

Restoring native fish assemblages to a regulated California stream using the natural flow regime concept

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Abstract. We examined the response of fishes to establishment of a new flow regime in lower Putah Creek, a regulated stream in California, USA. The new flow regime was designed to mimic the seasonal timing of natural increases and decreases in stream flow. We monitored fish assemblages annually at six sample sites distributed over ~30 km of stream for eight years before and nine years after the new flow regime was implemented. Our purpose was to determine whether more natural stream flow patterns would reestablish native fishes and reduce the abundances of alien (nonnative) fishes. At the onset of our study, native fishes were constrained to habitat immediately (<1 km) below the diversion dam, and alien species were numerically dominant at all downstream sample sites. Following implementation of the new flow regime, native fishes regained dominance across more than 20 km of lower Putah Creek. We propose that the expansion of native fishes was facilitated by creation of favorable spawning and rearing conditions (e.g., elevated springtime flows), cooler water temperatures, maintenance of lotic (flowing) conditions over the length of the creek, and displacement of alien species by naturally occurring high-discharge events. Importantly, restoration of native fishes was achieved by manipulating stream flows at biologically important times of the year and only required a small increase in the total volume of water delivered downstream (i.e., water that was not diverted for other uses) during most water years. Our results validate that natural flow regimes can be used to effectively manipulate and manage fish assemblages in regulated rivers.

Key words: assemblage structure; fish conservation; instream flow; introduced species; Mediterranean climate; Putah Creek, California, USA; stream fishes.

INTRODUCTION

The flow regime of a stream is often regarded as the “master variable” that determines composition of biotic assemblages (Poff and Ward 1989, Power et al. 1995, Matthews 1998). Many environmental factors that affect assemblage structure, including temperature, water chemistry, and physical habitat complexity, are determined by flow to a certain extent (Bunn and Arthington 2002). For streams in Mediterranean climates, such as northern California, USA, annual patterns of precipitation produce a hydrograph characterized by episodic high-discharge events during winter and by protracted periods of low flow throughout summer and early fall. Although the magnitude and frequency of hydrologic disturbance events such as extreme floods and extended low flows are highly variable from year to year, the timing (seasonality) of these events is largely predictable (Gasith and Resh 1999, Power et al. 2008). Thus, many native freshwater and riparian species have evolved

traits and life-history strategies to withstand natural hydrologic variability and to rapidly recover from disturbance (Bonada et al. 2007, Power et al. 2008, Yarnell et al. 2010). Conversely, alien (nonnative) species often lack biological and behavioral mechanisms to cope with region-specific flow regimes and are often disproportionately vulnerable (e.g., via physical displacement, recruitment failure, or direct mortality) to high and low stream flow conditions.

Water abstraction and management frequently alter the timing and magnitude of stream flows (Grantham et al. 2010) with adverse consequences for the diversity and abundance of native biota (Bunn and Arthington 2002). Such problems are particularly acute in California where dams, diversions, and inter-basin water transfers have dramatically altered the structure and function of many riverine and riparian ecosystems. For stream fishes, flow alteration often results in homogenized assemblages dominated by alien species that are favored by sport fisheries (e.g., sunfishes and basses) or by species that thrive in highly altered habitats (e.g., common carp [*Cyprinus carpio*] and red shiner [*Cyprinella lutrensis*]). In many regulated streams, native fishes have been partially or completely replaced by alien species that are better

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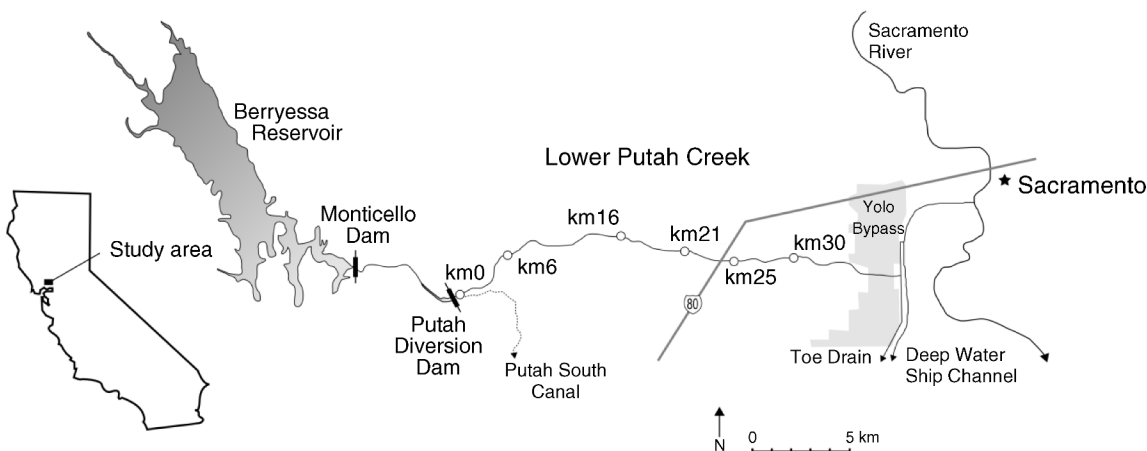


FIG. 1. Map of lower Putah Creek, Yolo and Solano counties, California, USA. Sample sites (open circles) are coded to reflect their approximate distance (in kilometers) downstream of the Putah Diversion Dam (e.g., km16 = 16.2 km below the diversion).

adapted to the new conditions that tend to include more constant flows, poorer water quality, and less habitat complexity (Moyle 2002, Moyle and Marchetti 2006). Consequently, the re-creation of naturally variable flow regimes in regulated rivers has been proposed as a technique to conserve, restore, and manage native fish populations and the vital ecosystem processes on which they depend (Poff et al. 1997, Propst and Gido 2004, Carlisle et al. 2010).

Here we examine the responses of fishes within lower Putah Creek (California) to the reestablishment of a natural flow regime that was mandated through legal action (Moyle et al. 1998). Marchetti and Moyle (2001) demonstrated the potential for recovery of native fishes in much of Putah Creek after a series of wet years fortuitously created flows that were similar to the historical natural regime. A negotiated settlement (the Putah Creek Accord; hereafter the “Accord”) was reached in 2000 that used the natural flow regime concept (Poff et al. 1997) to prescribe specific flow requirements for Putah Creek (see *Historical background* below). Annual monitoring to assess whether native fishes were responding to the new flow regime was also part of the Accord. The new flow regime required only a small percentage of available water, so flows were “natural” only in timing and not in total annual volume. In this study, we used eight years of pre-flow and nine years of post-flow Accord data to determine whether the new flow regime was successful at (1) reestablishing native fishes to lower Putah Creek and (2) reducing abundances of alien fishes. This paper represents a rare, long-term test of the natural flow regime concept as a tool to enhance native fish populations in regulated rivers.

STUDY AREA

This study was conducted in lower Putah Creek, a tributary of the Sacramento River in Yolo and Solano Counties, California, USA (Fig. 1). Putah Creek

originates in the Coast Range and flows freely eastward ~130 km before being impounded by Monticello Dam, forming Berryessa Reservoir (surface area = 8400 ha; storage capacity = 1.98 km³). Water releases from Monticello Dam flow ~13 km to a second dam, the Putah Diversion Dam (PDD), where most of the water is diverted south through the Putah South Canal to users in Solano County (Moyle et al. 1998). The stream section below the PDD (lower Putah Creek) flows ~37 km before reaching the Yolo Bypass and eventually emptying into the Sacramento River.

Stream flow in lower Putah Creek is regulated year-round except when large rainfall events cause Berryessa Reservoir to overflow. Uncontrolled releases can occur at any time between December and June and, combined with flows from tributaries upstream and downstream of the PDD, can deliver substantial pulses of water to lower Putah Creek. The maximum recorded mean daily discharge from Monticello Dam during the period of study (1991–2008) was 399.0 m³/s on 26 January 1997, which resulted in a mean daily discharge of 325.0 m³/s from the PDD into lower Putah Creek the following day.

Historical background

In 1957, the Putah Diversion Dam was constructed in conjunction with Monticello Dam and Berryessa Reservoir as part of the U.S. Bureau of Reclamation’s Solano Project. The project was principally designed to provide water for agricultural, municipal, and industrial uses, as well as flood control and recreational opportunities. Beginning in 1970, water was released below the diversion dam on a fixed schedule established by the California State Water Resources Control Board. While this schedule provided the minimum flows necessary to recharge groundwater aquifers and satisfy riparian water rights, it restricted permanent stream flow to a segment of the creek (~5 km) immediately below the PDD (Moyle et al. 1998).

In the summer of 1989, the third year of a five-year drought, >32 km of lower Putah Creek went dry, resulting in fish kills and harm to riparian wildlife. A lawsuit was subsequently filed (Putah Creek Council v. Solano Irrigation District and Solano County Water Agency, Sacramento Superior Court Number 515 766) to increase flows in lower Putah Creek. In 1996, the Court ordered, in part, a 50% increase in the minimum release schedule to maintain surface water flow from the PDD to its mouth in the Yolo Bypass (Fig. 1). The final flow regime was established in May 2000 with the signing of the Putah Creek Accord and immediately implemented. Three of the six operational requirements of the Accord were specifically designed to benefit fish and other aquatic organisms (Moyle et al. 1998).

Spawning and rearing flows for native fish.—This requirement was the ecological centerpiece of the Accord and was intended to secure spawning and rearing flows for spring-spawning native fishes. Specifically, the Accord mandated a short three-day pulse sometime between 15 February and 31 March to initiate spawning behavior, followed by a month-long release of elevated (i.e., higher than baseline) flows. Additionally, the Accord established a schedule of monthly baseline flows designed to maintain continuous lotic (flowing) conditions year-round from the PDD to the Yolo Bypass. During all but severe drought years, baseline flows were intended to provide cool-water rearing habitat for an assemblage of native fishes in much of the creek below the PDD. These flows were also expected to facilitate the survival of an assemblage of mostly alien fishes in the lowermost reaches, where flows would be lowest and water temperatures highest.

Pulse flows to attract and support anadromous fishes.—Supplemental (pulse) flows were provided to promote migration of fall-run chinook salmon (*Oncorhynchus tshawytscha*), except during times of severe drought. The Accord mandated minimum stream flows beginning in November and a five-day pulse flow in November or December to attract and enable adult chinook to migrate up Putah Creek from the Yolo Bypass. The specified springtime minimum flows were also designed to enhance rearing habitat for juvenile salmon and to facilitate outmigration.

Drought flows.—A drought flow schedule was created to ensure permanent stream flow from the PDD to the Interstate 80 crossing at all times, even during drought years when water levels would be low in the upstream reservoir. This was intended to provide suitable instream habitat for native fishes in at least a short segment of stream below the PDD.

METHODS

In 1991, six stream reaches were selected to represent typical habitats in lower Putah Creek and were established as permanent sample sites. Herein the six sites are coded km0, km6, km16, km21, km25, and km30 to reflect their approximate distances downstream of the

PDD (actual distances were 0.1, 6.3, 16.2, 20.6, 25.1, and 30.4 km, respectively). All sites were sampled annually from 1991 to 2008 (except 1992) in September or October during low (base) flow conditions. Thus, sampling included eight years of pre- and nine years of post-flow restoration data. Fish were captured by electroshocking using a Smith-Root model 2.5 GPP gas powered generator and pulsator (Smith-Root, Vancouver, Washington, USA) operated out of a small tow barge. Two anode poles were operated from the barge and each was attended by at least one netter to capture stunned fish. Electroshocking passes of equal effort by distance were conducted at each sample site across all years. Captured fish were held in buckets containing aerated water or in a live car until sampling was completed, whereupon fish were identified, enumerated, and returned to the creek. Unidentified sunfish and hybrids among all centrarchid species (i.e., green sunfish [*Lepomis cyanellus*] × bluegill [*Lepomis macrochirus*], green sunfish × redear sunfish [*Lepomis microlophus*], and redear sunfish × bluegill) were grouped as *Lepomis* spp.

DATA ANALYSES

Hydrology

To assess trends in stream flow in lower Putah Creek, records of mean daily flow releases from the PDD (water years 1977–2008) were obtained from Solano County Irrigation District (Elmira, California, USA). We used the indicators of hydrologic alteration (IHA) model of Richter et al. (1996) to contrast the periods 1977–1999 (pre-Accord) and 2000–2008 (post-Accord) and to assess how select attributes of the flow regime were affected by the flow Accord. The IHA model uses daily discharge values to calculate 33 flow metrics representing five broad categories: (1) flow magnitude, (2) magnitude and duration of annual extreme conditions, (3) timing of annual extreme conditions, (4) frequency and duration of high and low pulses, and (5) rate and frequency of changes (Nature Conservancy 2007).

Fish assemblages

Nonmetric multidimensional scaling (NMDS) ordinations were used to examine patterns in assemblage composition among the six sample sites during the pre-Accord (1991–1999) and post-Accord (2000–2008) periods. Bray-Curtis similarities were calculated for $\log_{10}(x + 1)$ -transformed fish abundance data and NMDS ordinations were used to illustrate similarities among sample sites. Optimal solutions (i.e., number of axes) were determined through low stress values and Monte Carlo randomization tests ($n = 100$ runs; McCune and Grace 2002). In ordination plots, sample sites are presented as ellipses that represent the 95% confidence interval surrounding the mean annual position (score) of each site in ordination space. Taxon scores were generated by weighted averaging. Distance calculations and ordinations were performed with PC-

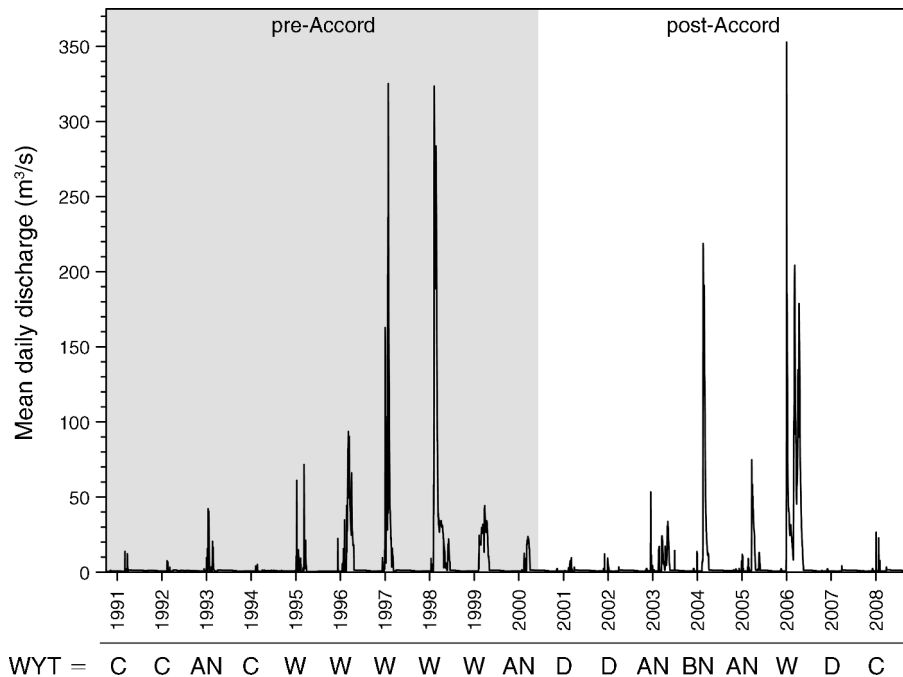


FIG. 2. Time series of mean daily discharge from the Putah Diversion Dam before (pre-Accord; shaded) and after (post-Accord; unshaded) implementation of a new flow regime. Water year types (WYT) appear below each year on the abscissa and are classified as wet (W), above normal (AN), below normal (BN), dry (D), and critically dry (C). See the *Introduction* for a description of the Accord.

ORD version 5.33 (MjM Software Design, Glenden Beach, Oregon, USA).

We used a nonparametric multi-response permutation procedure (MRPP) to test the null hypotheses of (1) no spatial differences in species composition among the six sample sites within either the pre- or post-Accord periods and (2) no changes in species composition at each sample site across periods (i.e., pre-Accord vs. post-Accord). Euclidean distances were calculated for untransformed abundance data and sample years were pooled in each analysis. MRPP produces two statistics: an agreement statistic (A) describing the degree of within-group homogeneity compared to that expected by chance (i.e., effect size) and a P value that estimates the probability that observed differences are due to chance. Values for the A statistic range from 1 to <0 ; $A = 1$ indicates complete within-group homogeneity, $A = 0$ indicates a level of heterogeneity within groups equal to that expected by chance, and $A < 0$ indicates more heterogeneity within groups than would be expected by chance. For ecological communities, values for A are commonly <0.1 and values ≥ 0.3 reflect strong differences between assemblages (McCune and Grace 2002). An overall significance test ($P < 0.05$) was followed by pairwise comparisons. We used Bonferroni-adjusted Type I error rates of $\alpha = 0.003$ (0.05/15) and $\alpha = 0.008$ (0.05/6) to assess significant differences in fish assemblages among sample sites and between time periods, respectively.

Lastly, a central premise of the flow Accord was that enhanced flows during March, April, and May would benefit spring-spawning native fishes. To test this hypothesis we examined the relationship between $\log_{10}(x + 1)$ -transformed mean spring discharge and the proportional abundance of native fish at each sample site using linear regression analysis.

RESULTS

Hydrology

The flow regime of lower Putah Creek exhibited high inter-annual variability during the period of study, chiefly due to precipitation events that caused Monticello Dam to spill. Of the 18 water years encompassed by our study, six were classified by the California Department of Water Resources as wet, four as above normal, one as below normal, three as dry, and four as critically dry (Fig. 2) (California Department of Water Resources water year classification index for the Sacramento Valley, *available online*).⁵ The implementation of the flow Accord had an effect on the magnitude, duration, and timing of stream flows in lower Putah Creek, as shown by IHA (Appendix). Mean monthly stream flow during the post-Accord period increased for eight months of the water year, with the greatest percentage gain occurring in the spring (April = +47% and May = +63%; Fig. 3). Additionally, the new flow

⁵ <http://cdec.water.ca.gov/cgi-progs/iodir/WSIHIST>

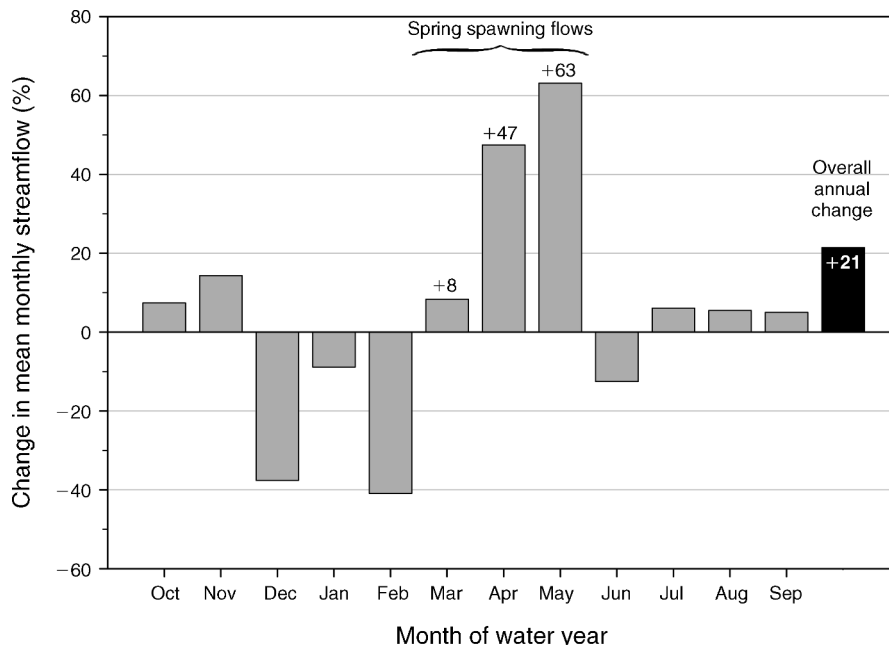


FIG. 3. Percentage change in mean monthly stream flow following implementation of the new flow regime. The pre-Accord period includes the water years 1979–1999, whereas the post-Accord period includes water years 2000–2008.

regime changed the magnitude and duration of annual extremes, with mean 1-, 3-, 7-, 30-, and 90-day minimum flows all increasing. Mean maximum flows calculated for these same time intervals decreased, but this reflected natural interannual variability in precipitation rather than a mandated change to the flow release schedule. Additionally, both the mean count and duration of low-flow pulses decreased in the post-Accord period (Appendix).

Fish assemblage composition

In total, 35 fish species (13 native, 22 alien) were captured in lower Putah Creek between 1991 and 2008. Most species were members of just four families: Centrarchidae ($n = 10$ species, 1 native), Cyprinidae ($n = 8$ species, 4 native), Ictaluridae ($n = 4$ species, all alien), and Salmonidae ($n = 3$ species, 2 native; Table 1). Seven species were considered rare based on presence (≤ 5 of the annual samples) or abundance ($< 5\%$ of the total assemblage at any site) and were excluded from subsequent analysis: Sacramento perch (*Archoplites interruptus*), spotted bass (*Micropterus punctulatus*), yellowfin goby (*Acanthogobius flavimanus*), brown bullhead (*Ameiurus nebulosus*), striped bass (*Morone saxatilis*), chinook salmon, and brown trout (*Salmo trutta*; Table 1).

Spatial and temporal distribution and abundance.—The NMDS analyses conducted for each time period indicated that two-dimensional ordinations were optimal, with both axes serving as significant ($P \leq 0.001$) predictors of species composition. Collectively, the two axes explained 89% and 94% of the variation in species

composition among sample sites for the pre-Accord and post-Accord periods, respectively. For the pre-Accord period, we interpreted the first NMDS axis (r^2 for axis 1 = 0.30; Fig. 4A) to represent a gradient between lentic-like conditions in the positive direction (e.g., increased frequency of large, deep pools, and slow-moving water) and increasingly lotic conditions in the negative direction. Fish taxa most positively correlated (Pearson) with the first axis were hitch (*Lavinia exilicauda*; $r = 0.51$), fathead minnow (*Pimephales promelas*; $r = 0.49$), black bullhead (*Ameiurus melas*; $r = 0.47$), Sacramento blackfish (*Orthodon microlepidotus*; $r = 0.47$), and goldfish (*Carassius auratus*; $r = 0.42$). The second axis (r^2 for axis 2 = 0.59) reflected a gradient in stream water temperature, with cooler locations exhibiting more positive values. Fish species most positively correlated with axis 2 were all native: Sacramento sucker (*Catostomus occidentalis*; $r = 0.88$), threespine stickleback (*Gasterosteus aculeatus*; $r = 0.69$), riffle sculpin (*Cottus gulosus*; $r = 0.69$), Sacramento pikeminnow (*Ptychocheilus grandis*; $r = 0.64$), and rainbow trout (*Oncorhynchus mykiss*; $r = 0.57$).

During the post-Accord period, sample sites exhibited increased separation in ordination space relative to the pre-Accord period, suggesting change in habitat conditions at most sites (Fig. 4). We inferred the first NMDS axis ($r^2 = 0.45$; Fig. 4B) to represent a gradient in physical habitat complexity; sample sites containing diverse meso-habitat types (e.g., riffles, runs, and pools) and abundant instream structure (e.g., aquatic vegetation and fallen trees) scored higher on axis 1. Species most positively correlated with the first axis during the

TABLE 1. Fish species collected at six permanent sample sites in Putah Creek, California, USA, before (Pre) and after (Post) implementation of the flow Accord.

Taxon	Common name	Taxon code	Origin	Sample site											
				km0		km6		km16		km21		km25		km30	
				Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
Atherinopsidae															
<i>Menidia audens</i>	Mississippi silverside	MSS	A	•				•		•	•	•	•	•	•
Catostomidae															
<i>Catostomus occidentalis</i>	Sacramento sucker	SKR	N	•	•	•	•	•	•	•	•	•	•	•	•
Centrarchidae															
<i>Archoplites interruptus</i>	Sacramento perch	†	N					•	•	•					
<i>Lepomis cyanellus</i>	green sunfish	GSF	A	•	•	•	•	•	•	•	•	•	•	•	•
<i>Lepomis gulosus</i>	warmouth	WRM	A								•	•	•	•	•
<i>Lepomis macrochirus</i>	bluegill	BGS	A	•	•	•	•	•	•	•	•	•	•	•	•
<i>Lepomis microlophus</i>	redear sunfish	RES	A					•	•	•	•	•	•	•	•
<i>Lepomis</i> spp.	various‡	LEP	A	•	•	•	•	•	•	•	•	•	•	•	•
<i>Micropterus dolomieu</i>	smallmouth bass	SMB	A	•	•	•	•	•	•	•	•	•	•	•	•
<i>Micropterus punctulatus</i>	spotted bass	†	A								•				
<i>Micropterus salmoides</i>	largemouth bass	LMB	A	•	•	•	•	•	•	•	•	•	•	•	•
<i>Pomoxis nigromaculatus</i>	black crappie	BCR	A								•	•	•	•	•
Cottidae															
<i>Cottus asper</i>	prickly sculpin	PSC	N	•	•	•	•	•	•	•	•	•	•		•
<i>Cottus gulosus</i>	riffle sculpin	RSC	N	•	•	•	•	•		•					•
Cyprinidae															
<i>Carassius auratus</i>	goldfish	GLF	A		•		•	•	•		•	•	•	•	•
<i>Cyprinella lutrensis</i>	red shiner	RSH	A					•	•	•	•	•	•	•	•
<i>Cyprinus carpio</i>	common carp	CRP	A	•	•		•	•	•	•	•	•	•	•	•
<i>Lavinia exilicauda</i>	hitch	HTC	N	•	•	•	•	•	•	•	•	•	•	•	•
<i>Lavinia symmetricus</i>	California roach	RCH	N	•	•									•	•
<i>Orthodon microlepidotus</i>	Sacramento blackfish	SBF	N							•		•	•	•	•
<i>Pimephales promelas</i>	fathead minnow	FHM	A							•		•	•	•	•
<i>Ptychocheilus grandis</i>	Sacramento pikeminnow	PKM	N	•	•	•	•	•	•	•	•	•	•	•	•
Embiotocidae															
<i>Hysterocarpus traski</i>	tule perch	TUP	N	•	•	•	•	•	•	•	•	•	•	•	•
Gasterosteidae															
<i>Gasterosteus aculeatus</i>	threespine stickleback	SBK	N	•	•	•	•				•				
Gobiidae															
<i>Acanthogobius flavimanus</i>	yellowfin goby	†	A												•
Ictaluridae															
<i>Ameiurus catus</i>	white catfish	WCF	A				•	•	•	•		•		•	•
<i>Ameiurus melas</i>	black bullhead	BBH	A	•	•					•	•	•		•	•
<i>Ameiurus nebulosus</i>	brown bullhead	†	A				•			•		•			
<i>Ictalurus punctatus</i>	channel catfish	CCF	A							•	•	•		•	•
Moronidae															
<i>Morone saxatilis</i>	striped bass	†	A												•
Percidae															
<i>Percina macrolepada</i>	bigscale logperch	BLP	A	•	•	•	•	•	•	•	•	•	•	•	•
Petromyzontidae															
<i>Lampetra tridentata</i>	Pacific lamprey	PLR	N	•	•	•	•	•	•	•	•	•	•		•
Poeciliidae															
<i>Gambusia affinis</i>	western mosquitofish	MSQ	A	•	•	•	•	•	•	•	•	•	•	•	•
Salmonidae															
<i>Oncorhynchus mykiss</i>	rainbow trout	RBT	N	•	•	•				•					
<i>Oncorhynchus tshawytscha</i>	chinook salmon	†	N		•										
<i>Salmo trutta</i>	brown trout	†	A	•											

Notes: The pre- and post-flow Accord periods represent water years 1991–1999 (except 1992; *N* = 8 years) and 2000–2008 (*N* = 9 years), respectively. Bullets indicate that a taxon was present during at least one of the annual surveys conducted during either the pre- or post-Accord periods. Sample site abbreviations reflect approximate distances (in kilometers) downstream of the Putah Diversion Dam. Origin abbreviations are: N, native; A, alien (nonnative). Taxon codes are used in Fig. 4.

† Excluded from ordinations due to rarity.

‡ The group *Lepomis* spp. includes centrarchid hybrids (see *Methods*).

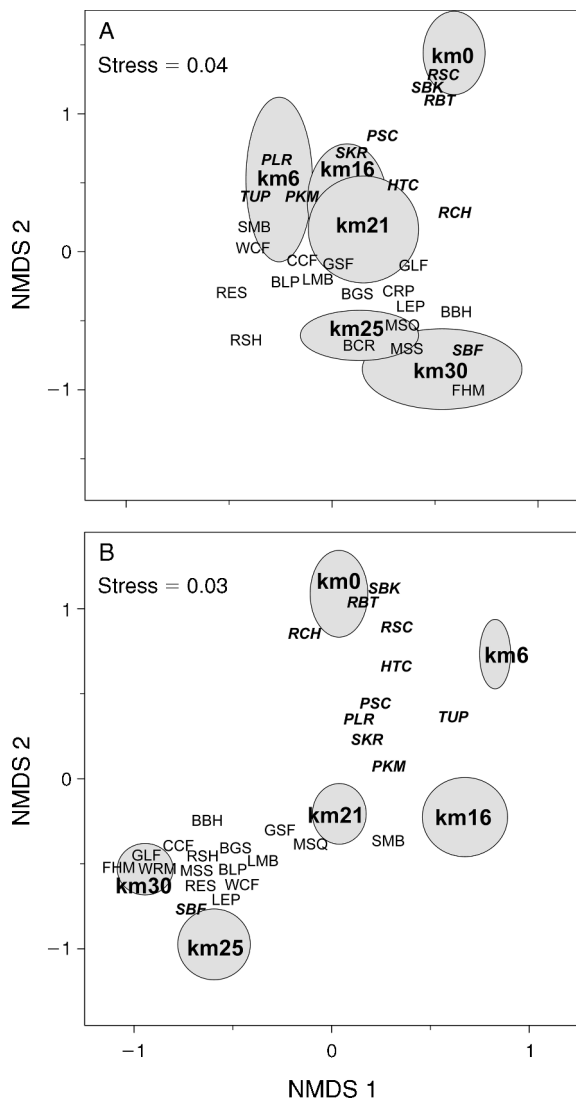


FIG. 4. Nonmetric multidimensional scaling ordinations of the lower Putah Creek fish assemblages at six sample sites (A) before and (B) after alteration of the flow regime. The sites, from upstream to downstream, are: km0, km6, km16, km21, km25, and km30. Shaded ellipses represent the 95% confidence interval surrounding the mean position of each sample site in ordination space. Taxon scores were generated by weighted averaging. Native taxa appear in boldface italic type, and taxon codes are provided in Table 1.

post-Accord period were tule perch (*Hysterocarpus traski*; $r = 0.77$), Sacramento pikeminnow ($r = 0.62$), Sacramento sucker ($r = 0.43$), and prickly sculpin (*Cottus asper*; $r = 0.43$). The second NMDS axis (r^2 for axis 2 = 0.49) again described a gradient in stream water temperature. Taxa most positively correlated with axis 2 were obligate cold-water natives: prickly sculpin ($r = 0.78$), riffle sculpin ($r = 0.77$), rainbow trout ($r = 0.78$), and threespine stickleback ($r = 0.71$; Fig. 4B).

Pairwise MRPP comparisons of the fish assemblages at each sample site during the pre-Accord period

revealed limited spatial heterogeneity. Only site km0 supported an assemblage that was significantly different (after Bonferroni adjustment) from those at all other sample sites (Table 2). Similarly, the composition of the fish assemblage at km6 was significantly different from all sample sites located downstream except km16. In general, with the exception of the two upstream-most sample sites (i.e., km0 and km6), adjacent sites during the pre-Accord period supported similar fish communities, as evidenced by low values of the MRPP A statistic. Conversely, pairwise MRPP comparisons conducted for the post-Accord period indicated that all sample sites except for km25 and km30 supported significantly different fish assemblages (Table 2). Notably, most site comparisons yielded A values ≥ 0.3 , suggesting strong longitudinal differences in fish assemblage structure during the post-Accord period.

For specific sample sites, MRPP contrasts revealed significant temporal changes in fish assemblage composition between the pre-Accord and post-Accord periods at sites km6 and km21 (Table 2).

Relationships between stream flow and native fishes

The flow regime of lower Putah Creek had a significant influence on the temporal and spatial distribution of native fishes. While the km0 sample site was largely dominated by native species across both the pre- and post-Accord periods (Fig. 5A), native species regained numerical dominance at sample sites km6, km16, and km21 during the course of our study (Fig. 5B–D). Most increases in the proportion of native species occurred prior to implementation of the flow Accord and were facilitated by consecutive wet water years that produced large-magnitude floods (e.g., peak discharges $>300 \text{ m}^3/\text{s}$ in 1998 and 1999; see Fig. 2) and protracted periods of elevated stream flow (i.e., week-long discharges $>75 \text{ m}^3/\text{s}$). Subsequent implementation of the flow Accord and the mandated enhanced spring flows in 2000 created conditions favorable for maintenance of native fishes. We found a positive relationship between mean spring discharge (1 March through 31 May) and the proportion of the fish assemblage composed of native species at the four upstream-most sites, though this relationship was only statistically significant at km16 ($r^2 = 0.30$, $F_{1,17} = 6.76$, $P = 0.02$; Fig. 6C) and km21 ($r^2 = 0.36$, $F_{1,17} = 9.14$, $P < 0.01$; Fig. 6D).

DISCUSSION

The change in flow regime of lower Putah Creek resulted in a dramatic shift in the fish fauna. At the onset of this study in 1991, fish assemblages in the lower creek were partitioned along an upstream–downstream gradient in flow, water temperature, canopy cover, and pool habitat (Marchetti and Moyle 2001) that reflected changes following dam construction and subsequent flow management. Alien fish outnumbered native fish at all sample sites except km0, immediately below the dam

TABLE 2. Matrix of *A* values derived from multi-response permutation procedure (MRPP) tests contrasting the fish assemblages at six sample sites before (upper half of matrix; values in italics) and after (lower half of matrix) implementation of the flow Accord.

Sample site	km0	km6	km16	km21	km25	km30
km0	0.06	<i>0.21*</i>	<i>0.13*</i>	<i>0.16*</i>	<i>0.23*</i>	<i>0.14*</i>
km6	<i>0.20*</i>	0.16*	<i>0.09</i>	<i>0.13*</i>	<i>0.19*</i>	<i>0.15*</i>
km16	<i>0.27*</i>	<i>0.15*</i>	0.05	<i>0.04</i>	<i>0.14*</i>	<i>0.07</i>
km21	<i>0.30*</i>	<i>0.23*</i>	<i>0.14*</i>	0.18*	<i>0.00</i>	<i>-0.00</i>
km25	<i>0.34*</i>	<i>0.28*</i>	<i>0.31*</i>	<i>0.31*</i>	-0.02	<i>0.00</i>
km30	<i>0.37*</i>	<i>0.30*</i>	<i>0.34*</i>	<i>0.30*</i>	<i>0.06</i>	0.04

Notes: The matrix diagonal (values in boldface) contains site-specific contrasts of the pre- and post-Accord fish assemblages (i.e., before vs. after tests). The MRPP *A* statistic describes the degree of within-group homogeneity compared to that expected by chance (i.e., effect size). Larger values for *A* indicate stronger differences between assemblages. Asterisks denote significant differences after Bonferroni adjustment for multiple comparisons. Sample site abbreviations reflect their approximate distances (in kilometers) downstream of the Putah Diversion Dam.

(Fig. 5). Beginning in 1997, a series of water years with high winter and spring flows displaced or suppressed alien species while creating advantageous spawning and rearing conditions for native fishes. By 1999, the proportion of native fish had greatly increased at the four upstream sites, driven by increases in abundance of Sacramento sucker and Sacramento pikeminnow. Marchetti and Moyle (2001) cited these changes as evidence that native fishes in lower Putah Creek could be enhanced by restoring a more natural flow regime.

The flow regime instituted in 2000 as a result of the Putah Creek Accord provided validation of the natural

flow regime concept by successfully maintaining native fish populations even when dry years intermittently recurred (e.g., 2001, 2002, 2007). The scheduled flows were designed to mimic the natural flow regime, principally in terms of the seasonal timing of increases and decreases in stream flow. Native fish assemblages in Putah Creek, and elsewhere in California, evolved under a Mediterranean-type hydrologic regime, with rain delivered in winter and spring followed by summer droughts with little or no precipitation. Consequently, most native species spawn in mid-February through mid-April and require hydrologic cues such as increased

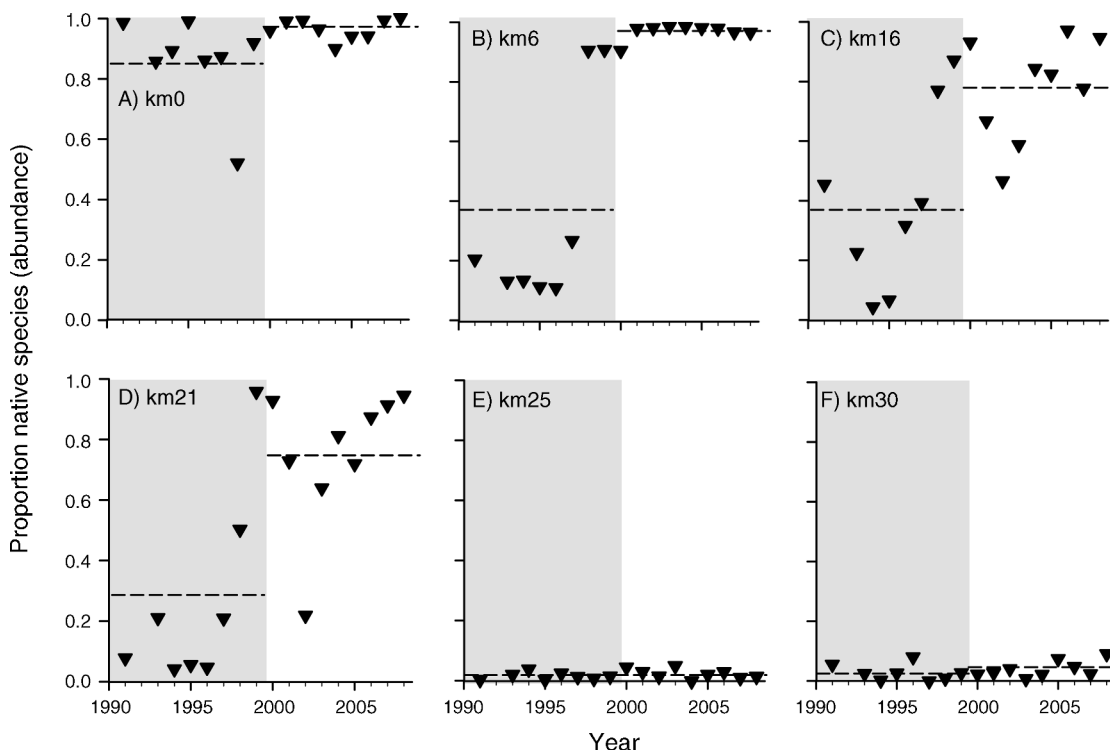


FIG. 5. Time series (1991–2008) of the proportion of the total fish assemblage composed of native species at six permanent sample sites. Sites are presented from upstream to downstream, and site codes (e.g., km0) reflect approximate distances downstream of the Putah Diversion Dam. The gray shaded region in each plot identifies the pre-Accord period (1991–1999). Horizontal dashed lines indicate the mean proportion of native species during each time period.

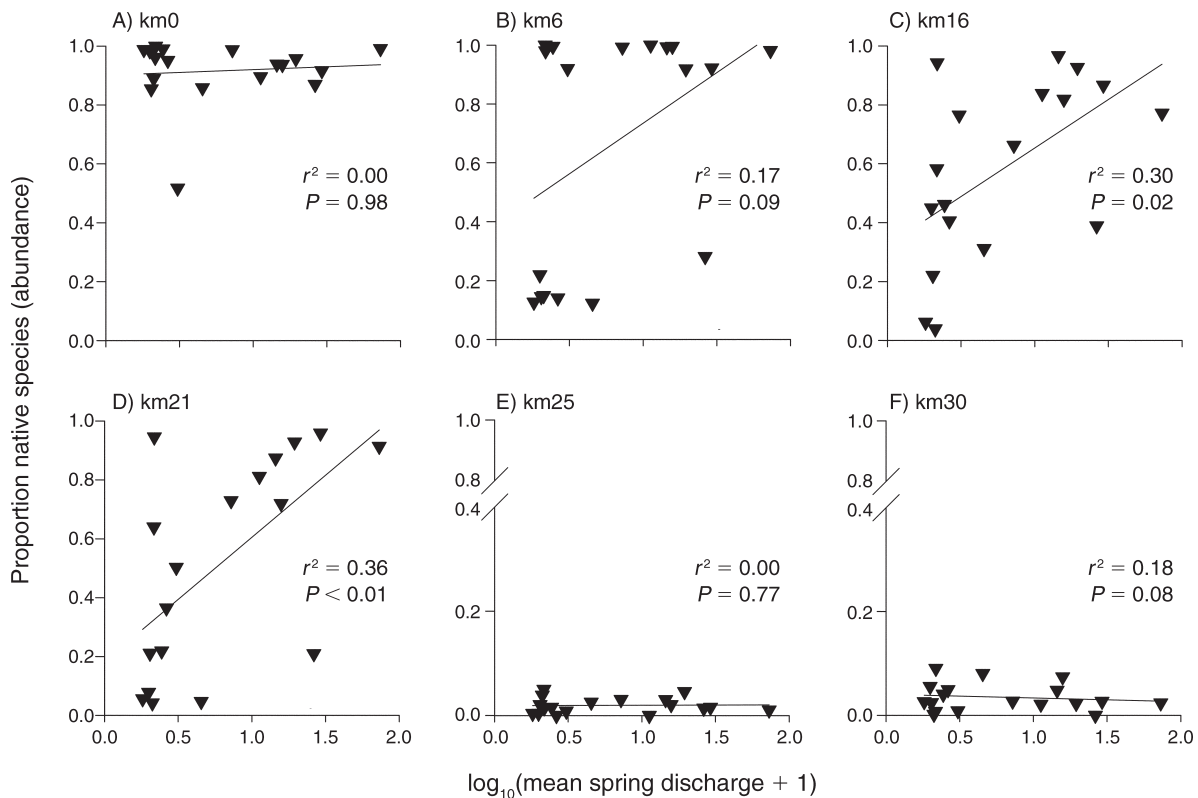


FIG. 6. Relationship between mean spring (1 March through 31 May) discharge and the proportion of the total fish assemblage composed of native species at six permanent sample sites. Site codes (e.g., km0) reflect approximate distances downstream of the Putah Diversion Dam. Proportion data were arcsine-square-root transformed prior to regression analysis. Discharge was measured as cubic meters per second.

stream flow or floodplain inundation to initiate spawning behavior (Moyle 2002). The new flow regime was explicitly designed to provide an initial pulse flow (3 days) in early spring, followed by 30 consecutive days of elevated flows and a gradual ramping of flows down to the minimum flows scheduled for that month. Further, it ensured sufficient water to provide cool ($<22^{\circ}\text{C}$) lotic (flowing) conditions throughout most of the lower creek during the warmest times of year.

Of the eight full water years analyzed since implementation of the Accord (2001–2008), one was classified by the California Department of Water Resources as below normal, three were classified as dry, and one was critically dry. Nonetheless, the new flow regime was successful at providing more water at biologically important times of the year across all water year types. Mean flows during the spring spawning season increased by $1.9 \text{ m}^3/\text{s}$, $5.8 \text{ m}^3/\text{s}$, and $1.5 \text{ m}^3/\text{s}$ in March, April, and May, respectively, compared to historical averages (1979–2000). Mean annual 90-d minimum flow was also $0.07 \text{ m}^3/\text{s}$ higher (+10.3%) during the post-Accord period, indicating that the new flow regime provided additional water during the critical low summer (base flow) period (Appendix).

Redistribution of native fishes

The NMDS analysis revealed a marked redistribution of fishes following the implementation of the flow Accord (Fig. 4). The native cold-water fish assemblage that was previously restricted to habitat immediately below the diversion dam (site km0) expanded downstream $>6 \text{ km}$. At the two middle sample sites (km16 and km21) native Sacramento pikeminnow, Sacramento sucker, tule perch, and hitch, which collectively represented a small proportion of the total fish assemblage before the flow Accord, became the numerically dominant taxa. The proportion of native species also increased by 39% and 49% at the km16 and km21 sites, respectively. Pairwise comparisons (MRPP) of fish assemblages at each sample site indicated a high degree of among-site homogenization prior to the flow Accord, especially from km16 to km30. In contrast, equivalent comparisons conducted for the post-Accord period revealed that the structure and composition of fish assemblages at all sample sites upstream of km30 were significantly different from one another.

We hypothesize that the shift in the fish fauna was driven by two major interacting factors, both of which were likely critical to the outcome. First was displacement of alien fishes by natural high flow events that

created long reaches of flowing water habitat and cooler temperatures. Displacement of alien fishes during high flow events has been reported elsewhere (e.g., Minckley and Meffe 1987, Valdez et al. 2001) and proposed as a mechanism that permits long-term coexistence of native and alien fishes in highly variable lotic ecosystems (Minckley and Meffe 1987, Schultz et al. 2003). Moreover, there is good evidence that natural flow regimes create conditions that discourage nonnative taxa adapted to systems with different environmental attributes (Baltz and Moyle 1993, Townsend 2003, Lytle and Poff 2004). Second was the creation of favorable spawning and rearing conditions for native fishes during spring, via mandated flow releases.

Persistence and dynamics of alien fishes

An unexpected but instructive occurrence during our study was an increase in the relative abundance of alien species in 1998 at km0, a site normally dominated by native cold-water fishes (Fig. 5A). This increase was driven by large numbers of green sunfish (34% of the total assemblage) that presumably either washed down from the reservoir during an uncontrolled spill or resulted from successful reproduction. The green sunfish, like many successful invaders, is an opportunistic species with high reproductive capacity and broad physiological tolerance (Moyle 2002, Garcia-Berthou 2007). Thus, there is a continuous threat of re-invasion given that the two upstream reservoirs contain many alien taxa (P. B. Moyle, *unpublished data*) and thereby potentially serve as “source” pools of nonnative fish to the lower creek. While high-discharge events such as the repeated floods that occurred in 1998 generally hinder persistence of alien species, extreme disturbances can concomitantly result in significant mortality or displacement of resident native fishes. In cases in which overall native fish abundance or diversity is reduced, alien species originating from upstream reservoirs may discover vacant habitats, rapidly colonize, and proliferate. Notably, for the km0 site, naturally variable stream flows the following year (1999) had a strong negative effect on green sunfish (reduced to 3% of the total assemblage) and allowed native fishes to regain numerical dominance of the assemblage. Green sunfish remained rare or absent from subsequent samples.

Evidence for the continued persistence of alien taxa in the upstream reaches through the post-Accord period was provided during a stream restoration project ~4 km downstream of the PDD in September 2011. When a series of large, deep (3–5 m) pools were isolated and drained, seven native fish species were found to account for 98% ($n = 1830$) and 97% ($n = 1574$) of the total fish assemblage in two pools that were inventoried (P. B. Moyle, *unpublished data*). Nonetheless, small numbers of alien fishes representing 10 species were also present, suggesting potential for proliferation if the flow regime were to return to its pre-Accord state.

It is also important to note that alien species are still abundant in the lowermost portion of Putah Creek, beginning at approximately km25. This segment of the creek is highly modified and characterized by low-gradient, warm summer water temperatures, large pools with sand and clay substrates, and low summer flows. Such conditions strongly favor benthic-nesting alien species such as bluegill, largemouth bass (*Micropterus salmoides*), and redear sunfish. Interestingly, at km30, the most downstream site with the lowest flows and highest summer water temperatures, there has been a dramatic shift in the fish assemblage, from one dominated by annual alien species (e.g., western mosquitofish [*Gambusia affinis*], Mississippi silverside [*Menidia audens*], and fathead minnow) to one dominated by a more complex community of longer-lived alien species (e.g., largemouth bass, bluegill). One native species, Sacramento blackfish, has apparently been excluded from downstream sites by the new flow regime. The reasons for this exclusion are not clear because Sacramento blackfish is a slow-water species with extraordinary tolerances for high temperatures and low dissolved oxygen levels and frequently co-occurs with alien species (Moyle 2002). Despite the persistence and dominance of alien fishes at downstream sites, implementation of a natural flow regime has allowed native species to regain dominance of >20 km of lower Putah Creek.

Conclusions

The restoration of natural flow regimes has been proposed, although seldom tested, as a conservation tool to manage and enhance fish populations in regulated rivers (Poff and Zimmerman 2010). Here we provide a rigorous example of how targeted changes to the flow regime successfully reestablished native fishes and reduced abundances of alien fishes throughout much of a regulated California stream. This favorable outcome was achieved by manipulating stream flows at key times of the year and only required a small increase in the total volume of water delivered downstream (i.e., not diverted) during most water years (Moyle et al. 1998). Our study supports a growing body of literature that shows the natural flow regime can be a powerful tool for restoring native fish populations.

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SUPPLEMENTAL MATERIAL

Appendix

Results of the indicators of hydrologic alteration (IHA) analysis for lower Putah Creek, California, USA (*Ecological Archives* A022-076-A1).