (Fig. 4). Varying flow produced a 6.2% increase and 4.7% decrease in escapement yet these differences were not statistically significant ($F_{2,297}$=2.19, p= 0.113). Similarly, variation in exports and ocean conditions did not yield statistically significant differences in escapement with p values of 0.656 and 0.114, respectively (Fig. 4).

The lack of significant changes in escapement with a 10% change in flow, exports and ocean conditions may reflect the type of data used to parameterize these relationships. The functions utilizing these inputs were constructed from data obtained from observational studies that had large error estimates associated with responses. Thus, large changes in these variables are required to produce a significant response in escapement. Temperature functions were parameterized with data from controlled experiments that produced small error estimates. Additionally, temperatures in the spawning and rearing area are close to the upper tolerance limit of Chinook salmon and even small changes have the potential to significantly affect the population.

Management of temperatures in the Sacramento River is a priority for stabilizing or increasing Chinook salmon populations. The Sacramento–San Joaquin Rivers represent the southern limit of Chinook spawning and stream temperatures can often approach the thermal tolerances for certain life stages [20]. Historically, Chinook salmon could avoid sub-optimal temperatures by utilizing higher elevation habitats [36]. However, these areas have been eliminated by the

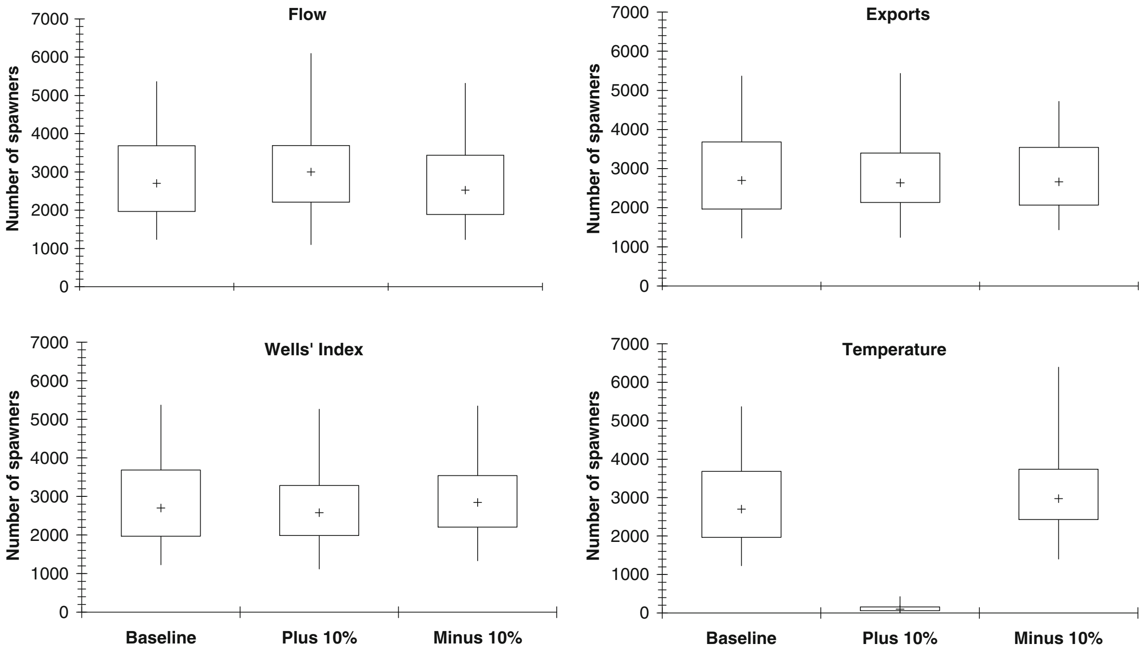

Fig. 4 Box and whisker plots of winter run escapement under baseline conditions, a 10% increase, and a 10% decrease in the four environmental inputs used in the IOS model

construction of impassable dams in the foothills of the Cascade and Sierra Nevada mountains [35]. Thus, understanding how population dynamics of Chinook are influenced by temperature-related mortality is essential for understanding how populations may be impacted by management actions or natural climate variations that may result in higher stream temperatures. The simulations conducted here do not represent any potential management or climate scenario, but instead demonstrate the utility of the IOS model for understanding this important driver of Chinook salmon population dynamics.

4 Summary and Conclusions

Our study developed and used a stochastic life cycle simulation model of winter-run Chinook salmon. The model brought together field monitoring data and laboratory studies to create six model stages that represent distinct salmon habitats and life stages. The model was created using GoldSim software and a free player version is available that will allow anyone to easily run and explore the IOS model. The model can be used to simulate population dynamics and mortality at each life stage for a period of years specified by the user. Our emphasis in developing this model was to allow managers a means to test and compare among alternative water management or restoration scenarios. A persistent problem in the management of anadromous salmonids has been the use of professional opinion in place of quantitative data to identify the life stages and/or habitats that will be affected by management actions [28]. The development of the IOS model provides a significant step such as recommended by Good et al. [12] to provide managers with the tools necessary for managers to make decisions based on the best quantitative data available. This was demonstrated by our simulation of variation in environmental parameters that revealed significant differences in escapement in response to higher and lower temperatures.

Sensitivity analysis revealed that uncertainty could be reduced by improving estimation of the mean values and uncertainty distributions of certain inputs and functional relationships between environmental variables and biological processes. This was particularly apparent for smolt-to-age-2 survival and ocean harvest that were uniform random variables. These variables had greater CVs than any other input and Sobol' indices indicated they could significantly influence model output. Additionally, river migration survival was not related to any environmental variables despite hypothesized relationships with flow because the data used was collected under a narrow range of conditions. Greater certainty in these relationships would improve model performance and reduce uncertainty in management and recovery actions based on IOS simulations. Although this model was specifically developed for winter run, the IOS model structure could easily be adapted for other salmon populations in the Sacramento-San Joaquin River system and serve as an example of how life cycle models can improve management of anadromous salmonids throughout their range. The IOS model will provide a much needed tool for resource managers and will continue to improve as more quantitative data becomes available.

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Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*

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ABSTRACT: Chinook salmon is an anadromous species that varies in size at freshwater emigration, which is hypothesized to increase population resiliency under variable environmental regimes. In California's Central Valley (USA), the majority of naturally spawned juveniles emigrate in 2 pulses: small juveniles (referred to as fry), typically ≤55 mm fork length (FL), emigrate from natal streams in February–March, whereas larger juveniles (smolts), typically >75 mm FL, emigrate in mid-April–May. In some river systems, there is a smaller pulse of emigrants of intermediate size (parr), typically 56 to 75 mm FL. Although the relative contribution of these migratory phenotypes to the adult population is unknown, management activities focus on survival of larger emigrants and most artificially produced fish (98%) are released from hatcheries at parr and smolt sizes. We reconstructed individual length at freshwater emigration for a sample of adult Central Valley Chinook salmon from 2 emigration years using chemical (Sr:Ca and Ba:Ca) and structural otolith analyses. The adult sample was comprised of individuals that emigrated as parr (mean = 48%), followed by smolts (32%) and fry (20%). Fry-sized emigrants likely represent natural production because fish ≤55 mm FL comprise <2% of the hatchery production. The distribution of migratory phenotypes represented in the adult sample was similar in both years despite apparent interannual variation in juvenile production, providing evidence for the contribution of diverse migratory phenotypes to the adult population. The contribution of all 3 migratory phenotypes to the adult population indicates that management and recovery efforts should focus on maintenance of life-history variation rather than the promotion of a particular phenotype.

KEY WORDS: Chinook salmon · Migratory phenotype · Otolith chemistry

INTRODUCTION

Many diadromous fishes display variation in juvenile migratory behavior. Individuals with distinct migratory phenotypes may experience differential survival and thus contribute to a population's resiliency, defined as its ability to persist following disturbances across variable environmental conditions (Holling 1973, Stearns 1992, Hilborn et al. 2003, Secor 2007, Bottom et al. 2009). Chinook salmon *Oncorhynchus tshawytscha* is an anadromous species that displays extensive variation in the size at, and timing of, freshwater emigration (Taylor 1990, Healey 1991, Quinn 2005, Waples et al. 2009). However, limited empirical data on the contribution of distinct migratory phenotypes to adult populations across years prevents a robust evaluation of the resiliency hypothesis. Certain approaches, such as artificial tagging studies and scale analyses, can be used to determine the contribution of migratory phenotypes; however, each of these methods has substantial

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logistic and interpretive limitations. Chemical and structural analyses of fish otoliths, which hold a record of aspects of an individual's environment, provide an alternative approach to generating empirical data on the contribution of migratory phenotypes without the need to recapture individuals (Campana 1999, Campana & Thorrold 2001).

Extensive agricultural land use conversion and water development within California's Central Valley (USA) (Fig. 1) have impacted the region's fall Chinook salmon (Moyle 2002), which are listed as a species of concern under the Endangered Species Act (Good et al. 2005). The majority of naturally spawned juveniles emigrate in 2 pulses: small juveniles (referred to as fry), typically ≤55 mm fork length (FL), emigrate from natal streams in February–March, whereas larger juveniles (smolts), typically >75 mm FL, emigrate in mid-April–May (Brandes & McLain 2001) (Fig. 2a–f). In some river systems, there is a smaller pulse of emigrants of intermediate size (parr), typically 56 to 75 mm FL (Fig. 2g–h). The movement patterns of these emigrant size classes are not well described, but it has been suggested that individuals remain in freshwater portions of the Sacramento–San Joaquin River Delta until they attain sizes >70 mm FL, at which point they enter the ocean (MacFarlane & Norton 2002). Additionally, although there is no information on the relative survival of these emigrant size classes, water and hatchery management strategies within the Central Valley focus on maximizing survival of smolt-sized emigrants (Brandes & McLain 2001, Williams 2001). For example, in-river flows are regulated to maximize survival during smolt emigration and >50% of hatchery juveniles are released as smolts and 2% as fry.

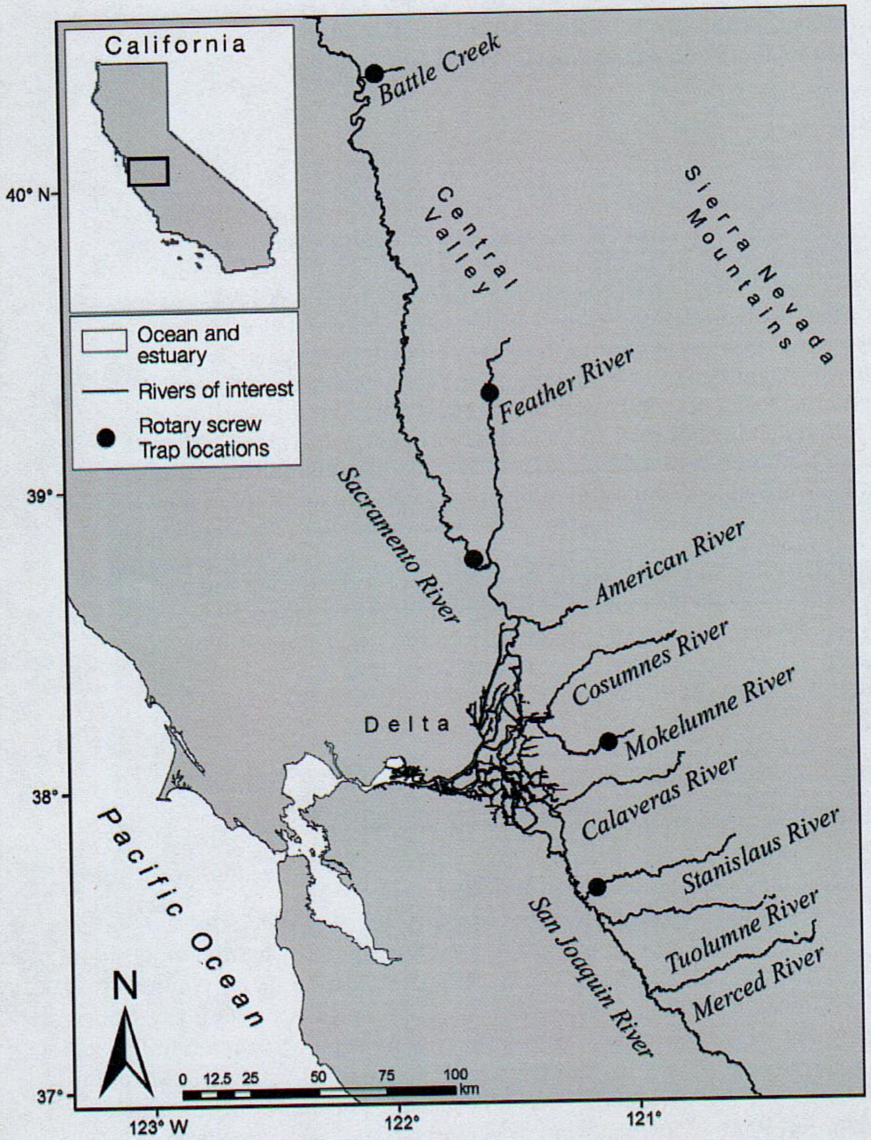

Fig. 1. General location of the Central Valley, California (inset). Major rivers, approximate rotary screw trap locations (●), and the Delta region are also identified

Numerous studies have used otolith Sr:Ca to reconstruct aspects of migratory history (e.g. Elsdon & Gillanders 2006, Thibault et al. 2007, Volk et al. 2010) and Sr:Ca and Ba:Ca have been combined to examine diadromous migrations (e.g. McCulloch et al. 2005, Bradbury et al. 2008, Crook et al. 2008, Milton et al. 2008). Such reconstructions are possible because otoliths grow continuously throughout the life of a fish and certain elements, such as Sr, are incorporated into an otolith in proportion to their water concentration. The ratio of Sr to Ca (Sr:Ca) is typically greater in marine waters (~8.5 mmol mol^{-1}) than in freshwater (<5 mmol mol^{-1}) although elevated values can occur in freshwater (Kraus & Secor 2004, Brown & Severin 2009). Therefore, variation in otolith Sr:Ca is often used to reconstruct diadromous migrations (e.g. Limburg 1995, Secor et al. 1995, Daverat et al. 2005). However, the utility of using otolith Sr:Ca is limited; the reason being that Sr and Ca water concentrations vary linearly (conservatively) along a salinity gradient, while Sr:Ca ratios display a curvilinear relationship with salinity which results in minimal variation in Sr:Ca above salinities of ~8 to 10 (Kraus & Secor 2004, Zimmerman 2005). Otolith Ba to Ca (Ba:Ca), which is also positively related to water Ba:Ca, may provide greater dis-

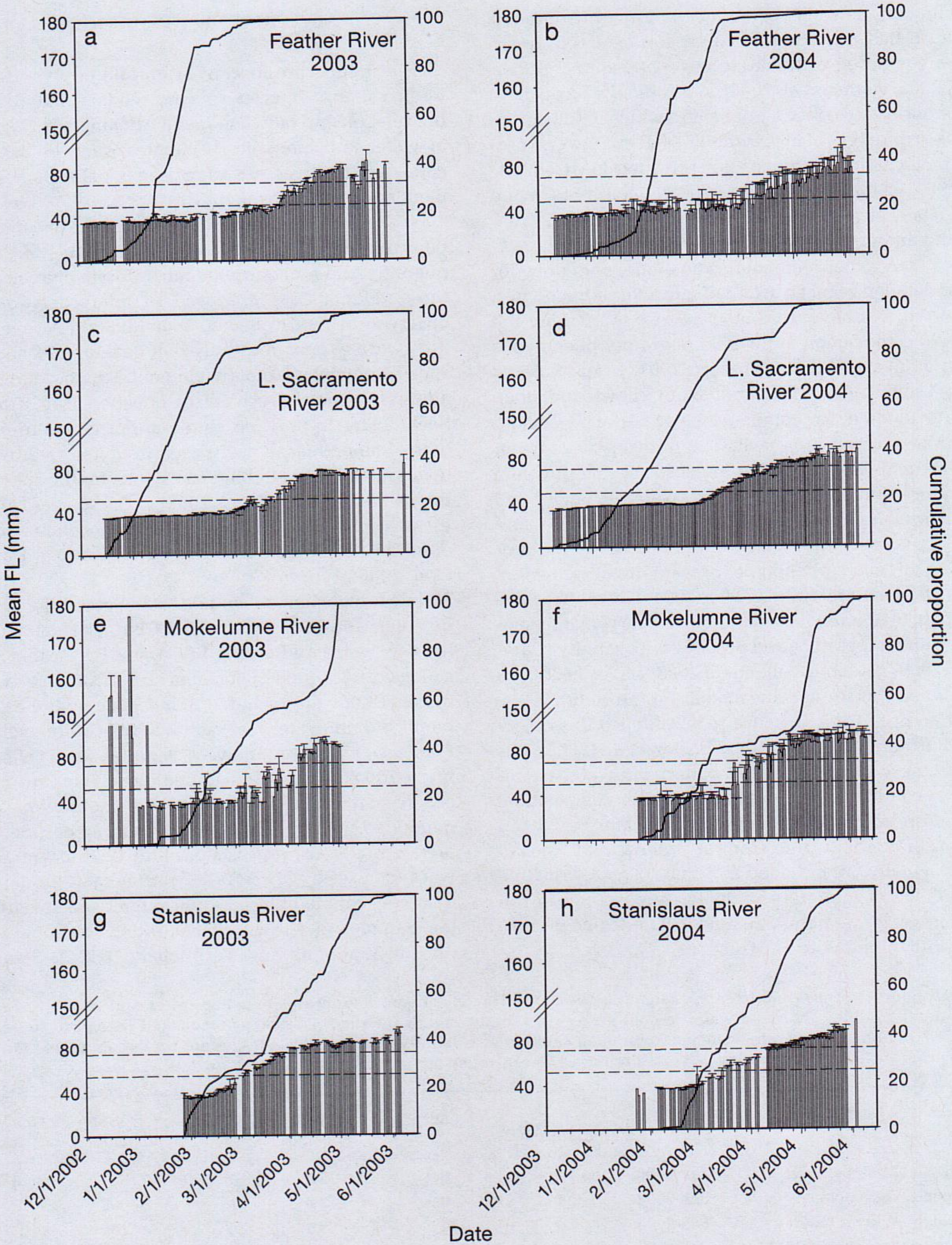

Fig. 2. *Oncorhynchus tshawytscha*. Size and timing of juvenile Chinook salmon emigration in the Central Valley, California. Mean (±SE) fork length (FL, mm; bars) and cumulative percent frequency of the total catch (solid line) are plotted against day of year (mo/d/yr). Data are from in-river rotary screw traps collections. In all cases, traps were placed in-river immediately prior to the first date with data presented. Data are included for 2003 and 2004 for (a,b) Feather River; (c,d) Lower Sacramento River; (e,f) Mokelumne River; and (g,h) Stanislaus River. Size designations for fry (≤55 mm FL), parr (56 to 75 mm FL), and smolt (>75 mm FL) are indicated by dashed lines

crimination between estuarine and marine habitats because Ba:Ca is often much greater (>50×) in freshwater compared with marine waters (Elsdon & Gillanders 2005, Hamer et al. 2006). Additionally, Ba displays non-conservative mixing behavior, which results in regions of enrichment at low salinities due to several processes, including desorption and resuspension (Coffey et al. 1997, Colbert & McManus 2005). Otolith Sr:Ca and Ba:Ca may be more useful in combination when discriminating among freshwater, estuarine, and marine residence than either elemental ratio alone, and allow for more detailed reconstruction of migratory phenotypes.

Few studies have used otolith Sr:Ca to quantify the relative contribution of juvenile migratory phenotypes in an adult population (Limburg 2001, Kraus & Secor 2004, Chino & Arai 2009) and, to our knowledge, none have evaluated the combined potential of Sr:Ca and Ba:Ca in such an approach. The primary objective of the present study was to reconstruct the juvenile migratory phenotypes of adult Central Valley fall Chinook salmon using otolith elemental (Sr:Ca and Ba:Ca) and structural analysis and determine the proportion of each phenotype present in a sample of adults that emigrated in 2003 or 2004. Given that rates of otolith elemental incorporation can vary among species, with temperature and possibly with salinity (Campana 1999, Elsdon & Gillanders 2003, Miller 2009), we developed species-specific models for the otolith incorporation of Sr:Ca and Ba:Ca to accomplish this objective. Furthermore, as noted by Elsdon et al. (2008), it is important to examine spatial patterns in water chemistry to confirm interpretations of otolith composition. Therefore, we also compiled data on water Sr:Ca and Ba:Ca throughout the Central Valley and coastal ocean. Finally, we obtained information on the relative abundance of migratory phenotypes observed in the juvenile emigrant population in 2003 and 2004 to compare with our adult reconstructions.

MATERIALS AND METHODS

Otolith incorporation of Sr and Ba in juvenile Chinook salmon. Species-specific models that describe the relationship between metal:calcium (Me:Ca) ratios of water and biogenic carbonates, such as those for corals and bivalves, are often used in palaeological and modern applications (e.g. Swart et al. 1999, Wei et al. 2000, Gaetani & Cohen 2006). In these cases, the relationships between water and carbonate Me:Ca are quantified under controlled laboratory conditions, and those relationships are used to interpret variations observed in field-collected individuals. However, we are aware of only one study that developed a species-specific model of otolith elemental incorporation to address a specific ecological question (see Kraus & Secor 2004). In previous studies, information from otoliths of other species were used to generate threshold levels indicative of habitat transitions for the species of interest (e.g. Hedger et al. 2008) or the species of interest was collected from representative locations to generate a baseline of otolith Me:Ca values (e.g. Daverat et al. 2005).

Here we developed models for the otolith incorporation of Sr and Ba in juvenile fall Chinook salmon using data on water and otolith Sr:Ca and Ba:Ca that were collected from field collections and laboratory experiments. Data were included in models only if measurements of both water and otolith Me:Ca were available (Table 1). For water analyses, samples were collected, filtered (0.45 µm), and acidified using standard methods (Eaton et al. 2005). Standard calibrations were generated with SPEX Certiprep® Group certified reference materials, and Ca, Sr, and Ba concentrations were measured with a Teledyne Leeman Prodigy inductively coupled plasma-optical emission spectrometer. Samples of known concentration (National Institute of Standards and Technology [NIST]; Standard

Table 1. Sources of juvenile Chinook salmon otoliths used to determine relationships between water and otolith Sr:Ca and water and otolith Ba:Ca. Mean water temperature (°C), salinity, and Sr:Ca and Ba:Ca ratios associated with each source are included. n: number of juveniles included for each category; trt: salinity × water Me:Ca treatment combination; OR: Oregon; CV: Central Valley; CA: California; CLC: controlled laboratory conditions; nd: no data available

Source of juveniles	Date	Water temperature (°C)	Salinity	Water Sr:Ca		Water Ba:Ca	
				mmol mol^{-1}	n	µmol mol^{-1}	n
Trask River hatchery, OR	Apr 2006	nd	0	2.6	9	84	8
Merced River hatchery, CV	Feb 2008	nd	0	3.4	11	1600	7
Mokelumne River hatchery, CV	Feb 2008	nd	0	5.1	7	1100	11
Coastal ocean, Southern OR, Northern CA	Jul 2008	nd	32	8.6	16	5	16
J. A. Miller (unpubl. data), CLC	nd	8.8, 11.9, 15.3	0, 5, 10, 15	1.5, 7.2, 7.8, 8.2	4–6 fish/trt	30, 60, 75, 135, 230, 520, 1035	4–6 fish/trt
Zimmerman (2005), CLC	nd	4.9–10.7	0, 6.3, 12.7, 18.6, 15.5, 33.0	2.8, 6.4, 7.4, 7.7, 7.9, 8.4	12 fish/trt	nd	nd

Reference Material 1643e) were introduced throughout the run to estimate accuracy: measured concentrations were within 2.0, 1.3, and 2.4 % of reported values for Ca, Sr, and Ba, respectively (n = 7). Precision was estimated with repeated measurements of the same sample (NIST 1643e) and varied by <2.5 % for all 3 elements (n = 3). For otolith analyses, sagittae were prepared using standard methods to minimize contamination (e.g. Miller 2009). Otolith ^{43}Ca, ^{86}Sr, and ^{138}Ba data were collected using a VG PQ ExCell inductively coupled plasma mass spectrometer (ICPMS) with a New Wave DUV193 excimer laser. The laser was set at a pulse rate of 10 Hz with a 40 µm diameter spot size and travelled at 5 µm s^{-1}. Limits of detection (ppm) were calculated as 3 standard deviations of background measurements: Ca = 0.02, Sr = 0.03, and Ba = 0.008. Normalized ion ratios were converted to elemental ratios as described in Miller (2007), converted to molar ratios based on the molar mass of Ca, Sr, and Ba, and presented as mmol mol^{-1} for Sr:Ca and µmol mol^{-1} for Ba:Ca. The mean percent relative standard deviations (%RSD) for NIST 612 glass during data collection were ^{43}Ca = 3.2, ^{86}Sr = 4.1, and ^{138}Ba = 4.4 %. A calcium carbonate standard of known composition developed by the US Geological Survey (USGS MACS-2) provided an estimate of accuracy: measured values were within 2 % of known values for both Sr:Ca and Ba:Ca. Linear and non-linear regression analyses were used to quantify the relationships between otolith and water Me:Ca using Statistica®. Data were examined for normality and homogeneity of variance prior to analysis.

Spatial patterns in water chemistry. In order to examine spatial patterns in water chemistry, we acquired existing data on Ca, Sr, and Ba water concentrations in coastal waters and within the Central Valley and collected additional samples from coastal areas and tributaries, including the Cosumnes, Mokelumne, Calaveras, Stanislaus, and San Joaquin Rivers (Fig. 1, Table A1 in Appendix 1). The purpose of this data collection effort was to provide an estimate of the variation in freshwater Sr:Ca and Ba:Ca observed in the Central Valley and determine if there were freshwater systems with elevated Sr:Ca that could confound interpretation of migratory history based on adult otoliths. Water samples were collected and processed as described above. Samples of known concentration (NIST 1643e) were introduced throughout the run to estimate accuracy: measured concentrations were within 2.5, 1.8, and 2.6 % of reported values for Ca, Sr, and Ba, respectively (n = 3). Precision was estimated with repeated measurements of the same sample (NIST 1643e) and varied by <3.2 % for all 3 elements (n = 3).

The relationships between water Sr:Ca and Ba:Ca and salinity (0 to 32) were predicted based on end member water concentrations similar to those observed in the Delta region, which is the downstream extent of freshwater in the Central Valley, and coastal waters. For our model, we assumed conservative mixing behavior for Ca, Sr, and Ba. However, it is important to note that Ba often displays non-conservative mixing with regions of Ba release, due to desorption and resuspension, between salinities of 1 and 15 (Coffey et al. 1997). Therefore, our Ba:Ca model represents a minimum estimate for water Ba:Ca at low salinities. It is likely that at low salinities Ba:Ca ratios often exceed values predicted based on conservative mixing, particularly during periods of high freshwater discharge (Coffey et al. 1997, Colbert & McManus 2005).

Back-calculation of juvenile size. The reconstruction of individual length at specific habitat transitions, such as freshwater emigration, based on otolith measurements requires an accurate back-calculation model. Therefore, we confirmed that otolith size provides a robust predictor of fall Chinook salmon size during the first year of life by collecting juveniles from several locations and brood years to quantify the relationship between fish and otolith size (Table 2). We measured juvenile FL (0.5 mm) prior to preservation, removed sagittal otoliths, and measured otolith width (OW, to the nearest µm) along the dorsal–ventral growth axis at the widest point. There were no significant differences in OW between left and right sagittae (n = 50, p > 0.40), and preliminary analysis indicated that OW was a better predictor of fish length than otolith length. All otolith distances were measured using a Leica® stereoscope and Image Pro Plus®. A linear regression analysis of FL and OW was completed for all juveniles.

Application to Central Valley fall Chinook salmon. Adult Chinook salmon were collected during the Ore-

Table 2. *Oncorhynchus tshawytscha*. Source, year of collection, and size range of juvenile Chinook salmon used to develop the relationship between otolith and fish size. n: number of juveniles included for each category; CV: Central Valley; OR; Oregon

Source	Year of collection	Fork length (mm)	n
Mokelumne River hatchery, CV	2008	40–48	7
Umpqua River hatchery, OR	2007	40–94	15
Trask River hatchery, OR	2007	43–88	8
Merced River hatchery, CV	2008	51–83	11
Rogue River hatchery, OR	2007	63–80	9
Coastal ocean, southern OR	2006–2007	84–125	52
Coastal ocean, off Columbia River	1999, 2000, 2002, 2006	98–166	21

gon ocean troll fishery in 2006. Biological data, including FL (cm), a tissue sample for genetic analysis, and several scales were collected from 2567 individuals. Otoliths were collected from a subset of those adults (n = 395). The region of origin for each individual was determined using a microsatellite DNA baseline, the Genetic Analysis of Pacific Salmonids, which identifies Central Valley fall Chinook salmon with a reported mean accuracy of 94.5% (Seeb et al. 2007). Fifty-nine percent of the fish were identified as Central Valley fall Chinook salmon. Only otoliths from fish identified as Central Valley fall Chinook salmon with >90% posterior probability of assignment were included in remaining analyses (n = 100). Scales were used to determine individual age and, hence, year of emigration. Individual age was determined by counting winter annuli on scales. Each scale was read by 2 observers, and disagreements were resolved during a joint third reading. Scales from other Central Valley adult Chinook salmon of known age were available and included to provide a test of ageing accuracy (n = 31): for these individuals, age was known due to the presence of coded wire tags (CWTs) (Jefferts et al. 1963).

Adult otoliths (n = 100) were prepared as described in 'Materials and methods', 'Otolith incorporation of Sr and Ba in juvenile Chinook salmon', except that 52% were prepared as transverse and 48% as sagittal sections. We visually inspected all sections for proper orientation and exposure of the core primordia to ensure that data were collected along the same dorsal–ventral axis on all samples. For 9 individuals, we prepared one otolith as a transverse section and one as a sagittal section to compare the back-calculated size estimates generated with the 2 preparations. Otolith ^{43}Ca, ^{86}Sr, and ^{138}Ba data were collected along transects that intersected the core region (Fig. 3) using methods similar to those described above. Limits of detection (ppm) were calculated as 3 SD of background measurements: Ca = 0.09, Sr = 0.09, and Ba = 0.007. The mean %RSDs for NIST 612 glass during data collection were ^{43}Ca = 3.0, ^{86}Sr = 4.4, and ^{138}Ba = 4.2%. External estimates of accuracy based on USGS MACS-2 were within 3 and 2% of known values for Sr:Ca and Ba:Ca, respectively.

We then combined otolith Sr:Ca and Ba:Ca data and structural analysis to determine individual length at freshwater emigration. For each individual, the OW at the time of freshwater emigration was determined by the initial and abrupt increase in otolith Sr:Ca, which indicates exit from freshwater, prior to stabilizing at brackish/ocean values (Fig. 3). This transition was verified by the occurrence of low or declining otolith Ba:Ca at the same time as the abrupt increase in otolith Sr:Ca. Threshold values for otolith Me:Ca during freshwater, brackish, and marine residence were determined based on our relationships between (1) otolith and water Me:Ca (see 'Results', 'Otolith incorporation of Sr and Ba in juvenile Chinook salmon') and (2) water Me:Ca and salinity (see 'Results', 'Spatial patterns in water chemistry'). Individual FL (mm) at freshwater emigration was estimated using the measurements of OW based on otolith Sr:Ca and Ba:Ca and the linear relationship between FL and OW developed for juvenile fall Chinook salmon (see 'Results', 'Back-calculation of juvenile size'). Confidence intervals (95% CI) for back-calculated size predictions were generated using standard methods ($\hat{Y}_i \pm t_{0.05(2)} \times s_{\hat{Y}i}$; Zar 1999).

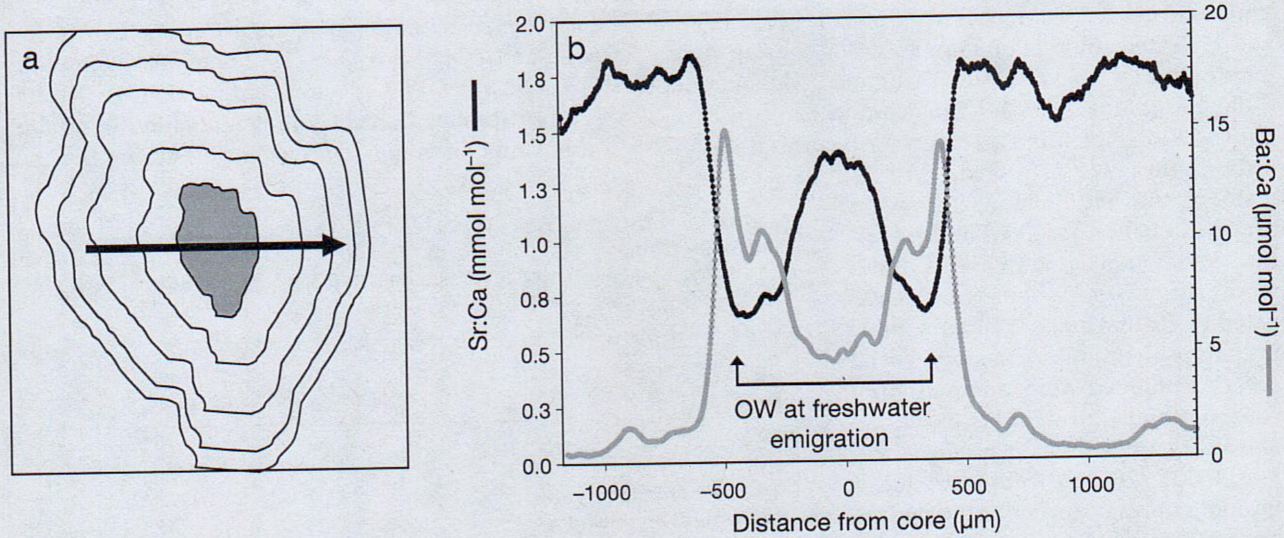

Fig. 3. *Oncorhynchus tshawytscha.* (a) Schematic of a sagittal section of an adult fall Chinook salmon otolith. Laser path for elemental analysis is identified. The core, which represents the egg and early juvenile life history, is shaded. (b) Sr:Ca (mmol mol^{-1}) and Ba:Ca (µmol mol^{-1}) across the otolith. Measurement of otolith width (OW) at freshwater emigration is identified

Production of juvenile fall Chinook salmon. We would need comprehensive data on the relative abundance of the phenotypes present in natural and hatchery juvenile production in 2003 and 2004 to estimate survival rates for each phenotype based on our adult sample. However, there are no estimates for total natural production in the Central Valley basin. Therefore, we used data available from in-stream rotary screw traps to describe the size and relative abundance of naturally produced juveniles. We compiled daily information on size and number of individuals collected in traps on the lower Sacramento, Feather, Mokelumne, and Stanislaus Rivers (Fig. 1). The data from these 4 traps combined represent the size and relative abundance of >70% of the natural production (Yoshiyama et al. 2000). All of these traps, except for the lower Sacramento River trap, are placed at river locations selected to maximize collection of naturally spawned emigrants. State hatcheries transport their production to estuarine waters for release so they would not be collected in-river. The only federal hatchery in the basin, i.e. the Coleman National Fish Hatchery on Battle Creek, releases juveniles in-stream and they could be collected in the lower Sacramento River trap. Additionally, estimates of total natural production upstream of a trap were available for the Feather and Mokelumne Rivers as well as a fifth trap on lower Battle Creek (Fig. 1). Trap data were obtained from the Bay Delta and Tributaries Project (http://bdat.ca.gov/) and R. Vincik, California Department of Fish and Game. For hatchery production, comprehensive data on the number and size of juveniles released in 2003 and 2004 are available from the Regional Mark Information System (www.rmpc.org/). Therefore, we compiled information on hatchery production from the 5 Central Valley hatcheries: the Coleman National Fish Hatchery and 4 state-run hatcheries, including the Nimbus, Feather River, Mokelumne River, and Merced River hatcheries. Release information is reported as fish lb^{-1}; therefore, Piper et al. (1982) was used to convert mass to FL. We used the data collected from traps and hatchery records to generate (1) daily mean size estimates and cumulative percent frequencies for emigrants, and (2) size-frequency distributions for in-stream and hatchery production in 2003 and 2004 for comparison with our adult reconstructions of size at freshwater emigration.

RESULTS

Otolith incorporation of Sr and Ba in juvenile Chinook salmon

For Sr:Ca, data were available across a range of temperatures (4.9 to 15.3°C), salinities (0 to 33), and water Sr:Ca ratios (1.5 to 8.6 mmol mol^{-1}) (Table 1). Otolith Sr:Ca increased curvilinearly as water Sr:Ca increased, and a polynomial regression provided the best fit to the data (Fig. 4a). For Ba:Ca, data were available across a range of temperatures (8.8 to 15.3°C), salinities (0 to 32), and water Ba:Ca ratios (5 to 1600 µmol mol^{-1}) (Table 1). Otolith Ba:Ca also increased as water Ba:Ca increased, although in a linear manner; therefore, a linear model was used to describe the relationship (Fig. 4b). It appears that otolith Ba:Ca may have reached a plateau of ~11 µmol mol^{-1} at water Ba:Ca ratios of ~1100 µmol mol^{-1}; however, data from fish reared at higher levels of Ba:Ca would be needed to draw any firm conclusions. It is important to note

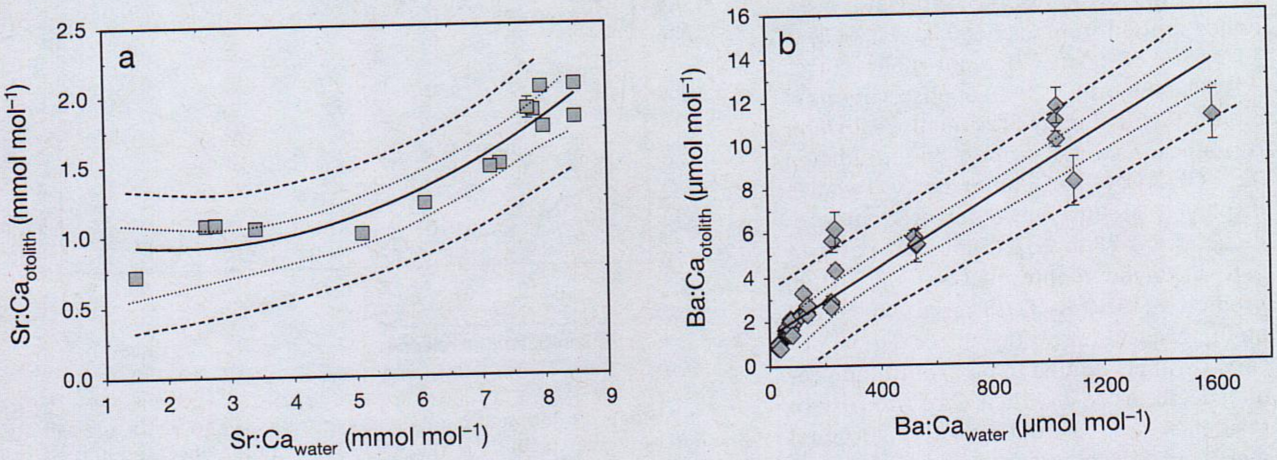

Fig. 4. *Oncorhynchus tshawytscha*. Relationships between otolith and water Sr:Ca and Ba:Ca. (a) Mean (±1 SE) otolith Sr:Ca versus water Sr:Ca (mmol mol^{-1}). Curve (solid line) was fit by following relationship: $y = 0.027$ (±0.011 SE) $x^2 - 0.118$ (±0.121 SE) $x +$ 1.043 (±0.266 SE) ($p < 0.001$, $r^2 = 0.89$, $n = 14$). (b) Mean (±1 SE) otolith Ba:Ca versus water Ba:Ca (µmol mol^{-1}). Curve (solid line) was fit by the following relationship: $y = 0.008$ (±0.0004 SE) $x + 1.37$ (±0.207 SE) ($p < 0.001$, $r^2 = 0.89$, $n = 38$). Estimates for the 95% confidence (dotted line) and prediction (dashed line) intervals are included

that although there were positive relationships between otolith and water Me:Ca ratios, the rate of incorporation declined as water Me:Ca increased. For example, at water Ba:Ca > 1000 μmol mol^{-1}, <1% was incorporated into otoliths, whereas at water Ba:Ca = 5 μmol mol^{-1}, 32% was incorporated into otoliths.

Spatial patterns in water chemistry

Observed freshwater Me:Ca within the Central Valley ranged from 2.41 to 5.48 mmol mol^{-1} for Sr:Ca and from 141 to 1679 μmol mol^{-1} for Ba:Ca (Table A1). Observed ocean Me:Ca averaged (±SD) 8.55 ± 0.33 mmol mol^{-1} for Sr:Ca and 5.03 ± 1.08 μmol mol^{-1} for Ba:Ca. We used the empirically derived relationships between otolith and water Me:Ca (Fig. 4) to predict otolith Me:Ca ratios for juvenile Chinook salmon from the Central Valley (Table A1). We then compared predictions with observed otolith Me:Ca values, which were generated by averaging across ~100 μm of each adult otolith during presumptive freshwater and marine residence (n = 99). Note that one otolith was removed from analysis (see 'Results', 'Application to Central Valley fall Chinook salmon').

Predictions for otolith Sr:Ca during freshwater residence ranged from 0.91 (±0.17 95% CI) to 1.20 (±0.09 95% CI) mmol mol^{-1} (Table A1). The majority (85/99) of otolith Sr:Ca observations during presumed freshwater residence fell within the predicted 95% CI (0.75 to 1.29 mmol mol^{-1}). Thirteen fish displayed otolith Sr:Ca lower than predicted (i.e. 0.62 to 0.74 mmol mol^{-1}) and one fish displayed otolith Sr:Ca higher than predicted (1.31 mmol mol^{-1}). Our predictions for otolith Ba:Ca during freshwater residence ranged from 2.47 (±0.35 95% CI) to 14.30 (±0.88 95% CI) μmol mol^{-1} (Table A1). The majority (83/99) of observations of otolith Ba:Ca during presumed freshwater residence also fell within the predicted 95% CI (2.12 to 15.18 μmol mol^{-1}). Two fish displayed otolith Ba:Ca lower than predicted (i.e. 1.78 to 2.10 μmol mol^{-1}) and 14 fish displayed otolith Ba:Ca higher than predicted (15.40 to 32.28 μmol mol^{-1}). For otolith Me:Ca during ocean residence, observed values tended to be lower than predicted. Observed otolith Sr:Ca during ocean residence ranged from 1.50 to 2.20 mmol mol^{-1} and 44% of the observations fell with the predicted range (2.01 ± 0.13 95% CI); the remaining observations were all less than predicted. Observed otolith Ba:Ca during ocean residence ranged from 0.35 to 1.31 μmol mol^{-1} and 12% of the observations fell with the predicted range (1.40 ± 0.40 95% CI); the remaining observations were all less than predicted. There was no overlap in the mean otolith Me:Ca ratios observed during presumed freshwater and marine residence.

We generated predictions for water Sr:Ca and Ba:Ca from salinities of 0 to 32 based on end member water Me:Ca values similar to those observed in the Delta region and coastal waters (Fig. 5). Based on predicted and observed values, residence in freshwater (with Sr:Ca < 7 mmol mol^{-1} and Ba:Ca > 80 μmol mol^{-1}) would result in otolith signatures distinct from residence in marine waters (with Sr:Ca > 7.0 mmol mol^{-1} and Ba:Ca < 80 μmol mol^{-1}; Fig. 5, Table A1). Given the predicted water Me:Ca ratios within the Central Valley, otolith Me:Ca ratios would not be distinct at salinities >3 for Sr:Ca and >6 for Ba:Ca. (Fig. 5). However, as noted, Ba release commonly occurs in low salinity waters. If localized enrichment of Ba occurs in low salinity waters and results in Ba:Ca > 80 μmol mol^{-1} while Sr:Ca remains greater than freshwater values (>7.0 mmol mol^{-1}), otolith signatures of fish residing in those waters would be distinct from freshwater or marine signatures. Based on these predictions and observations, otolith Sr:Ca < 1.5 mmol mol^{-1} with Ba:Ca > 2 μmol mol^{-1} indicates freshwater residence, otolith Sr:Ca ≥ 1.5 mmol mol^{-1} with Ba:Ca > 2 μmol mol^{-1} indicates brackish residence, and otolith Sr:Ca ≥ 1.5 mmol mol^{-1} with Ba:Ca < 2 μmol mol^{-1} indicates brackish/ocean residence.

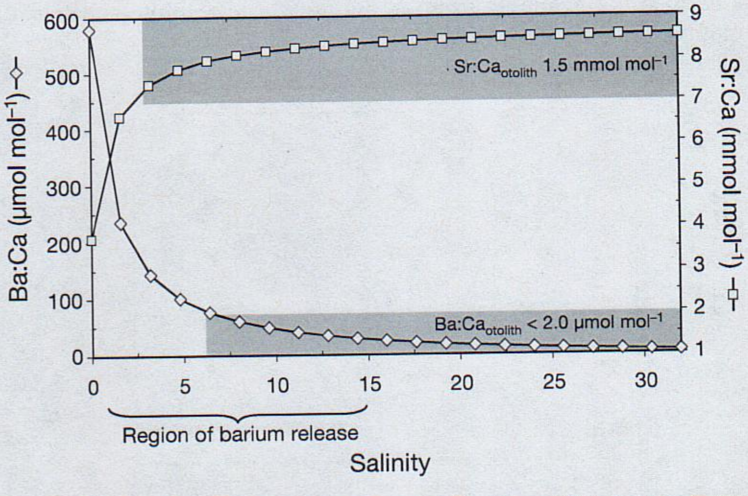

Fig. 5. Predicted relationship between water Ba:Ca and Sr:Ca and salinity. Freshwater values (salinity = 0) are within the range observed in the Central Valley Delta region. Shaded boxes indicate the water Me:Ca and salinities at which there would be minimal variation in otolith Me:Ca. Predicted values for otolith Ba:Ca and Sr:Ca at those water Me:Ca ratios and salinities are included in shaded boxes. Predictions were based on observed relationship between otolith and water Me:Ca, measured water Me:Ca, and the assumption of conservative mixing behavior

Back-calculation of juvenile size

For juveniles, FL (mm) was positively and linearly related to OW (µm) ($r^2 = 0.93$, $n = 123$, $p < 0.001$). Therefore, we used the following relationship to estimate FL based on OW:

$$FL = 0.060\ (\pm 0.002\ SE) \times OW + 6.91\ (\pm 2.19\ SE) \quad (1)$$

Fish were grouped into 10 mm bins based on back-calculated size at freshwater emigration.

Application to Central Valley fall Chinook salmon

Adult Chinook salmon ranged in size from 66 to 102 cm FL at capture, and their scales displayed 2 or 3 winter annuli except for one fish with 4 winter annuli. As the fish with 4 annuli was the only individual that emigrated in 2002, it was removed from the analysis. Therefore, all individuals included hereafter emigrated in 2003 ($n = 49$) or 2004 ($n = 50$). All the 31 known-age, CWT-fish were correctly aged (= 100% accuracy). There was no systematic difference in back-calculated size estimates (paired *t*-test, df = 9, $p = 0.46$) between transverse and sagittal sections and the mean difference in back-calculated size was <5%.

Overall, estimated length at freshwater emigration ranged from 33 to 104 mm FL. The error (95% CI) associated with individual back-calculations ranged from 2.3 to 10.7% and averaged 3.0%. Parr-sized individuals comprised the largest emigrant group in both 2003 and 2004 (mean ± SD across years = 47.5 ± 0.8%), followed by smolts (32.4 ± 6.2%), and fry (20.1 ± 5.4%; Fig. 6a). For 18 individuals, the transition from fresh to marine waters included a period during which otolith Sr:Ca was >1.5 mmol mol^{-1} and Ba:Ca was >2 µmol mol^{-1}, which is predicted to represent residence in brackish waters. Of the 18 individuals with this brackish otolith signature, 11 were fry, 6 were parr, and 1 was a smolt.

Juvenile production

Over 36 million fall Chinook salmon were released from state and federal hatcheries in 2003 and more than 27 million were released in 2004 (Fig. 6b). The majority of juveniles were released as smolts (54 to 65%), followed by parr (35 to 45%), with less than 2% released as fry. The majority of juveniles (>75%) collected in traps within the Sacramento River basin emigrated as fry in both 2003 and 2004 (Fig. 6c,d). Although some juveniles from the federal hatchery could be collected in the lower Sacramento River trap, the observed size distribution of fish collected in that trap indicates that the catch consisted of primarily natural production (Fig. 6b versus Fig. 6d). Juveniles from the Mokelumne and Stanislaus Rivers displayed more even distributions of emigrant size classes (Fig. 6e,f).

Given the low proportion of hatchery fish released at fry sizes (<2%), there is a high likelihood that the fry emigrants observed in the adult samples represent natural production. Additionally, there was greater natural production (3×) above the Feather River trap in 2004 than 2003, which resulted in more fry-sized emigrants (Fig. 6c). Similarly, the mean estimate of total natural production upstream of a trap on lower Battle Creek was greater (2.8×) in 2004 than in 2003 (581 677 and 206 266 juveniles in 2004 and 2003, respectively), and those catches comprised predominantly individuals <40 mm FL (i.e. >90%). Given that the Feather River and Battle Creek are estimated to contribute nearly 50% of the total production in the Central Valley (Yoshiyama et al. 2000), it appears that fry production was greater in 2004 than in 2003. Despite this apparent interannual variation in production, fry emigrants made up an average of 20% of the adult sample in both years (Fig. 6a), which indicates potentially greater fry survival in 2003 than 2004. Furthermore, our data indicate that parr emigrants represent a greater proportion of the adult sample than the juvenile emigrant population (Fig. 6a versus Fig. 6b–f), potentially a result of in-river growth of fry emigrants or greater rates of survival for parr emigrants.

DISCUSSION

Quantifying the extent of phenotypic variation in juvenile migratory behavior is the initial step in understanding if, and how, such variation contributes to the resilience of managed populations. Examining the role of phenotypic variation in managed populations is an important component of effective conservation. This is particularly true within the highly modified Central Valley, where freshwater flows are often re-allocated during smolt emigration to improve survival under the assumption that smolts contribute disproportionately to the adult population (Brandes & McLain 2001, Williams 2001). Additionally, studies examining survival of juveniles during migration through the riverine and Delta regions of the Central Valley focus on individuals >75 mm FL, a result of using telemetry methods that require relatively large individuals (i.e. >140 mm) (Perry et al. 2010) or focusing on hatchery fish (Kimmerer 2008). In the present study, the relative proportions of the juvenile migratory phenotypes present within adult samples were similar across both years, and there was no clear evidence that smolt-sized emigrants contributed disproportionately to the adult

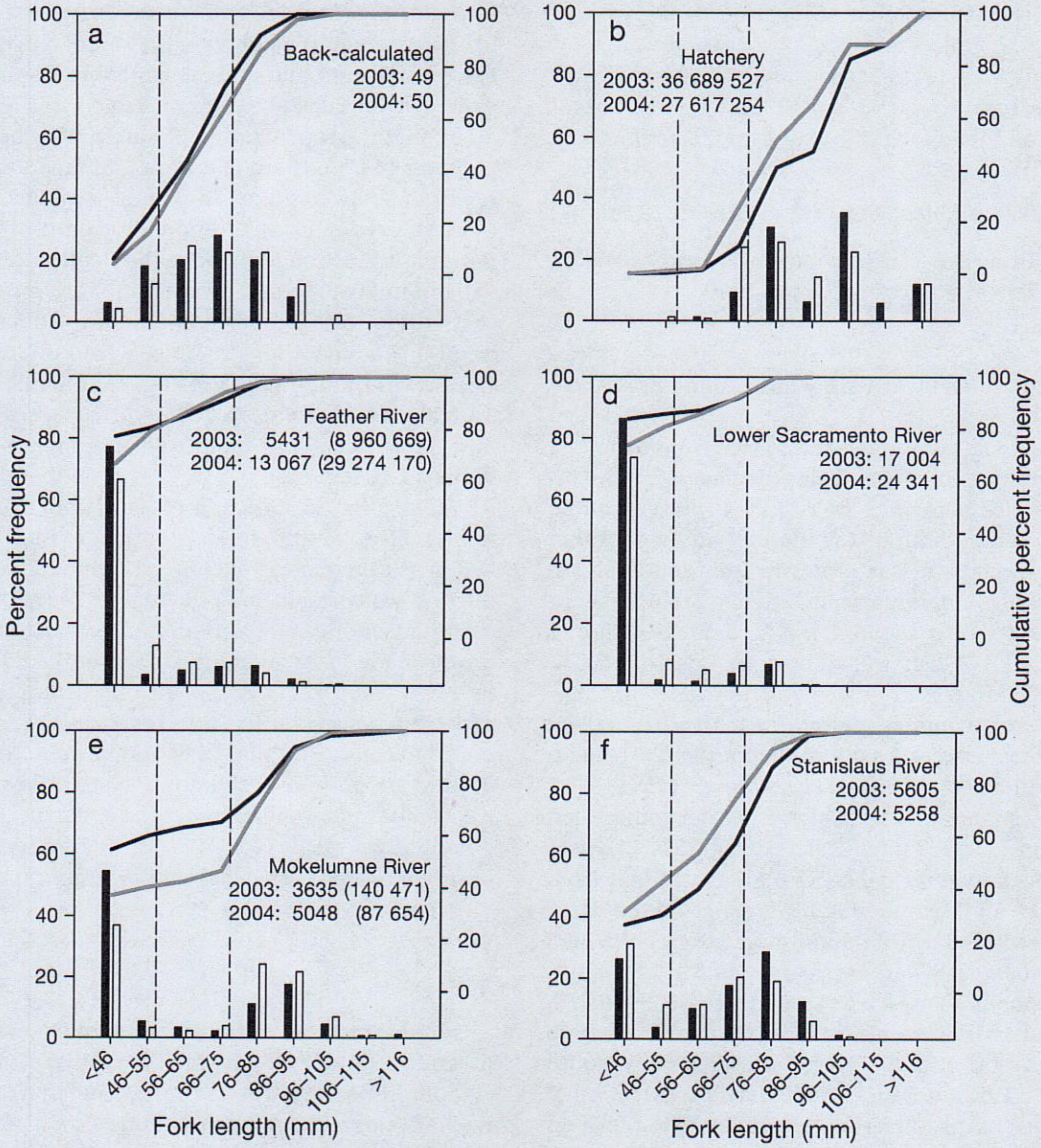

Fig. 6. *Oncorhynchus tshawytscha*. Size (fork length, mm) frequency distributions (bars) and cumulative percent frequency of occurrence (solid lines) for Central Valley fall Chinook salmon emigrants. (a) Back-calculated size at freshwater emigration for adult fall Central Valley Chinook salmon as determined based on otolith structure and chemistry. (b) Size of hatchery-produced Chinook salmon upon release. (c–f) Size of primarily naturally produced Chinook salmon collected in rotary screw traps: (c) Feather, (d) Lower Sacramento, (e) Mokelumne, and (f) Stanislaus Rivers. The numbers of fish used to generate each distribution are included. For the Feather and Mokelumne River traps, estimates for the total number of individuals produced upstream of the trap are included (95% CI: Feather River in 2003 = 7 158 975 to 13 851 505 and in 2004 = 20 186 009 to 37 851 505; Mokelumne River in 2003 = 95 974 to 310 357 and in 2004 = 67 068 to 134 898). Size designations for fry (≤55 mm FL), parr (56 to 75 mm FL), and smolt (>75 mm FL) are indicated by dashed lines. Filled bars and black lines represent 2003 emigrants and open bars and grey lines represent 2004 emigrants

population. Furthermore, similar proportions of juvenile migratory phenotypes were observed in both years despite the fact that natural production was apparently lower in 2003 than 2004, which likely resulted in fewer fry emigrants. Although the relative survival of distinct migratory phenotypes appears to vary across years, these 3 phenotypes likely consistently contribute to adult production. The adult Central Valley fall Chinook salmon used in the present study were collected within the Oregon salmon troll fishery. Central Valley fall Chinook salmon have been captured consistently in the Oregon troll fishery (Weitkamp 2010); however, additional information on the juvenile migratory phenotypes represented in additional samples of Central Valley adult fall Chinook salmon, including those collected from other fishery locations and on spawning grounds, is needed to evaluate the consistency of the observed patterns.

Although estuaries are known to provide rearing habitat for Chinook salmon (Reimers 1973, Healey 1991, Simenstad et al. 1982, Bottom et al. 2005, Volk et al. 2010), research in San Francisco Bay indicates that juvenile Chinook salmon may derive less benefit from estuarine residence than more northerly populations (MacFarlane & Norton 2002). During the 1997 emigration, juvenile Chinook salmon (68 to 110 mm FL) resided in the estuary for an average of 40 d and grew relatively slowly (mean = 0.18 mm d^{-1}) (MacFarlane & Norton 2002). Overall, their mean condition declined as they migrated through San Francisco Bay until they reached adjacent coastal waters where their growth rates accelerated (MacFarlane & Norton 2002). These observations led to the supposition that 'the ecological and evolutionary propensity of emigrating juveniles to conform to a strong ocean-type life history, with little estuarine dependency and a hastened ocean entry, may be another unique attribute of Central Valley Chinook salmon' (MacFarlane & Norton 2002, p. 255). However, MacFarlane & Norton (2002) estimated growth based on change in mean size, which may be biased by size-dependent emigration and may in fact underestimate actual growth. Additionally, smaller fish, which may display different patterns of growth and residence, may have been under-represented in their mid-water trawl collections. The relative importance of estuarine rearing may vary across years with different environmental conditions. In the present study, a substantial proportion of the fish (40%) entered brackish waters at sizes <65 mm FL. Extended estuarine residence may be important for smaller fall Chinook salmon emigrants in the Central Valley.

Hatchery fish account for an estimated 17 to 90% of the total adult fall Chinook salmon production in the Central Valley (Kjelson et al. 1982, Yoshiyama et al. 1998, Yoshiyama et al. 2000, Barnett-Johnson et al. 2007). The relatively large range in estimates of hatchery contribution is due, in part, to challenges associated with accurately identifying hatchery fish and interannual variation in the hatchery contribution. However, given that most hatchery fish are released at sizes >55 mm FL, it is likely that fry-sized emigrants observed in the present study represent natural production. Additional information on the origin of individual fish (hatchery versus naturally spawned) may be obtained through more detailed structural (Barnett-Johnson et al. 2007) or chemical (^{34}S:^{32}S, Weber et al. 2002) otolith analyses. Given the error rates associated with the identification of hatchery fish using structural analysis (~10%) and the instrumentation required for sulfur analysis (Weber et al. 2002), we did not incorporate either in the present study. Nonetheless, although fry-sized emigrants are consistently observed in lower rivers and estuaries (Collins 1892, Rich 1920, Reimers 1973), they remain a minor consideration in the Central Valley's water and salmon management practices (Brandes & McLain 2001, Williams 2001). It is plausible that fry emigrants comprise a migratory contingent, i.e. a subpopulation aggregate that share common migratory pathways and thus experience differential survival compared with other contingents (Hjort 1914, Clark 1968, Secor 1999).

Theoretically, the presence of diverse juvenile migratory contingents provides resilience for a population that confronts varying environmental conditions (Thorpe et al. 1998, Secor 1999, Waples et al. 2009). However, as noted earlier, empirical evidence for the survival of distinct migratory variants within the Central Valley has been difficult to acquire. Survival estimates based on comparisons between juvenile and adult abundance are problematic because they are confounded by large variations in sampling efficiency. Tagging studies have been initiated in several Central Valley river systems to quantify the relative contribution of juvenile migratory phenotypes to adult populations. However, low production of naturally spawned juveniles, low recapture rates, and the 3 to 5 yr required to examine adult returns have prevented robust conclusions using this methodology. Analysis of the structural variation in scales has been used on a limited basis to provide information on the relative contribution of migratory phenotypes (Reimers 1973). However, these studies require extensive baseline development and are highly subjective; they are best suited to differentiating between individuals that emigrate from freshwater in their first year of life (sub-yearlings) or in their second year of life (yearlings), rather than among size classes within the sub-yearling life history. Approaches similar to ours can be applied to other diadromous species, at finer spatial scales (e.g. within rivers), and over a period of several years to further examine how successful juvenile migratory behaviors vary under different environmental conditions without the need to recapture individuals.

Our results indicate that a combined marker approach (otolith Sr:Ca and Ba:Ca) holds promise for improving reconstructions of migratory history, but there are several factors to consider. For example, we observed that otolith Ba:Ca provided a slightly greater ability to differentiate residence in low salinity waters than otolith Sr:Ca in this species. However, by combining these 2 tracers, we were able to identify a pattern indicative of residence in brackish waters (i.e. otolith Sr:Ca > 1.5 mmol mol^{-1} and Ba:Ca > 2 µmol mol^{-1}). More detailed examination of the temporal and spatial variation in water Sr:Ca and Ba:Ca throughout San Francisco Bay and Delta during emigration may allow for more precise spatial determination of habitat use. Overall, the ability to reconstruct individual salinity history within a system largely depends on the freshwater Me:Ca values. Similar otolith chemical analyses in systems with greater freshwater Ba:Ca (>600 µmol mol^{-1}) and/or lower Sr:Ca (<4 mmol mol^{-1}) than the lower reaches of the Central Valley should provide additional salinity resolution (i.e. Volk et al. 2010).

For most populations of Chinook salmon, it is unclear how much variation in juvenile migratory behavior exists, how fluid that variation is, and whether survival varies among individuals with distinct migratory behaviors. Furthermore, it is not known if or how habitat modifications (such as the construction of dikes, levees, and bypass channels), freshwater discharge, harvest, and artificial propagation affect the relative proportion and survival of juvenile emigrants (but see Kimmerer 2008, Perry et al. 2010). As Healey (2009) notes, management strategies that enhance a dominant tactic (smolt-sized emigrants in this case) could reduce life-history diversity and result in a loss of population resilience. However, there is evidence that management practices can also result in the development of novel migratory phenotypes (i.e. a reservoir-rearing life history) (Connor et al. 2005). Lindley et al. (2009) indicate that hatchery production has reduced variation in juvenile size, condition, and migration timing in Central Valley fall Chinook salmon; they suggest that increased life-history diversity could reduce variability in adult production. The contribution of 3 juvenile migratory phenotypes to the Central Valley adult population indicates that a conservative management approach would focus on maintenance of life-history variation rather than the promotion of a particular phenotype.

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Appendix 1. Additional data on water and otolith chemistry

Table A1. Water Sr:Ca (mmol mol^{-1}) and Ba:Ca (µmol mol^{-1}) and predictions for Chinook salmon otolith Sr:Ca (mmol mol^{-1}) and Ba:Ca (µmol mol^{-1}). Data from Weber (2002) were collected monthly from October 1997 to September 1999; data from C. E. Zimmerman (unpubl. data) were collected in March, July, and November in 2003–2005; National Stream Quality Accounting Network (NASQAN; http://water.usgs.gov/nasqan/) data were collected approximately monthly from 1973–1995 (n = 46); and samples were collected in February 2008 for the present study. Predicted otolith Me:Ca ratios were based on observed otolith and water Me:Ca ratios (see 'Results' for details). For water Me:Ca, Weber (2002) = median values; all others = mean values ± SD. For predicted otolith Me:Ca, 95% CI are presented in parentheses. nd: no data available

Location	Water Sr:Ca (mmol mol^{-1})	Water Ba:Ca (µmol mol^{-1})	Predicted otolith Sr:Ca (mmol mol^{-1})	Predicted otolith Ba:Ca (µmol mol^{-1})	Source
Sacramento River	2.41	408	0.91 (0.17)	4.51 (0.36)	Weber (2002)
Upper Sacramento River	3.00 (0.75)	nd	0.93 (0.15)	nd	C. E. Zimmerman (unpubl. data)
Battle Creek	3.99	417	1.00 (0.12)	4.58 (0.37)	Weber (2002)
Mill Creek	3.42	288	0.95 (0.13)	3.59 (0.34)	Weber (2002)
Deer Creek	3.47	709	0.96 (0.13)	6.83 (0.53)	Weber (2002)
Upper Deer Creek	3.66 (0.75)	nd	0.97 (0.13)	nd	C. E. Zimmerman (unpubl. data)
Butte Creek	2.76	141	0.92 (0.15)	2.47 (0.35)	Weber (2002)
Feather River	3.07	440	0.93 (0.14)	4.76 (0.38)	Weber (2002)
Feather River Hatchery	3.18	446	0.94 (0.14)	4.81 (0.38)	Weber (2002)
American River	3.41	584	0.95 (0.13)	5.87 (0.45)	Weber (2002)
American River Hatchery	3.61	618	0.96 (0.13)	6.13 (0.47)	Weber (2002)
Upper Yuba River	2.89 (0.38)	nd	0.93 (0.15)	nd	C. E. Zimmerman (unpubl. data)
Northern Delta	3.94	595	0.99 (0.12)	5.95 (0.45)	Weber (2002)
Southern Delta	5.36	514	1.18 (0.09)	5.33 (0.41)	Weber (2002)
Mokelumne River	4.92	1140	1.11 (0.10)	10.15 (0.86)	Weber (2002)
Mokelumne River Hatchery	5.15	1168	1.14 (0.10)	10.37 (0.88)	Weber (2002)
Tuolumne River	3.75	708	0.98 (0.13)	6.82 (0.53)	Weber (2002)
Tuolumne River	3.96 (0.97)	nd	0.99 (0.12)	nd	C. E. Zimmerman (unpubl. data)
Merced River	3.21	1606	0.94 (0.14)	13.74 (1.25)	Weber (2002)
Upper Merced River	4.03 (0.57)	nd	1.00 (0.12)	nd	C. E. Zimmerman (unpubl. data)
Merced River Hatchery	3.32	1679	0.95 (0.14)	14.30 (1.31)	Weber (2002)
Upper Calaveras River	3.16 (0.55)	nd	0.94 (0.14)	nd	C. E. Zimmerman (unpubl. data)
Upper Stanislaus River	4.51 (0.39)	nd	1.05 (0.11)	nd	C. E. Zimmerman (unpubl. data)
San Joaquin River at Vernalis	5.30 (0.08)	425 (5)	1.17 (0.10)	4.64 (0.37)	NASQAN
Lower Cosumnes River	3.54 (0.08)	747 (61)	0.96 (0.13)	7.12 (0.55)	Present study
Lower Mokelumne River	5.37 (0.06)	1622 (6)	1.18 (0.10)	13.86 (1.26)	Present study
Lower Calaveras River	2.56 (0.10)	524 (144)	0.92 (0.16)	5.40 (0.41)	Present study
Stanislaus River	4.10 (0.12)	698 (52)	1.01 (0.12)	6.74 (0.52)	Present study
Lower San Joaquin River	5.48 (0.04)	468 (8)	1.20 (0.10)	4.97 (0.39)	Present study
Coastal ocean	8.55 (0.33)	5.03 (1.08)	1.98 (0.13)	1.41 (0.40)	Present study

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