

Flows, droughts, and aliens: factors affecting the fish assemblage in a Sierra Nevada, California, stream

JOSEPH D. KIERNAN^{1,2,3} AND PETER B. MOYLE²

¹*Fisheries Ecology Division, Southwest Fisheries Science Center, NOAA National Marine Fisheries Service, 110 Shaffer Road, Santa Cruz, California 95060 USA*

²*Center for Watershed Sciences, University of California at Davis, One Shields Avenue, Davis, California 95616 USA*

Abstract. The fishes of Martis Creek, in the Sierra Nevada of California (USA), were sampled at four sites annually over 30 years, 1979–2008. This long-term data set was used to examine (1) the persistence and stability of the Martis Creek fish assemblage in the face of environmental stochasticity; (2) whether native and alien fishes responded differently to a natural hydrologic regime (e.g., timing and magnitude of high and low flows); and (3) the importance of various hydrologic and physical habitat variables in explaining the abundances of native and alien fish species through time. Our results showed that fish assemblages were persistent at all sample sites, but individual species exhibited marked interannual variability in density, biomass, and relative abundance. The density and biomass of native fishes generally declined over the period of study, whereas most alien species showed no significant long-term trends. Only alien rainbow trout increased in both density and biomass at all sites over time. Redundancy analysis identified three hydrologic variables (annual 7-day minimum discharge, maximum winter discharge, and number of distinct winter floods) and two habitat variables (percentage of pool habitat and percentage of gravel substrate) that each explained a significant portion of the annual variation in fish assemblage structure. For alien taxa, their proportional contribution to the total fish assemblage was inversely related to mean annual streamflow, one-day maximum discharge in both winter and spring, and the frequency of springtime floods. Results of this study highlight the need for continuous annual monitoring of streams with highly variable flow regimes to evaluate shifts in fish community structure. Apparent successes or failures in stream management may appear differently depending on the time series of available data.

Key words: *assemblage structure; community ecology; drought; fish conservation; flow regime; introduced species; long-term data; Martis Creek; persistence.*

INTRODUCTION

Ecologists have long sought to understand the mechanisms and processes that affect persistence of populations and communities over time. There is an especially rich history of debate over mechanisms that determine the structure and dynamics of stream fish assemblages (Matthews 1998). Most disagreement has centered on the relative importance of density-dependent (deterministic) vs. density-independent (stochastic) processes. Density-dependent mechanisms, mainly competition, predation, parasitism, and disease, regulate populations via reductions in growth, reproductive output, or survivorship. Density-dependent regulation has been widely documented in streams (e.g., Elliott 1994, Jenkins et al. 1999, Lobon-Cervia 2007) and hypothesized to be the only force capable of producing populations with long-term stability (May 1976, Grossman et al. 1990, Murdoch 1994). Conversely, density-

independent mechanisms such as floods (Erman et al. 1988, Matthews 1998) and drought (Matthews and Marsh-Matthews 2003, Béche et al. 2009) affect fish populations via direct mortality during poor conditions or enhanced survivorship during periods of favorable conditions. While contemporary ecological theory suggests that both deterministic and stochastic processes act to structure riverine communities (Grossman and Sabo 2010), the perceived importance of each process is likely dependent upon the temporal and spatial scales used for study of the organisms and environments.

For streams in Mediterranean-type climates, streamflow has been deemed a “master variable” (Poff and Ward 1989, Power et al. 1995) because it influences many physical factors (e.g., water depth, current velocity, and habitat diversity) and ecological interactions (e.g., competition and predation) that limit distribution and abundance of stream biota. Moreover, a natural flow regime (Poff et al. 1997) is hypothesized to maintain native fish assemblages, where life histories are presumed to be synchronized with local flow dynamics. Conversely, the lack of persistence of alien

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³ E-mail: joseph.kiernan@noaa.gov

(nonnative) fishes may be caused by their inability to cope with hydrologic conditions that differ from those to which they are adapted (Moyle and Light 1996, Fausch et al. 2001). Riverine biota in California (USA) must contend with a strong seasonal pattern of flow (high in winter, low in summer) combined with natural hydrologic variability that creates frequent periods of extreme conditions such as floods and extended low flows (Gasith and Resh 1999, Grantham et al. 2010). Such periods of extreme flow may play a central role in structuring fish and invertebrate communities (Bêche et al. 2009).

Although long-term discharge data are available for many North American streams, quantitative records of fish assemblage composition, especially those collected with comparable sampling effort, are extremely rare (but see studies in Matthews 1998). This paucity of data has limited our ability to make robust assessments of stability and persistence in populations with generation times exceeding one year. Moreover, short-term studies often fail to capture the full range of hydrologic variability potentially experienced by fishes and may provide a spurious or incomplete picture of the importance of hydrologic disturbance to assemblage structure. For example, following a five year study (1979–1984) of Martis Creek, California, Moyle and Vondracek (1985) concluded that, despite interannual variability in streamflow, the fish assemblage was persistent and stable largely due to density-dependent mechanisms (e.g., segregation of species by habitat, microhabitat, and diet). However, when Strange et al. (1992) analyzed 10 years of data from the same stream they concluded that a pair of very large flood events precipitated a significant shift in the fish assemblage from dominance by native species to dominance by alien species.

Here we expand upon previous studies of Martis Creek and examine variability of the fish assemblage over 30 years (1979–2008). The extended temporal perspective of our study permits examination of community dynamics and population trends across many generations of the constituent species. Moreover, the period of study encompasses a range of hydrologic conditions including intense floods (1983, 1995, 2006) and extended drought (1987–1992), allowing us to assess the effect of hydrologic variability on assemblage structure. Our aim is to re-test hypotheses posed in Moyle and Vondracek (1985) and Strange et al. (1992). Specifically, (1) the Martis Creek fish assemblage is both persistent and stable through time, and (2) alien fishes are strongly affected by the timing (season) and magnitude of high-flow events. Additionally, we used three decades of hydrologic, physical habitat, and fish community data to examine the relative importance of various environmental factors in explaining the distribution and abundance of native and alien fish species within Martis Creek.

METHODS

Study site

Martis Creek is a tributary of the Truckee River in Nevada and Placer Counties, California, USA (39°19' N, 120°07' W). In 1979, four 40-m stream reaches were selected to represent typical habitats in the creek and were established as permanent sample sites. The sites were distributed along a 2.9-km stream segment bounded upstream by Martis Dam (elevation 1745 m) and downstream by a high-gradient riffle cascade. The four sample sites (hereafter S1, S2, S3, and S4) were located 0.1, 0.3, 1.2, and 2.4 km above the confluence with the Truckee River, respectively. The climate is Mediterranean and precipitation generally falls as snow or mixed snow and rain between October and May. Peaks in the annual hydrograph are produced by rain on snow events and spring snowmelt. Peak flows generally occur between January and early June and low (base) flows between August and November (Fig. 1A). Martis Dam was constructed in 1972 for flood control and formed 0.28-km² Martis Creek Reservoir (storage capacity = 1234 m³). The reservoir was originally designed to spill through a vertical standpipe; however, only temporary flood storage is currently permitted due to chronic seepage and active dam failure. Hence, reservoir outflows generally equaled inflows and annual discharge patterns in the study area mimicked the natural flow regime except that extreme high-flow events were dampened (Moyle and Vondracek 1985, Strange et al. 1992). Maximum daily discharge prior to dam construction was 50.9 m³/s (1 February 1963; period of record 1959–1971) compared to 17.3 m³/s (3 January 2006) during the post-dam era (U.S. Geological Survey [USGS] gage 10339400; data available online).⁴

Fish assemblage composition and sampling

The Martis Creek fish assemblage is a mixture of native and alien species, with the two most abundant predatory fishes being alien brown trout (*Salmo trutta*) and alien rainbow trout (*Oncorhynchus mykiss*; Table 1). Both species were introduced into the eastern Sierra Nevada in the late 19th century to improve fisheries and ultimately replaced the native Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) throughout its range, including Martis Creek (Moyle 2002). The two alien trout species coexist in many streams, although the life history of rainbow trout is closer to that of the native cutthroat trout. Presumably, resident native (non-trout) fish species maintain their populations in the face of predation by alien trout species because they coevolved with Lahontan cutthroat trout and have adaptations to reduce predation effects by trout.

From 1979 to 2008 (except 1986), fish populations were surveyed once annually in August or September during low-flow conditions. Annual summer sampling is

⁴ <http://waterdata.usgs.gov>

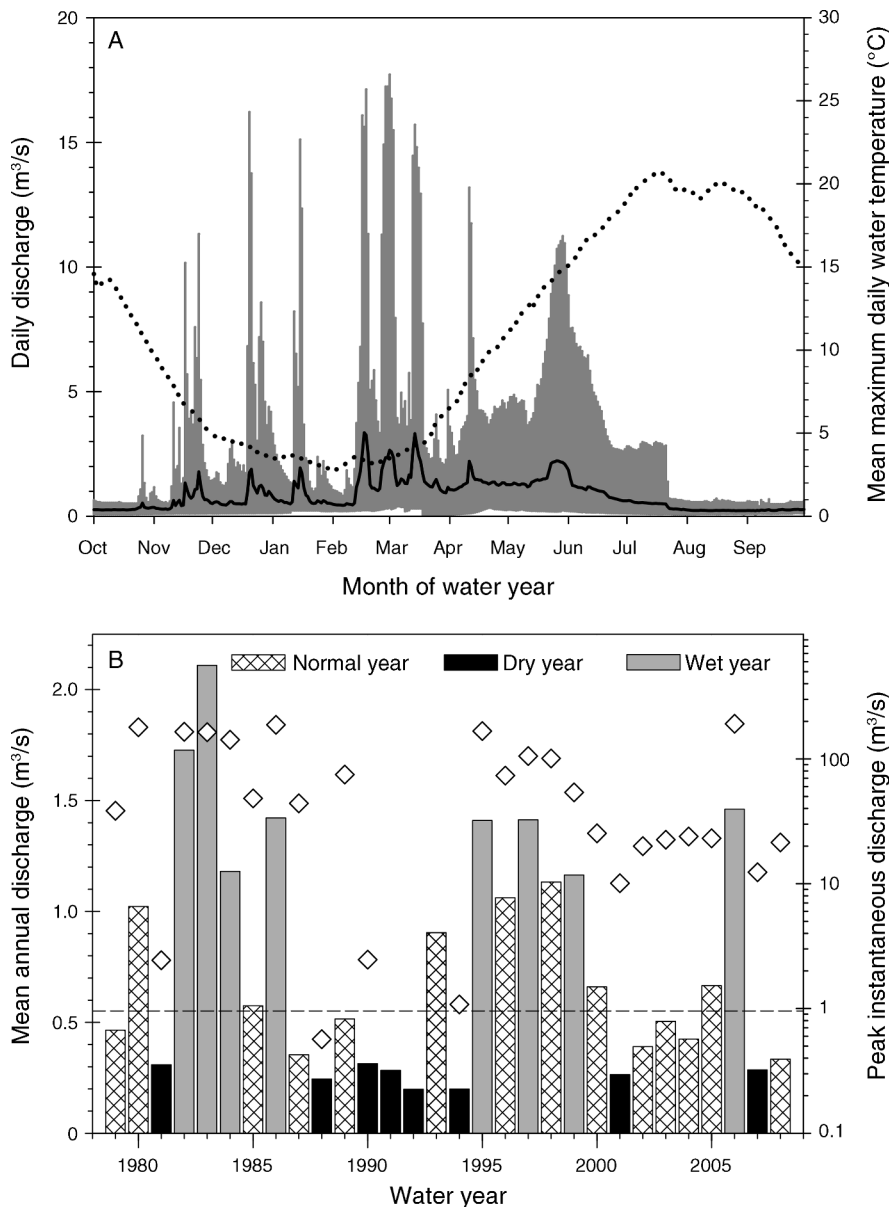


FIG. 1. Temporal dynamics of discharge and water temperature at Martis Creek, California, USA, 1979–2008. (A) Mean daily discharge (solid line) and maximum daily water temperature (dotted line). The gray shaded area represents the minimum and maximum recorded discharge for each day during the 30-year study. (B) Mean annual (bars) and peak instantaneous (diamonds) discharge during each water year of study. The horizontal dashed line represents median discharge for the complete hydrologic record (1974–2008). Gray, hatched, and black vertical bars indicate wet (≥ 75 th percentile), normal, and dry (≤ 25 th percentile) water year types, respectively. Note log scale for peak instantaneous discharge. Data are from USGS gaging station 10339400: <http://waterdata.usgs.gov>

typical for long-term studies of stream fishes (Matthews 1998 and references therein) because the interval and timing allows the annual success of reproduction to be easily determined (i.e., abundance of young-of-year fishes) and avoids problems with repeated sampling that might affect abundances of some species through mortalities or habitat disturbance. On each occasion, sample sites were isolated with block nets and fish were collected using a backpack electrofisher. Three-pass

removal sampling was conducted during most visits (106 of 115; 92%); however, single or two-pass sampling was occasionally employed due to equipment failures. Captured fish were identified to species and measured for standard length (± 1.0 mm). Biomass was determined by water displacement or by weighing with a Pesola spring scale (± 1.0 g; Pesola AG, Baar, Switzerland). Occasionally, masses were estimated from taxon-specific length–weight regression equations (P. B. Moyle,

unpublished data). Annual abundance estimates for each species were derived by maximum-likelihood estimation using MicroFish version 3.0 (Van Deventer and Platts 1989). Abundance and biomass totals were divided by the area sampled to generate annual estimates of species density (individuals/100 m²) and biomass (kg/100 m²) at each site. In most years, the majority of fish were young-of-year forming a size–age structure typical of minimally disturbed fish populations with relatively short-lived (<6–7 yr) adults. Hence, high abundance indicated successful spawning in the fall or spring prior to sampling.

Habitat variables

Twelve habitat variables were measured or estimated at each site across all years. Variables included: reach length, mean wetted width, mean depth, maximum depth, percentage of riffle, run, and pool habitat, and substrate composition. Wetted stream width and three depth measurements (± 1.0 cm, measured at 25, 50, and 75% wetted width) were quantified at 10 evenly spaced transects along the length of each sample site. Maximum depth was the deepest point in the entire sample reach. Substrate composition was visually estimated to the nearest 5% as sand/silt (<2 mm), gravel (2–64 mm), cobble (>64–256 mm), or boulder (>256 mm). Beginning in 1990, the proportion of stream habitat containing different forms of aquatic vegetation (i.e., emergent, submerged, floating mats, and filamentous algae) was also visually estimated ($\pm 5\%$; Appendix A).

Stream temperature and hydrologic attributes

Stream discharge and water temperature data were obtained from USGS gaging station 10339400 located 0.3 km downstream of Martis Creek Dam. We calculated mean weekly maximum stream temperature (i.e., 7-day running averages; MWMT) for each day of the year and summed the number of days MWMT $\geq 20^\circ\text{C}$ annually. A MWMT threshold of 20°C was chosen because it represents a sublethal level above which Paiute sculpin (*Cottus beldingi*), the most thermally intolerant species of the native fish assemblage, become increasingly rare (Moyle 2002). Mean daily discharge data representing the complete period of record (water years 1974–2008) were used to determine median annual stream flow (0.55 m³/s). Each study year was then classified as one of three water-year types based on mean annual flow: normal, wet (≥ 1.15 m³/s, 75th percentile), or dry (≤ 0.33 m³/s, 25th percentile). Because discharge data were unavailable for the period 1991–1993, we derived estimates of mean annual flow (Q_{maf} , [m³/s]) for these years using data for nearby Sagehen Creek (Nevada County, California; USGS gage 10343500). The relationship between Q_{maf} in the two basins was described by the equation $\log_{10}(Q_{\text{maf}}^{\text{Martis}}) = 0.32 + 0.95 \times \log_{10}(Q_{\text{maf}}^{\text{Sagehen}})$ ($r^2 = 0.98$, $F_{1,32} = 1517.98$, $P < 0.001$).

We identified a priori 14 attributes of the flow regime that we postulated were important to the Martis Creek fish assemblage (Appendix B: Table B1). Based on previous research in Martis Creek and knowledge of species life histories, we partitioned the hydrograph into winter (1 December–31 March) and spring (1 April–30 June) periods to examine how seasonal flow regimes influenced assemblage composition. Hydrologic variables were summarized using Indicators of Hydrologic Alteration (IHA) software version 7 (Richter et al. 1996, Nature Conservancy 2007) or calculated from the summary of annual statistics output generated by the IHA program. Following Fausch et al. (2001), we defined a flood event as any flow exceeding the 95th percentile mean daily discharge (i.e., the discharge exceeded 18 d/yr on average) for one or more days.

Data analyses

Fish assemblage structure, persistence, and stability.—Fish assemblages at each sample site were characterized in terms of rarefied species richness, Shannon's diversity index, evenness, and persistence. For the Martis Creek fish assemblage, we defined persistence as the continued presence of the constituent species over time, without regard to absolute or relative abundances. To quantify persistence we calculated rates of year-to-year assemblage turnover (T) at each site using the equation $T = (C + E)/(S_1 + S_2)$, where C and E represent the number of species that colonized or were extirpated between successive sample periods and S_1 and S_2 are the number of species present in each sample period (Diamond and May 1977). Turnover rates were averaged across all years and an index of persistence was calculated as $1 - \text{mean } T$ (Meffe and Minckley 1987). To assess long-term persistence at each site, we examined turnover between the assemblages documented at the onset (1979) and conclusion (2008) of the study, exclusively. Turnover index values ranged from 0 (no persistence) to 1.0 (complete persistence) with values >0.6 considered reasonable support for assemblage persistence (Meffe and Minckley 1987). We assumed the annual presence or absence of each fish species was measured without error.

We assessed stability (i.e., the degree of constancy in numbers or relative abundance) at both the level of individual populations and the entire fish community. For individual populations, we calculated coefficients of variation (CV) to quantify among year variability in abundance and biomass at each sample site. Following Freeman et al. (1988), populations were classified as (1) highly stable ($\text{CV} \leq 0.25$), (2) moderately stable ($0.25 < \text{CV} \leq 0.50$), (3) moderately fluctuating ($0.50 < \text{CV} \leq 0.75$), or (4) highly-fluctuating ($\text{CV} > 0.75$). For the full fish community, time-lag regression analysis (Collins et al. 2000) was used to assess assemblage change at each site over time. Specifically, we calculated Sorensen (Bray-Curtis) distances between each possible pair of years in the time series of annual species abundances

(1979–2008). Thus, a site sampled annually for 29 years yielded 28 one-year time lags, 27 two-year time lags, 26 three-year time lags, and so forth. The resulting distance values were then regressed against the square-root of their time lags to quantify differences in assemblage composition as a function of temporal separation. This method produced a measure of stability with three potential outcomes: (1) a regression line with a slope not significantly different from zero indicated either assemblage stability or complete stochastic variability, (2) a significant, positive, linear regression indicated an assemblage undergoing directional change, and (3) a significant, linear, and negative slope indicated an unstable assemblage converging on a structure characteristic of an earlier time period (Collins et al. 2000). For interpretation, the slope of the regression line indicated magnitude of assemblage change and model fit served as a measure of noise; low R^2 values suggested high stochastic variation between years, whereas higher R^2 values suggested a stronger signal of directional change (Angeler et al. 2009).

Non-metric multidimensional scaling (nMDS) ordinations were used to examine patterns in fish community structure at each sample site and identify years that contributed strongly to the results obtained from the time-lag regression analyses. For nMDS, Sorensen distances were calculated from the same matrices of fish abundance used in time-lag regression analyses. Optimal solutions (number of dimensions) were determined by examining stress values obtained using Monte Carlo permutation tests based on runs with real and randomized samples of the data ($N = 100$ each) and a stability criterion of 1.0×10^{-5} (McCune and Grace 2002). Two-dimensional ordination solutions were found to be optimal in all cases. Ordinations and distance calculations were performed in PC-ORD version 5.33 (MjM Software, Gleneden Beach, Oregon, USA).

Temporal trends in abundance and biomass.—Site-specific temporal trends in species abundance and biomass were assessed using nonparametric Spearman's rank correlation coefficients (r_s). Further, we used log-linear Poisson regression models with adjustments for overdispersion and serial correlation to identify significant changes in the annual abundance of each species and examine the synchrony of such changes across taxa. For this analysis, data from each sample site were pooled and the program TRIM (Trends and Indices for Monitoring Data; Pannekoek and van Strien 1996) was used to produce indexed estimates of mean annual abundance for each species. The stepwise selection procedure within TRIM was used to identify change points based on significant changes in slope (Wald tests; $\alpha = 0.05$) between successive years.

Habitat, hydrology, and fish assemblage structure.—Redundancy analysis (RDA) was used to relate fish community composition to potential explanatory variables. Candidate variables were selected a priori and included in-stream physical habitat parameters and

attributes of the flow regime, including water temperature (Appendix B). After correlation analysis to eliminate redundant ($r_s \geq 0.7$) variables, a reduced set of 17 explanatory variables were carried forward for potential inclusion in RDA models (Appendix B: Table B1). Separate RDAs were performed using (1) the full Martis Creek fish community, (2) alien taxa exclusively, and (3) native taxa exclusively. In each case, abundance data were square-root transformed and explanatory variables were standardized ($\mu = 0$, $\sigma = 1$) to account for different units of measurements. We used the forward selection procedure provided by the software package CANOCO (version 4.53; ter Braak and Šmilauer 2002) to identify variables that explained a significant amount of variance in community composition. Statistical significance was assessed at $\alpha = 0.05$ ($N = 499$ Monte Carlo permutations). However, all forward selected variables meeting the criteria of $P < 0.10$ were considered informative and presented in ordination diagrams. To quantify the fractions of variation in assemblage composition uniquely and jointly explained by the chosen sets of hydrologic ($N = 8$) and habitat variables ($N = 8$; Appendix B) we used variation partitioning following the methods in Borcard et al. (1992).

Finally, to test the hypothesis that alien fish populations are affected by the timing (season) and magnitude of high-flow events, we used Spearman's rank correlations to examine the relationship between the proportion of the total fish assemblage comprised of alien fishes and (1) mean annual discharge and (2) one-day maximum discharge. We also examined the relationship between seasonal flood frequency (number of distinct floods) and the proportional abundance of alien fishes using a generalized linear model with quasi-Poisson error distribution to correct for overdispersion, using R version 2.11 (R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Hydrologic trends

Despite high interannual variability in mean and peak discharge values (Fig. 1B), the long-term character of the Martis Creek hydrograph did not change between 1979 and 2008. Of the 33 hydrologic metrics generated by the IHA program to characterize magnitude, duration, timing, frequency, and rate of change of stream flows, only low pulse duration (i.e., periods within a year when daily flows were in the lower 25th percentile) exhibited a statistically significant trend over the period of study (slope = -2.49 , $F_{1,27} = 10.61$, $P < 0.01$, $R^2 = 0.34$; Appendix C).

Fish community composition

Collectively the four sample sites supported 14 species of fish over the 29 years of study (Table 1). Three species were present during all years, native Paiute sculpin and alien brown trout and rainbow trout, while native Tahoe

TABLE 1. Frequency of occurrence of fish species during annual surveys of four permanent sample sites (S1–4) in Martis Creek, California, USA, 1979–2008.

Species	S1 (<i>N</i> = 29)	S2 (<i>N</i> = 28)	S3 (<i>N</i> = 29)	S4 (<i>N</i> = 29)	All (<i>N</i> = 29)
Native					
Lahontan cutthroat trout (<i>Oncorhynchus clarki henshawi</i>)	3	2	1	1	0
Lahontan redbreast (<i>Richardsonius egregius</i>)	2	1	4	13	0
Lahontan tui chub (<i>Siphateles bicolor</i>)	0	1	0	1	0
Mountain sucker (<i>Catostomus platyrhynchus</i>)	3	7	6	16	0
Mountain whitefish (<i>Prosopium williamsoni</i>)	10	1	0	0	0
Paiute sculpin (<i>Cottus beldingi</i>)	28	27	19	18	14
Speckled dace (<i>Rhinichthys osculus</i>)	2	4	10	25	0
Tahoe sucker (<i>Catostomus tahoensis</i>)	7	14	17	28	6
Alien (nonnative)					
Bluegill (<i>Lepomis macrochirus</i>)	2	0	0	0	0
Brook trout (<i>Salvelinus fontinalis</i>)	2	0	0	0	0
Brown trout (<i>Salmo trutta</i>)	29	28	27	26	25
Green sunfish (<i>Lepomis cyanellus</i>)	0	1	3	12	0
Largemouth bass (<i>Micropterus salmoides</i>)	3	2	1	1	0
Rainbow trout (<i>Oncorhynchus mykiss</i>)	29	28	23	22	19

Notes: No sampling was conducted in 1986. *N* = number of years sampled at each site.

The “all” sites category indicates the number of years in which a given species was captured at all four sample sites (all three sites in 1990, as S2 was not sampled).

sucker (*Catostomus tahoensis*) were captured during every year except 1999. Spatially, no fish species was captured at all four sample sites during every year of study. Mean (± 1 SE) rarefied species richness was greatest at the upstream-most site (S4, 3.0 ± 0.2 species; *N* = 29) and lowest at S3 (2.5 ± 0.2 species; *N* = 29). Annual richness values (rarefied) ranged from 1.0 to 4.5 fish species at individual sample sites (Appendix D), and from 3.3 (year = 1988) to 7.5 (year = 1982) species at the scale of the entire creek (i.e., all sample sites pooled). Five species were rare in terms of abundance or frequency of occurrence (<25% of years): Lahontan cutthroat trout (*N* = 6 yr), Lahontan tui chub (*Siphateles bicolor*; *N* = 2 yr), bluegill (*Lepomis macrochirus*; *N* = 2 yr), brook trout (*Salvelinus fontinalis*; *N* = 2 yr), and largemouth bass (*Micropterus salmoides*; *N* = 2 yr) (Table 1). These species were not classified as resident populations and were excluded from all analyses except calculations of year-to-year assemblage turnover (indices of persistence).

Reach-scale assemblage persistence and stability

Fish assemblages at each sample site were moderately-persistent from year-to-year (mean persistence index [$1 - \bar{T}$], range = 0.77 to 0.86), but somewhat less so long term (i.e., contrasting 1979 and 2008, index range = 0.55 to 0.86; Appendix D). Despite overall assemblage persistence, the constituent species exhibited substantial interannual variability in density, biomass, and relative abundance (Fig. 2, Appendix E). Coefficient of variation calculations showed that native fishes were highly variable ($CV > 0.76$) in both density (CV_{den}) and biomass (CV_{bio}) over time, with a few exceptions (Appendix E). Among alien species, rainbow trout density was moderately stable at S1 ($CV_{den} = 0.47$) and moderately fluctuating at S2 ($CV_{den} = 0.64$).

Rainbow trout biomass was highly variable at all sites except S1 ($CV_{bio} = 0.71$). Brown trout density and biomass were both classified as moderately fluctuating at S1 ($CV_{den} = 0.53$, $CV_{bio} = 0.72$) and S2 ($CV_{den} = 0.72$, $CV_{bio} = 0.70$; Appendix E).

Time-lag regression analysis indicated significant directional change in fish assemblage structure at all four sample sites between 1979 and 2008 (slopes > 0 , $P \leq 0.002$ in all cases; Fig. 3A). However, the low regression coefficients associated with each model provided evidence that directional change across the 29-yr time series was weak. Additionally, the low proportion of variance explained by the linear models ($R^2 \leq 0.17$ in all cases) suggested stochastic variation in assemblage structure between sample years. Among the four sample sites, assemblage change was greatest at S3 (slope = 0.08, $P < 0.001$, $R^2 = 0.17$) and least pronounced at S1 (slope = 0.01, $P = 0.002$, $R^2 = 0.02$). Site-specific ordinations (nMDS) corroborated that assemblage structure was largely stochastic over both space and time (Fig. 3B). Nonetheless, the distribution of samples in ordination space revealed years of community dissimilarity that likely contributed to the observed patterns of directional change. Notably, fish assemblage structure in 1980 appeared as a peripheral point (> 2 SD from the centroid) in all four ordination plots (study sites) and the year 1988 represented a peripheral point in three of four ordinations (Fig. 3B). It is instructive to note that 1980 and 1988 were years in which native fishes accounted for the highest and lowest proportions, respectively, of total community density and biomass (Fig. 4B and D).

Trends in fish abundance and biomass

Most native fish populations exhibited trends of declining density and biomass over the period of study.

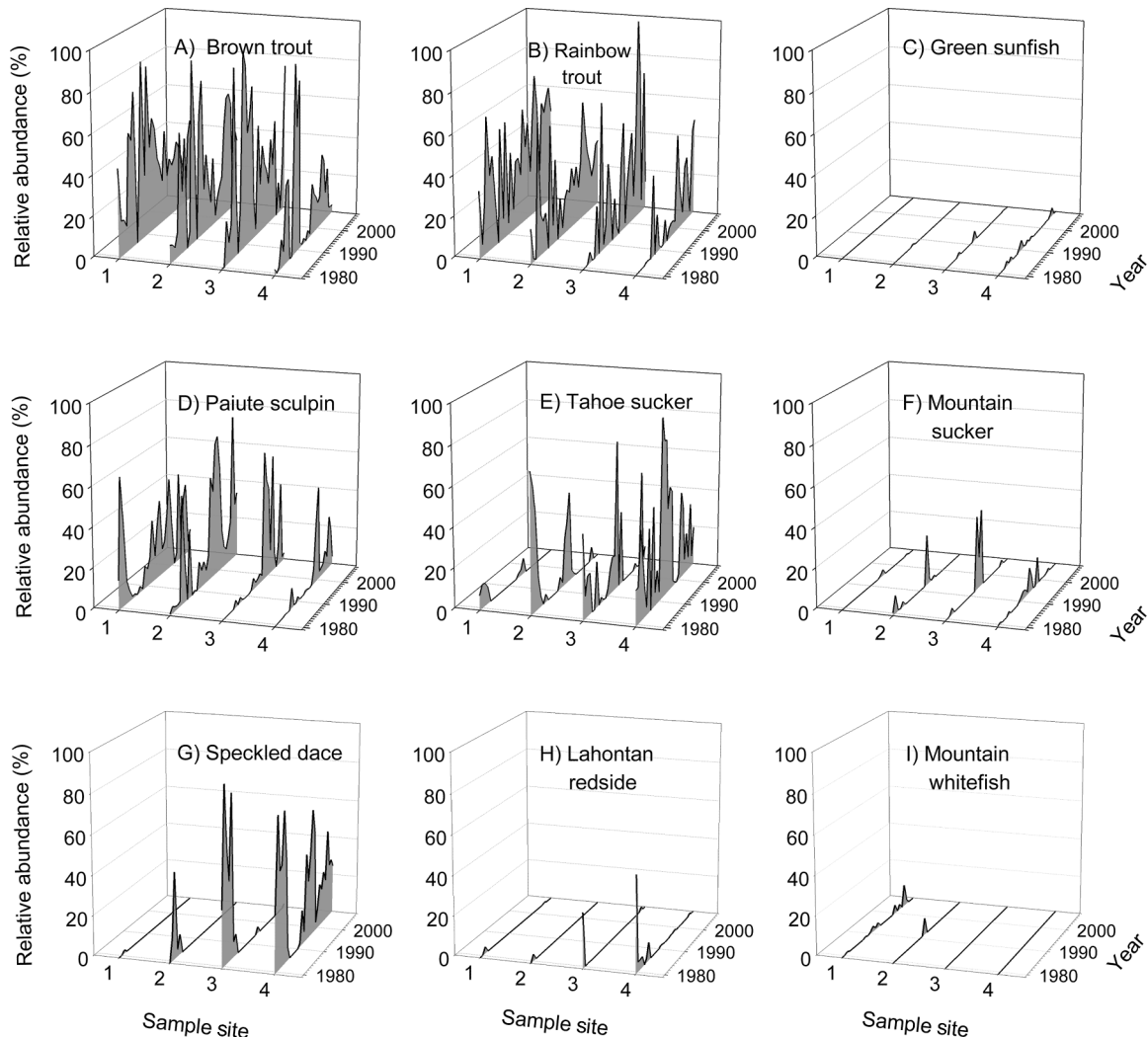


FIG. 2. Relative abundances (percentage of total fish community) of common species captured during annual surveys of four permanent sample sites in Martis Creek, California, 1979–2008. Alien fish are represented in plots A–C, and native fish are represented in plots D–I. Sample sites 1 and 4 represent the downstream-most and upstream-most locations, respectively (see *Methods: Study site*).

Only Paiute sculpin at sites S3 and S4 demonstrated statistically significant increases in density and/or biomass (Table 2). Temporal trends for alien species were inconsistent among sample sites. Rainbow trout were the only alien species to exhibit increases in both density and biomass at all sites over time (Table 2). The identification of significant change points on the indices of abundance generated for each species highlighted the marked lack of synchrony in the timing of population changes across taxa (Table 3). The Tahoe sucker population exhibited the greatest number of significant changes in abundance among the native species (five downturns, two upturns), while brown trout was the most mercurial of the alien taxa (eight downturns, six upturns; Table 3).

Overall, the highest mean (all sample sites) annual estimates of total fish density (499 ± 242 fish/100 m²)

and biomass (2.4 ± 0.4 kg/100 m²) occurred in 1981 (Fig. 4). Conversely, the lowest mean estimates of total density and biomass were recorded in 1991 (27 ± 10 fish/100 m²) and 1983 (0.4 ± 0.1 kg/100 m²), respectively. During the initial years of study (i.e., 1979–1982) fish assemblages were dominated by native species. Mean proportion of native fish peaked in 1980 ($92\% \pm 6\%$ of total density and $67\% \pm 20\%$ of total biomass) then abruptly declined until 1988 ($2\% \pm 2\%$ of total density, $2\% \pm 1\%$ of total biomass; Fig. 4). Although the proportion of native fishes subsequently increased between 1989 and 1994, it never rebounded to previous levels (e.g., 1981; Fig. 4).

Factors affecting species abundance

Forward selection procedures in RDA identified five variables that each explained a significant ($P < 0.05$)

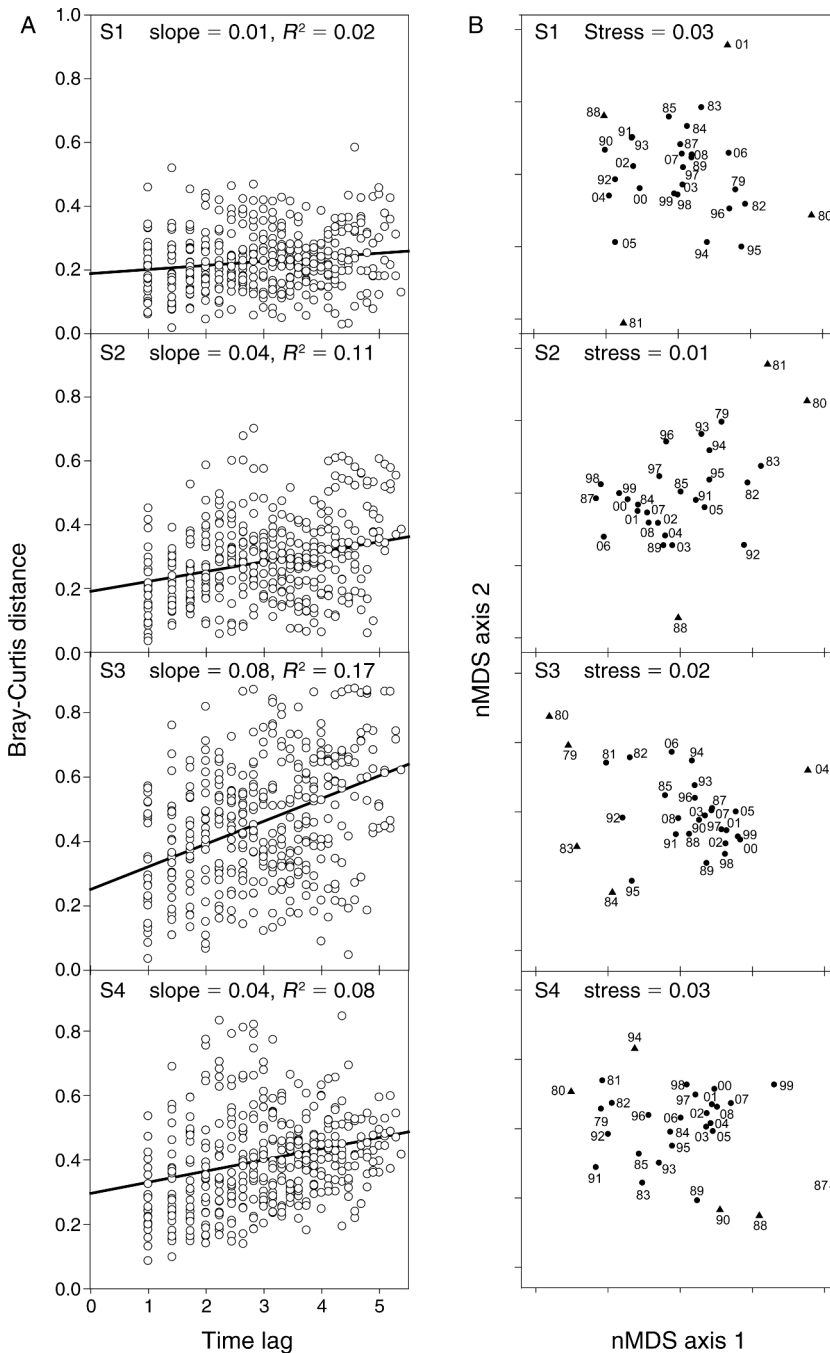


FIG. 3. (A) Time-lag and Bray-Curtis distance of change in fish density and (B) nonmetric multidimensional scaling (nMDS) ordinations by year for each sample site. For time-lag analyses, points represent differences in years for all year-to-year combinations plotted against Bray-Curtis distance. All regressions were statistically significant ($P \leq 0.002$). Time lag is plotted as the square root of the number of years. For nMDS ordinations, points represent fish assemblage structure in a specific year (e.g., 91 = 1991). Samples >2 standard deviations from the mean position (i.e., centroid) in ordination space are denoted with triangles. Cumulative r^2 values for axes 1 and 2 in final nMDS ordinations were 0.86 (S1), 0.81 (S2), 0.90 (S3), and 0.88 (S4).

portion of the variation in the Martis Creek fish community data (Fig. 5; Appendix B: Table B2). For the full fish community, the first two canonical axes explained approximately 14% and 4% of the total

variability in community composition, respectively (Fig. 5A). The highest conditional effects (lambda-A, additional variance explained by forward inclusion into the final model) were associated with the variables

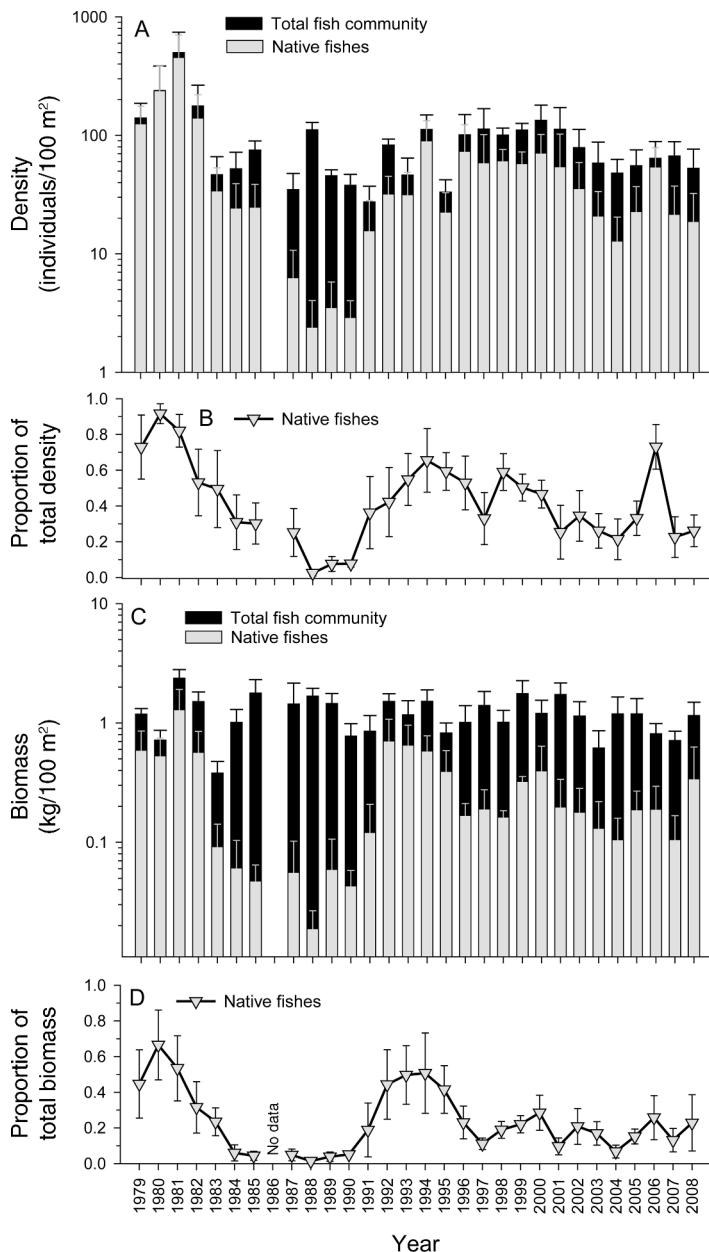


FIG. 4. Time series of density and biomass estimates for the fish assemblage in Martis Creek, California, 1979–2008. Bars (A, C) and triangles (B, D) represent the annual mean (+SE) of four sample stations. Black bars represent mean values for the full fish community, and gray bars represent mean values for native fishes exclusively. Note the log scale for panels (A) and (C).

percentage pool habitat (% pool; Monte Carlo permutation test, $\lambda = 0.06$, $F = 8.44$, $P < 0.01$), 7-day annual minimum discharge (7-day Q_{min} ; $\lambda = 0.05$, $F = 8.18$, $P < 0.01$), maximum winter discharge (Q_{max} winter; $\lambda = 0.04$, $F = 5.44$, $P < 0.01$), and percentage gravel substrate (% gravel; $\lambda = 0.03$, $F = 5.43$, $P < 0.01$) (Table B2). Analogous RDAs performed after restricting the fish assemblage to either alien (Fig. 5B) or native (Fig. 5C) taxa exclusively, indicated maximum winter discharge ($\lambda = 0.07$, $F = 9.59$, $P < 0.01$) and average stream depth (Ave. depth; $\lambda = 0.06$, $F = 7.47$, $P < 0.01$) had the highest conditional effects on alien fishes, whereas percentage pool habitat ($\lambda = 0.07$, $F = 10.54$,

$P < 0.01$) and 7-day annual minimum discharge ($\lambda = 0.07$, $F = 10.54$, $P < 0.01$) had the highest conditional effects on the native assemblage (Table B2).

Variance partitioning confirmed that the hydrologic and physical habitat data sets each explained significant ($P \leq 0.01$) proportions of the variation in fish assemblage structure. For both the full Martis Creek fish assemblage and the subset comprised of native taxa exclusively, habitat variables accounted for a slightly greater proportion of the total explained variance than did hydrologic factors (Fig. 5D). Conversely, hydrologic variables explained more of the variation in alien fish abundance than did physical habitat parameters, but there was considerable shared variance among the two

TABLE 2. Trend analysis (nonparametric Spearman's rank correlation) of species density and biomass at four sample sites (S1–4) in Martis Creek, California, 1979–2008.

Species	S1		S2		S3		S4	
	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
Native								
Lahontan redbside	-0.03	-0.27	-0.30	-0.30	-0.29	-0.33	-0.51	-0.48
Mountain sucker	0.17	0.02	-0.49	-0.47	-0.11	-0.13	-0.31	-0.40
Mountain whitefish	0.15	0.09	-0.06	-0.06				
Paiute sculpin	0.26	0.25	0.34	0.37	0.66	0.64	0.81	0.82
Speckled dace	-0.09	-0.09	-0.56	-0.56	-0.54	-0.53	-0.08	0.11
Tahoe sucker	-0.45	-0.43	-0.59	-0.53	-0.35	-0.46	-0.15	-0.06
Total native	0.23	0.27	-0.24	-0.26	-0.28	-0.24	-0.08	0.07
Alien (nonnative)								
Brown trout	0.06	0.30	-0.13	-0.36	-0.05	-0.33	0.13	0.07
Green sunfish			-0.16	-0.16	0.02	0.01	0.01	-0.12
Rainbow trout	0.38	0.53	0.08	0.14	0.58	0.36	0.80	0.73
Total alien	0.12	0.16	-0.06	-0.22	0.09	-0.13	0.44	0.30

Note: Significant ($P < 0.05$) values are shown in boldface type.

TABLE 3. Statistically significant increases (+) and decreases (-) in the mean annual abundance of select species in Martis Creek, California, 1979–2008.

Year	Water year type	Native						Alien (nonnative)		
		Lahontan redbside	Mountain sucker	Mountain whitefish	Paiute sculpin	Speckled dace	Tahoe sucker	Brown trout	Rainbow trout	Green sunfish
1979	Normal									
1980	Normal	-				+		-		
1981	Dry					-	+	+		
1982	Wet				-		-	-		
1983	Wet		-						-	
1984	Wet							+		+
1985	Normal	+								
1986	Wet	-						-		-
1987	Normal									
1988	Dry							+	-	
1989	Normal							-		
1990	Dry		+					-		
1991	Dry									
1992	Dry	+		+				+		-
1993	Normal			-				-		
1994	Dry			+				-		
1995	Wet		-				-			
1996	Normal						+			
1997	Wet		+				-	+		
1998	Normal							-		
1999	Wet		-							
2000	Normal					+				
2001	Dry				-					
2002	Normal				+		-			
2003	Normal									
2004	Normal									+
2005	Normal			-						
2006	Wet									-
2007	Dry				-		-	+	+	
2008	Normal									

Notes: Data from the four sample sites were pooled to produce indexed estimates of mean annual abundance for each species using the software package TRIM (trends and indices for monitoring data; Pannekoek and van Strien 1996). Years of increase (+) followed a statistically significant (Wald test, $\alpha = 0.05$) upturn in the indexed population trajectory (i.e., point at which the second derivative of the index curve turned significantly positive). Conversely, years of decrease (-) followed a statistically significant downturn in the indexed population trajectory (i.e., points at which the second derivative of the index curve was significantly negative). Data for the year 1986 were imputed by TRIM. See *Methods: Stream temperature and hydrologic attributes* for water year type definitions.

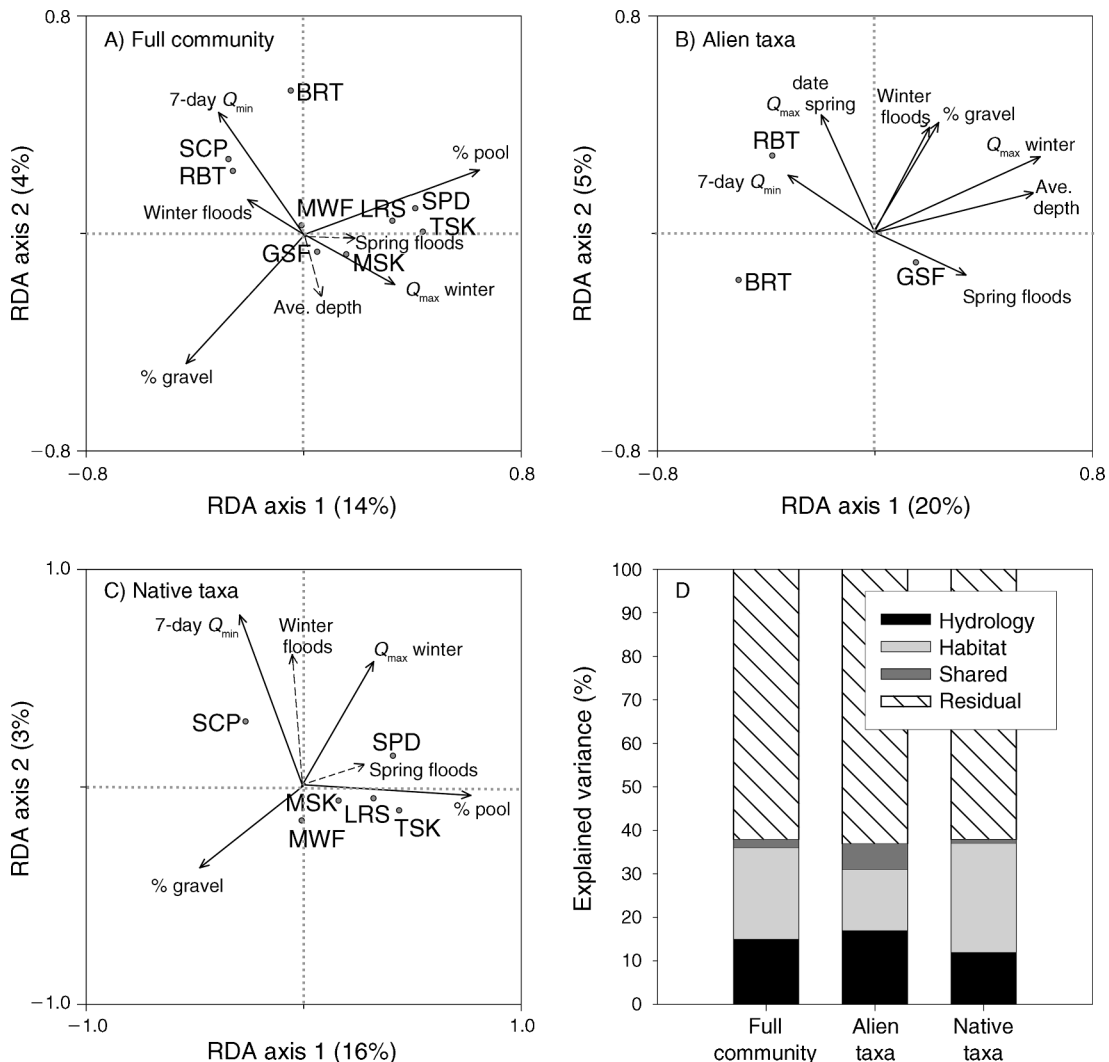


FIG. 5. Redundancy analysis (RDA) of forward-selected physical habitat and hydrologic variables contributing to the composition of (A) the full Martis Creek fish community, (B) alien taxa exclusively, and (C) native taxa exclusively. (D) Percentage of total variation in assemblage composition explained independently and jointly by the physical habitat and hydrologic variables considered ($N = 8$ each; see Appendix B: Table B2). Vectors in RDA plots represent the direction and strength of the relationship of an explanatory variable to the RDA axis. Solid vectors are significant at $\alpha = 0.05$, and dashed vectors are significant at $\alpha = 0.10$. For RDA ordinations, the percentage of variation explained by each of the first two axes is given in parentheses in each axis label. Species codes are: BRT, brown trout; GSF, green sunfish; LRS, Lahontan redbreast; MSK, mountain sucker; MWF, mountain whitefish; RBT, rainbow trout; SCP, Paiute sculpin; SPD, speckled dace; TSK, Tahoe sucker. Explanatory variables are defined in Table B1. Habitat and hydrological variables are defined in *Results: Factors affecting species abundance*.

groups of variables. In all cases, the majority of the variation in assemblage composition ($\geq 62\%$) was unexplained by the variables included in the analyses (Fig. 5D).

Stream discharge and community composition

For the fish community as a whole, there was an inverse relationship between the proportion of the assemblage comprised of alien species and mean annual discharge ($r_s = -0.47$, $P = 0.01$; Fig. 6A). One day maximum discharge values in both winter ($r_s = -0.39$, $P = 0.03$) and spring ($r_s = -0.50$, $P = 0.01$) were also negatively correlated with the proportional abundance

of alien species (Fig. 6B). Additionally, there was a negative relationship between the number of distinct floods events (count of floods ≥ 1 day in duration) in both winter and spring and the proportion of alien species, but only the latter season was statistically significant (quasi-Poisson regression, $t = -2.21$, $df = 25$, $P = 0.04$; Fig. 6C).

DISCUSSION

Assemblage persistence and stability

Our results both supported and refuted the previous findings of Moyle and Vondracek (1985) that the Martis

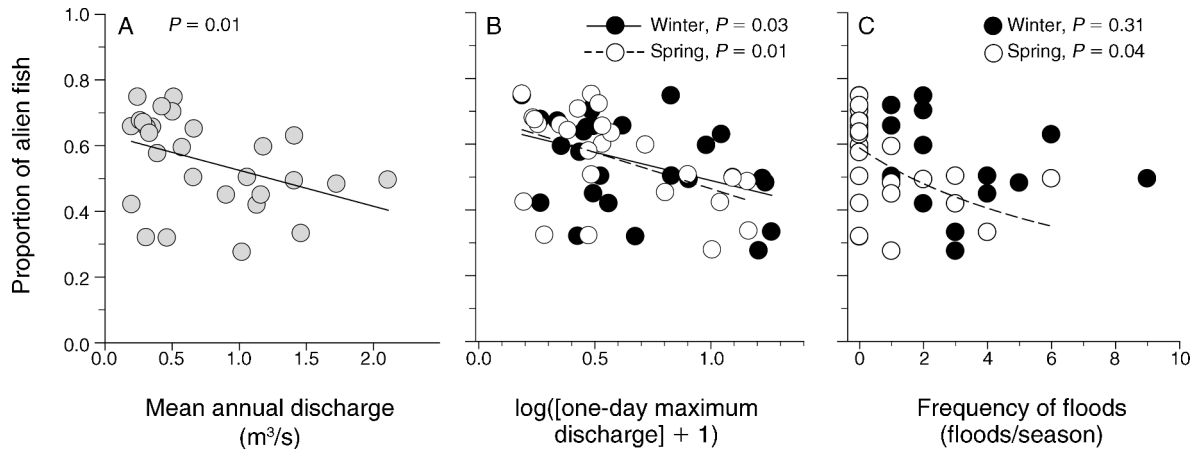


FIG. 6. Relationships between the proportion of the total fish community composed of alien species and (A) mean annual discharge (Spearman's rank correlation coefficient [r_s]= -0.47 , $P=0.01$), (B) maximum discharge during winter (1 December through 31 March; $r_s=-0.39$, $P=0.03$; measured as m^3/s), and spring (1 April through 30 June; $r_s=-0.50$, $P=0.01$) of each water year, and (C) the count of flood events during winter (quasi-Poisson regression, pseudo- $R^2=0.04$, $P=0.31$) and spring (quasi-Poisson regression, pseudo- $R^2=0.18$, $P=0.04$) of each year. Regression lines are presented to illustrate trends in the data.

Creek fish assemblage was persistent and stable over time. Evidence for assemblage persistence over three decades was provided by moderately-high persistence index values indicating consistent community composition in terms of species presence and absence. Deviations from complete persistence at each sample site were driven by the irregular capture of less abundant and rare taxa (i.e., green sunfish [*Lepomis cyanellus*], Lahontan cutthroat trout, bluegill, largemouth bass, and mountain whitefish [*Prosopium williamsoni*]) and not species extirpations. These species presumably originated from Martis Creek Reservoir and were either washed into the creek during large rainfall events that caused the reservoir to spill, or immigrated into our study site from the mainstem Truckee River. Nonetheless, at the scale of the entire 2.9-km stream segment, all seven species originally reported by Moyle and Vondracek (1985) to represent the core fish assemblage (i.e., brown trout, rainbow trout, speckled dace [*Rhinichthys osculus*], Lahontan redbreast, mountain sucker [*Catostomus platyrhynchus*], Tahoe sucker, and Paiute sculpin) remained extant and were routinely captured in Martis Creek at the end of the 29-year study.

Although the Martis Creek fish community as a whole was persistent over time, individual species commonly exhibited high interannual variability in their absolute and relative abundances and rank order, contrary to the hypothesis of assemblage stability (i.e., constancy of numbers) proposed by Moyle and Vondracek (1985). The dynamics and instability of the constituent populations resulted in multiple changes to the structure of the fish assemblage between 1979 and 2008, as illustrated by the time series of proportional abundance of native fishes (Fig. 4). During initial years of study the Martis Creek fish assemblage was dominated by native species (Tahoe sucker, Lahontan redbreast, Paiute sculpin, and

speckled dace) with concordant relative abundances, and trout were generally uncommon (Moyle and Vondracek 1985). In 1983, low winter stream flows were followed by severe flooding during the spring. This sequence of hydrologic events was associated with relatively high recruitment of alien brown trout and poor recruitment of all spring spawning species (Strange 1995). For several years following 1983, flood events were infrequent or of short duration (except 1986; see Fig. 1B) and brown trout were consistently the dominant species, both in terms of numbers and biomass.

A second significant shift in community structure occurred as a result of prolonged drought from 1987–1992. During the second year of drought conditions (1988), remnant native fish populations remained depressed while brown trout reached their highest mean density and relative abundance observed during the study. Following this peak in abundance, brown trout populations declined for three consecutive years to a low mean density of <10 individuals/100 m^2 at each site in 1991 before bouncing back slightly the following year. Consequently, 1991 represented the year with the lowest total community density (mean = 38 ± 9 fish/100 m^2) and marked the start of a temporary rebound by the native fish assemblage, driven by increases in Tahoe sucker and speckled dace. It is instructive to note that extended drought conditions had markedly different effects on the population trajectories of native and alien species. The populations of all alien species exhibited at least one statistically significant downturn in their indexed populations during the drought, with brown trout exhibiting two such declines between 1987 and 1992. Conversely, populations of native species were either largely unaffected or exhibited significant increases during this same time period.

Hydrology and fish assemblage structure

Based on the natural flow regime paradigm (Poff et al. 1997) and our knowledge of the life history requirements of the different species (Moyle 2002), we hypothesized that alien fishes would be strongly and disproportionately limited by hydrologic factors. While our results largely supported this prediction, year-to-year community assembly was strongly context dependent. Redundancy analysis identified five hydrologic and two habitat variables that significantly ($P < 0.05$) explained the distribution and abundance of alien fishes, with maximum winter discharge contributing most strongly. In contrast, native fish assemblage structure was modeled by two habitat and two hydrologic variables with percentage pool habitat contributing most significantly. With respect to high stream flows, the proportion of the total fish assemblage composed of alien species was inversely related to mean annual discharge, one-day maximum discharge, and frequency of spring (but not winter) flood events. It is important to note that overall effects of flow regime on the abundance of alien species in our study were likely tempered by the fact that the two dominant nonnatives, rainbow trout and brown trout, while functionally and morphologically similar, differed in their susceptibility to various elements of the flow regime. Brown trout were the sole fall-spawning species in the fish community and had a less flexible temporal spawning window (based on photoperiod) than rainbow trout. Consequently, developing brown trout eggs and alevins were especially susceptible to mortality during winter flood events that scoured the streambed, as has been reported elsewhere (Spina 2001, Cattaneo et al. 2002).

Does the flow regime have primacy?

In some years the magnitude, frequency, and timing of flow events produced unambiguous effects on fish community structure, whereas in other years, hydrologic effects were subtle or obscure. Initial support for the importance of stream flow in structuring the Martis Creek fish community was provided by Strange et al. (1992), who modeled assemblage dynamics over 10 years and found that high interannual variability in the flow regime generated two distinct equilibria: an assemblage dominated by native fishes and one dominated by alien brown trout. Specifically, fall-spawning brown trout were hypothesized to be favored in years where winter floods were absent and spring floods reduced native fishes, and native fish were predicted to dominate in years when winter flows were high (Strange et al. 1992). However, these predictions had mixed success during subsequent years. For example, 1997 was characterized by heavy winter flooding (six distinct flood events during winter; none during spring) and thus expected to favor native species. Nevertheless, brown trout were the dominant species that year (mean relative abundance = $37.2\% \pm 4.6\%$), with numbers dominated by young-of-year, and the proportion of the community comprised of

native fish exhibited a marked decline (Fig. 4). In contrast, 2006 was characterized by extreme high-flow events during the winter (3 January mean daily $Q = 17.3 \text{ m}^3/\text{s}$, [highest in the post-dam era]), late winter (4 March mean daily $Q = 17.1 \text{ m}^3/\text{s}$), and spring (5 April mean daily $Q = 13.4 \text{ m}^3/\text{s}$). This broad distribution of flood events across multiple seasons resulted in a fish assemblage dominated by Paiute sculpin ($45.2\% \pm 10.4\%$), rainbow trout ($21.5\% \pm 12.0\%$), and Tahoe sucker ($20.3\% \pm 12.1\%$), while brown trout accounted for a scant $4.1\% \pm 1.3\%$ (range = 1.5% to 7.8%) of the assemblage when pooled across all sample sites.

Whereas the role of high stream flows in shaping ecological processes has been well documented in a variety of systems (e.g., Resh et al. 1988, Grimm and Fisher 1989, Wootton et al. 1996), droughts represent an important but understudied part of the flow regime that can dramatically alter community composition and ecosystem functioning (Bêche 2005, Bêche and Resh 2007, Power et al. 2008). Bêche et al. (2009) proposed that both the severity and duration of drought events are important in structuring fish and invertebrate communities in Mediterranean-type streams, and this hypothesis appears to be supported by the dynamics of the Martis Creek fish assemblage. During dry water years, the amount of total available habitat is reduced, which presumably results in increased inter- and intraspecific competition and predation by brown trout, largely to the detriment of native species. This is consistent with the finding of Propst et al. (2008) that native fish assemblages can persist through periods of drought, but their ability to do so is reduced when alien predators are present. However, while an isolated low water year may facilitate brown trout production, periods of prolonged drought appear to have a disproportionate negative effect on brown trout populations. This is most likely because brown trout live 5–8 years with only one or two reproductive age classes (Moyle 2002), making them especially vulnerable to prolonged adverse conditions and the cumulative effects of reduced recruitment.

The future of the Martis Creek fish assemblage

We believe that a mixed native and nonnative fish assemblage will continue to persist into the future. However, rainbow trout may ultimately displace brown trout as the dominant predator in the system. Rainbow trout, like the endemic trout it replaced in the basin (Lahontan cutthroat trout) is a spring spawning species and well adapted to the Mediterranean-type flow regime. Results of our trend analyses indicated a positive increase in rainbow trout density and biomass at all sites over time, although such trends were not always statistically significant (Table 2). The greatest disparity in density between the two trout species occurred in 1988 with average estimates of 103 ± 16 vs. 6 ± 2 individuals/100 m^2 (mean \pm SE) for brown trout and rainbow trout, respectively. Since that time, however, populations of the two species have exhibited markedly different trends,

with rainbow trout increasing in abundance and brown trout declining. For example, prior to the end of drought conditions in 1993, rainbow trout were captured at all four sample sites during ~40% of the annual collections. Since 1993, rainbow trout have been documented at all sites during 90% of annual surveys and every year since 1996. During recent years the Martis Creek fish community appears to have exhibited a reversal in the relative abundances of rainbow trout and brown trout. Hence, the community has assumed a state that is ecologically and functionally closer to the original stream assemblage given that rainbow trout, like the native cutthroat trout it replaced, spawns during the spring.

Whether or not the rainbow trout dominated assemblage will be able to persist will depend, in part, on the effects of climate change. Climate change is expected to produce appreciable changes to hydrology. Snowmelt discharge hydrographs like those that characterize Martis Creek contain three major attributes that can affect the distribution and abundance of aquatic biota: peak flow, the spring pulse, and base flow (Cayan et al. 2001). Although climate change scenarios project little change to the total annual precipitation in California's Sierra Nevada mountains, the region is expected to experience an advancement in the timing of precipitation events and an increase in the ratio of rain to snow (Knowles and Cayan 2002, Miller et al. 2003). This temporal shift will result in more peak flows occurring during the winter, increased frequency of high-flow events, diminished spring pulses, and protracted periods of low (base) flows. While this scenario is likely to adversely affect all fishes to some extent, we predict the ability of the native fishes, especially Tahoe sucker and speckled dace, to cope with variation and reduction in streamflow (Moyle 2002) will give them an edge.

We acknowledge that our findings may have been an artifact of our sampling design (e.g., sampling conducted once annually during late summer base flow) or how we selected, defined, and quantified our potential explanatory variables (e.g., spring and winter floods). Further, the large unexplained component of variation that accompanied some analyses implied that fish community composition varied temporally and spatially in response to environmental and/or biological mechanisms not accounted for in our study (e.g., trophic resource availability or biotic interactions). For example, early research on Martis Creek provided evidence that predation by alien brown trout suppressed native fish populations, but that their ability to do so was dependent upon hydrologic conditions (Moyle 1994, Strange 1995). Moreover, Moyle and Vondracek (1985) reported segregation by habitat, microhabitat, and diet as strong evidence for deterministic regulation of the fish assemblage during some years. Proxies for density-dependence (e.g., predation and competition) were not included as potential explanatory variables in our study, thus limiting our ability to assess the relative importance

of deterministic vs. stochastic processes. Despite these potential shortcomings, our study provides a unique and valuable long-term perspective on the dynamics of a riverine fish assemblage in the face of environmental stochasticity.

Implications for the management and conservation of stream fishes

The contribution of long-term data sets to our understanding of ecological pattern and process has long been recognized (e.g., Likens 1989, Magnuson 1990, Burt 1994). Often, judgments concerning community dynamics based on short time series of qualitative data or on irregular surveys spaced over time can be misleading. A principal tenet guiding studies of community persistence is that the length of the investigation should exceed at least one complete turnover of the constituent species (Connell and Sousa 1983) in order to avoid Frank's (1968) tautology. However, our results clearly demonstrate that, for fish in lotic systems subjected to highly variable hydrologic regimes, annual samples collected over multiple decades may be necessary to successfully capture the full range of environmental conditions that influence assemblage dynamics. Moreover, our results show that, even when robust long-term data sets are available, demographic responses to environmental factors can vary over time and space and general patterns in community composition may be difficult to ascertain. The data from Martis Creek led to different conclusions after 5, 10, and 30 years of study. Fish community structure may be strongly influenced by the specific temporal sequence of stochastic hydrologic events (i.e., succession of wet and dry years) and multiple alternate states may be possible, especially in species-depauperate systems. These results indicate the need for continuous annual monitoring of streams, especially those with dynamic flow regimes, because apparent successes or failures in stream management may appear in a different light under long-term study.

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LITERATURE CITED

- Angeler, D. G., O. Viedma, and J. Moreno. 2009. Statistical performance and information content of time lag analysis and redundancy analysis in time series modeling. *Ecology* 90:3245–3257.
- Bêche, L. A. 2005. Long-term variability, disturbance, and biological traits of aquatic invertebrates in Mediterranean-climate streams. Dissertation. University of California, Berkeley, California, USA.

- Bêche, L. A., P. G. Connors, V. H. Resh, and A. M. Merenlender. 2009. Resilience of fishes and invertebrates to prolonged drought in two California streams. *Ecography* 32:778–788.
- Bêche, L. A., and V. H. Resh. 2007. Short-term climatic trends affect the temporal variability of macroinvertebrates in California Mediterranean streams. *Freshwater Biology* 52:2317–2339.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055.
- Burt, T. P. 1994. Long-term study of the natural environment—perceptive science or mindless monitoring? *Progress in Physical Geography* 18:475–496.
- Cattaneo, F., N. Lamouroux, P. Breil, and H. Capra. 2002. The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* 59:12–22.
- Cayan, D. R., S. A. Kammerdiener, M. D. Dettinger, J. M. Caprio, and D. H. Peterson. 2001. Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society* 82:399–415.
- Collins, S. L., F. Micheli, and L. Hartt. 2000. A method to determine rates and patterns of variability in ecological communities. *Oikos* 91:285–293.
- Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* 121:789.
- Diamond, J. M., and R. M. May. 1977. Species turnover rates on islands: dependence on census interval. *Science* 197:266–270.
- Elliott, J. M. 1994. *Quantitative ecology and the brown trout*. Oxford University Press, Oxford, UK.
- Erman, B. C., E. D. Andrews, and M. Yoder-Williams. 1988. Effects of winter floods on fishes in the Sierra Nevada. *Canadian Journal of Fisheries and Aquatic Sciences* 45:2195–2200.
- Fausch, K. D., Y. Taniguchi, S. Nakano, G. D. Grossman, and C. R. Townsend. 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. *Ecological Applications* 11:1438–1455.
- Frank, P. W. 1968. Life histories and community stability. *Ecology* 49:355–357.
- Freeman, M. C., M. K. Crawford, J. C. Barrett, D. E. Facey, M. G. Flood, J. Hill, D. J. Stouder, and G. D. Grossman. 1988. Fish assemblage stability in a southern Appalachian stream. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1949–1958.
- Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics* 30:51–81.
- Grantham, T. E., A. M. Merenlender, and V. H. Resh. 2010. Climatic influences and anthropogenic stressors: an integrated framework for streamflow management in Mediterranean-climate California, U.S.A. *Freshwater Biology* 55:188–204.
- Grimm, N. B., and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8:293–307.
- Grossman, G. D., J. F. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes: a review. *Environmental Management* 14:661–671.
- Grossman, G. D., and J. L. Sabo. 2010. Preface: structure and dynamics of stream fish assemblages. Pages 401–405 in K. B. Gido and D. A. Jackson, editors. *Community ecology of stream fishes: concepts, approaches, and techniques*. Symposium 73. American Fisheries Society, Bethesda, Maryland, USA.
- Jenkins, T. M., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. Effects of population density on individual growth of brown trout in streams. *Ecology* 80:941–956.
- Knowles, N., and D. R. Cayan. 2002. Potential effects of global warming on the Sacramento/San Joaquin watershed and the San Francisco estuary. *Geophysical Research Letters* 29:1891–1895.
- Likens, G. E. 1989. *Long-term studies in ecology: approaches and alternatives*. Springer-Verlag, New York, New York, USA.
- Lobon-Cervia, J. 2007. Density-dependent growth in stream-living Brown Trout (*Salmo trutta*). *Functional Ecology* 21:117–124.
- Magnuson, J. J. 1990. Long-term ecological research and the invisible present. *BioScience* 40:495–501.
- Matthews, W. J. 1998. *Patterns in freshwater fish ecology*. Chapman and Hall, New York, New York, USA.
- Matthews, W. J., and E. Marsh-Matthews. 2003. Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology* 48:1232–1253.
- May, R. M. 1976. Models for single populations. Pages 4–25 in R. M. May, editor. *Theoretical ecology, principles and applications*. W. B. Saunders, Philadelphia, Pennsylvania, USA.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon, USA.
- Meffe, G. K., and W. L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *American Midland Naturalist* 117:177–191.
- Miller, N. L., K. E. Bashford, and E. Strem. 2003. Potential impacts of climate change on California hydrology. *Journal of the American Water Resources Association* 39:771–784.
- Moyle, P. B. 1994. Biodiversity, biomonitoring, and the structure of stream fish communities. Pages 171–186 in S. Loeb and A. Spacie, editors. *Biological monitoring of freshwater ecosystems*. Lewis Publishing, Boca Raton, Florida, USA.
- Moyle, P. B. 2002. *Inland fishes of California: revised and expanded*. University of California Press, Berkeley, California, USA.
- Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78:149–161.
- Moyle, P. B., and B. Vondracek. 1985. Persistence and structure of the fish assemblage in a small California stream. *Ecology* 66:1–13.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- Nature Conservancy. 2007. Indicators of hydrologic alteration, version 7 user's manual. <http://www.nature.org/initiatives/freshwater/files/ihav7.pdf>
- Pannekoek, J., and A. van Strien. 1996. TRIM (TRends and Indices for Monitoring data). Research paper 9634. Statistics Netherlands, Voorburg, The Netherlands.
- Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. *BioScience* 47:769–784.
- Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805–1818.
- Power, M. E., M. S. Parker, and W. E. Dietrich. 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts on fish. *Ecological Monographs* 78:263–282.
- Power, M. E., A. Sun, G. Parker, W. E. Dietrich, and J. T. Wootton. 1995. Hydraulic food-chain models. *BioScience* 45:159–167.
- Propst, D. L., K. B. Gido, and J. A. Stefferud. 2008. Natural flow regimes, nonnative fishes, and native fish persistence in arid-land river systems. *Ecological Applications* 18:1236–1252.

- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433–455.
- Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* 10:1163–1174.
- Spina, A. P. 2001. Incubation discharge and aspects of brown trout population dynamics. *Transactions of the American Fisheries Society* 130:322–327.
- Strange, E. M. 1995. Pattern and process in stream fish community organization: field study and simulation modeling. Dissertation. University of California, Davis, California, USA.
- 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.
- ter Braak, C. J. F., and P. Šmilauer. 2002. Canoco reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca, New York, USA.
- Van Deventer, J. S., and W. S. Platts. 1989. Microcomputer software system for generating population statistics from electrofishing data—user's guide for Microfish 3.0. General Technical Report INT-254. USDA Forest Service, Ogden, Utah, USA.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558–1561.

SUPPLEMENTAL MATERIAL

Appendix A

Characteristics of the four permanent sample sites (S1–S4) in Martis Creek, California, 1979–2008 (*Ecological Archives* A022-062-A1).

Appendix B

Computational approach used in redundancy analysis (RDA) and variance partitioning (*Ecological Archives* A022-062-A2).

Appendix C

Results of the indicators of hydrologic alteration analysis for Martis Creek, California, 1979–2008 (*Ecological Archives* A022-062-A3).

Appendix D

Summary of fish community metrics for each permanent sample site in Martis Creek, California, 1979–2008 (*Ecological Archives* A022-062-A4).

Appendix E

Coefficients of variation for species density and biomass at four sample sites in Martis Creek, California, 1979–2008 (*Ecological Archives* A022-062-A5).