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Spatial-Temporal Distribution and Habitat Associations of Age-0 Splittail in the Lower San Francisco Estuary Watershed

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The Splittail (*Pogonichthys macrolepidotus*) is a cyprinid endemic to the San Francisco Estuary and its lower watershed. Although it was recently removed from the Federal Endangered Species Act list of threatened species, it is still a species of concern because of uncertainties regarding its abundance and distribution. Because little information is available on early life stages for which to base management decisions, we examined historical long-term monitoring data and conducted a field study in 2002 and 2003 to examine the distribution and habitat associations of age-0 Splittail. During winter and spring, adults migrate from the upper San Francisco Estuary and the Sacramento-San Joaquin Delta upstream into freshwater tributaries and floodplains to spawn. Although previous work suggested a decreasing upstream range for this species, we found that catch data for age-0 Splittail (≤ 50 mm fork length) during a monitoring program spanning 28 years (1976–2003) indicated the upstream-most distribution in the Sacramento River has remained persistent at 232–296 km upstream from the estuary. Additionally, centers of distribution in the Sacramento and San Joaquin Rivers varied according to hydrology; distance upstream was similar in years of high and intermediate river flows, but increased during low flow years. In all years, age-0 Splittail became abundant in April or May and by June and July had a center of distribution downstream at the margin of the Sacramento-San Joaquin Delta. Our field study showed that in addition to these two primary tributaries, substantial spawning also occurred in other smaller tributaries with previously uncertain importance to Splittail production, namely the Petaluma River, Napa River, and Butte Slough. We also found that age-0 Splittail favor low velocity shallow-water habitats. Compared to main channel habitats, age-0 Splittail were 6.5 times more common in backwaters in upstream riverine locations, and 3.5 times more common in offchannel intertidal habitats in downstream tidal locations. Our study demonstrates the distribution of Splittail is more widespread than previously believed and underscores the importance of offchannel habitats as nursery areas for age-0 fish.

Cyprinids represent the largest family of fishes and are widely distributed over North America, Eurasia, and Africa (Moyle and Cech, 2004). They are found in a variety of habitats and often exhibit complex migratory behaviors (Lucas and Baras, 2001). As with many other groups of fishes, long-term or long-distance rheotactic migrations exhibited by cyprinids are commonly associated with reproductive events. These spawning migrations often occur in dynamic physical habitats and situations where environmental requirements of individual species vary by life stage (Matthews, 1998; Lucas and Baras, 2001; Moyle and Cech, 2004). Such energetically demanding behavior has likely evolved to ensure that eggs are deposited in optimal physical habitats (e.g., temperature, salinity, water velocity, substrate type) and that offspring are able to find favorable rearing habitats (e.g., productive floodplain or low velocity offchannel habitats). Subsequent downstream movement of offspring is often triggered by environmental cues, such as seasonally induced changes in physical habitat, food supply, predation risk, and their interactions. Habitat and hydrodynamic manipulations characteristic of many highly developed regions throughout the world can pose serious problems to fish populations if they dramatically alter natural processes or migration corridors (Stanford et al., 1996; Ross, 1997; Lucas and Baras, 2001).

The Splittail (*Pogonichthys macrolepidotus*) is relatively unique among North American cyprinids in that it makes annual spawning migrations from brackish estuarine habitats into upstream freshwater tributaries and floodplains (Daniels and Moyle, 1983; Sommer et al., 1997; Moyle et al., 2004). Endemic to the San Francisco Estuary and its lower watershed in California's Central Valley (Moyle, 2002; Moyle et al., 2004), it is a large cyprinid (adults attain lengths > 400 mm; Moyle, 2002) with broad environmental tolerances (Young and Cech, 1996). Based largely upon catches of ripe adults and larvae, spawning is believed to occur on flooded terrestrial vegetation (Caywood, 1974; Sommer et al., 2002; Crain et al., 2004). Typically, larvae and juveniles remain upstream until inundated river margins and floodplains begin to dry, promoting emigration downstream to tidal freshwater and brackish portions of the San Francisco Estuary. Although reproduction occurs in all years, the strongest year-classes are produced in extremely wet years when areas of large floodplains and river margins are inundated for extended periods of time (Sommer et al., 1997).

The Splittail is of high importance for local resource managers. Concerns about apparent long-term abundance declines lead to its listing as a threatened species by the U.S. Fish and Wildlife Service (USFWS) in 1999. Primary factors believed to be associated with the decline included water management practices that altered important spawning and rearing habitat (Meng and Moyle, 1995). Splittail was delisted in 2003 but remains a Species of Special Concern by USFWS, the California Department of Fish and Game, and the CALFED Bay-Delta Program, a large local restoration effort (T. R. Sommer, R. Baxter, and F. Feyrer, unpubl.). Setting objectives for the conservation of Splittail has been hindered because very little data are available on its early life stages (Moyle et al., 2004). Specific uncertainties include the distribution and habitat associations of young Splittail.

Our goals for this study included resolving uncertainties regarding the spawning distribution of adults (as inferred by the presence of age-0 fish), downstream emigration patterns of age-0 fish, and habitat associations of age-0 fish. We hoped that this information would be useful for the management of the species, particularly with respect to ambitious habitat restoration efforts in the San Francisco Estuary ecosystem (Moyle et al., 2004). We addressed the following specific questions: (1) Has the upstream-most distribution of age-0 Splittail in the Sacramento River changed since monitoring began in 1976? Understanding the upstream range of Splittail is important because there is some concern that the range has been decreasing (Moyle et al., 2004). (2) How are age-0 Splittail distributed in the Sacramento and San Joaquin Rivers, and how are distributions affected by river flow? Hydrology significantly affects the production of Splittail (Sommer et al., 1997); thus, we sought to determine whether there is also an effect on distribution. (3) Are other tributaries of the San Francisco Estuary important for spawning? Moyle et al. (2004) suggested that Splittail production is largely limited to the Sacramento River and the upper San Francisco Estuary with periodic production from other regions only in extremely wet years. (4) In what habitats are age-0 Splittail present? Although some information has been collected about depth and velocity distributions of age-0 (Sommer et al., 2002), little is known about the preferred habitats of young Splittail.

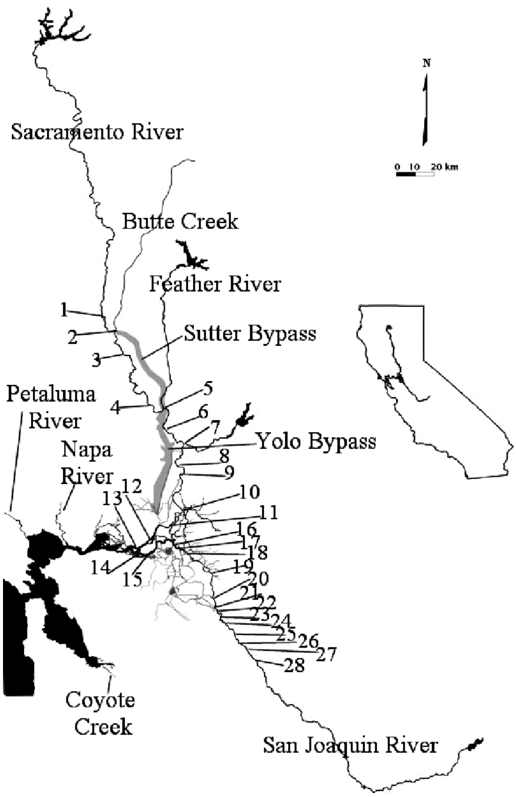

Fig. 1. Study area in the San Francisco Estuary and its lower watershed. Long-term monitoring sites included in this study from the Sacramento and San Joaquin Rivers and their distance (km) upstream from the confluence of the two rivers are numbered as follows: (1) Colusa State Park, 232, (2) Ward's Landing, 222, (3) South Meridian, 209, (4) Knight's Landing, 145, (5) Verona, 129, (6) Elkhorn, 114, (7) American River, 95, (8) Garcia Bend, 79, (9) Clarksburg, 69, (10) Koket, 39, (11) Isleton, 27, (12) Rio Vista, 23, (13) Sherman Island, 2, (14) Antioch Dunes, 2, (15) Eddo's Marina, 8, (16) Medford Island, 42, (17) Venice Island, 42, (18), Lost Isle, 51, (19) Dad's Point, 66, (20) Dos Reis, 82, (21), Mossdale, 90, (22) Wetherbee, 93, (23) Big Beach, 101, (24) Durham Ferry, 109, (25) Sturgeon Bend, 119, (26) Route 132, 124, (27) North of Tuolumne River, 134, (28) Grayson, 140.

Materials and Methods

Study area.—The San Francisco Estuary (Fig. 1) is the largest estuary on the Pacific coast of the

United States. It receives water from California's two largest rivers—Sacramento (from the north) and San Joaquin (from the south)—which drain a watershed encompassing 40% of California's surface area (100,000 km^2). The rivers converge to form the Sacramento–San Joaquin Delta, a complex network of tidal freshwater channels covering 3000 km^2. Water from the delta flows through Suisun and San Pablo Bays before entering San Francisco Bay and exiting through the Golden Gate to the Pacific Ocean. The delta is primarily a freshwater environment; however, both Suisun and San Pablo Bays are brackish, and San Francisco Bay is marine. Because of the Mediterranean climate, rainfall and, thus, freshwater flow into the estuary is highly seasonal, occurring mainly in late winter through spring. The system is also subject to extreme interannual variation in freshwater flows, with periodic droughts and floods.

The geographic extent of our study took place from the confluence of the Sacramento and San Joaquin Rivers upstream approximately 296 km (Ord Bend) in the Sacramento basin and 140 km (Grayson) in the San Joaquin basin (Fig. 1). We also sampled two tributaries to San Pablo Bay, Napa and Petaluma Rivers. Napa River joins San Pablo Bay at its northeastern corner near Carquinez Strait, and Petaluma River joins at the northwestern corner at Black Point. The lower reaches of both of these tributaries where we sampled are slightly brackish intertidal sloughs except when spring runoff produces periods of freshwater flow. We also sampled lower Coyote Creek, a tributary to south San Francisco Bay with historical records of Splittail (Snyder, 1905; Aceituno et al., 1976), once in June 2002 but did not collect any Splittail.

The Sacramento River and its major floodplains, the Yolo and Sutter Bypasses, provide the most substantial spawning and rearing habitat for Splittail (Sommer et al., 1997; Sommer et al., 2001; Moyle et al., 2004). Since the 1920s, habitat available to Splittail for spawning and rearing along the Sacramento River has diminished. Initial losses occurred as long segments of the lower River were straightened and leveed, reducing habitat complexity and limiting floodplain access. Since the 1960s, levees and river banks have been rip-rapped, which has supplanted vegetation used as spawning substrate and early rearing habitat (Crain et al., 2004; Moyle et al., 2004). Levees on the Sacramento River currently extend from river kilometer (rkm) 312 at Chico Landing downstream to Collinsville (rkm 0). Levee configuration differs through three reaches downstream of Chico Landing and has important implications in terms of Splittail spawning and rearing habitat: the river from (1) Chico Landing to Colusa (rkm 232) is characterized by setback levees enclosing remnant floodplain ("flood terraces") and a narrowly meandering river channel; (2) from Colusa to Verona (rkm 129) is tightly leveed and contains fewer and much narrower flood terraces, many of which are actively eroding and targeted for rip-rap; and (3) from Verona to Collinsville (rkm 0) is also tightly leveed and contains extensive, narrow flood terraces between Verona and Sacramento but is almost completely rip-rapped from Sacramento to Collinsville. Several weirs along the levees facilitate flood flows into the engineered Sutter and Yolo Bypass floodplains during high flow events. Because of the extensive levee system, access for Splittail to these floodplains has been limited to swimming up their respective perennial channels ("toe drains") or by spilling over a weir.

The flood control system on the San Joaquin River differs from that of the Sacramento River in two important ways. First, set-back levees and channel meander are common from rkm 200 and extending downstream to rkm 93, providing access to remnant flood terraces throughout this reach. Second, dams control a much larger proportion of the annual runoff as compared to the Sacramento River and significantly limit the frequency and duration of floodplain inundation.

Data sources.—To examine trends in distribution, we examined data from a long-term monitoring program, implemented by USFWS, which began in 1976 and is on-going (Sommer at al., 1997; Brandes and McLain, 2001). The primary goal of the program has been to monitor the abundance and distribution of juvenile Chinook salmon (*Onchorhynchus tshawytscha*) and resident fishes in the Sacramento-San Joaquin Delta and upstream into the Sacramento and San Joaquin Rivers. Monitoring involves weekly sampling with beach seines at fixed sites; we used data from a subset of these sites for this analysis (Fig. 1). Sampling was conducted with a 15.2 × 1.2-m beach seine with 3.2mm mesh pulled perpendicular onto shore during daylight hours. Fishes collected were identified to species, measured for fork length (mm) and returned to the water.

To provide supplemental information on the range and habitat use of age-0 Splittail, we conducted additional sampling during spring and summer (April through July) of 2002 and 2003. Our sampling focused on the Sacramento, San Joaquin, Napa, and Petaluma Rivers (Fig. 1). In addition to these primary rivers, we also sampled Butte Slough, the section of Butte Creek adjacent to Sutter Bypass, which joins the Sacramento River near Verona. Within each region, we targeted all possible areas that we could access and effectively sample with beach seines. Sampling was conducted with a 15.2 × 1.2-m beach seine with 3.2 mm mesh during daylight hours; one to four hauls were conducted at each site. Following each sample, we measured water temperature (C) and specific conductance (μS) and characterized substrate as the visually estimated proportional coverage of each of the following components: mud, sand, clay, pavement, cobble, pebble, detritus, and silt. We sampled most regions on a weekly basis, resulting in a total of 354 beach seine hauls.

Data analysis.—We analyzed data from the long-term monitoring program to address the first two study questions. The data analysis was limited to fish ≤ 50 mm because of our focus on age-0 distributions. For question one, has the upstream-most distribution of age-0 Splittail in the Sacramento River changed, we compared the upstream-most distribution of Splittail to that based on the sampling effort in each year that sampling occurred. We limited this analysis to the months of May and June because that is when age-0 Splittail are most abundant.

To address question two, how are age-0 Splittail distributed in the Sacramento and San Joaquin Rivers and how are distributions affected by river flow, we standardized the data to a single point in the estuary (Dege and Brown, 2004). We plotted the mean position of the population in terms of distance (km) upstream from the confluence of the Sacramento and San Joaquin Rivers during spring and summer and then visually compared distributions among low, intermediate, and high flow years. Although our analysis was largely a qualitative examination of the data, we feel it provided a valid assessment of temporal distribution patterns within the limitations of the available data.

Associated river flow conditions for these analyses focused on the months of January through March, the primary period of Splittail upstream migration and initial spawning (Moyle et al., 2004). Mean flows for the study periods were calculated from mean daily flow data for the Sacramento and San Joaquin Rivers (obtained from the California Department of Water Resources' DAYFLOW Database; publicly available at http://www.iep.water.ca.gov) and then classified into low, intermediate, and high flow years (Table 1). Intermediate flow years were classified by bounding the mean annual flow for the study period by ± 25%; years falling below or above this range were classified as low or high, respectively. This technique provided a conservative classification scheme, which allowed us to elaborate on general patterns in the fish distribution data.

TABLE 1. MEAN JANUARY THROUGH MARCH DAILY FLOW CONDITIONS (m^3/SEC) AND CLASSIFICATION (LOW, INTERMEDIATE, OR HIGH; DETAILS IN MATERIALS AND METHODS) IN THE SACRAMENTO AND SAN JOAQUIN RIVERS.

Year	Sacramento River	San Joaquin River
1993	1380 - intermediate	—
1994	452 - low	56 - low
1995	1815 - high	243 - intermediate
1996	1552 - intermediate	273 - intermediate
1997	1594 - high	741 - high
1998	1,859 - high	505 - high
1999	1496 - intermediate	234 - intermediate
2000	1371 - intermediate	206 - intermediate
2001	592 - low	85 - low
2002	734 - low	63 - low
2003	1048 - intermediate	57 - low

The mean position of the population for each month during April to July (only to June for the San Joaquin River) was calculated as a weighted average. We multiplied the river location (km) of a site by abundance (number of fish/m^3), summed across all sites, and then divided by total abundance. Because not all years had a continuous data series caused by inconsistent sampling effort or unmeasured fish, the Sacramento River analysis was limited to 1993–2003 ($N =$ 2026 seine hauls) and the San Joaquin River analysis to 1994–2003 (N = 2846 seine hauls). Ninety-seven percent of all possible site-by-month sample combinations were available for the Sacramento River time series. The missing datapoints were not spatially or temporally biased based upon visual assessment so we made no subsequent adjustments to the data. A larger proportion of the site by month sample combinations were missing from the San Joaquin River time series. To correct for this problem, we grouped individual sites into nine geographic regions, coincidentally resulting in another matrix with 97% of all possible datapoints for which we made no further adjustments.

We analyzed data from our field study to address study questions three and four. For question three, are other tributaries of the San Francisco Estuary important spawning regions, we summarized our catches according to the five major regions that were sampled and compared log(x + 1) -transformed abundances (number of fish/m^2) with analysis of variance and Tukey's

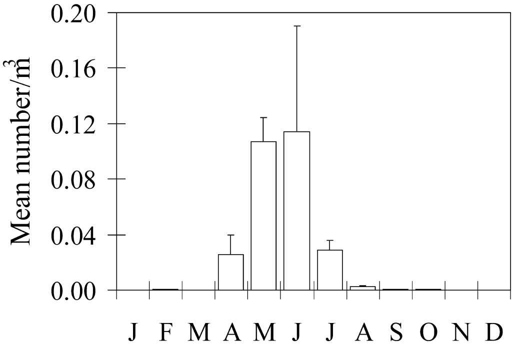

Fig. 2. Mean monthly abundance of age-0 Splittail collected in beach seine samples between 1976 and 2003. Error bars represent 95% confidence intervals.

HSD posthoc multiple comparison test for unequal sample size. For question four, in what habitats are age-0 Splittail present, we used binary logistic regression to determine the habitat variables associated with the presence of age-0 Splittail. We specifically chose logistic regression because it can be used with both discrete and continuous independent variables and does not assume linearity and normally distributed errors as in the case of simple linear regression (Trexler and Travis, 1993). We derived two separate regression models, one for upstream nontidal habitats and one for downstream tidal habitats. Prior to each regression, we used principal components analysis (PCA) to identify colinear habitat variables. We retained one representative variable of those that were colinear (those that exhibited similar PCA loadings) for further analysis in the logistic regression models. The upstream model included a binary predictor factor (backwater), which indicated whether the sample was taken from the main river channel or a backwater. Backwaters were defined as bodies of water distinct from the main channel. They were connected to the main channel at a single point and exhibited no current. The size and permanency of these habitats was directly related to river stage. The downstream model also included a binary predictor factor (offchannel), which indicated whether the sample was taken from the main channel or in offchannel intertidal habitat. Offchannel intertidal habitat was characterized as broad shoals or smaller channels adjacent to main channels that completely dewatered at low tides. All statistical tests were considered significant at $P \leq 0.05$.

Results

The upstream-most distribution of age-0 Splittail in the Sacramento River has been largely

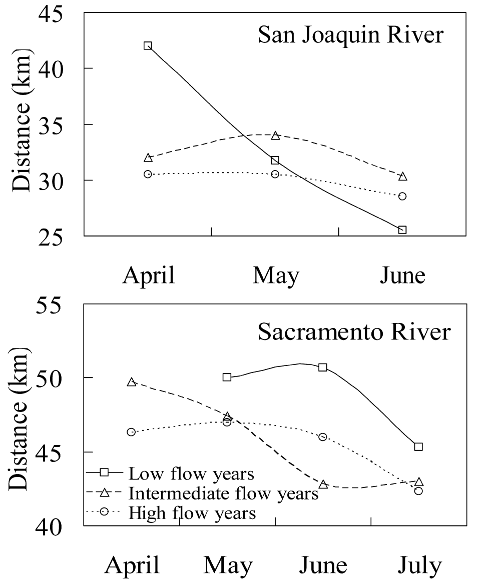

Fig. 3. Mean monthly upstream distances of the center of distribution for age-0 Splittail in the Sacramento and San Joaquin Rivers under different flow conditions. Datapoints are connected by smooth lines to facilitate interpretation.

unchanged since long-term monitoring began in 1976. Splittail were not collected at the upstream-most sampling location in only one of 19 years (1981). The maximum upstream distribution of both sampling effort and Splittail has typically been located at either 232 (Colusa State Park) or 296 (Ord Bend) km upstream of the confluence of the Sacramento and San Joaquin Rivers. The only exceptions were 1976 (79 km) and 1977–1980 (97 km). Only limited data are available from other programs to determine whether the maximum upstream distribution of Splittail exceeded the range of beach seine sampling (see Discussion).

Abundance peaked from April to July during the long-term monitoring program (Fig. 2). In both the Sacramento and San Joaquin Rivers, centers of distribution varied according to river flow conditions; distance upstream was similar in years of high and intermediate river flows but typically furthest upstream during low flow years (Fig. 3). By June and July of all years, the center of distribution was downstream at the upper margin of the Sacramento–San Joaquin Delta (Fig. 3).

Overall, Splittail were relatively common in samples during our field study in 2002 and 2003; frequency of occurrence in samples (the percentages of samples in which Splittail were present) for each watershed we sampled was:

TABLE 2. RESULTS OF BINARY LOGISTIC REGRESSION ANALYSES USING HABITAT VARIABLES AS PREDICTORS OF THE PRESENCE OF AGE-0 SPLITTAIL PERFORMED SEPARATELY ON UPSTREAM NONTIDAL HABITATS (TEST THAT ALL SLOPES ARE ZERO: $G = 13.03$, DF = 6, $P = 0.04$) AND DOWNSTREAM TIDAL HABITATS (TEST THAT ALL SLOPES ARE ZERO: $G = 46.27$, DF = 7, $P < 0.01$). Both models adequately explained patterns in the data as indicated by goodness-of-fit tests (details given in Results). Asterisks denote meaningful variables for each model based upon a significant P-value and odds ratio.

Predictor	Coef.	SE Coef.	Z	P	Odds ratio
Upstream nontidal habitat model					
Constant	−0.63	1.68	−0.37	0.71	
*Backwater	1.86	0.71	2.64	<0.01	6.45
Temperature	0.06	0.09	0.70	0.49	1.06
Sp. conduct.	<−0.01	<0.01	−1.19	0.23	1.00
Sand	<0.01	0.01	0.27	0.79	1.00
Pavement	−0.01	0.01	−1.26	0.21	0.99
Pebble	<0.01	0.02	0.40	0.69	1.01
Downstream tidal habitat model					
Constant	−5.61	1.66	−3.38	<0.01	
*Offchannel	1.25	0.54	2.33	0.02	3.50
*Temperature	0.31	0.08	4.04	<0.01	1.37
Sp. conduct.	<0.01	<0.01	2.00	0.05	1.00
Mud	−0.02	0.01	−2.93	<0.01	0.98
Clay	0.08	0.08	1.04	0.29	1.09
Cobble	0.01	0.08	0.16	0.87	1.01
Silt	−0.08	0.07	−1.11	0.26	0.92

Napa River, 44; Sacramento River, 33; Petaluma River, 33; San Joaquin River, 27. Across locations, abundance was significantly higher in the Sacramento River (mean = 0.13) than the San Joaquin River (mean = 0.01; $F = 3.17$, MS = 0.01, df = 4, $P = 0.01$) but did not significantly differ among other location comparisons (mean abundances for other locations: Napa River = 0.09, Petaluma River = 0.05, Butte Slough = 0.03).

Age-0 Splittail were most common in offchannel habitats. In the logistic regression analyses, backwater was the only significant prediction variable of presence/absence of Splittail for the upstream nontidal habitat model, whereas offchannel and temperature were the only significant variables with meaningful odds ratios for the downstream tidal habitat model (Table 2). Both models did an adequate job of explaining the patterns in the data as indicated by a Pearson goodness-of-fit test (upstream model: Chi-square = 71.47, df = 67, $P = 0.33$; downstream model: Chi-square = 90.11, df = 74, $P = 0.10$). The upstream non-tidal model indicated that age-0 were 6.5 times more likely to be found in backwater habitats, and the downstream intertidal model indicated that age-0 were 3.5 times more likely to be found in offchannel habitats, irrespective of other habitat characteristics.

DISCUSSION

The maximum upstream distribution of Splittail appears to be greater than previously believed. Meng and Moyle (1995) concluded that the population was mostly limited to the San Francisco Estuary. Although the population appears to congregate seasonally in the estuary after the reproductive season, our data show that distribution consistently ranged at least 232–296 km upstream from the estuary. Moreover, the consistent capture of Splittail at the most upstream sampling location suggests that the sampling limit of the long-term monitoring survey was well within the habitat range of Splittail rather than at the periphery. This is supported by published reports and recent observations. Sommer et al. (1997) reported Splittail observed as far upstream as Hamilton City (rkm 331) on the Sacramento River. More recent observations by the California Department of Fish and Game confirm the periodic presence of Splittail at this location (Table 3). The current maximum upstream observation of Splittail (adults only) is the Red Bluff Diversion Dam (rkm 391; Baxter, 1999; T. R. Sommer, R. Baxter, and F. Feyrer, unpubl.). We know of no other sampling conducted between Hamilton City and Red Bluff or above Red Bluff to establish the upstream limit to spawning. Upstream dams

TABLE 3. TOTAL ANNUAL AGE-0 SPLITTAIL CATCH FROM JANUARY TO JUNE WITHIN BUTTE SLOUGH ADJACENT TO SUTTER BYPASS BY CALIFORNIA DEPARTMENT OF FISH AND GAME (CDFG) ROTARY SCREW TRAP MONITORING (RST) AND TOTAL MONTHLY AGE-0 SPLITTAIL CATCH NEAR THE GLENN-COLUSA IRRIGATION DISTRICT INTAKE (GCID; RIVER KILOMETER 331) BY CDFG RST.

Year	Total annual Butte Slough RST catch	Monthly GCID RST catch						
		Jun	Jul	Aug	Sep	Oct	Nov	Dec
1994				2	2	2	1	
1995				3	3		1	1
1996	2994					4		4
1997	1[a]		4	4	5	5		
1998	11,525[a]						3	
1999	85,856			1		1		
2000	334,146							
2001	58,476	2						
2002	196[b]							

[a] Because of extreme flow conditions traps were not deployed for most of 1997 and part of 1998.
[b] The number of traps deployed declined from three to one in 2002.

such as Shasta on the Sacramento River and Millerton on the San Joaquin River have undoubtedly limited the absolute distance Splittail can migrate upstream. However, it is unclear how abundant Splittail were in these regions historically or whether reproduction occurred at the limits of their distribution.

Splittail are strongly affected by river flow conditions. Previous studies (Meng and Moyle, 1995; Sommer et al., 1997) demonstrated that the strongest year classes are produced in the wettest years because of extensive floodplain inundation. Our analyses show that age-0 distributions are also affected by river flow conditions; centers of distribution were furthest upstream in low versus high and intermediate river flow years. We believe there are three mechanisms behind this pattern. First, large, low-elevation floodplains in the Yolo and Sutter Bypasses on the Sacramento River, typically are inundated during high and intermediate river flow years; hence, adults do not have to migrate as far upstream to find suitable spawning habitat. It is during these wet years that large numbers of Splittail are produced on floodplains and subsequently appear in the adjacent river channel in high abundance when floodwaters recede (Sommer et al., 1997). Second, changes in stage height and current velocity during high and intermediate flow years appear to cause Splittail larvae to disperse off of floodplains resulting in downstream displacement; Sommer et al. (1997) found significantly higher concentrations of Splittail larvae within bypass discharge plumes compared to other habitats in the main river channel. Under this scenario, young Splittail may be transported downstream of their hatch location, potentially all the way to the Sacramento–San Joaquin Delta, before they are large enough for capture by sampling gear that targets juveniles. Finally, lower Splittail production in Sutter and Yolo Bypasses in dry years may effectively shift the center of age-0 distribution further upstream. The lack of lower river spawning habitat caused by contiguous riprapped banks necessitates migration to at least the American River confluence (rkm 95) and generally past Verona (rkm 129) to locate sizable areas of riparian vegetation susceptible to inundation by modest river stage increases.

Environmental factors may also influence the early summer downstream migration of age-0 Splittail from spawning regions to the Sacramento-San Joaquin Delta. This migration is probably triggered when river stage declines and the amount of upstream low velocity off-channel habitat is reduced. Food availability and temperature preferences may also influence age-0 Splittail migrations, as suggested for another large migratory cyprinid native to the western United States, the Colorado Pikeminnow (*Ptychocheilus lucius*; Osmundson et al., 1998). There is limited evidence suggesting some Splittail exhibit alternative life-history strategies in the form of permanent or at least prolonged upstream residency. Rotary screw trap monitoring by the California Department of Fish and Game has collected juveniles year-round near the Glenn-Colusa Irrigation District intake (rkm 331) from 1994 to 2001 (Table 3). The duration that such fish remain upstream is not known, nor is it known why they remain upstream when the majority of the population moves downstream to the delta and estuary. Alternative or divergent migratory pathways are known for many fishes (Secor, 1999; Moyle, 2002); however, mechanisms behind such patterns are poorly understood. It is plausible that in the dynamic environment of the San Francisco Estuary, these individuals constitute a contingency population to ensure persistence of the species in the face of unpredictable environmental conditions (Secor, 1999).

The migratory behavior exhibited by Splittail appears to be a trait shared by many native fishes inhabiting large river systems of the western United States. Several species of cyprinids and catostomids make similar long-distance migrations in the Colorado River (Moyle, 2002). In the San Francisco Estuary watershed, Splittail is one of a suite of large-sized cyprinids that live as adults in the fresh and brackish water portions of the upper estuary and migrate upstream for spawning. The Sacramento Pikeminnow (*Ptychocheilus grandis*) migrates upstream to spawn in late spring or early summer (Moyle, 2002). However, in contrast to Splittail, most Sacramento pikeminnow offspring remain in upstream habitats until significant outflow events occur the following spring (M. Nobriga, F. Feyrer, and R. Baxter, unpubl.). Hitch (*Lavinia exilicauda*) and Sacramento Blackfish (*Orthodon macrolepidotus*) also make upstream spawning migrations but are relatively unstudied in the Sacramento–San Joaquin Delta. Although migrations have not been fully documented for Sacramento Blackfish, adults and young-of-year have been collected seasonally in association with inundation events of upstream floodplains (Harrell and Sommer, 2003; Crain et al., 2004; Sommer et al., 2004). Studies in nearby Clear Lake (Lake County, CA) have shown that Hitch exhibit spring spawning migrations into tributaries and that offspring immediately return downstream to the lake (Murphy, 1948). Moyle (2002) suggested that this behavior contributed to the success of Hitch in that it enabled them to spawn in intermittent streams that dry in summer. The same statement can be made for Splittail in regards to spawning on seasonally inundated floodplains and river margins.

Splittail and other native fishes appear to share general migration characteristics (i.e., upstream spawning migrations triggered by environmental cues such as flooding) with numerous other cyprinids worldwide, but with subtle differences that can be attributed to their local environment (Lucas and Baras, 2001). Perhaps the most similar behavior is exhibited by the cyprinid *Hemibarbus barbus* in the Chikugo River of Japan (Lucas and Baras, 2001). Once mature, adults migrate from low salinity (2‰) tidal waters upstream 20–40 km into the middle reaches of the river for spawning. Offspring ultimately move downstream and become abundant in tidal waters by midsummer. A review by Lucas and Baras (2001) found that movement of cyprinids between fresh and brackish water appears most common in Europe and Asia, whereas upstream migration following flooding appears most common in the Middle East and Africa. Lucas and Baras (2001) also noted that many cyprinids in Mediterranean climates remain in upstream disconnected waters during summer and rejoin main stem reaches when flows increase and inundate the previously isolated habitats. Although the local conditions are well suited for it, Splittail apparently do not exhibit this behavior. Feyrer et al. (2004) found Splittail absent from perennial habitats in the Yolo Bypass floodplain between inundation events.

Regions of substantial Splittail production appear to be more widespread than previously believed. Moyle et al. (2004) suggested there was little evidence for persistent production outside of the San Francisco Estuary and lower Sacramento River. Our data documenting abundant age-0 Splittail in 2002 (a dry year) and 2003 (a moderately wet year) in the Petaluma, Napa, and San Joaquin Rivers indicate these regions are important regions of Splittail production. Persistent observations of Splittail in Butte Slough (this study; California Department of Fish and Game, unpublished data [Table 3]) and the Cosumnes River (Caywood, 1974; Crain et al., 2004) suggest that smaller tributaries can have substantial Splittail production. The levels of genetic diversity, gene flow, and the degree of relatedness among fish spawning at these geographically disparate regions is unknown. Such information would be vital in identifying evolutionarily significant units or management units and aid in the formulation and implementation of actions that might be needed to help conserve this species of concern.

Age-0 Splittail are most common in offchannel habitats, specifically backwaters in upstream riverine locations and broad shoals or channels of intertidal habitat in downstream tidal locations. Off-channel habitats are important for a number of native fishes of the western United States (Tyus and Hines, 1991; Modde et al., 2001; Scheerer, 2002) and cyprinids in general (Holland and Huston, 1985; Holland, 1986; Shaeffer and Nickum, 1986). In this system, such habitats probably represent optimal rearing locations because they are typically warmer, shallower, and more productive than adjacent channel habitats. We found, on average, that backwaters were two degrees warmer than immediately adjacent main channel habitats in instances when we had side-by-side samples (range: 0.0–8.9; SD: 2.9). Corollary explanatory mechanisms are provided by Sommer et al. (2001). They showed that offchannel floodplain habitat provided optimal rearing conditions compared to the adjacent Sacramento River channel for juvenile Chinook salmon because of warmer water temperatures and enhanced food resources. In a model floodplain study (Sommer et al., 2002), age-0 Splittail were most abundant in the shallowest habitats available near vegetation. The relative risk of predation in offchannel versus adjacent channel habitats is unknown and should be studied; studies on young cyprinids have shown that habitat use can be governed by food availability and predation risk (Garner, 1996; Harvey, 1991; MacRae and Jackson, 2001).

Our findings have several immediate implications for habitat restoration and conservation that exemplify scenarios encountered in highly regulated systems throughout the world. First, the continued loss of low-velocity shallow water habitats caused by the construction of riprapped levees that prevent channel meander, characteristic of so many large regulated rivers, is problematic for many native species including Splittail. Because these habitats are important nursery areas for young Splittail and other native fishes (Moyle, 2002), existing upstream backwaters and downstream tidal marshes should be preserved, and future restoration projects should consider incorporating these low-velocity offchannel habitats. Additionally, creating such habitats so that they are seasonally inundated will limit their use by alien fishes while maximizing their benefit for natives (Brown, 2003). Second, the Splittail's potential risk to catastrophic events such as extinction are probably somewhat lower than previously believed since the species occupies a significantly greater range than that considered when it was first petitioned for listing as a threatened species. However, this also indicates that conservation and restoration efforts will have to be greatly expanded in scope to provide optimal benefits to Splittail.

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Literature Cited

Aceituno, M. E., M. L. Caywood, S. J. Nicola, and W. I. Follet. 1976. Occurrence of native fishes in Alameda and Coyote creeks, California. Calif. Fish Game 62:195–206.

Baxter, R. D. 1999. Status of splittail in California. *Ibid.* 85:28–30.

Brandes, P. L., and J. S. McLain. 2001. Juvenile Chinook Salmon abundance, distribution, and survival in the Sacramento–San Joaquin Estuary, p. 39–138. *In:* Contributions to the biology of Central Valley salmonids. R. L. Brown (ed.). California Fish and Game, Fish Bulletin 179, Vol. 2, Sacramento.

Brown, L. R. (ed.). Issues in San Francisco Estuary tidal wetlands restoration. San Francisco Estuary and Watershed Science 1:2(October 2003); http://repositories.cdlib.org/jmie/sfews/vol1/iss1/art2.

Caywood, M. L. 1974. Contributions to the life history of the Splittail *Pogonichthys macrolepidotus* (Ayres). Unpubl. master's thesis, California State Univ., Sacramento.

Crain, P. K., K. Whitener, and P. B. Moyle. 2004. Use of a restored central California floodplain by larvae of native and alien fishes, p. 125–140. *In:* Early life history of fishes in the San Francisco Estuary and watershed. F. Feyrer, L. R. Brown, R. L. Brown, and J. J. Orsi (eds.). American Fisheries Society, Symposium 39, Bethesda, MD.

Daniels, R. A., and P. B. Moyle. 1983. Life history of the Splittail (Cyprinidae: *Pogonichthys macrolepidotus*) in the Sacramento–San Joaquin Estuary. Fish. Bull. 84:105–117.

Dege, M., and L. R. Brown. 2004. Effect of outflow on spring and summer distribution and abundance of larval and juvenile fishes in the upper San Francisco Estuary, p. 49–65. *In:* Early life history of fishes in the San Francisco Estuary and watershed. F. Feyrer, L. R. Brown, R L Brown, and J. J. Orsi (eds.). American Fisheries Society, Symposium 39, Bethesda, MD.

Feyrer, F., T. R. Sommer, S. C. Zeug, G. O'Leary, and W. Harrell. 2004. Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA), with implications for the conservation of native fishes. Fish. Manag. Ecol. 11:335–344.

Garner, P. 1996. Diel patterns in the feeding and habitat use of 0-group fishes in a regulated river: the River Great Ouse, England. Ecol. Freshwater Fish 5:175–182.

Harrell, W. C., and T. R. Sommer. 2003. Patterns of adult fish use on California's Yolo Bypass floodplain, p. 88–93. *In:* California riparian systems: processes and floodplain management, ecology, and restoration. P. M. Faber (ed.). 2001 Riparian Habitat and Floodplains Conference Proceedings, Riparian Habitat Joint Venture, Sacramento, CA.

HARVEY, B. C. 1991. Interaction of abiotic and biotic factors influences larval fish survival in an Oklahoma stream. Can. J. Fish. Aquat. Sci. 48:1476–1480.

HOLLAND, L. E. 1986. Distribution of early life stages of fishes in selected pools of the upper Mississippi River. Hydrobiologia 136:121–130.

———, AND M. L. HUSTON. 1985. Distribution and food habits of young-of-year fishes in a backwater lake of the upper Mississippi River. J. Freshwater Ecol. 3:81–91.

LUCAS, M. C., AND E. BARAS. 2001. Migration of freshwater fishes. Blackwell Science, Iowa State Univ. Press, Ames.

MACRAE, P. M. S., AND D. A. JACKSON. 2001. The influence of Smallmouth Bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. Can. J. Fish. Aquat. Sci. 58:342–351.

MATTHEWS, W. J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, London.

MENG, L., AND P. B. MOYLE. 1995. Status of Splittail in the Sacramento-San Joaquin Estuary. Trans. Am. Fish. Soc. 124:538–549.

MODDE, T., R. T. MUTH, AND G. B. HAINES. 2001. Floodplain wetland suitability, access, and potential use by juvenile razorback suckers in the Middle Green River, Utah. *Ibid.* 130:1095–1105.

MOYLE, P. B. 2002. Inland fishes of California. Rev. exp. Univ. of California Press, Berkeley.

———, AND J. J. CECH JR. 2004. Fishes: an introduction to ichthyology. 5th ed. Prentice Hall, Englewood Cliffs, NJ.

———, R. D. BAXTER, T. R. SOMMER, T. C. FOIN, AND S. A. MATERN. 2004. Biology and population dynamics of Sacramento Splittail (*Pogonichthys macrolepidotus*) in the San Francisco Estuary: a review. San Francisco Estuary and Watershed Science 2:2(May 2004), Article 3; http://repositories.cdlib.org/jmie/sfews/vol2/iss2/art3.

MURPHY, G. I. 1948. Notes on the biology of the Sacramento Hitch (*Lavinia e. exilicauda*) of Clear Lake, California. Calif. Fish Game 34:101–110.

OSMUNDSON, D. B., R. J. RYEL, M. E. TUCKER, B. D. BURDICK, W. R. ELMBLAD, AND T. E. CHART. 1998. Dispersal patterns of subadult and adult Colorado Squawfish in the upper Colorado River. Trans. Am. Fish. Soc. 127:943–956.

ROSS, M. R. 1997. Fisheries conservation and management. Prentice Hall, Englewood Cliffs, NJ.

SCHEERER, P. D. 2002. Implications of floodplain isolation and connectivity on the conservation of an endangered minnow, Oregon Chub, in the Willamette River, Oregon. Trans. Am. Fish. Soc. 131:1070–1080.

SECOR, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish. Res. 43:13–34.

SHAEFFER, W. A., AND J. G. NICKUM. 1986. Backwater areas as nursery habitat for fishes in pool 13 of the upper Mississippi River. Hydrobiologia 136:131–140.

SOMMER, T. R., R. BAXTER, AND B. HERBOLD. 1997. Resilience of Splittail in the Sacramento-San Joaquin Estuary. Trans. Am. Fish. Soc. 126:961–976.

———, M. L. NOBRIGA, W. C. HARRELL, W. BATHAM, AND W. J. KIMMERER. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. Can. J. Fish. Aquat. Sci. 58: 325–333.

———, L. CONRAD, G. O'LEARY, F. FEYRER, AND W. C. HARRELL. 2002. Spawning and rearing of Splittail in a model floodplain wetland. Trans. Am. Fish. Soc. 131:966–974.

———, W. C. HARRELL, R. KURTH, F. FEYRER, S. C. ZEUG, AND G. O'LEARY. 2004. Ecological patterns of early life stages of fishes in a river-floodplain of the San Francisco Estuary, p. 111–123. *In:* Early life history of fishes in the San Francisco Estuary and watershed. F. Feyrer, L. R. Brown, R. L. Brown, and J. J. Orsi (eds.). American Fisheries Society, Symposium 39, Bethesda, MD.

SNYDER, J. O. 1905. Notes on the fishes of the streams flowing into San Francisco Bay, California. U.S. Bur. Fish. Rpt. 1904:327–338.

STANFORD, J. A., J. V. WARD, W. J. LISS, C. A. FRISSEL, R. N. WILLIAMS, J. A. LICHATOWICH, AND C. C. COUTANT. 1996. A general protocol for restoration of regulated rivers. Reg. Riv. Res. Manag. 12:391–413.

TREXLER, J. C., AND J. TRAVIS. 1993. Nontraditional regression analyses. Ecology 74:1629–1637.

TYUS, H. M., AND G. B. HAINES. 1991. Distribution, habitat use, and growth of age-0 Colorado Squawfish in the Green River Basin, Colorado and Utah. Trans. Am. Fish. Soc. 120:79–89.

YOUNG, P. S., AND J. J. CECH JR. 1996. Environmental tolerances and requirements of Splittail. Trans. Am. Fish. Soc. 125:664–678.

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