RIVER RESEARCH AND APPLICATIONS

River. Res. Applic. (2009)

Published online in Wiley InterScience
(www.interscience.wiley.com) DOI: 10.1002/rra.1293

EFFECTS OF HYDROLOGIC INFRASTRUCTURE ON FLOW REGIMES OF CALIFORNIA'S CENTRAL VALLEY RIVERS: IMPLICATIONS FOR FISH POPULATIONS[†]

LARRY R. BROWN* and MARISSA L. BAUER

U.S. Geological Survey, Placer Hall, 6000 J Street, Sacramento, CA 95819-6129, USA

ABSTRACT

Alteration of natural flow regimes is generally acknowledged to have negative effects on native biota; however, methods for defining ecologically appropriate flow regimes in managed river systems are only beginning to be developed. Understanding how past and present water management has affected rivers is an important part of developing such tools. In this paper, we evaluate how existing hydrologic infrastructure and management affect streamflow characteristics of rivers in the Central Valley, California and discuss those characteristics in the context of habitat requirements of native and alien fishes. We evaluated the effects of water management by comparing observed discharges with estimated discharges assuming no water management ('full natural runoff'). Rivers in the Sacramento River drainage were characterized by reduced winter–spring discharges and augmented discharges in other months. Rivers in the San Joaquin River drainage were characterized by reduced discharges in all months but particularly in winter and spring. Two largely unaltered streams had hydrographs similar to those based on full natural runoff of the regulated rivers. The reduced discharges in the San Joaquin River drainage streams are favourable for spawning of many alien species, which is consistent with observed patterns of fish distribution and abundance in the Central Valley. However, other factors, such as water temperature, are also important to the relative success of native and alien resident fishes. As water management changes in response to climate change and societal demands, interdisciplinary programs of research and monitoring will be essential for anticipating effects on fishes and to avoid unanticipated ecological outcomes. Published in 2009 by John Wiley & Sons, Ltd.

KEY WORDS: flow regime; hydrologic infrastructure; water management; native fishes; alien fishes; dams; California

Received 27 February 2009; Revised 22 May 2009; Accepted 9 June 2009

INTRODUCTION

There is wide consensus among aquatic ecologists that alteration of natural flow regimes often results in negative effects on native biota (e.g. Williams *et al*., 1993; Webb *et al*., 1999; Pringle *et al*., 2000; Moyle and Mount, 2007). Studies around the world have clearly shown the importance of natural flow regimes in maintaining the condition of rivers, floodplains and estuaries (Arthington *et al*., 1992; Sparks, 1995; Walker *et al*., 1995; Poff *et al*., 1997; Bunn and Arthington, 2002; Poff *et al*., 2007). In addition, it has been well established that degradation of river ecosystems can have negative effects on the ecosystem services that humans expect to derive from rivers, including commercial, recreational and subsistence fisheries, water purification, flood storage, recreation and aesthetic values (Postel and Richter, 2003; Richter *et al*., 2003; Annear *et al*., 2004). Despite the acceptance of the 'natural flow-regime paradigm' (Richter *et al*., 1996; Poff *et al*., 1997; Lytle and Poff, 2004; Poff *et al*., 2006a), tools for defining and implementing ecologically appropriate flow regimes in managed river systems are only now being developed (Arthington *et al*., 2006; Kondolf *et al*., 2007; Mathews and Richter, 2007; Richter and Thomas, 2007). This interface between water management and maintenance of aquatic resources represents a difficult challenge to resource managers (Postel, 1996, 2000; Jackson *et al*., 2001).

An integral part of the strategy for meeting this challenge is to understand how past and present water management has affected the flow regime of river ecosystems and how the resulting flow regimes have affected aquatic biota (e.g. Poff *et al*., 2007). The Central Valley of California (Figure 1) provides an excellent opportunity

*Correspondence to: Larry R. Brown, U.S. Geological Survey, Placer Hall, 6000 J Street, Sacramento, CA 95819-6129, USA.
E-mail: lrbrown@usgs.gov

[†]This article is a U.S. Government work and is in the public domain in the U.S.A.

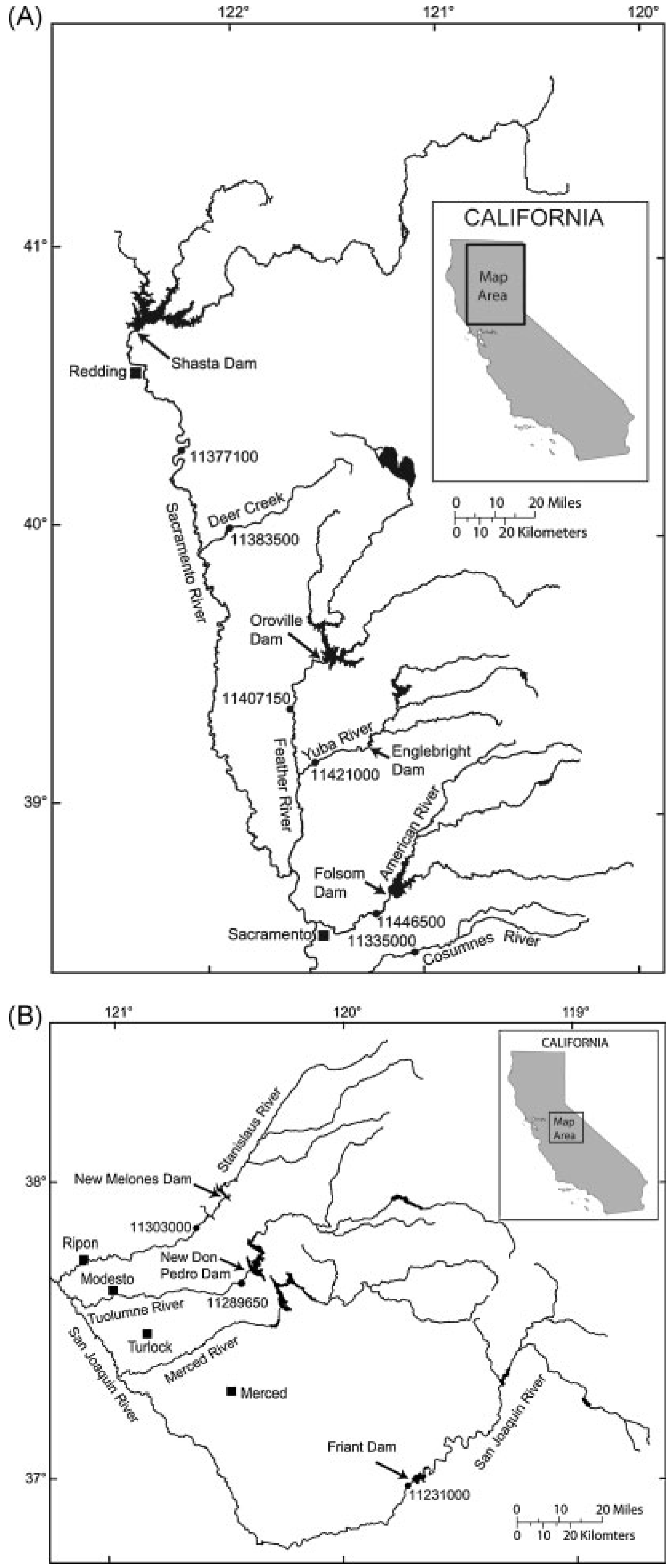

Figure 1. Study basins in the (A) Sacramento River drainage system, including the Cosumnes River, and (B) San Joaquin drainage system

DOI: 10.1002/rra

to evaluate the effects of water management on flow regime. The Central Valley encompasses two large river drainages, the Sacramento River drainage to the north and the San Joaquin River drainage to the south. These drainages include about 40% of surface area of California but collect about 50% of the surface runoff. An extensive system of hydrologic infrastructure, including dams, reservoirs, diversions and aqueducts, not only supports extensive agricultural and municipal uses within the Central Valley but provides drinking water to many areas of densely populated California (Mount, 1995; CALFED, 2007; Lund *et al*., 2007). In total, the system provides water to about 25 million Californians and supports a multi-billion dollar agricultural economy.

Water development in the Central Valley has had widespread effects on aquatic resources of which fish populations are the best studied. Dam construction has isolated anadromous fish populations from large portions of their historical spawning habitat (Yoshiyama *et al*., 2001) with negative effects on population structure (Schick and Lindley, 2007). Hydrologic infrastructure, used as a surrogate for water management, has been associated with the success of introduced fishes, which compete with and prey on native fishes (Light and Marchetti, 2007). Restoration of flows has been associated with recovery of native fishes (Marchetti and Moyle, 2001). May and Brown (2002) suggested that different strategies of water management in the Sacramento and San Joaquin drainages had different outcomes for native species. The rivers in the San Joaquin River drainage are generally managed for water diversions into canal systems, which seem to favour introduced fishes (Brown, 2000; Brown and Ford, 2002). The rivers in the Sacramento River system are generally managed for in-channel water delivery to large diversion pumps in the Sacramento-San Joaquin Delta. These operations seem to aid in maintenance of native fish populations in the freshwater river channels (May and Brown, 2002); however, there is evidence for some negative effects in the Delta (Sommer *et al*., 2007). Thus, it is clear that flow regime is important to California fish communities but the discussion of this relationship has remained general. The main reason for lack of detail is that no comprehensive assessment of the ecological implications of flow regime exists for California river systems.

The purpose of this paper is to provide an ecologically-oriented assessment of the streamflow characteristics of selected Central Valley rivers. We include four major rivers in the Sacramento River system (American, Yuba, Feather and Sacramento), three major rivers in the San Joaquin River system (San Joaquin, Tuolumne and Stanislaus) and two of the largest remaining undammed streams in the Central Valley (Deer Creek and Cosumnes River) (Figure 1). We use the Indicators of Hydrologic Alteration (IHA) software (TNC, 2007) to address our primary question: How does the existing hydrologic infrastructure and management affect the streamflow characteristics of each river compared to natural flows? We also interpret these results in the context of existing knowledge of how native and alien fishes respond to streamflow characteristics.

METHODS

Our basic approach was to compare estimates of 'full natural runoff' (FNR) with measured streamflow (observed; OBS) for the time period after completion of the most recent major unpassable downstream dam (Table I). We chose this comparison to avoid potential problems with before–after dam construction comparisons, such as variability associated with climate oscillations like the Pacific Decadal Oscillation or ongoing climate change (Barnett *et al*., 2008). We obtained estimates of FNR for the rivers of interest through the late 1990s from a data set prepared by the National Weather Service for a comprehensive study of river infrastructure conducted by the U.S. Army Corps of Engineers (2002). Data through 2006 were obtained from the California Data Exchange Center (CDEC; http://cdec.water.ca.gov/). Observed flow data were generally obtained from USGS gauges (Table I).

Estimates of FNR are calculated based on a number of measurements from the upper watershed, including precipitation, gauge records and reservoir levels. Basically, inflows from precipitation are adjusted for water storage, water diversions and reservoir releases to estimate flows in the absence of such manipulation (CDEC; http://cdec.water.ca.gov/). These estimates should not be interpreted as 'true' unimpaired historical streamflows because the reconstructions do not account for changes in the historic channel configuration (e.g. loss of side channels) or changes in land use (e.g. deforestation, agriculture).

On the Feather River, we incorporated OBS data from the California Department of Water Resources, which we obtained from CDEC for water years 1999 to the present (a water year starts on 1 October of the previous year and ends on 30 September) because the USGS gauge was discontinued. We calculated a regression for a period of

DOI: 10.1002/rra

Table I. U.S. Geological Survey stream gauge numbers, watershed characteristics and dam characteristics for rivers analysed in this study. Pre-dam storage capacity refers to the summed capacity of all reservoirs that existed before completion of the dam described in previous columns

Station name	USGS gauge number	Drainage area (km^2)	Maximum elevation (m)	Mean elevation (m)	Name of dam	Year completed	Storage capacity (10^6 m^3)	Pre-dam storage capacity (10^6 m^3)
Sacramento River drainage								
Sacramento River above Bend Bridge near Red Bluff	11377100	23 051	4303	1207	Shasta	1943	5472	192
Feather River near Gridley	11407150	9521	2783	1518	Oroville	1967	4364	1934
Yuba River near Marysville	11421000	3468	2761	1287	Englebright	1941	86	271
American River at Fair Oaks	11446500	4890	3162	933	Folsom	1956	1246	46
Deer Creek near Vina	11383500	539	2394	1280	none			
San Joaquin River drainage								
Stanislaus River below Goodwin Dam near Knights Ferry	11302000	2554	3519	1617	New Melones	1978	2985	261
Tuolumne River below LaGrange Dam near La Grange	11289650	3983	3973	1790	New Don Pedro	1970	2504	825
San Joaquin River below Friant	11251000	4341	2119	2119	Friant	1941	642	462
Mokelumne River drainage								
Cosumnes River at Michigan Bar	11335000	1388	2355	933	none			

DOI: 10.1002/rra

Table II. Selected flow variables and definitions (see TNC, 2007 for details) used in this paper. Criteria for flow events (floods, pulses and extreme low flows) are based on values derived from the full natural runoff (FNR) data record

Variable	Definition
Annual mean daily discharge*	Mean of daily discharge.
Flow predictability*	Ranges from 0 (low predictability) to 1 (high predictability). The sum of constancy (C), a measure of temporal invariance and contingency (M), a measure of periodicity. See Colwell (1974) for details.
Constancy/predictability*	C/(C+M), the proportion of predictability due to constancy.
Flood free season*	Number of days in the longest period common to all water years when flows are at or below the 75th percentile of the FNR data record in every year.
30-day minimum flow ($m^3 s^{-1}$)†	Minimum of 30-day running average of daily flows.
30-day maximum flow ($m^3 s^{-1}$)†	Maximum of 30-day running average of daily flows.
Baseflow†	Minimum 7-day running average of daily flows/annual mean flow for year.
High pulse frequency†	Frequency of flow events with flows greater than the 75th percentile of the FNR data record.
High pulse duration (d)†	Duration in days of high flow pulses.
Low pulse frequency†	Frequency of flow events with flows less than the 25th percentile of the FNR data record.
Low pulse duration (d)†	Duration in days of low flow pulses.

*These values are calculated for the entire period of record.
†These values are calculated for each water year.

overlap between 1 January 1993 and 30 September 1998. The state gauge gave slightly lower readings (State gauge $= 0.92 \times$ USGS gauge, $r^2 = 0.98$). We did not correct the state readings for this analysis but keep the discrepancy in mind when interpreting results.

We analysed flow records using the IHA software. These analyses were conducted using the default nonparametric option analyses built into the software. We concentrated our analyses on variables at time scales of monthly or longer (Table II), because estimates of FNR can vary somewhat from day to day, especially during low flow periods when measurement error can be large relative to estimated values. During the summer low flow period, FNR is sometimes estimated as a small negative number due to errors in measurements such as reservoir volumes. All such values were converted to zeros for analyses. We compared values of our selected flow variables between the FNR and OBS time periods using the nonparametric Mann–Whitney *U* test.

We selected a number of fish species as representative of native anadromous, native resident and alien resident fishes commonly occurring in the rivers analysed in this study (Table III) (Brown, 2000; Marchetti and Moyle, 2001; Brown and Ford, 2002; May and Brown, 2002; Moyle, 2002). Although the environmental tolerances and habitat utilization of the adults of these species often broadly overlap (Brown and Moyle, 1993, 2005; Moyle, 2002), the spawning requirements of the species are fairly specialized and it has been hypothesized that relative spawning success is a major factor determining the relative population sizes of native and alien species (Marchetti and Moyle, 2000; Brown and Ford, 2002). Therefore, we compiled information on spawning characteristics of each species and discuss observed hydrologic changes in the context of species spawning success.

RESULTS

The rivers we examined varied widely in drainage area and reservoir storage capacity (Table I). Except for the Yuba River and the San Joaquin River, the downstream dam of interest in this study added significant storage capacity to the system (Table I). Differences in water management in the Sacramento and San Joaquin drainages are clearly shown by differences in annual mean daily discharge (Table IV). In the Sacramento drainage, annual mean daily discharge for the OBS data was within 20% of the FNR value for all the rivers. In the San Joaquin River drainage, annual mean daily discharge for the OBS data was 33–52% of the FNR data.

Flow predictability (constancy + periodicity) did not exhibit large differences between the FNR and OBS data; however, there were larger differences in the constancy/predictability ratio between the FNR and OBS data. The

DOI: 10.1002/rra

Table III. Spawning characteristics of selected native and alien fishes

Species	Common name	Spawning period*	Spawning temperature*	Spawning behavior‡	Spawning habitat*	Spawning substrate*
Native anadromous						
Oncorhynchus mykiss	Rainbow trout (steelhead)	Dec–June	$< 13°C$	Simple nester	Flowing water	Gravel
Oncorhynchus tshawytscha	Chinook salmon (fall-run)	Oct–Mar	5–13°C	Simple nester	Flowing water	Gravel–cobble
Resident native						
Catostomus occidentalis	Sacramento sucker	Mar–May	12–18°C	Broadcast	Riffles, flowing water	Gravel–cobble
Cottus asper	Prickly sculpin	Feb–Jun	8–13°C	Complex nester	Flowing water	Cobble
Cottus gulosus	Riffle sculpin	Feb–Apr	$< 15°C$	Complex nester	Riffles, flowing water	Cobble
Ptychocheilus grandis	Sacramento pikeminnow	Apr–May	15–20°C	Broadcast	Riffles, flowing water	Gravel–cobble
Mylopharodon conocephalus	Hardhead	Apr–May	15–20°C†	Broadcast	Riffles, flowing water	Gravel
Resident alien						
Cyprinella lutrensis	Red shiner	June–July	15–30°C	Simple nester	No or little flow	Substrate, vegetation, other structure
Dorosoma petenense	Threadfin shad	Apr–Aug	$> 20°C$	Broadcast	No or little flow	Vegetation, other structure
Lepomis macrochirus	Bluegill	Spring	> 18–21°C	Complex nester	No or little flow	Mud–gravel
Lepomis microlophus	Redear sunfish	Summer	> 21–24°C	Complex nester	No or little flow	Mud–gravel
Menidia audens	Mississippi silverside	Apr–Sep	15–30°C	Broadcast	No or little flow	Vegetation, other structure
Micropterus salmoides	Largemouth bass	Apr–June	15–24°C	Complex nester	No or little flow	Sand–gravel
Micropterus dolomieu	Smallmouth bass	May–July	> 13–16°C	Complex nester	No or little flow	Sand–cobble
Micropterus coosae	Redeye bass	Late spring	> 17–21°C	Complex nester	Flowing water	Gravel

*Approximate spawning period, spawning temperature, spawning habitat and spawning substrate based on Moyle (2002). Exact spawning periods dependent on water temperatures and other environmental factors.
†Assumed to be similar to Sacramento pikeminnow based on Moyle (2002).
‡Based on Meador and Goldstein and Meador (2004). Broadcast, eggs distributed indiscriminately across spawning substrate; simple nester, use a rudimentary nesting surface that is excavated in the substrate or constructed from substrate; complex nester, some level of parental care provided by adult.

DOI: 10.1002/rra

Table IV. Values for selected hydrologic parameters calculated for estimated full natural runoff (FNR) and observed (OBS) flows

	Flow record	Annual mean daily discharge ($m^3 s^{-1}$)		Flow predictability		Constancy/ predictability		Flood-free season (d)	
		FNR	OBS	FNR	OBS	FNR	OBS	FNR	OBS
Sacramento River drainage									
Sacramento River above Bend Bridge near Red Bluff	1945–2006	351	352	0.53	0.61	0.76	0.85	70	23
Feather River near Gridley	1968–2006	167	135	0.35	4.42	0.48	0.80	99	39
Yuba River near Marysville	1944–2006	79	69	0.36	0.30	0.43	0.60	17	66
American River at Fair Oaks	1957–2006	108	106	0.35	0.44	0.39	0.82	35	23
Deer Creek near Vina	1921–2006	na	9	na	0.44	na	0.71	na	86
San Joaquin River drainage									
Stanislaus River below Goodwin Dam near Knights Ferry	1979–2006	48	23	0.36	0.39	0.47	0.74	19	85
Tuolumne River below LaGrange Dam near La Grange	1972–2006	75	28	0.36	0.28	0.39	0.53	22	49
San Joaquin River below Friant	1944–2006	70	23	0.38	0.35	0.43	0.67	26	111
Mokelumne River drainage									
Cosumnes River at Michigan Bar	1908–2006	na	14	na	0.35	na	0.33	na	94

greater values for the OBS data indicate that a greater portion of predictability is due to constancy of flow. The flood-free season was generally shorter for the OBS data in the Sacramento River drainage rivers, except for the Yuba River, and was longer for the OBS data in the San Joaquin River drainage.

Patterns in monthly flow were very different between the FNR and OBS data for all streams in the Sacramento River drainage (Figure 2). In general the hydrograph was flattened. Winter–spring high discharges, generally March

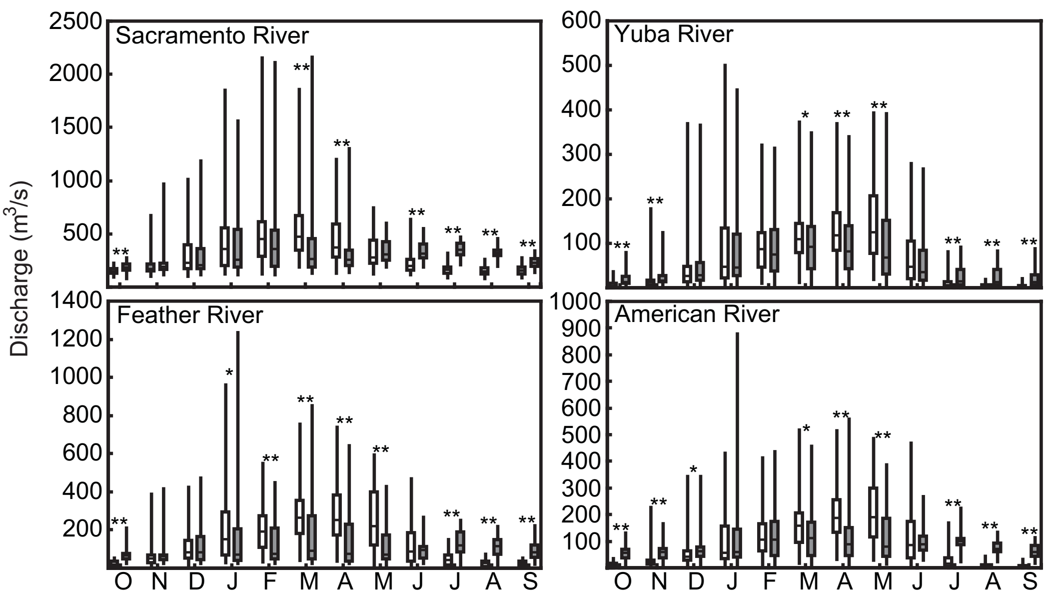

Figure 2. Median monthly discharge for estimated full natural runoff (open bars) and observed flow (filled bars) for rivers in the Sacramento River drainage. Statistically significant differences are indicated by asterisks (*, $p < 0.05$, **, $p < 0.01$). Key to boxplots: median, horizontal line; box, 25th and 75th percentiles; whiskers, range

DOI: 10.1002/rra

through May, were reduced by dam operations. Discharges in the remaining months were augmented or unchanged. In the Feather River, significant declines also occurred in January and February (Figure 2).

Patterns in monthly discharge were also very different between FNR and OBS data for all streams in the San Joaquin River drainage (Figure 3). In contrast to the rivers in the Sacramento River drainage, the OBS data were characterized by water withdrawal from the system. Median monthly OBS flows were similar to or less than FNR

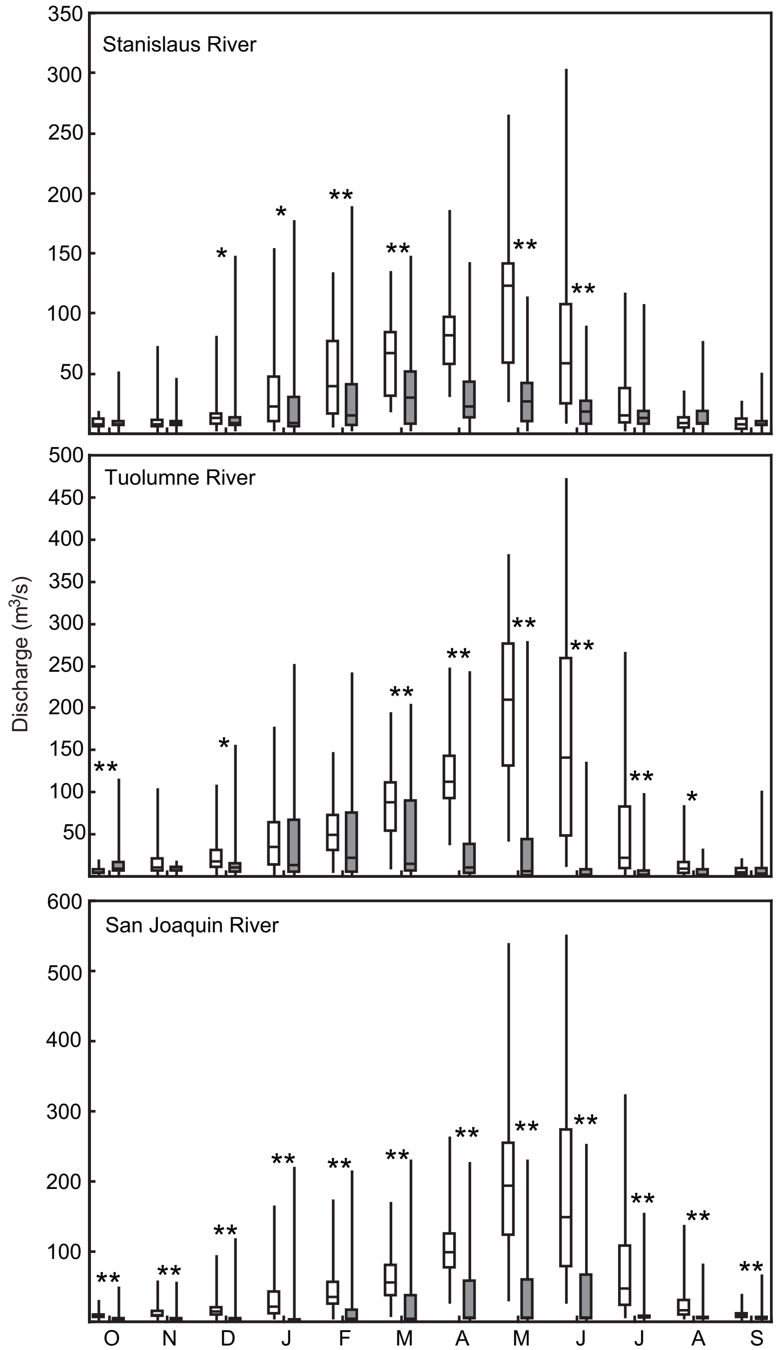

Figure 3. Median monthly discharge for estimated full natural runoff (open bars) and observed flow (filled bars) for rivers in the San Joaquin River drainage. Statistically significant differences are indicated by asterisks (*, $p < 0.05$, **, $p < 0.01$). Key to boxplots: median, horizontal line; box, 25th and 75th percentiles; whiskers, range

DOI: 10.1002/rra

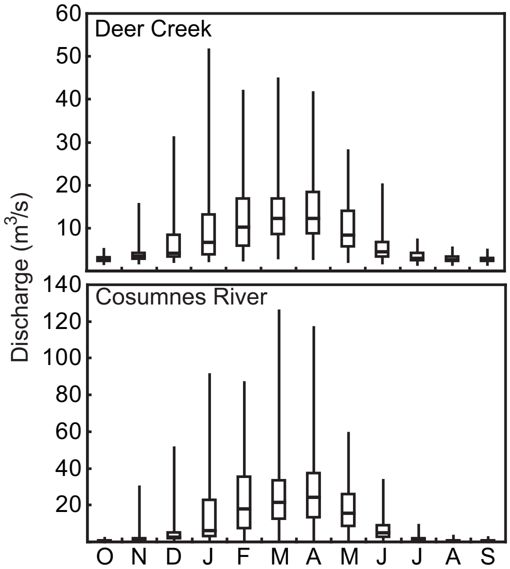

Figure 4. Median monthly discharge for Deer Creek and Cosumnes River, which do not have major storage reservoirs in their drainages. Key to boxplots: median, horizontal line; box, 25th and 75th percentiles; whiskers, range

flows in almost every comparison. There was a slight but statistically significant augmentation in October in the Tuolumne River. The largest differences in median discharge occurred in April, May and June.

Patterns for monthly flow for the two undammed streams (Figure 4) are most similar to the FNR data for the Sacramento and Feather Rivers (Figure 2). Highest flows occurred in February, March and April for these rivers with high flows extending through May. The other rivers tended to have their highest flows several months later in April, May or June. Low flows in Deer Creek approached zero and surface water flow ceased in the Cosumnes River in some years.

Values for the selected IHA statistics differed between FNR and OBS data in almost all cases (Table V). The 30-day minimum flow was always greater for the OBS data than for the FNR data in the Sacramento River drainage rivers. This variable was lower or unchanged for OBS data compared to FNR data in the San Joaquin River drainage rivers. The 30-day maximum flow was typically lower for the OBS data than for the FNR data in the Sacramento River drainage, although the changes were not always statistically significant (Table V). Differences were much greater in the San Joaquin River drainage with OBS values of 28% or less of FNR values.

The augmentation of low flows during the natural low flow period of the late fall and early winter resulted in an elevated baseflow index for all the rivers analysed (Table V). This difference is obvious in the monthly median flows for Sacramento River drainage rivers (Figure 2). In the San Joaquin River drainage rivers, the difference is due to required minimum flows during periods when FNR data have minimal or zero flow. The median number of low flow pulses (flows $<$ 25th percentile) and high flow pulses (flows $>$ 75th percentile) were less in the OBS data compared to the FNR data for all rivers. The median duration of low flow pulses was greater in all rivers in the OBS data compared to the FNR data. The median duration of high flow pulses was also greater in the OBS data compared to the FNR data in the San Joaquin River drainage rivers and in the Feather and American Rivers in the Sacramento River drainage. There was no statistically significant difference between FNR and OBS data in high flow pulse duration in the Sacramento River or Yuba River (Table V).

DISCUSSION

Although the magnitude of median monthly flows varied tremendously among the different rivers, FNR hydrographs were very similar in form. Late summer to early winter flows were uniformly low, increased later in the winter and peaked during snow melt in April or May. Flows declined rapidly from the peak through June and July.

DOI: 10.1002/rra

Table V. Statistical comparisons between estimated full natural runoff (FNR) and observed flows (OBS) for values of selected hydrologic parameters for each river studied.

	30-day minimum flow ($m^3 s^{-1}$)	30-day maximum flow ($m^3 s^{-1}$)	Baseflow	High pulse frequency	High pulse duration (d)	Low pulse frequency	Low pulse duration (d)
Sacramento River drainage							
Sacramento River							
FNR	122 (76–205)**	957 (207–2316)*	0.32 (0.15–0.62)**	8 (0–15)**	3 (1–90) ns	18 (1–44)**	2 (1–5)**
OBS	164 (81–275)	778 (250–2203)	0.46 (0.22–0.68)	6 (0–14)	3 (1–64)	2 (0–11)	6 (1–96)
Feather River							
FNR	21 (0–47)**	523 (57–1441)*	0.08 (0–0.30)**	8 (0–15)**	3 (1–14)**	21 (1–39)**	2 (1–4)**
OBS	34 (11–79)	262 (67–1274)	0.29 (0–0.52)	2 (0–7)	11 (1–68)	1 (0–13)	7 (1–30)
Yuba River							
FNR	1 (0–16)**	245 (18–857) ns	0 (0–0.19)**	8 (1–12)**	3 (1–82) ns	14 (0–61)**	2 (1–57)**
OBS	8 (1–50)	198 (1–809)	0.09 (0.01–1.00)	4 (0–12)	4 (1–178)	0 (0–12)	11 (2–730)
American River							
FNR	3 (0–30)**	303 (45–1108) ns	0.01 (0–0.07)**	8 (0–13)**	3 (1–15)**	18 (3–37)**	2 (1–9)**
OBS	34 (7–82)	206 (47–1044)	0.31 (0.07–0.80)	3 (0–9)	10 (1–149)	0 (0–4)	7 (1–77)
Deer Creek	2 (1–5)	28 (3–84)	0.29 (0.10–0.68)	6 (0–12)	4 (1–47)	2 (0–14)	17 (1–156)
San Joaquin River drainage							
Stanislaus River							
FNR	6 (1–20) ns	137 (32–341)**	0.05 (0.01–0.29)**	9 (0–21)**	2 (1–8)*	23 (3–48)**	2 (1–4)**
OBS	6 (<1–17)	38 (11–182)	0.32 (<0.01–0.52)	1 (0–6)	21 (1–93)	3 (0–12)	23 (2–105)
Tuolumne River							
FNR	4 (1–16)**	267 (65–517)**	0.02 (0–0.07)**	10 (2–19)**	2 (1–7)**	34 (10–57)**	2 (1–5)**
OBS	1 (1–24)	53 (6–377)	0.07 (0–0.48)	0 (0–8)	11 (1–89)	3 (0–19)	9 (1–367)
San Joaquin River							
FNR	5 (2–44)**	221 (58–589)**	0.06 (0.01–0.23)**	12 (1–13)**	3 (1–51)**	15 (0–37)*	2 (1–19)**
OBS	2 (1–34)	19 (4–273)	0.20 (0.01–0.57)	1 (0–5)	12 (1–70)	1 (0–7)	40 (2–1317)
Mokelumne River drainage							
Cosumnes River							
	<1 (0–2)	53 (1–217)	0.01 (0–0.05)	4 (0–10)	5 (1–169)	2 (0–8)	27 (1–138)

*$p < 0.05$; **$p < 0.01$. *ns*, not significant

DOI: 10.1002/rra

The effects of water management on this natural hydrograph varied from river to river but the general results were very different in the Sacramento and San Joaquin River drainages.

In the Sacramento River drainage, where in-channel water deliveries to the Sacramento San Joaquin Delta are the primary water management activity, rivers were characterized by a flattened hydrograph in the OBS data. Spring discharges were lower for OBS data compared to the FNR data. Conversely, late summer and fall discharges were augmented in the OBS data. Despite the changes in timing of discharge, annual mean discharge did not change appreciably. From the standpoint of the life history characteristics of the fish species of interest, the augmented summer flows in the Sacramento River drainage would be a disadvantage to the alien resident species that prefer spawning habitat with little or no flow (Table III). Presumably, the high summer discharges would minimize the availability of low velocity habitat, and the range of summer variability suggests that the availability of such habitat would vary from year to year. For native species, the reduced spring discharges likely limit the availability of riffle spawning habitat in relation to historical conditions and reduce any spawning cues from rising or falling hydrographs, but the flattened hydrograph probably maintains the existing spawning habitat for longer into the summer. However, the utilization of such spawning habitat would also depend on temperature conditions (Table III). The major exception to the pattern is the Yuba River, which has minimal storage capacity compared to the other dammed rivers. The Yuba River hydrograph was very similar to the undammed Deer Creek hydrograph.

In the San Joaquin River drainage, rivers were characterized by water diversions into canal systems. River discharges were much lower in the OBS data compared to the FNR data, particularly during months of spring snowmelt. However, in contrast to the Sacramento River drainage, summer discharges were not augmented. The dominance of low discharge through much of the year likely provides better environmental conditions for alien species compared to the Sacramento River drainage. For example, the large reductions in spring discharge would limit the availability of the moving water habitats favoured for spawning by native species. The low flows for much of the spring, summer and fall occur during a period of high air temperatures and likely promote warmer water temperatures, which would favour the alien species.

These inferences regarding fish responses to altered hydrographs are consistent with previous work resulting from studies addressing particular rivers (e.g. Marchetti and Moyle, 2001; Brown and Ford, 2002) or studies of more than one river (Brown, 2000; May and Brown, 2002) over relatively short timescales (1–3 years). These studies basically show that native resident species make up a larger proportion of the stream fish assemblage compared to alien resident species during years of higher flow. Marchetti and Moyle (2001) documented increased populations of native fishes at downstream sites in Putah Creek, a Sacramento River drainage stream, after changes in water management provided increased flows, especially during spring. Brown (2000) documented dominance of resident alien species in rivers of the San Joaquin River drainage at the end of a 5-year drought but recent surveys on the Merced River suggest that native resident species have increased since the drought ended (Stillwater Sciences, 2008). Similarly, Brown and Ford (2002) documented the decline of resident native fishes in the Tuolumne River, during the drought and their recovery when the drought ended.

Although results from previous studies have been useful in developing a conceptual understanding of the responses of native and alien resident fishes to flow (Brown and Moyle, 2005), there are no comprehensive, state-wide long-term monitoring programs for resident fishes in California, making it difficult to determine if such patterns are stable over time and space either within a single river or among rivers. There is also a lack of process-oriented studies to establish the mechanisms associated with fluctuations in fish assemblage composition. Although we believe we make a strong argument for the importance of differential spawning success, it is likely that other ecological interactions are also important. Differences in flow regime affect availability of habitat for juvenile and adult fishes. Competition and predation may also be important. Predation of alien species on native species is commonly inferred to be important in California streams (Moyle, 2002; Brown and Moyle, 2005) with some support from focused research (e.g. Brown and Moyle, 1991; Brown and Brasher, 1995; Gard, 2004). Developing useful management strategies and documenting the results of such strategies will require long-term research and monitoring conducted in a framework of adaptive management (Richter and Thomas, 2007; Souchon *et al*., 2008).

While analyses of flow regimes are critical to developing our understanding of the effects of water management on biotic resources, other factors are also important. We know that temperature is important, especially for anadromous salmonids (Moyle, 2002). The resident native and alien species also have different temperature requirements (Table III) that likely influence their relative success (Brown and Ford, 2002). For example, a reach of the Feather River with a relatively low, steady discharge of cold water is able to maintain populations of native fishes, including salmonids, while downstream reaches with augmented flow but warmer water temperatures support a mix of native and alien fishes (Seesholtz *et al*., 2004). In unaltered California rivers, flow and temperature covary seasonally, but the installation of temperature control devices that release water from selected depths in a reservoir or other infrastructure have disconnected temperature and flow. Water temperature management through controlled release of water of different temperatures from different depths in a reservoir has become a key feature of managing anadromous salmonids in the Sacramento River drainage. Such temperature management may help or hinder resident native fishes. For example, the Sacramento River downstream of Shasta Reservoir is managed to provide cold water to winter-run Chinook salmon throughout the summer. This management strategy likely favours native residents that can spawn at cooler temperatures. The interactions among flow, land use and geomorphology to provide different habitat features is also likely important (Poff *et al*., 2006b), but this is largely unstudied in regulated California rivers except in relation to Chinook salmon. Such interactions will affect the availability of low flow habitats favoured by most alien species presently occurring in Central Valley rivers.

The 'natural flow-regime paradigm' (Richter *et al*., 1996; Poff *et al*., 1997; Lytle and Poff, 2004; Poff *et al*., 2006a), has generally been considered as appropriate for California streams. Deer Creek, a tributary to the Sacramento River without a major dam, has largely maintained a native fish community (Baltz and Moyle, 1993). Baltz and Moyle (1993) suggest that the natural flow regime and associated environmental conditions are more favourable for native species than for alien species. However, there is increased recognition that this view may be too simplistic. Propst *et al.* (2008) studied the Gila River, a relatively unaltered arid southwest US stream and found that natural low flows promoted expansion of alien species, which compromised persistence of native fish assemblages. They concluded that natural flow regimes were important for the conservation on native fish assemblages but only if alien predators and competitors are actively removed or excluded. A recent study in the Cosumnes River, the largest undammed river in the Central Valley, found the system to be highly invaded by redeye bass *Micropterus coosae* (Moyle *et al*., 2003). Stream reaches with large numbers of redeye bass had few native fishes, suggesting that absence of large dams alone is not sufficient to guarantee persistence of native species. Given that restoring a natural flow regime may not benefit native fishes when alien fishes are present, it may be possible to target specific hydrologic conditions to favour native species, irrespective of whether those conditions are natural. Richter and Thomas (2007) suggest that substantial ecological benefits can be derived by modifying dam operations to mimic key aspects of the natural flow regime in situations where the full natural flow regime cannot be restored.

In California and elsewhere, a major impediment to developing river management strategies is the paucity of data on the linkages between hydrologic modification and biological responses (Pringle *et al*., 2000; Arthington *et al*., 2006; Murchie *et al*., 2008). Previous studies of the hydrology of Central Valley rivers have not generally focused on biotic effects of hydrologic changes. Previous work has focused instead on geomorphic effects, particularly sediment transport, or changes in amount and timing of runoff and potential downstream effects of that runoff, often in relation to climate change (Mount, 1995; Dettinger and Cayan, 2003; Knowles and Cayan, 2004; Knowles *et al*., 2006; Singer, 2007). Useful biological metrics and modelling approaches are being developed (Kennen *et al*., 2008; Konrad *et al*., 2008; Murchie *et al*., 2008); however, local and regional monitoring data are needed to calculate the metrics or apply approaches to understand the responses of local systems to hydrologic modification (Arthington *et al*., 2006) and develop appropriate management strategies.

In recent years, numerous studies have addressed impending changes in water supply and water management in relation to climate change and growing human demand (e.g. Gordon *et al*., 2008; Palmer *et al*., 2008). In turn, hydrologic alterations will occur that will likely have major effects on biodiversity of native aquatic species. Barnett *et al.* (2008) indicate that climate change has already had major effects on the hydrological cycle in the western United States, including California. California governmental agencies are beginning to consider effects on water supply and water management. The present challenge is to not only assess how climate change might affect timing and quantity of runoff but to understand how those changes will affect water management (e.g. reservoir operations) and how the resulting hydrology and associated environmental conditions will affect populations of organisms and their habitats.

It would seem prudent to invest similar effort in understanding biological responses to a variety of factors resulting from climate change, including water management driven changes in hydrologic regime, water temperature and geomorphic habitat changes. We stress that such considerations should be holistic. Water management in the Central Valley is complex, with water delivered from Sacramento River reservoirs to diversion pumps in the Sacramento–San Joaquin Delta at the confluence of the Sacramento and San Joaquin Rivers. Thus, changes in water management can affect hundreds of kilometres of river habitat. The effects of such changes should be evaluated for the entire ecosystem rather than selected species of management interest (e.g. Chinook salmon). In California, and elsewhere in the world, integrated, interdisciplinary programs of monitoring, research, and monitoring will be essential to avoiding unanticipated ecological outcomes as water is managed for human needs (Arthington *et al*., 2006; Poff *et al*., 2007; Murchie *et al*., 2008).

ACKNOWLEDGEMENTS

The authors thank the reviewers for their many comments which significantly improved the manuscript. This paper is based upon work supported by a grant from the CALFED Science Program. This paper is contribution no. 11 to the CASCADE project (Computational Assessments of Scenarios of Change for the Delta Ecosystem, Project SCI-05-C01-84).

REFERENCES

Annear T, Chisholm I, Beecher H, Locke A, Aarrestad P, Coomer C, Estes C, Hunt J, Jacobson R, Jobsis G, Kauffman J, Marshall J, Mayes K, Smith G, Wentworth R, Stalnaker C. 2004. *Instream Flows for Riverine Resource Stewardship* (revised edition). Instream Flow Council: Cheyenne, WY.

Arthington A, Bunn SE, Poff NL, Naiman J. 2006. The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications* **16**: 1311–1318.

Arthington AH, King JM, O'Keefe JH, Bunn SE, Day JA, Pusey BJ, Bluhdorn DR, Tharme R. 1992. Development of an holistic approach for assessing environmental flow requirements of riverine ecosystems. In *Proceedings of an International Seminar and Workshop on Water Allocation for the Environment*, Pigram JJ, Hooper BP (eds). Centre for Water Policy Research: University of New England; 69–76.

Baltz DM, Moyle PB. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* **3**: 246–255.

Barnett TP, Pierce DW, Hidalgo HG, Bonfils C, Santer BD, Das T, Bala G, Wood AW, Nozawa T, Mirin AA, Cayan DR, Dettinger MD. 2008. Human-induced changes in the hydrology of the western United States. *Science* **319**: 1080–1083.

Brown LR. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes* **57**: 251–269.

Brown LR, Brasher A. 1995. Effects of predation by Sacramento squawfish (*Ptychocheilus grandis*) on habitat choice of California roach (*Lavinia symmetricus*) and rainbow trout (*Oncorhynchus mykiss*) in artificial streams. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 1639–1646.

Brown LR, Ford TJ. 2002. Effects of flow on the fish communities of a regulated California river: implications for managing native fishes. *River Research and Applications* **18**: 331–342.

Brown LR, Moyle PB. 1991. Changes in habitat and microhabitat use of an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 849–856.

Brown LR, Moyle PB. 1993. Distribution, ecology, and status of the fishes of the San Joaquin River drainage, California. *California Fish and Game* **79**: 96–114.

Brown LR, Moyle PB. 2005. Native fish communities of the Sacramento-San Joaquin watershed, California: a history of decline. In *Fish Communities of Large Rivers of the United States*, Rinne F, Hughes R, Calamusso R (eds). American Fisheries Society: Bethesda, Maryland; 75–98.

Bunn SE, Arthington AH. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**: 492–507.

CALFED. 2007. *2007 CALFED Annual Report*. CALFED Bay-Delta Program: Sacramento.

Colwell RK. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55:1148–1153.

Dettinger MD, Cayan DR. 2003. Interseasonal covariability of Sierra Nevada streamflow and San Francisco Bay salinity. *Journal of Hydrology* **277**: 164–181.

Gard M. 2004. Interactions between an introduced piscivore and a native piscivore in a California stream. *Environmental Biology of Fishes* **71**: 287–295.

Goldstein RM, Meador MR. 2004. Comparisons of fish species traits from small streams to large rivers. *Transactions of the American Fisheries Society* **133**: 971–983.

Gordon LJ, Petersen GD, Bennett EM. 2008. Agricultural modifications of hydrological flows create ecological surprises. *Trends in Ecology and Evolution* **23**: 211–219.

Jackson RB, Carpenter SR, Dahm CN, McKnight DM, Naiman RJ, Postel SL, Running SW. 2001. Water in a changing world. *Ecological Applications* **11**: 1027–1045.

Kennen JG, Kauffman LJ, Ayers MA, Wolock DM, Bolarullo SJ. 2008. Use of an integrated flow model to estimate ecologically relevant hydrologic characteristics at stream biomonitoring sites. *Ecological Modeling* **211**: 57–76.

Kondolf GM, Boulton AJ, O'Daniel S, Poole GC, Rahel FJ, Stanley EH, Wohl E, Bang A, Carlstrom J, Cristoni C, Huber H, Koljonen S, Louhi P, Nakamura K. 2007. Process-based ecological river restoration: visualizing three-dimensional connectivity and dynamic vectors to recover lost linkages. *Ecology and Society* **11**(2): 5. Available at: http://www.ecologyandsociety.org/vol11/iss2/art5/

Konrad CP, Brasher AMD, May JT. 2008. Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biology* **53**: 1983–1998.

Knowles N, Cayan DR. 2004. Elevational dependence of projected hydrologic changes in the San Francisco Estuary and watershed. *Climatic Change* **62**: 319–336.

Knowles N, Dettinger MD, Cayan DR. 2006. Trends in snowfall versus rainfall in the western United States. *Journal of Climate* **19**: 4545–4559.

Light T, Marchetti MP. 2007. Distinguishing between invasions and habitat changes as drivers of diversity loss among California's freshwater fishes. *Conservation Biology* **21**: 434–446.

Lund J, Hanak E, Fleenor W, Howitt R, Mount J, Moyle P. 2007. *Envisioning Futures for the Sacramento-San Joaquin Delta*. Public Policy Institute of California: San Francisco.

Lytle DH, Poff NL. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution* **19**: 94–100.

Mathews R, Richter BD. 2007. Application of the indicators of hydrologic alteration software in environmental flow setting. *Journal of the American Water Resources Association* **43**(5): 1–14.

Marchetti MP, Moyle PB. 2000. Spatial and temporal ecology of native and introduced fish larvae in lower Putah Creek, California. *Environmental Biology of Fishes* **58**: 75–87.

Marchetti MP, Moyle PB. 2001. Keeping alien fishes at bay: effects of flow regime and habitat structure on fish assemblages in a regulated California stream. *Ecological Applications* **11**: 75–87.

May JT, Brown LR. 2002. Fish communities of the Sacramento River Basin: implications for conservation of native fishes in the Central Valley, California. *Environmental Biology of Fishes* **63**: 373–388.

Mount JF. 1995. *California Rivers and Streams: The Conflict Between Fluvial Process and Land Use*. University of California Press: Berkeley.

Moyle PB. 2002. *Inland Fishes of California*. (revised and expanded). University of California Press: Berkeley.

Moyle B, Mount JF. 2007. Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Sciences* **104**: 5711–5712.

Moyle PB, Crain PK, Whitener K, Mount JF. 2003. Alien fishes in natural streams: fish distribution, assemblage structure, and conservation in the Cosumnes River, California, U.S.A. *Environmental Biology of Fishes* **68**: 143–162.

Murchie KJ, Hair KPE, Pullen CE, Redpath TD, Stephens HR, Cooke SJ. 2008. Fish response to modified flow regimes in regulated rivers: research methods, effects, and opportunities. *River Research and Applications* **24**: 197–217.

Palmer MA, Reidy Liermann CA, Nilsson C, Flörke M, Alcamo J, Lake PS, Bond N. 2008. Climate change and the world's river basins: anticipating management options. *Frontiers in Ecology and Environment* **6**(2): 81–89.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC. 1997. The natural flow regime: a paradigm for river conservation and restoration. *Bioscience* **47**: 769–784.

Poff NL, Bledsoe BP, Cuhaciyan CO. 2006a. Hydrologic variation with land use across the contiguous United States: geomorphic and ecological consequences for stream ecosystems. *Geomorphology* **79**: 264–285.

Poff NL, Olden JD, Pepin DM, Bledsoe BP. 2006b. Placing global stream flow variability in geographic and geomorphic contexts. *River Research and Applications* **22**: 149–166.

Poff NL, Olden JD, Merritt DM, Pepin DM. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences* **104**: 5732–5737.

Postel SL. 1996. *Dividing the Waters: Food Security, Ecosystem Health, and the New Politics Of Scarcity*. Worldwatch Institute: Washington, D.C.

Postel SL. 2000. Entering an era of water scarcity: the challenges ahead. *Ecological Applications* **10**: 941–948.

Postel SL, Richter B. 2003. *Rivers for Life: Managing Water for People and Nature*. Island Press: Washington, D.C.

Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical–temperate comparisons. *Bioscience* **50**: 807–823.

Propst DL, Gido KB, Stefferud JA. 2008. Natural flow regimes, nonnative fishes, and native fish persistence in arid-land river systems. *Ecological Applications* **18**: 1236–1252.

Richter BD, Baumgartner JV, Powell J, Braun DP. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* **10**: 1–12.

Richter BD, Matthews R, Harrison DL, Wigington R. 2003. Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications* **13**: 206–224.

Richter BD, Thomas GA. 2007. Restoring environmental flows by modifying dam operations. *Ecology and Society* **12**: 12. Available at: http://www.ecologyandsociety.org/vol12/iss1/art12/

Schick RS, Lindley ST. 2007. Directed connectivity among fish populations in a riverine network. *Journal of Applied Ecology* **44**: 1116–1126.

Seesholtz A, Cavallo BJ, Kindopp J, Kurth R. 2004. Juvenile fishes of the lower Feather River: distribution, emigration patterns, and associations with environmental variables. In *Early Life History of Fishes in the San Francisco Estuary and Watershed*, Feyrer F, Brown LR, Brown RL, Orsi JJ (eds). American Fisheries Society: Symposium 39: Bethesda, Maryland; 141–166.

Singer MB. 2007. The influence of major dams on hydrology through the drainage network of the Sacramento River basin, California. *River Research and Applications* **23**: 55–72.

DOI: 10.1002/rra

Sommer T, Armor C, Baxter R, Breuer R, Brown L, Chotkowski M, Culberson S, Feyrer F, Gingras M, Herbold B, Kimmerer W, Mueller-Solger A, Nobriga M, Souza K. 2007. The collapse of pelagic fishes in the upper San Francisco Estuary. *Fisheries* **32**(6): 270–277.

Souchon Y, Sabaton C, Deibel R, Reiser D, Kershner J, Gard M, Katapodis C, Leonard P, Poff NL, Miller WJ, Lamb BL. 2008. Detecting biological responses to flow management: missed opportunities; future directions. *River Research and Applications* **24**: 506–518.

Sparks RE. 1995. Need for ecosystem management of large rivers and their floodplains. *Bioscience* **45**: 169–182.

Stillwater Sciences. 2008. *The Merced River Alliance Project Final Report. Volume II: Biological Monitoring and Assessment Report*. Stillwater Sciences: Berkeley, California.

TNC (The Nature Conservancy). 2007. *Indicators of Hydrologic Alteration Version 7 User's Manual*. The Nature Conservancy: Charlottesville, Virginia.

U.S. Army Corps of Engineers. 2002. *Sacramento and San Joaquin River Basins California Comprehensive Study Interim Report*. U.S. Army Corps of Engineers: Sacramento District. Available at: http://www.spk.usace.army.mil/projects/civil/compstudy/reports.html

Walker KF, Sheldon F, Puckridge JT. 1995. A perspective on dryland river ecosystems. *Regulated Rivers* **11**: 85–104.

Webb RH, Wegner DL, Andrews ED, Valdez RA, Patten DT. 1999. Downstream effects of Glen Canyon Dam on the Colorado River in Grand Canyon—a review. In *The Controlled Flood in Grand Canyon*, Webb RH, Schmidt JC, Marzolf GR, Valdez RA (eds). AGU Monograph 110: Washington, D.C; 1–21.

Williams JD, Warren Jr. ML, Cummings KS, Harris JL, Neves RJ. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries 18(9):6–22

Yoshiyama RM, Gerstung ER, Fisher FW, Moyle PB. 2001. Historical and present distribution of chinook salmon in the Central Valley drainage of California. In *Contributions to the Biology of Central Valley Salmonids*, Brown R (ed). Fishery Bulletin 179: California Department of Fish and Game: Sacramento, California; 71–176.

DOI: 10.1002/rra