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Alien fishes in natural streams: fish distribution, assemblage structure, and conservation in the Cosumnes River, California, U.S.A.

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Synopsis

The Cosumnes River is the largest stream without a major dam on its mainstem in the Sacramento–San Joaquin drainage, central California, U.S.A. We studied its fishes over a 3-year period to answer the following questions: (1) Was the native fish fauna still present? (2) Why were alien fishes so abundant in a river system with a 'natural' flow regime, which elsewhere has been shown to favor native fishes? (3) Were there assemblages of fishes that reflected environmental differences created by the underlying geology? (4) Were there features of the watershed that consistently favored native fishes or that could be managed to favor native fishes? Of the 25 species collected, 17 were alien species; 14 species (five native) were abundant or widely distributed enough to use in detailed analyses. Of the native species, only rainbow trout, *Oncorhynchus mykiss*, still occupied much of its native range in headwater streams. Other native species have been extirpated or persisted mainly above barriers to alien invasions. The most widely distributed alien species was redeye bass, *Micropterus coosae*, previously unknown from the river, whose abundance was associated with low-numbers of native species. Other aliens were found primarily in low-land habitats on the valley floor or foothills. Canonical Correspondence Analysis indicated that both native and alien species located on environmental gradients determined largely by elevation, temperature, flow, and emergent vegetation, but the associations with these variables were not strong. While most alien fishes were found in lowland sections of river flowing through agricultural regions, the general relationships between species abundance and landscape-level variables were weak. Assemblages of fishes were poorly defined mixtures of native and alien species. The strikingly distinct geological regions of the basin no longer supported distinct fish assemblages. Species distributions were highly individualistic, reflecting dynamic patterns of introductions, invasions, and local extinctions, as well as physiological tolerances and life history patterns. Most native fishes are likely to persist in the Cosumnes River only if summer flows are increased and if populations above natural barriers are protected from further invasions by alien species, especially redeye bass. General conclusions from this study include: (1) altered habitats can support native species under some circumstances; (2) new fish assemblages with characteristics of 'natural' communities are likely to develop in invaded systems; (3) restoring flow regimes to favor native fishes may require restoring minimum summer flows as well as high channel-forming flows. However, reversing or even reducing, the impact of the predatory redeye bass, pre-adapted for California streams, is probably not possible.

Introduction

Most temperate streams are degraded to some degree as the result of physical alteration, pollution, removal of water for human use, and invasions of alien (non-indigenous to the stream) species, resulting in declines of native biota (Moyle & Leidy 1992, Ward et al. 2001). Management and rehabilitation of stream ecosystems is difficult because of the strong interactions of stream flow and local water quality with both natural and anthropogenic factors, such as climate, geology, land use, and water removal (Schlosser 1995, Richards et al. 1996, Aparicio et al. 2000). Nevertheless, major restoration efforts for aquatic ecosystems are underway in many parts of the world. Fishes are frequently the focus of stream management and rehabilitation because they are easy to sample and identify, often have economic value, have high public awareness of their value, and can be good indicators of stream and watershed condition. In relatively undisturbed (by humans) streams, fishes tend to group into fairly predictable assemblages of co-evolved species, which are usually tied to factors such as elevation, gradient, channel size and shape, and location of natural barriers (Matthews 1998, Pusey & Kennard 1996, Lamouroux et al. 2002). This is especially true in the streams of central California, U.S.A. (Moyle 2002). While biotic interactions influence fish abundance and assemblage structure in streams (Baltz et al.1982, Taylor 1996), they seem to play only a small role in comparison to physical factors such as annual variation in stream flow (Grossman et al. 1998, Oberdorff et al. 1998, Marsh-Matthews & Matthews 2000).

Understanding the relationships among landscapes, stream hydraulics, and fish assemblages is important for developing management schemes for many watersheds, but the relationships have less meaning where streams have been highly altered by human activity and are invaded by alien species. Watersheds dominated by agriculture, for example, tend to have reduced diversity of native fishes, more alien species, and less predictability in assemblage structure (Wasler & Bart 1999, Brown 2000). Likewise, dams and diversions drastically alter flow regimes and hydrologic processes (Mount 1995); they create serial discontinuities within normally continuous stream ecosystems (Ward & Stanford 1983), resulting in dramatic changes in fish assemblages (Bain et al. 1988, Aparico et al. 2000). The changes in flows and habitats often favor alien species (Godinho & Ferreira 2000, Marchetti & Moyle 2001, Brown & Ford 2002), which in turn can alter assemblages further through predation and competition (Strange et al. 1992, Brown & Moyle 1997). These observations have led to the concept that rehabilitation of a stream (as indicated by fish assemblages with desirable characteristics) requires re-creation of a natural flow regime (Poff et al. 1997) while also requiring restoration of the surrounding watershed to a more sustainable condition (Poff et al. 1997, Fausch et al. 2002). A basic problem with this approach is often the lack of baseline information upon which to set goals for stream and watershed rehabilitation (Ward et al. 2001). This is particularly a problem in California's Central Valley, where almost all streams have long been dammed, diverted, channelized, and otherwise heavily altered, yet where there is also a growing interest in improving the condition of streams and watersheds and in restoring native fish assemblages (May & Brown 2002, Moyle 2002).

Because of this interest, the Cosumnes River has become a focus of major conservation efforts as the largest stream flowing into California's Central Valley without a major dam on its main stem and a presumed natural flow regime. The Cosumnes River was therefore assumed to have native fish assemblages that reflected natural environmental gradients, especially those related to the striking changes in underlying geology and could therefore be a model for restoration efforts of more modified streams. It was also assumed that the entire watershed could be managed as a refuge for native aquatic organisms, particularly fishes, although the watershed was little studied. Preliminary surveys, however, indicated that alien fishes were common throughout the watershed. The broad purpose of this study was therefore to document the distribution and abundance of fishes in the watershed in relation to natural and anthropogenic features at both local (reach) and watershed scales in order to assist agencies and private conservation organizations in developing conservation strategies for the basin.

Specific questions included: (1) Was the native fish fauna still intact? We expected that at least isolated populations of all native fishes would be present and that these remnants could then become the focus of conservation efforts. (2) Why are alien fishes so common in a river system with an apparent natural flow regime, which elsewhere in California has been shown to favor native fishes (Baltz & Moyle 1993, Marchetti & Moyle 2001, Brown & Ford 2002)? (3) Are there assemblages of fishes that reflect environmental differences created by the underlying geology? We hypothesized that a lack of strong patterns would indicate assemblages were still undergoing change as the result of alien invasions. (4) Are there features of the watershed that consistently favor native fishes or that can be managed to favor native fishes?

We were also interested in addressing some related basic questions about the nature of stream fish assemblages containing alien species: Do alien species and persistent native species form distinct assemblages in response to environmental gradients? Are assemblages dominated by alien species found mainly in highly altered environments?

Study area

The Cosumnes River watershed flows from the west side of the Sierra Nevada range in central California (Figure 1). It drains about 3 000 km^2 and ranges in elevation from around 2 400 m at the headwaters to near sea level at its outlet in the Mokelumne River, just before the river enters the Sacramento–San Joaquin delta. Only about 16% of the watershed lies above 1 500 m, so much of the flow of the river is derived from rainfall, rather than snow melt; this results in higher winter flood pulses and, relative to other Sierran drainages, smaller spring flood flows. At the main gauging station on the river (Michigan Bar, located about 58 km above the mouth, below the confluence of the three forks), flows range from no-flow during critical dry years to a peak flow of 2 650 $m^3\ s^{-1}$ during an exceptional event in January 1997. The annual mean runoff as measured at Michigan Bar is $\sim$452 million $m^3\ yr^{-1}$, with a peak in mean daily flow typically occurring in February (Figure 2). While there are no large dams on the main stem or on the three major forks of the Cosumnes River, a diversion on Camp Creek sends over 28.3 million $m^3\ yr^{-1}$ across the basin to Sly Park Reservoir on Sly Park Creek, from which the water is pumped into the adjacent American River watershed. Two other large diversions (Crawford Ditch, Plymouth Ditch) remove over 8.6 million $m^3\ yr^{-1}$ and 135 smaller diversions remove up to 6.9 million $m^3\ yr^{-1}$ (Quidachay et al. 2000). The database on water rights kept by the State Water Resources Control Board shows over 575 potential diversions in the watershed, although many are apparently not active at the present time because the water allocated for diversion exceeds the natural summer flow. During winter and spring, surface diversions do not appear to have a significant impact on the Cosumnes River hydrograph. However,

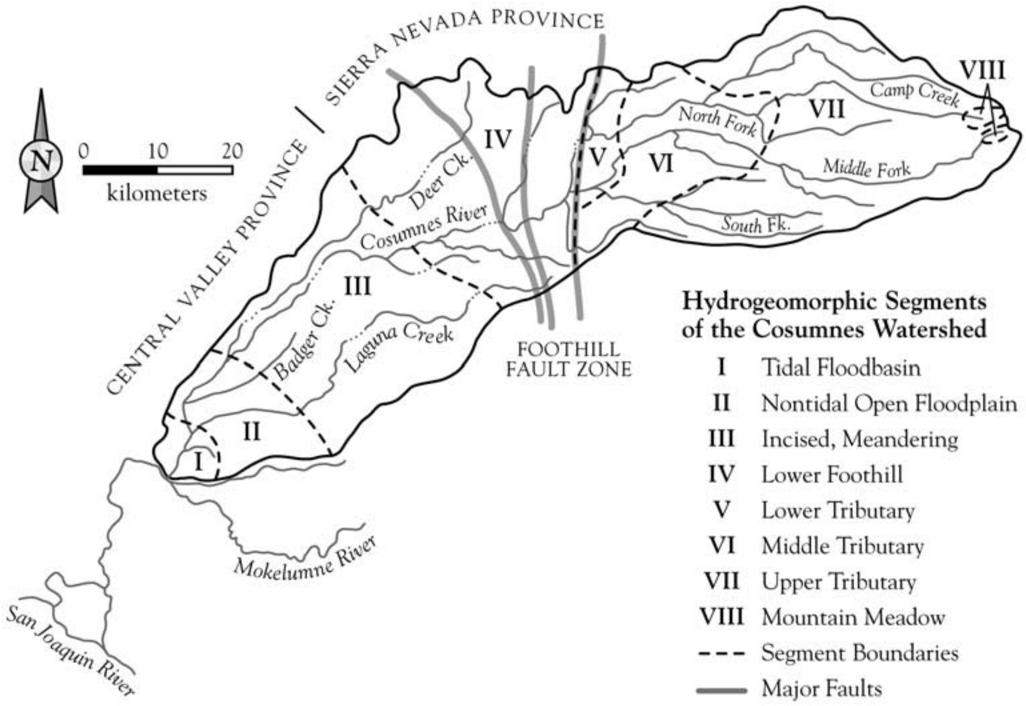

Figure 1. Map of the Cosumnes River watershed, California, showing the major geologic regions, fault zones, and stream reaches.

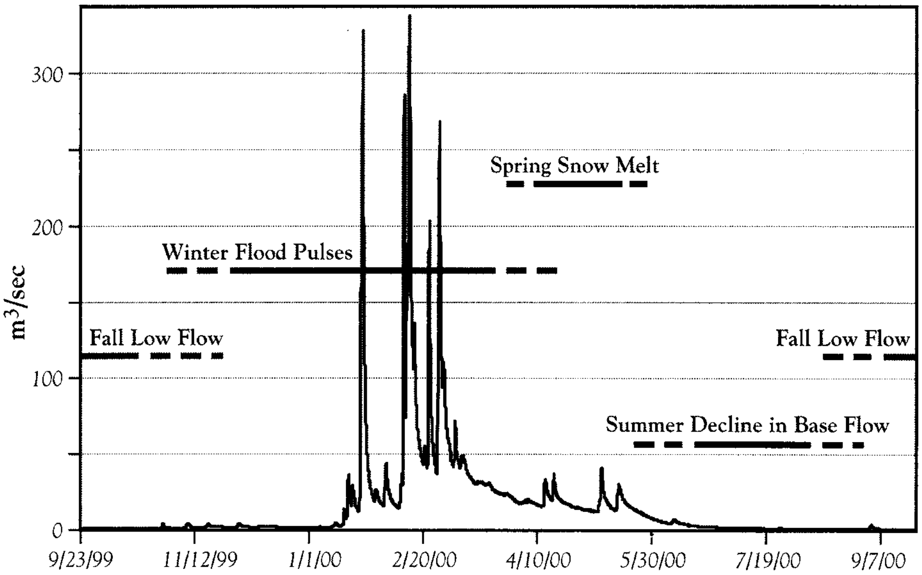

Figure 2. Annual hydrograph, Cosumnes River at Michigan Bar, water year 2000. The hydrograph can be broken into four distinct hydrologic periods: (1) During late November through late March, Pacific storms produce the large seasonal flood pulses. (2) From late March through late May, snowmelt runoff dominates the flow. (3) From late May through early September there is no precipitation while irrigation and evapotranspiration rates increase, so there is gradual decline in base flow. (4) From September through November, the flows are at their minimum, with extended periods of no-flow conditions.

in summer and fall, when flows are naturally low, these diversions may be important, particularly in tributaries of the watershed. Recent work has demonstrated that high rates of groundwater pumping in the lower watershed has exacerbated low-flow and non-flow conditions (Mount et al. 2001). Increasing agricultural and urban use of groundwater has lowered groundwater tables as much as 30 m in some reaches of the river. The lowered groundwater has converted the lower Cosumnes from an influent river, where shallow groundwater provided base flow support, to an effluent river, where groundwater is recharged by rapid seepage into the riverbed. This condition, which has been conspicuous since the 1950s, is an important contributor to the extended period of no-flow conditions in the lower watershed.

The Cosumnes basin flows through the Sierra Nevada and Central Valley physiographic provinces (Figure 1). The Central Valley province contains the low-gradient, alluvial sections of river that are linked to broad floodplains that make up much of the valley floor. The Sierra Nevada province includes the steep-gradient, bedrock-controlled watersheds of the Sierra Nevada. The portions of the Cosumnes that lie within the Central Valley province can be divided into three distinct segments based on their geologic, hydrologic, and land use/land cover characteristics. The tidal flood basin segment (I, Figure 1) includes the portion of the Cosumnes from the confluence with the Mokelumne River, upstream 8 km to the limits of tidal influence (Twin Cities Road bridge). Historically, the river here consisted of multiple, shifting channels in broad floodplain, which supported a mosaic of aquatic and terrestrial habitats, including riparian forest, seasonal and perennial wetlands, permanent sloughs, and seasonal floodplain lakes. During low-flow conditions, diurnal tidal fluctuations impact water levels in the sloughs and in the mainstem river. Much of the tidally influenced floodplain today is farm fields protected by low-levees that do not prevent seasonal flooding. It is also the site of major efforts to restore natural habitats, including seasonally flooded areas.

The nontidal open floodplain segment (II, Figure 1) is 8 km in length and contains multiple shallow, channels. The bed of the channels is dominated by sand, with a gravel–sand transition zone occurring in the uppermost portions (Constantine 2001). Discontinuous low-levees and riparian forests flank the channel. Flow in the nontidal, open floodplain reach of the Cosumnes decreases rapidly during the summer, typically becoming discontinuous by late August due to lowered groundwater conditions (Mount et al. 2001).

The incised meandering river segment (III, Figure 1) is 35 km in length and extends from the Highway 16 bridge (elevation 15 m) to the highway 99 bridge (elevation 3 m). Within this reach, the Cosumnes River and its adjacent floodplain make up a narrow valley inset into Pleistocene alluvial fan deposits (Constantine et al. in press). The river channel is lined with agricultural levees throughout this reach and contains limited riparian vegetation. Historically, the floodplain was dominated by riparian forest, grassland, and oak savannah. Today, almost all the adjacent floodplain is used for vineyards and irrigated row crops, with scattered single-family homes. The levees, coupled with bank stabilization efforts, appear to have induced a long-term cycle of channel degradation (Constantine 2001). A number of reaches in this segment contain deep (1–2 m) pools where the river has incised through a clay duripan; these pools typically hold water through the summer. Historically, shallow groundwater supported base flows during late summer and early fall but the lowered groundwater table has created an extended period of low-flow and dry conditions.

The upper reaches of the Cosumnes River lie within the Sierra Nevada province, extending from the top of the watershed at 2 400 m elevation down to 15 m (Highway 16 bridge) (Figure 1). This portion of the watershed consists of steep, narrow, bedrock-controlled valley floors with steep valley-side slopes and moderate gradient drainage divides. The geographic distribution of geologic units of variable erosional resistance, along with the active tectonic uplift and westward tilting of the Sierra Nevada range, accounts for the diversity of landscapes and aquatic habitat within the upper watershed (Mount 1995). The Sierra Nevada today is a mixture of private and public lands (mainly El Dorado National Forest) that have been extensively logged, crossed by roads, and converted to agriculture (especially vineyards), with urbanization a small but increasing use. We divide the stream network of this province into four reaches: lower foothill mainstem, lower tributaries, upper tributaries, and mountain meadows.

The lower foothill mainstem segment (IV, Figure 1) originates at 52 m, approximately where the three forks of the Cosumnes converge, and drops to 15 m elevation where the incised meandering river reach begins. Within this reach the mainstem channel is alternately confined and unconfined, with numerous 'step-pools' that are often quite deep (2–4 m). The largest cascade (Latrobe Falls) in the entire watershed occurs in erosion-resistant rock adjacent to the Foothill Fault Zone. Substrate conditions vary, but are dominated by medium to coarse gravels. Flows in the lower foothill mainstem reach are perennial, but typically low ($<0.3\,m^3\,s^{-1}$) by late summer, affected in part by numerous small diversions upstream. Portions of this reach were heavily altered by hydraulic mining during the late 1800s and by gold dredging of stream placers in the 1900s. Land use today is dominated by grazing, with minor urbanization.

Above the lower foothill mainstem reach, the Cosumnes River divides into three high-order tributaries: the North, Middle, and South Forks. The confluence of the Middle and North Forks occurs in the large north–south valley adjacent to the Foothill Fault Zone (Figure 1). The South Fork joins the Middle Fork upstream of this valley. The forks of the Cosumnes contain three distinct reaches of varying length. The characteristics of these reaches are a function of their elevation and geology.

A lower tributary segment (IV, Figure 1) occurs within the lowermost Middle and North Forks of the Cosumnes. Channels within this reach are relatively low-gradient ($<20\,m\,km^{-1}$), alternately confined and unconfined, with diverse riffles and pools or narrow bedrock channels with alternate bars. Substrates vary from sand to coarse gravels. Flow within this lower reach is perennial, although typically low ($<1\,m^3\,s^{-1}$) in late summer and early fall. Significant land use/land cover change is taking place in this reach, principally associated with vineyards, grazing, and urbanization.

A middle tributary segment (V, Figure 1) occurs in all three forks of the Cosumnes. The South Fork flows across the southern edge of a large formation of granite about 5 km in a confined, bedrock channel with numerous cascades. Above this high-gradient reach (a presumed barrier to fish movement), the South Fork flows through fairly erosible metamorphic rocks. The channel is consequently a low-gradient (slope $<20\,m\,km^{-1}$) reach, often unconfined, with abundant alluvium in the bed. The middle tributary reach of the Middle and North Forks are confined, largely bedrock channels with moderate gradients ($20–30\,m\,km^{-1}$), narrow valley floors, and steep valley-side slopes with conifer and mixed conifer/hardwood plant communities. The Middle Fork flows through the relatively homogeneous center of the granite formation with a relatively constant gradient but no significant cascades. In contrast, the North Fork flows along the heterogeneous northern edge of the granite. Differential erosion during down cutting of the North Fork has produced at least four major cascades with gradients of over $100\,m\,km^{-1}$ for 1.5 km, reaching as much as $160\,\mathrm{m\,km^{-1}}$ gradients. All three forks are perennial, although sections of the South Fork may cease flowing in late September or early October, especially in dry years due to local surface diversions.

An upper tributary segment (VI, Figure 1) occurs in all three forks of the Cosumnes River. This reach is dominated by steep bedrock channels ($>30\,\mathrm{m\,km^{-1}}$) and occurs almost entirely within El Dorado National Forest. Summer flows are low but continuous, particularly near large springs.

The Middle and North Forks of the Cosumnes River originate in small, high mountain meadows above 2 200 m (mountain meadow segment, VII, Figure 1). The meadows are Pleistocene glacial troughs, reflecting the limited extent of glacial advance into the watershed. They support sinuous, spring-fed streams that are relatively undisturbed.

Methods

In July, August, and September of 1999, 2000, and 2001, we sampled a total of 44 sites throughout the watershed. We sampled 24 of the sites just once in the 3-year period, we sampled 14 twice, and we sampled eight all 3 years. We chose sites based on: (1) data from previous surveys, (2) representation of watershed habitats (an effort was made to sample throughout the watershed), and (3) accessibility. Accessibility was a particular problem because much of the watershed is privately owned and it was often difficult to obtain permission for access from landowners. Nevertheless, sampling sites were well distributed throughout the watershed.

At each site, we sampled 50–100 m of stream for fish using the most effective technique or combination of techniques. For 40 of the 44 sites, electrofishing was the principal technique applied, using a Smith-Root Type 12 Backpack electrofisher. Each site was subjected to a single pass with the electrofisher and two people using dip nets captured fish. In areas with wide, shallow, sandy-bottomed pools, electrofishing was supplemented by sampling with a $10 \times 1.3\,\mathrm{m}^2$ bag seine (8 mm mesh). At four wide, shallow lowland sites, seining was the sole method of sampling. For both techniques, fish were kept alive in buckets until they were measured (standard length) and returned alive to the water. Pools too large and deep to electrofish or seine were surveyed using mask and snorkel by two observers; all fish were counted and lengths estimated. Snorkeling surveys were useful mainly for determining the presence of large individuals of some species and for determining the presence of rare species not captured by other techniques.

At each site, the following environmental variables were measured or estimated, following Brown & Moyle (1993): (1) length, (2) mean width from three transects, (3) average depth from 30 measurements, (4) maximum depth, (5) percent water surface shaded by tree canopy, (6) percentage of bottom consisting of mud, sand, gravel, cobble, boulder, and bedrock, according to the Wentworth particle scale, (7) percent bottom covered separately with macrophytes, filamentous algae, and emergent vegetation, (8) percent of site with surface turbulence from fast-flowing water, and (9) percent of each site classified as run, riffle, or pool. We determined flow ($\mathrm{m^3\,s^{-1}}$) using a Marsh-McBirney Model 2000 flow meter, using 10 equal spaced measurements of depth and velocity on a single transect. We measured turbidity (NTU) with an HF Scientific DRT-15 CE Turbidimeter, while we measured conductivity and temperature (°C) with a Hanna HI 991300 multimeter.

We determined stream gradient ($\mathrm{m\,km^{-1}}$) and elevation (m) from topographic maps. We determined land use, vegetation types, and road densities for a 500 m wide circle around each site by calculating the number of hectares in each category. We broke land use into 13 categories (evergreen forest, mixed forest, shrub land, grassland, low-intensity residential, orchards and vineyards, urban, open water, exposed soil and rock, pasture and grain fields, wetlands, and row crops). We broke vegetation into nine categories according to dominant species (red fir, pine, mixed conifer, canyon live oak, manzanita, blue oak, annual grassland, exposed rock and soil, and urban–agricultural landscapes). The Geographic Information System (GIS) data sets used in analysis of land use and road length were USGS land use/land cover data (1990), GAP Analysis Vegetation data, and USGS Digital Line Graph (DLG) transportation linework. We screen digitized each sampling site on a 1 : 24 000 scale USGS quad (DRG) using ArcView 3.2. The USGS data is classified LandSat TM imagery and is in raster format with a 30 m cell size. The GAP Analysis data is classified LandSat TM imagery (1990). We classified the data using WHR habitat types and generalized for this analysis. The DLG road data was from the DLG-3 series and is at a 1 : 100 000 scale. We updated the roads data set using transportation data maintained by the California Department of Transportation in 1993. We completed the rest of the

GIS analysis using a customized set of Arc Macro Language (AMLs) programs in ARC/INFO. The sampling points were individually buffered with a radius of 500 m. The resulting circle was used to determine land use, vegetation types, and road densities around each sampling site.

We calculated the numbers of dams and potential diversions upstream of each sample site from the jurisdictional dams data set (dams over 5 m high) and the water rights data set, both maintained by the State Water Resources Control Board. Both data sets were completed in the early 1990s and have not been updated in recent years. We calculated the upstream drainage area of each sample site from a 30 m Digital Elevation Model (USGS DEM) and determined the number of dams falling in this area.

Extensive water quality data (23 variables) were available for sites throughout the watershed, including stream reaches that included most of our sampling sites (R. Dahlgren, University of California, Davis, unpublished data). However, a preliminary analysis indicated water quality variables beyond those that we collected at our sites had relatively low-variability and therefore had little impact on fish distribution. The only exception was the data from Deer Creek, which indicated high levels of nitrogen and phosphorus in the water from effluent from a sewage treatment plant. Even so, we did not use the more extensive water quality data set in this study.

The total number of fish of each species captured at each site was log transformed and standardized (mean 0, SD 1) for analysis, while the percentage of each species was arc sine transformed. The analysis was run independently using the following data: (1) combined numbers of individuals of each species captured in both electrofishing and seining, (2) combined numbers captured in electrofishing, seining, and snorkeling, (3) percentages of each species captured by electrofishing, seining, and snorkeling combined, and (4) combined numbers captured by electrofishing and snorkeling per m^2 sampled, excluding large pools. Detrended correspondence analysis (DCA) indicated that sites sampled in multiple years showed few differences among years, with the exception of a few sites that were dry after the first year; therefore, only data from the first year of sampling at each site was used in the final analysis. To determine how environmental factors influenced the distribution of species or groups of species, we used direct gradient analysis (canonical correspondence analysis (CCA)), with the CANOCO 4.0 program of ter Braak & Smilauer (1998), following Marchetti & Moyle (2001). CCA shows patterns in multivariate data. In this case it is useful for indicating how a variety of fish species simultaneously respond to environmental factors at a number of sites by correlating environmental variables with sample scores (ter Braak & Verdonschot 1995). The CCA was run separately with the site-specific data that characterized instream conditions and with the land use and vegetation data from the GIS analyses. Only the 14 most abundant or widely distributed species were used in the CCA; they included the most abundant species at one or more sites or species that made up more than 0.5% of the total fish sampled. Simple correlation analysis was also run on the abundance data for the 14 species to look for strong patterns of co-occurrence (assemblages) as found in Moyle & Nichols (1973) for the adjacent San Joaquin River drainage. Finally, to look at patterns of co-occurrence among species, a simple matrix was constructed showing the percentage of times each species occurred with each other species.

Results

Species distributions

Of the 25 species captured during the study, 18 were alien species (Table 1). We collected an additional 10 species (8 aliens) in a separate study on fish use of flood plains in the tidal reaches (Table 1). Six species (common carp, brown bullhead, prickly sculpin, hitch, bigscale logperch, inland silverside) were represented by just a few individuals at one or two sites. Of the three anadromous species present (Pacific lamprey, American shad, chinook salmon), only Pacific lampreys were widely distributed (eight sites in the main river), as larvae. We observed American shad as adults in early summer in big pools in the lowermost reaches of the river, which subsequently dried up. We collected juvenile shad once in large numbers at a site near the mouth of the river in the tidal zone. We did not collect chinook salmon but we recorded them as spawners in the winter.

Of the native warm water fishes, Sacramento pikeminnows and Sacramento suckers were most widely distributed (15 sites and 17 sites, respectively), occurring in three and four of the river segments, respectively (Table 1). However, we observed most pikeminnows either as young of year in reaches that subsequently dried up or as large adults in deep pools dominated by alien fishes. They were abundant mainly

Table 1. Fishes of the Cosumnes River watershed above the tidal floodplain segment, collected at 44 sites, 1999–2001.

Species	Number of sites	Elevation (m) Mean (range)	River segments	Life history
Pacific lamprey, *Lampetra tridentata**#	8	94 (11–232)	CV3, SN1	A
American shad, *Alosa sapidissima*	1	8	CV2	A
California roach, *Lavinia symmetricus**#	8	559 (341–622)	SN2	R
Hitch, *L. exilicauda*	1	3	CV2	R
Sacramento pikeminnow, *Ptychocheilus grandis**#	15	40 (3–134)	CV2,CV3,SN1	R
Golden shiner, *Notemigonus crysoleucas*#	4	18 (11–31)	CV2	R, A
Common carp, *Cyprinus carpio*	2	15 (11–18)	CV2	A?
Sacramento sucker, *Catostomus occidentalis**#	17	176 (3–622)	CV2, CV3, SN1, SN2	R, A
White catfish, *Ameiurus catus*#	5	34 (8–110)	CV3, SN1, SN2	R
Black bullhead, *A. melas*	2	20 (8–31)	CV2	R
Chinook salmon, *Oncorhynchus tshawytscha**	0[1]	−(3–11)	CV2, CV3	A
Rainbow trout, *Oncorhynchus mykiss**#	22	1111 (512–2201)	SN3, SN4, SN5	R
Brook trout, *Salvelinus fontinalis*#	2	2186 (2170–2201)	SN5	R
Brown trout, *Salmo trutta*#	11	1164 (561–2042)	SN3, SN4, SN5	R
Western mosquitofish, *Gambusia affinis*	6	38 (3–122)	CV2, SN2	R
Green sunfish, *Lepomis cyanellus*#	8	156 (8–622)	CV3, SN1, SN2	R
Redear sunfish, *Lepomis microlophus*	6	201 (3–597)	CV2, CV3, SN1, SN2	R
Bluegill, *Lepomis macrochirus*	7	77 (3–341)	CV2, CV3, SN1, SN2	R
Redeye bass, *Micropterus coosae*#	31	137 (8–561)	CV2, CV3, SN1, SN2	R
Largemouth bass, *Micropterus salmoides*#	9	48 (3–341)	CV2, CV3. SN1, SN2	R
Spotted bass, *Micropterus punctulatus*#	4	12 (3–31)	CV2, CV3, SN1	R
Smallmouth bass, *Micropterus dolomieu*	3	83 (18–158)	CV3	R
Bigscale logperch, *Percina macrolepida*	1	14	CV3	R
Striped bass, *Morone saxatilis*#	1	8	CV2	A
Prickly sculpin, *Cottus asper**	3	11 (8–13)	CV2, SN1, SN2	R

Native fishes are indicated by *, while fishes used in the analyses are indicated by #. River segments are CV1 (tidal floodplain, not included in this study), CV2 (nontidal floodplain), CV3 (incised, meandering river), SN1 (lower foothill mainstem), SN2 (lower tributary), SN3 (middle tributary), SN4 (upper tributary), SN5 (mountain meadow). For life-history, A indicates anadromous or adfluvial while R indicates resident.

[1]Chinook salmon and American shad migrate into the river to spawn in the fall and the juveniles migrate out before our summer sampling period, although some shad were collected in isolated pools in the lower reaches of the river.

in upper Deer Creek, a small tributary. Sacramento suckers had a similar distribution pattern except that they were common in one of the two reaches above natural barriers to alien fishes. These reaches also supported California roach (sites sites). Roach were usually the most abundant fish in the small streams where found (mean, 66% of individuals). Prickly sculpin were found only twice in our samples, but we observed them in large numbers in boulder rip–rap in the tidal reach of the river. Additional sampling in 2002 indicated that a low-elevation tributary, Deer Creek, supports a small population of sculpin (unpublished data). We found hitch in small numbers in one nontidal floodplain site.

The most widely distributed alien species was redeye bass (31 sites, four river segments) and it was often the most common species where found as well (average, 56% of individuals present). Prior to this study, this species was not known from the watershed; it was introduced into nearby Stanislaus River and Alder Creek (American River drainage) in 1962 and 1964 (Moyle 2002). The upstream limits of redeye bass seemed to be determined mainly by the presence of high-gradient reaches of stream that form barriers to movement. However, their presence above Latrobe Falls, a presumably impassible barrier on the mainstem Cosumnes River, indicates that they are subject to transplantation by anglers. Two other centrarchid species (bluegill, redear sunfish) were also widely distributed (four river segments) but they were usually uncommon where found, suggesting many were escapees from stock ponds (Table 1). Green sunfish (eight sites), however, were the only fish in one small tributary, Indian Creek, and were also abundant in Big Canyon Creek (18% of fish collected). The remaining alien species also appeared to be either stock pond escapees or were present only in large permanent pools in the nontidal and alluvial segments of the lower river. Striped bass were abundant only in a series of pools below a road crossing that formed a partial barrier to upstream movement. Of the three resident salmonids, native rainbow trout were the most widely distributed in sites in the upper-half of the watershed (22 sites, three river segments) and usually dominated by number as well (mean, 58% of individuals present). Alien brown trout occurred at 11 upper watershed sites but were dominant only in two locations, a headwater meadow stream and Sly Park Creek below Sly Park Dam, where flows are maintained by a small release from the dam. Brown trout were the only species at the meadow site, which was isolated from the rest of the system by a high waterfall. Alien brook trout were found at only two headwater meadow sites, where they made up over 88% of the fish present.

Species ecology

Rainbow trout and brown trout showed nearly identical association with environmental variables (Table 2). Both were widely distributed in cool, small, high-gradient streams in the upper tributary segments of the watershed. These streams have alternating runs, riffles, and pools and coarse substrates. They typically were found mainly with each other although rainbow trout were the more abundant of the two species. Brook trout, in contrast, were found in only small, shallow, cool (18–22°C, summer temperatures), meadow streams (mountain meadow segment) in which rainbow trout were present but uncommon.

California roach were found at mid-elevation sites (lower tributary segment) with moderate flows, cool temperatures, clear water, large deep pools, and complex substrates (Table 2). They were often most abundant in reaches where water flowed through pools sculpted in bedrock and boulder. Alien species (brown trout) were uncommon where roach were found and they most often co-occurred with rainbow trout and Sacramento suckers. Although genetic evidence suggests roach in the Cosumnes River have been isolated from other roach populations for a long time (Jones 2001), they presumably were once much more widely distributed in the watershed, occupying similar habitats now occupied by alien species, especially redeye bass and green sunfish. At one site on Deer Creek, they switched from being the most abundant species, with multiple age classes, at the beginning of the study, to being <25% of the fishes in 2002, entirely large individuals (unpublished data). Green sunfish became the dominant species at this site, indicating extirpation of the roach is likely, as has happened elsewhere in California (Moyle 2002).

Sacramento suckers occupy a wide elevation range in the lower watershed and were found at sites with a wide variety of characteristics (four river segments). Adults were most typically associated with cool clear water and deep pools although juveniles were often found in shallow, sandy-bottomed areas in the valley floor reaches, especially during the first year of our study when flows persisted into July. These fish perished when the stream dried up.

Sacramento pikeminnow were once the principal native piscivore in the lower Cosumnes River, but today

Table 2. Means of selected environmental variables affecting distribution of common fish species in the Cosumnes basin during the summer low-flow period.

Variable	Gradient	Flow	Temp.	Turbidity	Conductivity	Max. depth	Avg. width	Avg. depth	Sand	Cobble	Boulder bedrock	Riffle	Pool
Units	%	cfs	•C	NTU	µS	cm	m	cm	%	%	%	%	%
Pacific lamprey	1	20	25	3	126	168	16	72	26	33	34	19	37
California roach	2	6	18	1	131	128	8	48	15	30	35	33	40
Sacramento pikeminnow	<1	11	24	6	177	151	12	55	47	13	29	9	65
Golden shiner	<1	2	21	109	403	86	6	31	7	2	50	7	67
Sacramento sucker	1	9	23	5	177	121	11	46	39	15	33	14	51
White catfish	<1	6	24	4	103	144	14	47	71	7	21	4	74
Rainbow trout	2	5	17	1	75	87	5	34	11	31	31	33	31
Brook trout	2	0	19	1	44	33	2	2	12	6	19	23	40
Brown trout	2	6	17	2	45	62	5	27	5	30	34	31	24
Green sunfish	1	1	23	61	408	79	6	37	35	13	29	9	65
Redeye bass	1	15	25	3	157	158	12	57	39	22	31	13	49
Largemouth bass	<1	9	25	7	168	88	13	41	47	0	37	4	64
Spotted bass	<1	4	24	8	119	171	7	47	70	30	22	33	40
Striped bass	<1	0	25	2	93	110	10	50	35	33	55	19	37

they are present only in small numbers at a few warm sites in the alluvial river segment, a few sites in the lower foothill mainstem segments and in one refuge site, upper Deer Creek. Some of our collections were of young-of-year in shallow sandy flowages during the first year of the study, when flows persisted well into the summer, while most of the remainder were a few adults in deep rocky pools. Pikeminnows were typically found with alien species, including redeye bass, and with Sacramento suckers

Pacific lampreys were collected as ammocoetes at a number of locations in the main river where there was permanent water. They were most abundant above Latrobe Falls, demonstrating the ability of adult lampreys to climb over this barrier. They were typically found in the lower foothill mainstem segment in warm, clear, low-gradient reaches with abundant sand and gravel, flowing water, and deep pools (Table 2). Curiously, the most abundant fishes at sites where lampreys were collected were alien species, especially redeye bass. Presumably, the fact the ammocoetes are mostly buried in soft bottoms during the day allows them to avoid predation by the bass.

Redeye bass were the most abundant fish in permanent waters of the mainstem. They were found mainly in clear, warm water where the main habitats were deep pools and runs and bottoms were predominately sand and gravel (Table 2). Where redeye bass were abundant, other fishes were typically scarce. We observed different sizes of bass using virtually all available microhabitats: small (<50 mm SL) juveniles in shallow inshore areas, larger fish (50–150 mm SL) in runs and riffles, and large fish (150–250 mm SL) in the pools, often in loose aggregations. In a few areas, redeye bass co-occurred with smallmouth bass, largemouth bass, and spotted bass, but even in these areas redeye bass tended to be the most abundant *Micropterus*. Smallmouth bass were rare, but largemouth bass and spotted bass were common in warm, low-elevation pool habitats in the alluvial river segment (Table 2). Spotted bass were found only in the deepest pools, while largemouth bass were common in flowing habitats as well, including some that dried up by mid summer.

Green sunfish were associated mainly with bedrock and sand-bottomed pools in small warm streams, mainly in the lower tributary segment, which typically were turbid with algae and had high conductivities (Table 2). Occasionally they would be seen in larger pools on the mainstem as well. Their presence above barriers suggests movements by humans and presence in stock ponds, along with bluegill, redear sunfish, and largemouth bass (both occasional captures in upstream sites). Where green sunfish were present, native fishes were rare or absent and other aliens were common.

White catfish had a curious distribution because they were present as juveniles both in warm, deep pools in the mainstem alluvial segment and in the clear shallow pools of the lower foothill mainstem above Latrobe Falls. They were never abundant but consistently present indicating populations in stock ponds and perhaps some natural reproduction in the river itself. Common associates were other alien fishes.

Golden shiners were generally present in pools and runs of the nontidal floodplain segment of the main river. They were often trapped in summer reaches as the river dried up and our data reflect collections from stagnant pools with high turbidity and conductivity (Table 2). They were abundant in the sloughs and ponds of the tidal reach of the river and seemed to recolonize riverine reaches on an annual basis.

Striped bass, abundant in the estuary below the river mouth, were consistently present in the nontidal floodplain segment of the river before the river dried up and aggregated in large numbers in a series of pools below a road crossing, which was a partial barrier to further movement. The fish became trapped in these pools and eventually died when the pools dried up. When a passage way under the road was constructed in 2001 to allow better access to spawning areas for chinook salmon, large volumes of sand that had accumulated behind the road crossing moved through the passage way and filled in the pools, effectively eliminating the bass from the river. In 2002, the sand had been partially flushed out by winter flows and the bass returned (unpublished data).

Fish assemblages

The four CCAs run on different combinations of fish abundance data all indicated that species separated on environmental gradients determined largely by elevation, temperature, flow, and emergent vegetation, so only the analysis based on percentage of species from electrofishing and seining combined will be presented here (Figure 3). The CCA identified three weak groups

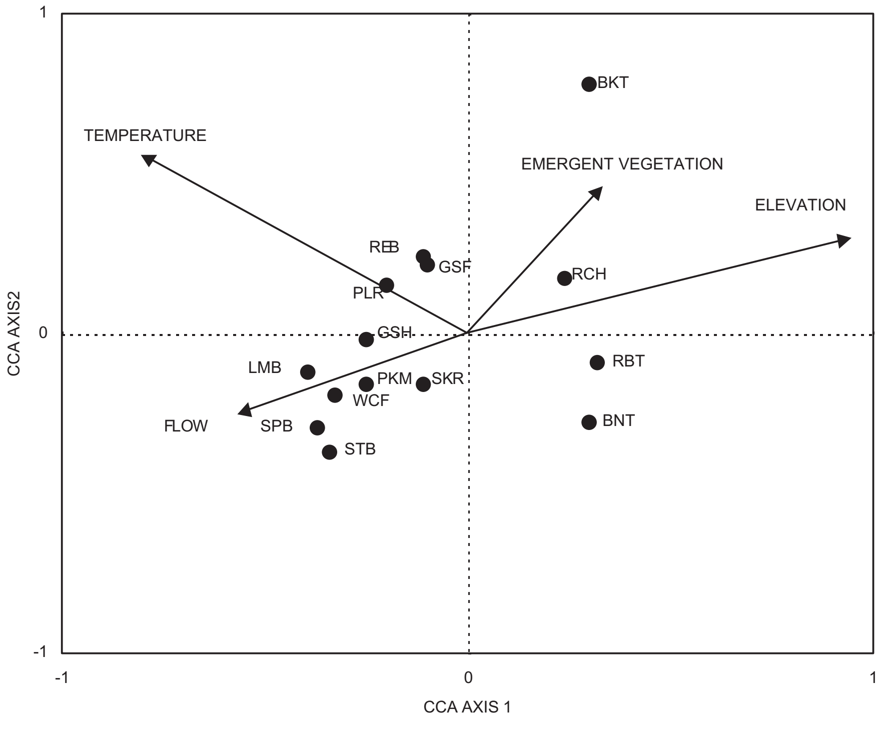

Figure 3. CCA diagram showing the relationship between abundance of fishes in the Cosumnes River watershed and site-specific environmental variables. RBT, rainbow trout; BKT – brook trout; BNT – brown trout; SKR – Sacramento sucker; PKM – Sacramento pikeminnow; REB – redeye bass; LMB – largemouth bass; RCH – California roach; PLR – Pacific lamprey; GSF – green sunfish; WCF – white catfish; SPB – spotted bass; GSH – golden shiner; STB – striped bass.

of species. The first group, mostly aliens, was found at lower elevations mainly in warm, nontidal floodplain and alluvial segments or in big pools in lower foothill mainstem segment. The second group, which clearly has broad overlap with the first group, consisted of Pacific lamprey ammocoetes and two aliens (redeye bass, green sunfish). It is associated with warm water, mainly in reaches with moderate gradients and flow. Redeye bass typically dominated these stream reaches to the point where other species, such as pikeminnow and redear sunfish, were present in only low-numbers. Green sunfish were abundant mainly in small tributaries, including one from which redeye bass were absent. A third group consisted of rainbow trout and brown trout, which had similar requirements for cooler water at higher elevations and almost always occurred together, typically (two exceptions) with rainbow trout dominating. Two species, California roach and brook trout fell outside the groupings of species. California roach occurred in clear cool tributaries above barriers that prevented invasion by redeye bass, usually dominating the reaches in which they occurred, although suckers and rainbow trout were often present with them. Brook trout were isolated in a small headwater tributary that flowed through mountain meadows, with lots of emergent vegetation in the water. The weakness of the groupings is reflected in the fact that each CCA only explained about 20–21% of the variance in factors determining fish distributions.

The weakness of the groupings is also apparent when the matrix of correlation coefficients based on numbers (log transformed) of fish captured in electrofishing and seining, are examined (Table 3). Only 17 of 91 (18%) possible combinations were significant ($p < 0.05$). In contrast, Moyle & Nichols (1973), working in nearby watersheds, found 40% of the combinations were significant. Seven of these combinations were between pikeminnow and other species, reflecting both the wide distribution (15 sites) of pikeminnow in low-elevation habitats and its consistent low-abundance; its abundance was positively correlated with that of Pacific lamprey, Sacramento sucker, white catfish, redeye bass, largemouth bass, and spotted bass and negatively correlated with that of rainbow trout. The only consistent group of intercorrelated species was redeye bass, Sacramento pikeminnow, Pacific lamprey, and white catfish, a cluster of species that occurred together in the foothill segments (but was not a cluster in the CCA). This is not a natural assemblage because: (1) the sites were dominated by redeye bass, (2) pikeminnows and lampreys were remnants of the original native fish fauna, and (3) white catfish were an anomalous presence in small numbers. In addition, the species involved in this assemblage were all commonly found in association with other species of fish, typically at more than 25% of the sites where the species was found (Table 4). The most exclusive group of fish was the three trout species but only two species occurred together in any one locality and about half the sites, only rainbow trout were present. California roach occurred only with rainbow trout, brown trout, green sunfish, and Sacramento sucker but never all at one site together. All other species co-occurred in at least one locality with 8–12 of the 13 possible other common species, as well as with several uncommon alien species (Table 4).

Landscape patterns

The distribution of fishes in the Cosumnes basin only weakly reflected broad patterns of land use and vegetation types (Figure 4) in contrast to elsewhere in the Central Valley (May & Brown 2002). The CCA for vegetation types explained only 3% of the variance in fish distribution, so is not considered further here. The CCA for land use explained only 11% of the variance and was driven mainly by the number of small dams upstream from each site, the presence of open areas (mainly hydraulic mining debris and levees), and deciduous forest (Figure 3). The fish clustered around the weighted mean with a tendency for alien species to have a positive relationship with dams and for roach and the three trout to be associated with forest and lack of dams. The lack of strong associations of fish with vegetation types and land use reflects the lack of consistent association of fish species and assemblages with the underlying geology, despite striking shifts in topography that take place in the watershed (Figure 1). While there are some general patterns (e.g., most warmwater aliens are found in the Central Valley province, most trout are found in the upper stream reaches in the Sierra Nevada province), the different geologic reaches do not have the same set of species in all areas, unlike streams dominated by native fishes elsewhere in California (Moyle 2002).

Even natural barriers have limited effectiveness in separating groups of fishes. In the Sierra Nevada province, the lower foothill mainstem segment contains a major barrier to fish movement (Latrobe Falls), although it is possible that it was historically navigable by native fishes during periods of high water. Only Pacific lampreys move over the falls on a regular basis today. The presence of redeye bass and other alien

Table 3. Pearson correlation coefficients between abundances of fish species at 44 sites in the Cosumnes basin.

	PLR	RCH	PKM	GSH	SKR	WCF	RBT	BKT	BNT	GSF	REB	LMB	SPB	STB
PLR	1.000													
RCH	−0.138	1.000												
PKM	0.374**	−0.280	1.000											
GSH	−0.024	−0.087	0.137	1.000										
SKR	0.105	0.195	0.351*	0.317*	1.000									
WCF	0.612**	−0.150	0.358*	−0.068	0.249	1.000								
RBT	−0.253	0.188	−0.514**	−0.160	−0.299*	−0.275	1.000							
BKT	−0.065	−0.091	−0.133	−0.041	−0.121	−0.071	0.114	1.000						
BNT	−0.125	0.037	−0.255	−0.079	−0.110	−0.136	0.186	−0.083	1.000					
GSF	−0.127	0.035	−0.013	−0.038	−0.022	−0.060	−0.224	−0.084	−0.160	1.000				
REB	0.567**	−0.255	0.401**	−0.095	−0.103	0.352*	−0.374**	−0.121	−0.162	−0.085	1.000			
LMB	−0.078	−0.191	0.440**	0.424**	0.285*	−0.026	−0.350*	−0.090	−0.173	−0.041	−0.116	1.000		
SPB	−0.106	−0.147	0.463**	−0.067	0.029	0.084	−0.269	−0.070	−0.134	0.057	0.063	0.398**	1.000	
STB	−0.062	−0.086	0.109	−0.039	−0.114	0.122	−0.158	−0.041	−0.078	−0.079	−0.114	0.272	0.208	1.000

*Indicates significance at 5% level; **Indicates significance at 1% level. RBT – rainbow trout; BKT – brook trout; BNT – brown trout; SKR – Sacramento sucker; PKM – Sacramento pikeminnow; REB – redeye bass; LMB – largemouth bass; RCH – California roach; PLR – Pacific lamprey; GSF – green sunfish; WCF – white catfish; SPB – spotted bass; GSH – golden shiner; STB – striped bass.

Table 4. Patterns of co-occurrence of fishes at 44 sites in the Cosumnes River basin.

No. sites	% of species found at individual species sites	PLR	RCH	PKM	GSH	SKR	WCF	RBT	BKT	BNT	GSF	REB	LMB	SPB	STB
8	PLR	100	0	88	13	38	38	13	0	0	13	100	25	13	0
8	RCH	0	100	0	0	50	0	88	0	38	38	0	13	0	0
15	PKM	47	0	100	20	80	33	0	0	0	13	67	53	27	7
4	GSH	20	0	75	100	75	25	0	0	0	50	50	75	25	25
17	SKR	18	24	71	18	100	29	24	0	24	12	53	41	24	6
5	WCF	60	0	100	20	100	100	0	0	0	40	80	40	60	20
22	RBT	5	32	0	0	18	0	100	9	45	9	9	0	0	0
2	BKT	0	0	0	0	0	0	100	100	0	0	0	0	0	0
11	BNT	0	27	0	0	27	0	91	0	100	0	9	0	0	0
8	GSF	13	38	25	25	25	25	25	0	0	100	38	25	38	13
13	REB	62	0	77	31	69	31	15	0	8	23	100	38	23	8
9	LMB	22	11	89	33	78	22	0	0	0	22	56	100	33	11
4	SPB	25	0	100	25	100	75	0	0	0	50	75	75	100	25
1	STB	0	0	100	100	100	100	0	0	0	100	100	100	100	100

Species abbreviations are as in Table 2 Values show the percentage of sites at which the species is found which also contain the other species, so each species pair has two values. Thus pikeminnows (PKM) are found at 88% of the sites containing Pacific lamprey (PLR), while lamprey are found at only 47% of the sites containing pikeminnows. Number of sites refers to sites at which each species in the next column were observed.

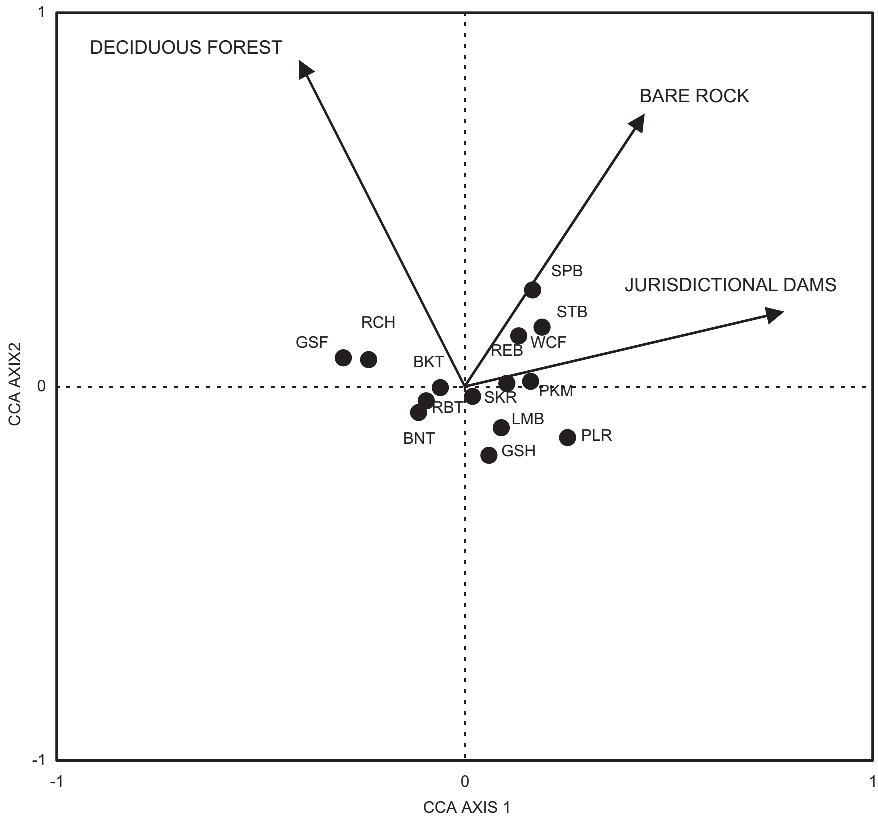

Figure 4. CCA diagram showing the relationship between abundance of fishes in the Cosumnes River and land use and vegetation variables. Abbreviations are as in Figure 2.

species both above and below the falls indicates that humans moved them there. The upstream limits of redeye bass in the North and South Forks are the high gradient reaches in the lower tributary segment, above which are the two principal remaining populations of California roach in the watershed. In the Middle Fork a similar gradient barrier is absent because of the uniform underlying geology, which allows redeye bass to extend upstream to the point where the water is cool enough to support rainbow trout. Presumably the cool water and increasing gradients keep the bass from penetrating higher. High gradient reaches (including 35 m high waterfalls) also separate the mountain meadow reaches from downstream reaches, which is presumably the reason the two separate meadow reaches support different kinds of alien trout: brook trout (North Fork) and brown trout (Middle Fork), reflecting different introduction histories. The meadow habitat, however, also seems to favor brook and brown trout because rainbow trout, also presumably from introductions, are abundant in the forested reaches above the barriers but below the meadows.

Discussion

Is the native fish fauna still intact?

Studies of other watersheds in the region have indicated that most expected species of native fishes are still present, if only in isolated pockets (Brown & Moyle 1993, Brown & Ford 2002, May & Brown 2002). We collected only seven of 11 expected native species. Native species that were expected but missing included hardhead, *Mylopharodon conocephalus*, speckled dace, *Rhinichthys osculus*, anadromous rainbow trout (steelhead), and riffle sculpin, *Cottus gulosus*. A fifth species, chinook salmon, was not collected but was present during the winter months as spawners in the lower foothill mainstem segment and as juvenile out migrants in the lower river (unpublished data).

Hardhead and speckled dace should have been present even though there are no reliable records of their presence. Suitable habitat for them exists in the watershed and they are present in the watersheds on both sides of the Cosumnes, the American River on the north and the Mokelumne River on the south. It seems likely they have been extirpated from the watershed in recent years; redeye bass and green sunfish now occupy most of the suitable habitat for both species. There are also no recent records of steelhead in the watershed, although we found resident rainbow trout to be common in upstream areas that may once have been accessible to the anadromous form. The absence of migratory fish presumably reflects the multiple factors that have caused the decline of native steelhead throughout central California, leading to their listing as a threatened species under the federal Endangered Species Act of 1973 (Moyle 2002). Although riffle sculpin are also present in both adjacent watersheds, they may have been absent from the Cosumnes basin due to natural causes. The cold swift water they require is limited even in the upper most parts of the Cosumnes drainage and is present mainly above barriers that would likely have prevented natural colonization by this benthic fish (Moyle 2002).

Our data suggest the Sacramento pikeminnow is likely the next species to be extirpated from the watershed, except perhaps for the population in Deer Creek. Young-of-year pikeminnows were observed mainly in areas that dried up later in the summer and most other fish observed were large individuals. Their distribution largely overlapped that of redeye bass, which suggests that predation (or other interactions) with the bass is responsible for their decline. This fits with the overall pattern of gradual disappearance of native fishes from the Cosumnes basin.

Why are alien fishes so abundant in a river system with a 'natural' flow regime?

The Cosumnes River and its tributaries are dominated by alien fishes, except for high elevation streams that maintain rainbow trout populations and for a few reaches that have been protected from invasion by downstream barriers. The dominance of alien fishes, the scarcity of native fishes (and the absence of some species) was not anticipated because the river is the last Central Valley tributary without a dam on its mainstem. As a rule in California and elsewhere, streams with altered flow regimes, especially those with dams that reduce high flow events, favor alien fishes (Moyle 2002), unless the flow regimes are managed to favor native fishes (Marchetti & Moyle 2001). Thus native fishes and fish assemblages tend to be most abundant in unregulated or lightly regulated tributaries to the main rivers. The restricted distribution and abundance of native fishes except rainbow trout in the Cosumnes basin can be attributed to a variety of interacting factors, in order of importance: (1) altered flow regime, (2) predatory alien fishes, and (3) habitat alteration.

Altered flow regime. While the Cosumnes River lacks a major mainstem dam to capture high winter flows, it does have hundreds of small diversions and a few larger ones that reduce summer flows. Thus much of the flow of Camp Creek, a large tributary, is diverted for storage in Sly Park Reservoir for eventual delivery to water users in the American River basin. More importantly, pumping of ground water for agricultural and urban use has depleted the aquifer below the lower river causing the river to dry up in summer. The Cosumnes River was historically a perennial stream from headwaters to mouth, with flows in later summer supported by upwelling ground water (Fleckenstein et al. 2001). Thus the lower reaches have become dry in summer except for a few large pools which favor alien 'pond' fishes (centrarchid basses and sunfishes, catfishes); these alien fishes have continuous sources of colonists from stock ponds and from the tidal sloughs downstream (unpublished data). In the lower and middle tributary reaches, reduction in summer flows may increase temperatures enough to shift the balance in some areas to alien fishes; native fishes are generally favored by cooler temperatures and permanent flows in such situations (Marchetti & Moyle 2001). Overall, the Cosumnes still has high winter flows that are important for maintaining channel processes and floodplains but has greatly reduced summer flows in most of the lower-half of the basin.

Predatory alien fishes. The most surprising finding of this study was the abundance of redeye bass in so much of the river. In places 90% or more of the fish observed or captured were redeye bass. In these areas native fishes were found as only a few individuals, usually near heavy cover. This redeye bass was introduced by the California Department of Fish and Game in the 1960s because foothill streams contained mainly native fishes that were deemed unsuitable for food or sport by most anglers. It was chosen because its native streams in the southeastern U.S.A. seemed to be similar to the foothill streams of the Central Valley (Moyle 2002). After the initial introduction, its presence was largely ignored because it apparently failed to spread and because most anglers had little interest in it, due to its small adult size (20 cm TL is a large fish). Its spread into the Cosumnes basin occurred without official sanction or notice. All surveys prior to ours identified redeye bass as smallmouth bass. The redeye bass is obviously well adapted to warm foothill streams where different size classes occupy different microhabitats in riffles, runs, and pools and feed on a wide variety of invertebrates (unpublished data). It is a very aggressive species, even to swimming humans, and we suspect that it has eliminated native fishes from its habitats by predation on early life history stages or by competitive interactions with other size classes.

Predation may have caused of elimination or reduction of native fishes from permanent pools in the lower reaches of the river. We found four species of piscivorous centrarchid basses in these pools (sometimes all four together), as well as striped bass. The main native fishes we observed in these pools were large (20–40 cm TL) Sacramento suckers and pikeminnows, fishes that are capable of living 10–20 years (Moyle 2002). It is significant that we found reaches of stream dominated by native fishes other than trout only above barriers. In one case, Deer Creek, the barrier appeared to be lower stream reaches that were dry in summer or highly polluted by agricultural waste. Ironically, flows in reaches containing native fishes are partially maintained by discharge from a sewage treatment plant. In other cases, the barriers were high-gradient sections of stream. Likewise, it is significant that we found young-of-year pikeminnows in the nontidal river segment only during 1999, a wet year with extended summer flows, in shallow, sandy-bottomed habitat containing few other fishes. These fish were lost when the stream dried up in late summer. Presumably the adults observed in upstream pools were able to spawn in the high flows but their young could persist temporarily into the summer only in seasonal shallow streams that excluded the alien predators.

Habitat alteration. Most of the Cosumnes watershed has been altered to one degree or another as indicated by the high frequency of roads everywhere. The most severely altered reaches are on the valley floor, where the river has been confined between levees and surrounded by intensive farming. But even the uppermost reaches have been affected by logging, grazing, and highways, resulting in increased sedimentation, increased temperatures due to removal of riparian trees and other changes. The pervasiveness of habitat alteration throughout the basin suggests that it has been a factor in the decline of native fishes but the continued presence of native fishes in some areas where aliens have not invaded suggests that it is often not the ultimate cause of extirpation.

Are there assemblages of fishes that reflect environmental differences created by the underlying geology?

The underlying geology of the Cosumnes basin creates a series of streams reaches that are distinctly different in their fish habitats. Historically each distinct reach either supported a distinct group of native fishes or was fish-free, as was the case of the mountain meadow reaches (Moyle 2002). Fishes with similar physiological requirements formed groups of ecologically segregated species (Moyle 2002). The cold upper reaches contained mainly rainbow trout, which gave way to reaches supporting different groups of native minnows and suckers, which in turn yielded to various warm-water and migratory fishes on the valley floor. Today the underlying geology still plays a role in fish distribution: trout (three species) dominate the upper reaches, fragmented groups of native fishes are found in the mid-elevation reaches, and a diverse group of warm-water alien fishes dominates the reaches in the valley floor and lower foothills. However, species distributions are highly individualistic, reflecting patterns of introductions, invasions and local extinctions, as well as physiological tolerances. The patterns suggest that changes in distribution and abundance are still occurring. For example, in Big Canyon Creek, a mid-elevation intermittent stream, we collected only redeye bass, green sunfish, and western mosquitofish. When the creek was sampled in 1979, redeye bass were present but the most abundant fish were Sacramento suckers and pikeminnows (BLM unpublished data). Likewise, in the course of our study, a site on Deer Creek (a stream heavily impacted by treated sewage water) shifted from being dominated by California roach to being dominated by green sunfish, with little evidence of recent successful reproduction by the roach.

Are there features of the watershed that consistently favor native fishes or that can be managed to favor native fishes?

Contrary to most other studies on stream fishes (e.g., Poff 1997, Waite & Carpenter 2000, Ross et al. 2002) the relationships of fish distribution and abundance in this study with patterns of land use, vegetation type, and water quality were weak. Presumably, this was because alien fishes have not invaded all the areas where they are capable of living and because native fishes have fragmented distribution patterns, reflecting past and on-going local extirpations. Geologic barriers that prevent invasions of alien species into upstream areas are important features for maintaining enclaves of native fishes such as California roach. However, evidence of recent movement of fishes by humans and the presence of numerous stock ponds, usually planted with centrarchid fishes to support fisheries, suggests that even these barriers are ephemeral. Thus the completeness with which the Cosumnes River watershed has been altered and invaded indicates that natural features that might normally protect native fishes are largely absent. Reversal of the trend towards complete dominance by alien species will require active management of the fishes and the watershed including actions such as restoration of flows to reaches that now dry up, eradication of trout from former fishless areas, and vigorous protection of remaining reaches dominated by native fishes (including eliminating upstream sources of alien fishes).

Conclusions

The Cosumnes River basin has been thoroughly invaded by alien fishes, to the increasing exclusion of native fishes. There is little evidence for predictable assemblages of interacting species. Even associations of species with strong patterns of geology, land use, and vegetation types are weak. We anticipate the fish assemblages will continue to change as alien species expand their ranges, as new species invade, and as native species become increasingly rare. Despite this extreme situation, the fishes of the Cosumnes basin provide some insights useful in managing invaded watersheds elsewhere.

Altered habitats can support native fishes. Practically every abuse possible to a watershed has been perpetrated on the Cosumnes basin, from placer gold mining in the 19th century to intense agriculture and urbanization in the present era. While the areas with the most extreme alteration support almost entirely alien fishes, some of the less altered areas (mainly at higher elevations) still support native fishes, especially above natural barriers. Interestingly enough, even the extremely altered valley floor reaches still support seasonal runs of migratory fishes (chinook salmon, Pacific lamprey, Sacramento sucker), although such runs are no doubt greatly diminished from historic numbers. This suggests that even altered habitats, if properly managed, can support native fishes.

New fish assemblages with characteristics of 'natural' communities are likely to develop in invaded systems. Fish assemblages in streams are dynamic because of two conflicting trends: the strong environmental gradients characteristic of streams favor discrete groups of fishes adapted to different sets of conditions on a longitudinal scale, while the high temporal variability in stream conditions promotes variability in composition of local fish assemblages (Matthews 1998). Thus the predictable fish assemblages frequently observed in streams are naturally forged under conditions likely to promote seeming chaos, at least in the short term. Native fish assemblages in streams in California's Central Valley have remarkably well-developed structure with strong persistence through fluctuating conditions, a reflection in part of long evolution in isolation (Moyle & Nichols 1973, Moyle 2002). In the Cosumnes River, the native fish assemblages have been disrupted and new assemblages are being formed, made up of mixtures of native and alien species. At present, the picture is one of the ecological chaos but with some emergent structure. The local assemblages reflect ongoing complex interactions of species' physiological tolerances and life-history requirements with geology, altered flow regimes, land use, habitat quality, and patterns of introduction and invasion. Biotic interactions between native and alien species are clearly also an important structuring force. Clusters of species with similar physiological tolerances are present in the various stream segments within the watershed but the composition of the assemblages overlap widely and continue to change. Presumably, barring additional introductions, more predictable assemblages will eventually form in each of the geologically distinct river reaches, although native species, except rainbow trout, are likely to be relegated to positions as minor players or driven to extinction. We assume these results are transferable to other regions of the world where alien fishes are not yet as pervasive as they are in California (e.g., Godinho & Ferreira 2000; Aparico et al. 2000). The extent to which invasions of new species are allowed to occur will determine the extent to which native fishes make up the new, mixed assemblages.

Restoring natural flow regimes to favor native fishes requires restoring both high and low-flows. If there is any hope for native fishes remaining as important components of the stream ecosystem in the Cosumnes basin it lies in improving the flow regime. Using the natural flow regime as a model upon which to base flows in regulated streams in a useful concept in stream management, especially in the western USA (Poff et al. 1997). In general, the more the flow regime of a stream resembles the historic regime, the more likely native fishes are to dominate its fauna (Marchetti & Moyle 2001). In regulated streams, often the most severe problem is reduction of high flows needed for channel forming events and attraction and export of migratory fishes, so much of the emphasis in restoring natural flow regimes has been in restoring high-flow events. Our study shows that restoring minimum flows is equally important in many rivers.

In the Cosumnes basin, the high flows still follow historic patterns, but summer flows are greatly reduced, with some once-perennial reaches becoming dry or intermittent. In addition, high flows tend to diminish more rapidly at the low-end of the hydrograph, increasing the likelihood of stranding of fish in unfavorable habitats (Fleckenstein et al. 2001). As a result, long sections of stream used for spawning and rearing by natives are now dry during critical periods. Where summer flows still exist, their reduction has presumably resulted in increased water temperatures and decreased riparian growth (a source of habitat structure), which favor alien species (Marchetti & Moyle 2001). Methods available for restoring low-flows and perhaps native fishes include reducing ground water pumping, reducing upstream diversions, releasing water from Sly Park Reservoir (down Sly Park Creek), and transferring water from the American River by way of the Folsom South Canal. Such actions would benefit anadromous fish by providing better flows for salmon spawning and rearing, as well as more habitat for larval lampreys. They would also provide rearing habitat for juvenile Sacramento suckers and other native fishes. Unfortunately, changing the flow regime is unlikely to reverse or even reduce the impact of redeye bass on native fishes in permanent sections of stream because they are preadapted for free-flowing Central California streams.

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