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EFFECTS OF FLOW REGIME ON FISH ASSEMBLAGES IN A REGULATED CALIFORNIA STREAM

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Abstract. The fishes in Lower Putah Creek, a regulated stream in the Central Valley of California, were sampled over a 5-yr period, 1994–1998. Distinct fish assemblages were observed in the lower 37 km of stream using two-way indicator species analysis (TWINSPAN) and canonical correspondence analysis (CCA). The assemblages segregated in an upstream-to-downstream manner. Distinct differences were found between assemblages of native and nonnative fishes and their association with environmental variables and habitat use. Native fishes tended to cluster in areas with colder temperatures, lower conductivity, less pool habitat, faster streamflow, and more shaded stream surface. Numbers of nonnative fish were negatively correlated with increased streamflow, and numbers of native fish were positively correlated with increased flow. Hydrologic variability between years and seasons indicated that flow regime had a large effect on the fish assemblages. This study provides a clear demonstration of how native fishes in streams of the western United States exhibit different habitat requirements and respond to temporal variation in flow in a different manner than nonnative fishes. It supports the concept that restoration of natural flow regimes, in company with other restoration measures, is necessary if the continued downward decline of native fish populations in the western United States is to be reversed.

Key words: assemblage structure; canonical correspondence analysis; fish conservation; flow regime; introduced species; ordination; Putah Creek, California; regression; stream fishes.

Introduction

Many streams in western North America have highly altered flow regimes, the result of dams and diversions impounding and removing a significant portion of their water. The changed flow regimes have profound effects on the ecology of the streams at multiple trophic levels and at multiple spatial scales (Ligon et al. 1995, Poff et al. 1997). Effects on streams include changes in physical characteristics such as channel structure, sediment transport, and thermal regime, and changes in biological characteristics such as species diversity, trophic structure, and community composition (Ward and Stanford 1983, Bain et al. 1988, Ligon et al. 1995, Ward and Stanford 1995, Imbert and Stanford 1996, Poff et al. 1997).

Usually the most obvious ecological effect of stream regulation is a collapse or change in fish populations. This has led to the development of various modeling tools to aid fisheries managers in developing flow regimes to favor economically important species, such as the instream flow incremental methodology and its associated physical habitat simulation model (Mathur et al. 1985). However, these techniques have generated significant criticism, particularly for their simplifying assumptions (Mathur et al. 1985, Pert and Erman 1994, Castleberry et al. 1996, Williams 1996) and their typical focus on single species (Moyle and Baltz 1985, Moyle et al. 1998). Two related responses to these criticisms are to recommend flow regimes in regulated streams that favor native fish assemblages (Moyle et al. 1998) or to recommend ''natural'' flow regimes (Power et al. 1996, Poff et al. 1997). But how do we manage for native fish assemblages in streams that also contain many alien species such as occurs in streams of the western United States? And how do we develop a natural flow regime when much of the annual flow is diverted? Answering these questions is crucial for the conservation of native stream biota in regulated streams.

We have attempted to answer these general questions through the study of lower Putah Creek, Yolo County, California, a stream from which most of the water has been diverted for over 40 yr. Putah Creek is fairly typical of streams in the western United States, with its strongly seasonal flow regime (high flows in winter and spring, low flows in summer) and with low richness of native species. The native species are strongly stratified by elevation into assemblages of one to seven species (Moyle and Herbold 1987, Brown and Moyle 1993). Fortuitously, our 5-yr study encompassed a series of unusually dry years followed by a series of unusually wet years. This allowed us to directly examine the effects of naturally restored flows on fish assemblages existing in a stream from which most of the water had previously been diverted. Natural climatic conditions essentially created an experiment for us in which stream flow was changed abruptly from conditions

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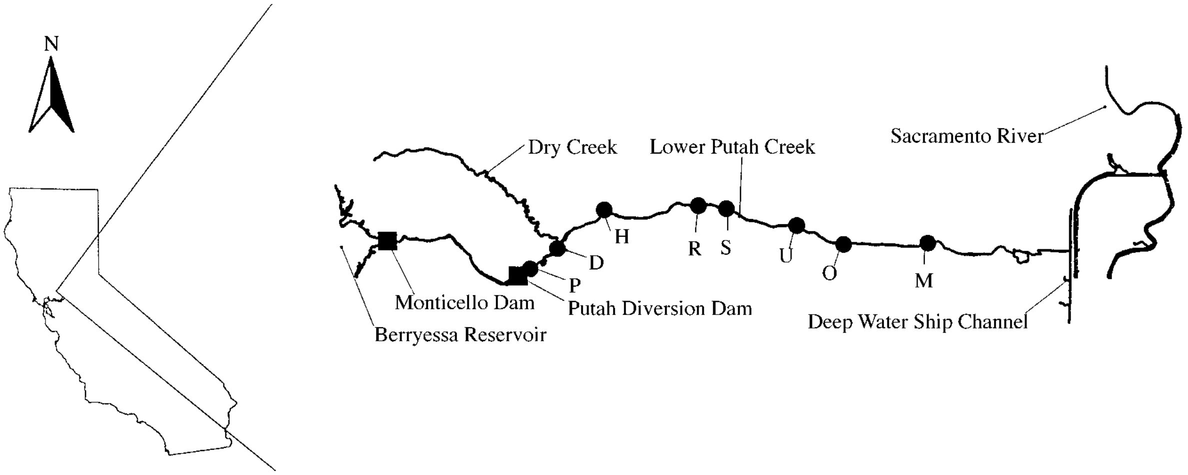

FIG. 1. Map of Lower Putah Creek, Yolo County, California, USA, and sample sites. Key to abbreviations: P = Putah Diversion Dam, D = Dry Creek, H = Highway 505, R = Russell Ranch, S = Stevenson Road, U = UC Davis Campus, O = Old Davis Road, and M = Mace Boulevard.

characteristic of a dammed stream to conditions similar to a natural flow regime. The abrupt change in the flow regime permitted us to test the general hypothesis that restoration of native stream biota in the western United States requires restoration of natural flow regimes (Stanford et al. 1996, Poff et al. 1997). More specifically, the conditions allowed us to test the hypothesis that a more natural flow regime favors native fishes and suppresses alien fishes. We addressed the following questions: (1) Do predictable fish assemblages exist in Putah Creek in response to the progressive change in environmental conditions downstream from the dam? (2) What habitat conditions favor native fish assemblages? (3) How do seasonal and annual flow regimes affect the balance between native and nonnative fishes, both annually and seasonally?

METHODS

Study area

We sampled the juvenile and adult fish in lower Putah Creek (Yolo County, California) over five years (1994–1998) in late spring and early fall. Putah Creek is a tributary to the Sacramento River with its headwaters in the Coast Range of California. It is fairly typical of such tributaries in its flow regime and fish fauna. From the Coast Range, the creek flows ~129 km east before it is impounded by Monticello Dam, forming Berryessa Reservoir. The releases from Monticello Dam flow ~13 km to Putah Diversion Dam (PDD; Fig. 1). The stream reach beween the two dams is intensely managed as a cold water trout stream. Below PDD (referred to as the lower creek), the creek flows ~37 km across the alluvial plain of the western Central Valley before emptying into Cache Slough and eventually the Sacramento River (Fig. 1). The width of the lower creek channel ranges from 5 to 25 m wide and the channel is deeply incised and channelized in places.

Lower creek hydrology is dominated by regulated flows during most months and years. Exceptions occur during winters of high rainfall when Berryessa Reservoir fills up and spills, recreating natural high flow events ($\geq$393 m^3/sec was recorded in January 1997). During years of drought, diversion of water can dry up much of the lower creek during the summer and fall (no measurable flow was recorded for eight months at the sample station farthest downstream in 1994). Dry years are defined for this study as years in which total annual flow is <50% of the 40-yr average (40-yr average = 1.8×10^8 m^3), and wet years are defined as years in which total yearly flow is >200% of the 40-yr average. The years of 1994 (total flow = 2.4×10^7 m^3) and 1995 (total flow = 6.4×10^7 m^3) were considered dry years. The years of 1997 and 1998 were considered wet years (total flow = 4.5×10^8 and $>7.3 \times 10^8$ m^3, respectively). High flow events can occur anytime during the months of December through April in years of high rainfall. Low flow periods occur on a regular basis in July through October but are exacerbated by prolonged periods of drought and reduction in releases from Putah Diversion Dam (Moyle et al. 1998). This hydrologic pattern is typical for streams in a Mediterranean climate, with low flows in summer (0.05–0.85 m^3/sec) and high flows (5.66 m^3/sec) for short periods during most winters.

Fish sampling

Eight permanent sampling sites were established along the lower creek: Putah Diversion Dam (P), Dry Creek (D), the Highway 505 bridge (H), Russell Ranch (R), Stevenson Road area (S), University of California Davis campus (U), Old Davis Road bridge (O), and Mace Boulevard bridge (M) (Fig. 1). The sites were chosen to be representative of the diversity of habitat in the lower creek and for their ease of access. Each

PLATE. 1. Student assistants, Ryon Kurth, Lisa Konyescni, and Pat Crain, electrofishing Russell Ranch site on lower Putah Creek (Yolo County, California) summer of 1997.

site was sampled in September 1994, in May and August 1995, in June and September 1997, and in September 1998.

At each site, a combination of backpack electrofishing (Smith Root Type 15A backpack shocker, Smith-Root, Incorporated, Vancouver, Washington, USA; see Plate 1), hand seining (6 m length with 6-mm mesh), and gill netting (two nets, each 15 × 2 m, with 5-cm^2 and 2.5-cm^2 mesh) was used. All techniques were not used at every site due to site-specific limitations. Sample reaches ranged from 20 to 80 m in length and utilized five to nine person hours per sample. A combination of aquatic habitats (pools, riffles, and runs) were sampled within each site. All fish sampled were identified to species, counted, measured (standard length) to the nearest millimeter, and then released.

Environmental sampling

Twelve environmental variables were measured or estimated at each sampling site including: streamflow (cubic meters per second), maximum depth (in centimeters), average depth (in centimeters), turbidity (in centimeters), surface temperature (in degrees Celsius), specific conductance (in microSiemens), percent canopy cover (percentage of stream surface shaded at noon), an index of instream aquatic cover, percentage of substrate in various particle size classes, and percentage of habitat as pools and riffles (Table 1). Environmental variables were chosen based on stream sampling experience in California (e.g., Brown and Moyle 1993). Flow was calculated from a width and depth transect, where current velocity was measured at 60% of the stream depth with a handheld current meter

TABLE 1. Environmental and faunal assessment variables average values and standard deviation (in parentheses) for the eight sample sites along lower Putah Creek, 1994–1998.

Variable	Putah Diversion Dam (0.0)	Dry Creek (3.5)	Highway 505 (4.8)	Russell Ranch (16.1)	Stevenson Road (18.5)	UC Davis Campus (23.3)	Old Davis Road (26.6)	Mace Blvd. (33.0)
Flow (m^3/s)†	0.7 (0.4)	0.6 (0.3)	0.5 (0.3)	0.7 (0.4)	0.7 (0.4)	0.7 (0.4)	0.5 (0.3)	0.7 (0.6)
Maximum depth (cm)	104 (27)	107 (41)	118 (26)	112 (46)	84 (12)	196 (68)	128 (20)	118 (32)
Average depth (cm)	42 (11)	31 (12)	59 (10)	50 (15)	34 (9)	84 (18)	67 (12)	73 (17)
Water clarity (cm)‡	82 (50)	96 (49)	71 (34)	86 (37)	101 (61)	63 (43)	37 (14)	25 (21)
Temperature (°C)†	13 (4)	18 (2)	22 (3)	22 (2)	22 (1)	24 (2)	23 (2)	23 (2)
Conductivity (μS)†	224 (59)	262 (45)	316 (38)	479 (108)	538 (48)	531 (57)	565 (117)	623 (190)
Shade (%)†	62 (17)	35 (15)	28 (14)	41 (17)	23 (15)	16 (12)	20 (10)	12 (8)
Cover‡	15 (3)	13 (3)	10 (2)	12 (3)	12 (2)	8 (6)	7 (2)	4 (3)
Silt (%)	18 (21)	14 (8)	41 (14)	36 (17)	13 (9)	97 (8)	83 (12)	93 (14)
Gravel (%)	30 (19)	53 (10)	13 (8)	28 (18)	47 (29)	3 (8)	5 (8)	3 (8)
Pool (%)†	22 (8)	17 (12)	63 (39)	32 (24)	15 (8)	97 (8)	98 (3)	100 (0)
Riffle (%)	43 (14)	52 (9)	0 (0)	29 (15)	36 (23)	2 (4)	0 (0)	0 (0)
Crayfish‡	0.7 (0.8)	1.5 (0.5)	2.0 (0.9)	1.7 (0.8)	1.7 (0.8)	0.3 (0.5)	1.7 (0.8)	1.7 (1.2)
Mollusc‡	1.2 (1.3)	1.5 (1.0)	1.8 (1.5)	2.8 (0.4)	0.8 (1.0)	0.2 (0.4)	0.2 (0.5)	0.7 (0.8)

Note: River kilometers downstream of Putah Diversion Dam are indicated in parentheses under station name headings.
† Included in CCA ordination by forward selection of variables at $\alpha = 0.10$.
‡ See *Methods: Experimental sampling* for description of variables.

TABLE 2. Common and scientific names of fishes collected in Lower Putah Creek during 1994–1998.

Common name	Scientific name	Origin	TWIN-SPAN groupings
Pacific lamprey	*Lampetra tridentata*	N	A1
Threadfin shad	*Dorosoma petenense*	I	†
Chinook salmon	*Oncorhynchus tshawytscha*	N	†
Rainbow trout	*Oncorhynchus mykiss*	N	A1
Brown trout	*Salmo trutta*	I	†
Goldfish	*Carassius auratus*	I	†
Carp	*Cyprinus carpio*	I	B2
California roach	*Lavinia symmetricus*	N	A1
Hitch	*Lavinia exilicauda*	N	A1
Golden shiner	*Notemigonus crysoleucas*	I	†
Red shiner	*Cyprinella lutrensis*	I	B2
Sacramento blackfish	*Orthodon microlepidotus*	N	B2
Fathead minnow	*Pimephales promelas*	I	B2
Sacramento pikeminnow	*Ptychochelius grandis*	N	A2
Sacramento sucker	*Catostomus occidentalis*	N	A1
White catfish	*Ameiurus catus*	I	B2
Black bullhead	*Ameiurus melas*	I	B2
Channel catfish	*Ictalurus punctatus*	I	B2
Western mosquitofish	*Gambusia affinis*	I	‡
Inland silverside	*Menidia beryllina*	I	B2
Threespine stickleback	*Gasterosteus aculeatus*	N	A1
Striped bass	*Morone saxatilis*	I	†
Green sunfish	*Lepomis cyanellus*	I	B1
Warmouth	*Lepomis gulosus*	I	†
Bluegill	*Lepomis machrochirus*	I	B2
Hybrid (bluegill × green sunfish)	*Lepomis* spp.	I	B1
Redear sunfish	*Lepomis microlophus*	I	†
Smallmouth bass	*Micropterus dolomieu*	I	A2
Largemouth bass	*Micropterus salmoides*	I	B1
White crappie	*Pomoxis annularis*	I	†
Black crappie	*Pomoxis nigromaculatus*	I	B2
Bigscale log perch	*Percina macrolepida*	I	B2
Tule perch	*Hysterocarpus traski*	N	A2
Prickly sculpin	*Cottus asper*	N	A1
Riffle sculpin	*Cottus gulosus*	N	A1

Note: Origin codes: N = native, I = introduced.
† Not included in analysis due to rarity.
‡ Not enumerated due to sampling inconsistency.

(Marsh-McBirney Flowmate 2000, Marsh-McBirney, Incorporated, Frederick, Maryland, USA). Maximum depth was the measured depth at the deepest portion of the sample reach. Average depth was estimated using the flow-transect data. Water clarity (turbidity) was measured using the depth at which a bronze plate attached to a top-setting depth rod was no longer visible in the water. Specific conductance was measured using a portable YSI salinity/conductivity/temperature meter (Model 33, YSI, Incorporated, Yellow Springs, Ohio, USA). An index of aquatic cover was developed by visually estimating and combining five separate elements of aquatic cover present in the creek (submerged aquatic vegetation, emergent or instream riparian vegetation, undercut banks, surface turbulence, root wads) using a 1–5 scale (0 = not present, 1 = low abundance, 3 = moderate abundance, 5 = highly abundant). The percentage of substrate categories (silt/mud, sand, gravel, cobble, boulder, and bedrock) was visually estimated for each reach sampled. In addition, the abundance of two large-sized aquatic invertebrate taxa (crayfish and molluscs) was visually assessed. The same 1–5 scale used for aquatic cover was used to estimate the abundance of crayfish and mollusks over the entire sample reach.

Data analysis

All variables expressed as percentage data were arcsin (square-root x) transformed prior to analysis so their distribution more closely approximated normality. For classification and ordination, all fish abundance data was log $(x + 1)$ transformed to down-weight large numbers and to account for variation in catch. Ten species known to be present in the creek were not included in the analysis (Table 2) either because: (1) the species was not present in at least three of the samples, (2) the species did not make up at least 5% of the sampled fauna at one or more sites, or (3) in the case of the western mosquitofish (*Gambusia affinis*), the species was not sampled in a consistent manner.

We simultaneously analyzed the species and environmental data using classification and ordination tech-

TABLE 3. Environmental variable mean values and standard deviation for the four TWINSPAN site groups along lower Putah Creek, 1994–1998.

Variable	A1 (N = 9)		A2 (N = 18)		B1 (N = 7)		B2 (N = 14)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Flow (m^3/s)†	0.68	0.36	0.74	0.32	0.45	0.40	0.61	0.42
Maximum depth (cm)	100.0	23.3	122.1	57.7	113.1	43.9	138.5	40.0
Average depth (cm)	37.2^{a}	11.8	47.9^{a}	19.4	58.8^{ab}	17.3	75.0^{b}	17.6
Water clarity (cm)	87.9^{a}	51.3	88.2^{a}	46.0	61.8^{ab}	32.2	36.8^{b}	29.7
Temperature (°C)†	13.8^{a}	3.7	21.0^{b}	1.8	23.6^{b}	2.3	23.1^{b}	1.8
Conductivity (μS)†	241.0^{a}	57.9	433.2^{b}	138.3	456.3^{bc}	106.0	585.0^{c}	151.9
Shade (%)†	51.1^{a}	21.4	30.3^{b}	17.4	26.9^{b}	15.8	15.4^{b}	10.1
Cover‡	14.7^{a}	2.9	11.2^{ab}	2.9	8.9^{bc}	3.5	6.1^{c}	4.4
Silt (%)	18.3^{a}	16.8	28.1^{a}	25.1	61.9^{b}	26.4	91.9^{c}	12.5
Gravel (%)	40.0^{a}	21.2	32.3^{ab}	25.5	14.4^{bc}	9.8	3.1^{c}	7.5
Pool (%)†	21.1^{a}	7.8	31.7^{a}	32.0	75.6^{b}	32.5	99.6^{b}	1.4
Riffle (%)	47.2^{a}	13.9	26.4^{b}	23.2	8.8^{bc}	13.6	0.0^{c}	0.0
Crayfish‡	1.1^{a}	0.9	1.6^{ab}	0.9	1.8^{ab}	0.9	0.7^{ac}	0.8
Mollusc‡	1.2^{a}	1.3	1.6^{ab}	1.3	1.7^{ab}	1.1	0.2^{ac}	0.6

Notes: Bold variables were found to have differences between TWINSPAN groups using one-way ANOVA and a Bonferroni adjustment for multiple unplanned comparisons among means ($\alpha = 0.05$). Within rows, values with the same letters are not significantly different.

† Included in CCA ordination by forward selection of variables at $\alpha = 0.10$.

‡ See *Methods: environmental sampling* for description of variables.

niques. We used the two-way indicator species analysis program (TWINSPAN) developed by Hill (1979) to perform sampling site and species classification. TWINSPAN classification was limited to two levels because further divisions only served to isolate single species and sites. Differences among TWINSPAN site groupings for the 15 environmental variables were tested using single-factor ANOVA and a Bonferroni test for multiple unplanned comparisons among means. Analysis was performed using SYSTAT (1998).

To investigate the association between fish assemblages and environmental variables, we utilized direct gradient analysis (canonical correspondence analysis [CCA]). We used the CANOCO 4.0 program developed by ter Braak and Smilauer (1998). CCA aids in the recognition and description of patterns in multivariate data; in particular it describes how a suite of species simultaneously responds to environmental factors at multiple sites by correlating environmental variables with sample scores (ter Braak and Verdonschot 1995). The ordination technique employed (CCA) follows recommendations in ter Braak (1986), Palmer (1993), and ter Braak and Verdonschot (1995).

Thirteen environmental variables and two macroinvertebrate abundance measures (Table 3) were initially included in the ordination. These variables were tested for significance by forward selection utilizing the Monte Carlo test ($\alpha = 0.1$, with 99 random permutations) provided by CANOCO. The only variables retained were those chosen by forward selection as contributing significant variation to the ordination: flow, temperature, conductivity, percent canopy and percent pools (Table 4).

Site ordination diagrams were used to assess within-year variation for each sample site (Fig. 2; Gower et al. 1994). Comparisons were made for each site between late spring (May or June) and late summer (August or September) samples in 1995 and 1997. Similar comparisons were used to investigate sample site trajectories between wet and dry years (September 1994 and September 1998; Fig. 2).

To investigate the relationships between the abundance of nonnative and native species and streamflow, we regressed abundance of the two groups at each site as a function of annual streamflow. Analysis was performed using SigmaPlot 4.0 (1997).

RESULTS

Ordination

The first two canonical axes explained a total of 29% of the variation in species distribution (19% and 10%, respectively; Table 4). Inter-set correlations indicated that environmental gradients in temperature, conductivity, canopy and percent pools contributed significantly to the first canonical axis, whereas gradients in temperature and percent pools contributed significantly to the second canonical axis (Table 4). The first axis separated species longitudinally (upstream and downstream) and by species origin (native and nonnative), while the second axis further separated species by temperature requirements, percentage of pools, and streamflow.

Species associations

Thirty-five fish species (including one hybrid) have been collected in Lower Putah Creek since 1994 (M. Marchetti, *unpublished data*), of which 13 are native to the drainage (Table 2). The ordination plot of species scores and environmental variables indicated a separation of native and nonnative species (Fig. 3). Most of the native species (except Sacramento blackfish)

TABLE 4. Summary statistics for the canonical correspondence analysis of fish abundance and environmental variables.

Variable	Axis 1	Axis 2	Axis 3
Eigenvalue	0.494	0.247	0.096
Species-environment correlations	0.912	0.853	0.619
Cumulative percentage variation			
Explained by species only	19.2	28.9	32.6
Explained by species + env. var.	51.8	77.7	87.8
Inter-set correlations with axes			
Streamflow	0.258	0.126	−0.319
Temperature	−0.774	0.391	−0.036
Conductivity	−0.745	0.120	0.162
Pools (%)	−0.774	−0.346	−0.196
Shade (%)	0.641	−0.140	−0.006

Note: Total inertia = 2.566.

tended to be in regions associated with increased canopy, higher streamflow, decreased conductivity, cooler temperatures, and fewer pools, while most of the nonnative species (except green sunfish and smallmouth bass) had an opposite association with these variables (Fig. 3).

The TWINSPAN results showed a similar separation of native and nonnative species (Fig. 3). The first division among species separated most native species from nonnative species. The second division produced four distinct species groups. Group A1 contained all native species (threespine stickleback, prickly sculpin, riffle sculpin, rainbow trout, Pacific lamprey, hitch, and California roach). Group A2 contained two native (Sacramento pikeminnow and tule perch) and one nonnative species (smallmouth bass). Group B1 contained three nonnative taxa, green sunfish, largemouth bass, and bluegill × green sunfish hybrid. Group B2 contained the bulk of the nonnative taxa (bluegill, largemouth bass, black bullhead, common carp, channel catfish, white crappie, fathead minnow, inland silverside, black crappie, bigscale logperch, and red shiner) and a single native species (Sacramento blackfish).

Site associations

The ordination and classification results indicated spatial associations among sites. Individual sample sites were associated with similar suites of environmental variables and were arranged in a general upstream to downstream gradient (Fig. 2). The upstream sites were associated with increased canopy and flow, decreased conductivity, cooler temperatures and fewer pools, while the downstream sites had opposite associations. The second TWINSPAN division produced four groupings that suggested a similar spatial pattern.

The four TWINSPAN groups defined by the second level of classification had significantly different (one-way ANOVA with Bonferroni adjustment $\alpha = 0.05$) average values for 12 of the original 14 environmental variables (Table 3). The upstream group (A1) was often (8 out of 11 variables) significantly different from the downstream groups (B1and B2). Group A2 was often intermediate between groups A1 and B2, although there was significant overlap among groups.

Patterns in site characteristics among time periods were also observed in the ordination plots (Fig. 2). Site variation between the early and late seasons generally had a two-part structure. The six sites in the middle and lower reaches (H, R, S, U, O, and M) showed lower flows and more pools from early to late summer. The two upstream sites (P and D) responded very little over the same seasonal periods.

Site variation between dry and wet years showed similar, but reversed patterns (Fig. 2). The six middle and lower reach sites (H, R, S, U, O, and M) changed between September 1994 and September 1998 with increased flow and fewer pools. The two most upstream sites (P and D) showed decreases in temperature and conductivity.

Regression

Nonnative fish abundance decreased in response to increasing streamflow at four middle and lower reach sites (Russell Ranch, Stevenson Road, University of California [UC] Davis Campus, and Old Davis Road) over the six sample periods (Fig. 4). Using an exponential decay regression equation ($y = ae^{-bx}$), the abundance of nonnative fish vs. flow was significant ($\alpha = 0.05$) at all four sites (Russell Ranch, no. exotics = $266.6e^{-3.11(\mathrm{flow})}$; Stevenson Road, no. exotics = $225.3e^{-5.48(\mathrm{flow})}$; UC Davis, no. exotics = $394.3e^{-2.14(\mathrm{flow})}$; Old Davis Road, no. exotics = $107.6e^{-2.81(\mathrm{flow})}$). The effect of elevated streamflow was reduced after streamflows became >0.8 m^3/sec. Fish abundance at all other sites exhibited no significant relationship with streamflow.

The Stevenson Road site exhibited a significant ($\alpha = 0.05$) positive relationship between native fish abundance and decreased streamflow (Fig. 4) using an exponential growth regression model ($y = e^{ax}$); Stevenson Road, no. natives = $e^{5.22(\mathrm{flow})}$). All other sites exhibited no significant relationship with streamflow, although the Russell Ranch and UC Davis sites had generally increasing trends when streamflow was <1.0 m^3/sec.

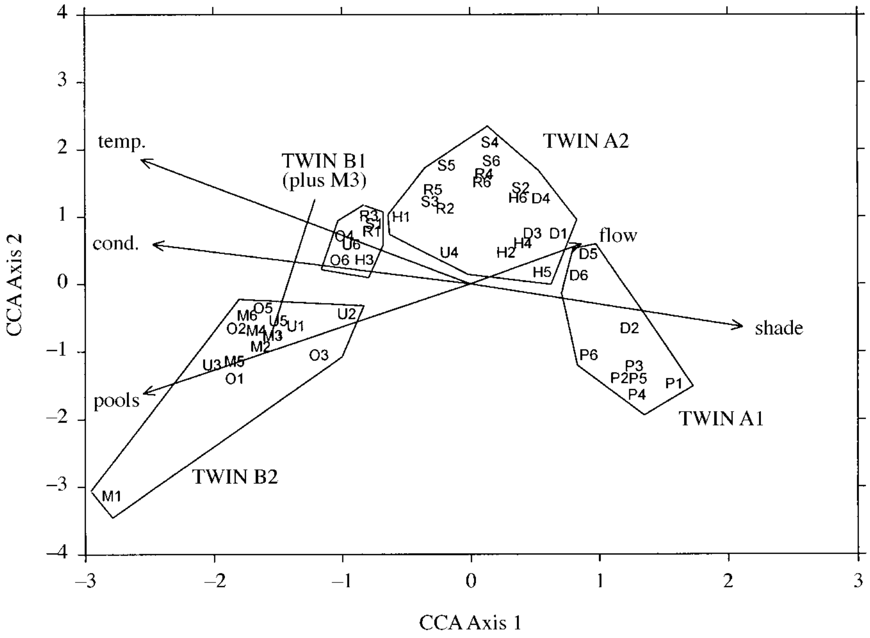

FIG. 2. Plot of results of canonical correspondence analysis showing site scores and the five environmental variables on the first two canonical axes. The two-character code for site scores refers to site name (letters) and sample date (numbers). See Fig. 1 for site names. Number 1 refers to September 1994 samples, no. 2 to May 1995 samples, no. 3 to August 1995 samples, no. 4 to June 1997 samples, no. 5 to September 1997 samples, and no. 6 to September 1998 samples. TWINSPAN groups are enclosed in polygons. Arrows represent the correlation of physical variables with the canonical axes. Nine site scores (P2, P3, S2, S3, U5, M2, M3, O2, and O5) were slightly altered on the figure to facilitate visual interpretation of the plot. Key to abbreviations: cond. = specific conductance, temp. = stream temperature.

DISCUSSION

The native fishes of Putah Creek are favored by a combination of suitable habitat conditions and a flow regime that resembles the natural flow regime of the stream. While alien fishes can invade the habitats favored by native fishes, their ability to persist seems to be limited by high flow events. High flow events also allow the native fishes to become abundant in habitats otherwise dominated by nonnative species. These results seem to validate the natural flow regime paradigm (Power et al. 1996, Poff et al. 1997).

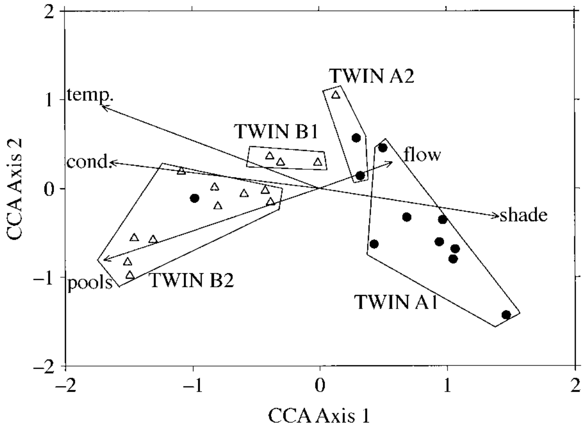

FIG. 3. Plot of results of canonical correspondence analysis showing species occurrence and the five environmental variables on the first two canonical axes. Native species are represented by solid circles, nonnative species by gray triangles. TWINSPAN groups are enclosed in polygons. See Table 2 for exact species membership in TWINSPAN groups. Arrows represent the correlation of physical variables with the canonical axes. Key to abbreviations: cond. = specific conductance, temp. = stream temperature.

Do predictable fish assemblages exist in Putah Creek?

Lower Putah Creek has very little drop in elevation (27 m over 37 km), yet the patterns of fish distribution and abundance were very similar to those found over much wider elevational gradients in Central Valley streams, including Putah Creek above Berryessa Reservoir (Moyle 1976, Moyle et al. 1982). Upper elevation reaches have a cold-water fauna dominated by trout and sculpins, mid-elevation foothill reaches contain mainly endemic cyprinids and suckers, and lower elevation reaches contain mainly alien fishes adapted to slow-water habitats. As predicted by Ward and Stanford (1979, 1983), Monticello and Putah Diversion dams on Putah Creek have created a compression of the natural longitudinal gradient of physical and ecological factors within the stream, compressing the fish assemblages into narrow zones. Before the construction of the dams, the three major fish assemblages observed in the creek would have been spread over the entire

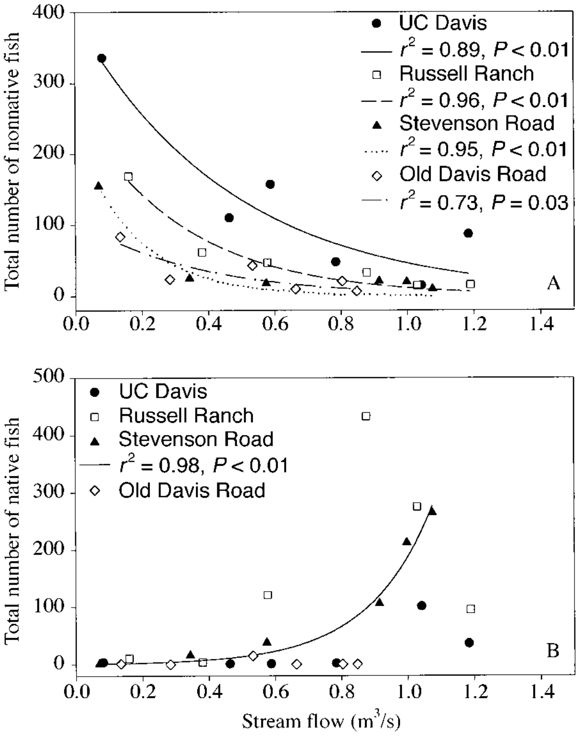

FIG. 4. (A) Number of nonnative fish collected at middle reach sites plotted against stream flow. Regression equations are of the form $y = ae^{-bx}$. (B) Number of native fish collected at middle reach sites plotted against stream flow. Regression equation is of the form $y = e^{ax}$.

watershed. It should be noted, however, that the faunal compression caused by the dams has resulted in a native fish assemblage that historically would have been regarded as transitional between the foothill cyprinid–sucker assemblage and the original native fish assemblage found on the valley floor. Hitch, threespine stickleback, and tule perch are typically low-elevation species although these fishes today are uncommon where alien fishes predominate (Moyle 1976, Moyle et al. 1998).

What habitat conditions favor native fishes?

The forward selection procedure in CANOCO indicated that five environmental variables contributed most heavily to the ordination and were therefore important in structuring the fish assemblages in Putah Creek: specific conductance, temperature, amount of pool habitat, canopy (a measure of riparian cover), and flow. The native fishes were consistently associated with high water quality, flowing water, and structurally complex habitats. These results agree with other studies of factors determining the composition of stream fish assemblages in the Central Valley drainage (Moyle 1976, Taylor et al. 1982, Brown and Moyle 1993). Because of the compressed nature of the stream gradient, other factors often identified as affecting fish assemblages, such as gradient, watershed size, elevation, and forest cover (Hawkes et al. 1986, Matthews and Robison 1988, Matthews et al. 1992, Maret et al. 1997) did not have much influence.

How does flow regime affect native and nonnative fishes?

Changes in the fish assemblages at each site through time (both within and between years) in combination with the regression analyses suggest strongly that streamflow influenced fish assemblage composition, particularly at the middle and lower sites. These sites became favorable for nonnative species when flows declined and unfavorable when flows increased. The pattern is progressive in time as well as in space. Back-to-back years of high flows in the creek increased the abundance of native fishes between years and decreased the abundance of alien fishes. This implies that there are large differences between wet years (1998) and dry years (1994) in terms of community response. Dry years shifted the environmental conditions favoring nonnative assemblages upstream and wet years shifted environmental conditions to those favoring native assemblages downstream.

CONCLUSIONS

The fortuitous combination of extreme dry and extreme wet years we encountered during the five years of our study provided an unusual opportunity to test the hypothesis that a more natural flow regime favors native fishes in a regulated stream (Poff et al. 1997). In Putah Creek, conditions for native species improved during years with large peak flows in winter and sustained flows in summer, while alien species were favored during years without high peak flows and with intermittent summer flows. The natural flow regime of Putah Creek is typical of streams of the western United States, where peak flows result from winter rains and spring snowmelt and low flows result from summers with little precipitation. Likewise, the flattened hydrograph of the regulated creek is typical of other regulated streams but especially those in California (Mount 1995, Poff et al. 1997). It is widely recognized that a natural hydrograph reduces the invasibility of undammed streams by alien fishes (Baltz and Moyle 1993, Stanford et al. 1996). However, natural experiments such as the 1994–1998 flow regime of Putah Creek, which allow this idea to be tested with the potential for determining mechanisms, are rare (Strange et al. 1992). Understanding how a more natural flow regime favors native fishes and other organisms can help to establish favorable flow regimes in regulated streams with minimal costs in additional releases of water from dams (Power et al. 1996).

In Putah Creek, the high winter and spring flows apparently flushed many nonnative fish from the creek, while simultaneously creating conditions that favored reproduction by the native fishes, which mostly spawn in mid-February through mid-April (Marchetti and

Moyle 2000). The flushing effects of high flow events have been observed in other western streams (Meffe 1984). The higher summer flows also favored native fishes by providing longer reaches of cool flowing water where juveniles of the native fishes could find suitable conditions for rearing, while simultaneously reducing the favorability of the habitats for spawning and rearing of alien fishes. Most of the nonnative fishes are summer spawners, in warm (>24°C) quiet water (Moyle 1976). The improvement of habitats for native fishes while simultaneously decreasing the abundance of alien fishes are synergistic actions because alien species can limit native species through competition and predation (Ross 1991, Lodge 1993, Moyle and Light 1996, Marchetti 1999).

Putah Creek provides an example where adaptive management could be implemented to provide flows for native fishes, while not providing much reduction in water available for human use. In years where large natural flows occur (1997, 1998), little water would have to be released from storage beyond what is required to maintain summer base flows for native species. During years with very little flow (1994, 1995), however, maintenance of native fishes may require augmenting base flows and occasionally releasing large pulse flows in winter (Moyle et al. 1998). Fortunately, the native fishes are adapted for surviving multiyear periods of adverse flow conditions (Moyle et al. 1982) so they can persist through an extended drought, provided the alien fishes are kept at bay or that suitable habitat refuges exist for the native fishes. Thus, an adaptive management scheme focused on native fish assemblages would necessarily include consideration of other environmental variables in addition to streamflow. One such management option might include increasing riparian vegetation along the lower portions of the creek. This would create more shaded aquatic habitat and would cool water temperatures, favoring native fishes, perhaps reducing water costs during periods of drought.

Our study of lower Putah Creek provides a clear demonstration of how native fishes in streams of the western United States respond to annual and seasonal variation in flow in a different manner than nonnative fishes and how they exhibit different habitat requirements. The study supports the concept that restoration of natural flow regimes, in company with other restoration measures, is necessary if the continued downward decline of native fish populations in the western United States is to be reversed.

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LITERATURE CITED

Bain, M. B., J. T. Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. Ecology **69**:382–392.

Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecological Applications **3**:246–255

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

Castleberry, D. T., J. J. Cech, Jr., D. C. Erman, D. Hankin, M. Healey, G. M. Kondolf, M. Mangel, M. Mohr, P. B. Moyle, J. Nielsen, T. P. Speed, and J. G. Williams. 1996. Uncertainty and instream flow standards. Fisheries **21**(8): 20–21.

Gower, A. M., G. Myers, M. Kent, and M. E. Foulkes. 1994. Relationships between macroinvertebrate communities and environmental variables in metal-contaminated streams in south-west England. Freshwater Biology **32**:199–221.

Hawkes, C. L., D. L. Miller, and W. G. Layher. 1986. Fish ecoregions of Kansas: stream fish assemblage patterns and associated environmental correlates. Environmental Biology of Fishes **17**:267–279.

Hill, M. O. 1979. TWINSPAN, a fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Microcomputer Power, Ithaca, New York, USA.

Imbert, J. B., and J. A. Stanford. 1996. An ecological study of a regulated prairie stream in western Montana. Regulated Rivers: Research and Management **12**:597–615.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams: a geomorphic perspective. Bioscience **45**:183–192.

Lodge, D. M. 1993. Species invasions and deletions: community effects and responses to climate and habitat change. Pages 367–387 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Marchetti, M. P. 1999. An experimental study of competition between the native Sacramento perch (*Archoplites interruptus*) and introduced bluegill (*Lepomis macrochirus*). Biological Invasions **1**:1–11.

Marchetti, M. P., and P. B. Moyle. 2000. Spatial and temporal ecology of native and introduced larval fish in Lower Putah Creek (Yolo Co. CA). Environmental Biology of Fishes **58**(1):73–87.

Maret, T. R., C. T. Robinson, and G. W. Minshall. 1997. Fish assemblages and environmental correlates in least-disturbed streams of the Upper Snake River Basin. Transactions of the American Fisheries Society **126**:200–216.

Mathur, D., W. H. Bason, E. J. Purdy, Jr., and C. A. Silver. 1985. A critique of the instream flow incremental methodology. Canadian Journal of Fisheries and Aquatic Sciences **42**:825–831.

Matthews, W. J., D. J. Hough, and H. W. Robison. 1992. Similarities in fish distribution and water quality patterns in streams of Arkansas: congruence of multivariate analysis. Copeia **1992**(2):296–305.

Matthews, W. J., and H. W. Robison. 1988. The distribution of the fishes of Arkansas: a multivariate analysis. Copeia **1998**(2):358–374.

Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator–prey fish species. Ecology **65**:1525–1534.

Mount, J. F. 1995. California rivers and streams: the conflict between fluvial processes and land use. University of California Press, Berkeley, California, USA.

Moyle, P. B. 1976. Inland fishes of California. University of California Press, Berkeley, California, USA.

Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Transactions of the American Fisheries Society **123**:498–507.

Moyle, P. B., and B. Herbold. 1987. Life-history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe. Pages 25–32 *in* W. J. Matthews and D. C. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Oklahoma, USA.

Moyle, P. B., and T. Light. 1996. Fish invasions in California: Do abiotic factors determine success? Ecology **77**:1666–1670.

Moyle, P. B., M. P. Marchetti, J. Baldridge, and T. L. Taylor. 1998. Fish health and diversity: justifying flows for a California stream. Fisheries **23**(7):6–15.

Moyle, P. B., J. J. Smith, R. A. Daniels, and D. M. Baltz. 1982. A review. Pages 255–256 *in* P. B. Moyle, editor. Distribution and ecology of stream fishes of the Sacramento–San Joaquin drainage system, California. University of California Publications in Zoology 115. University of California Press, Berkeley, California, USA.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology **74**:2215–2230.

Pert, E. J., and D. C. Erman. 1994. Habitat use by adult rainbow trout under moderate artificial fluctuations in flow. Transactions of the American Fisheries Society **123**:913–923.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience **47**:769–784.

Power, M. E., W. E. Dietrich, and J. C. Finlay. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. Environmental Management **20**:887–895.

Ross, T. S. 1991. Mechanisms structuring stream fish assemblages: are there lessons from introduced species? Environmental Biology of Fishes **30**:359–368.

SigmaPlot. 1997. SigmaPlot: 4.0 for Windows 95, NT and 3.1. SPSS, Chicago, Illinois, USA.

Stanford, J. A., J. V. Ward, W. J. Liss, C. A. Frissell, R. N. Williams, J. A. Lichatowich, and C. C. Countant. 1996. A general protocol for restoration of regulated rivers. Regulated Rivers **12**:391–501.

Strange, E. M., P. B. Moyle, and T. C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology of Fishes **36**:1–15.

SYSTAT. 1998. SYSTAT 8.0 Statistics. SPSS, Chicago, Illinois, USA.

Taylor, T. L., P. B. Moyle, and D. G. Price. 1982. Fishes of the Clear Lake Basin. Pages 171–224 *in* P. B. Moyle, editor. Distribution and ecology of stream fishes of the Sacramento–San Joaquin drainage system, California. University of California Publications in Zoology 115. University of California Press, Berkeley, California, USA.

ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**:1167–1179.

ter Braak, C. J. F., and P. Smilauer. 1998. CANOCO for windows version 4.0. Center for Biometry, Wageningen, The Netherlands.

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences **57**(3):255–289.

Ward, J. V., and J. A. Stanford. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. Pages 35–55 *in* J. V. Ward and J. A. Stanford, editors. The ecology of regulated streams. Plenum Press, New York, New York, USA.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems. Pages 29–42 *in* T. D. Fontaine and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan, USA.

Ward, J. V., and J. A. Stanford. 1995. The serial discontinuity concept: extending the model to floodplain rivers. Regulated Rivers: Research and Management **10**:159–168.

Williams, J. G. 1996. Lost in space: minimum confidence intervals for idealized PHABSIM studies. Transactions of the American Fisheries Society **125**:458–465.