

Importance of Flood Dynamics versus Intrinsic Physical Habitat in Structuring Fish Communities: Evidence from Two Adjacent Engineered Floodplains on the Sacramento River, California

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Abstract.—We examined the factors structuring fish communities at two adjacent engineered floodplain systems on the Sacramento River, California: Yolo and Sutter bypasses. We intensively sampled fishes at each location during January–June 2002 and 2004 by rotary screw trap, collecting a total of 126,635 fish comprised of 29 species. Nonmetric multidimensional scaling indicated that distinct fish communities persisted between the locations during our study, despite nearly identical hydrographs and water temperature regimes. Regression models evaluated with an information-theoretic approach also indicated that location was an important factor explaining the abundances of selected species. Overall, Yolo Bypass had more species and a greater proportion of native species than did Sutter Bypass. Sutter Bypass had a greater proportion of species classified as freshwater, while Yolo Bypass had a greater proportion of species classified as either estuarine or anadromous. We believe these results are related to substantial differences in the underlying physical habitat within the floodplains, which are primarily associated with connectivity to the adjacent river. Although the dynamic flooding that occurs at both locations appeared unable to override the underlying physical habitat differences in structuring the overall fish communities, it was important in controlling the abundances of two prominent native species, Chinook salmon *Oncorhynchus tshawytscha* and splittail *Pogonichthys macrolepidotus*, which represented 79% of all individuals collected; splittails spawn on the inundated floodplains, and age-0 individuals of both species use these areas as rearing habitat. Our results have important restoration implications in that they illustrate the importance of both flood pulse dynamics and underlying physical habitat associated with connectivity in structuring river–floodplain fish communities.

Structuring of freshwater fish communities is influenced by many interacting factors operating at varying scales (Matthews 1998). Most mechanisms considered important in structuring fish communities can be broadly categorized as either biotic or abiotic factors. These factors often interact along spatial and temporal gradients, which can influence their perceived importance (Jackson et al. 2001). Thus, it is critical to understand the underlying spatiotemporal dynamics of fish communities to effectively model the perceived structuring mechanisms.

River–floodplain systems exhibit perhaps the most extreme spatiotemporal variation among freshwater habitats (Power et al. 1995; Puckridge et al. 1998). The rise and fall of flood waters can vary by amplitude, frequency, timing, and duration and thus can dramatically alter landscapes across interacting spatiotemporal scales. The predictability of flood dynamics varies regionally (Puckridge et al. 1998); nonetheless, the influence of the flood pulse on fish communities, food webs, and biological productivity appears to be

generally common and widespread (Junk et al. 1989; Winemiller 1996; Sommer et al. 2004a).

In many regions, especially temperate North America, there has been a substantial loss of natural floodplain connectivity due to human disturbances (Ward and Sanford 1995; Vitousek et al. 1997). In the United States alone, 98% of rivers are regulated (Vitousek et al. 1997). A variety of activities, including water storage, conveyance, flood control, and navigation enhancements, have contributed to river modification and impaired natural floodplain inundation. Recent modeling studies have indicated that these factors can also affect habitats internal to the floodplain (Gergel 2002) as well as their fisheries (Halls and Welcomme 2004). However, there is a growing interest in restoring river–floodplain connectivity because of increased understanding of the ecological importance of floodplain habitat to river ecosystems (e.g., Junk et al. 1989; Gutreuter et al. 1999; Sommer et al. 2001a). A fundamental question regarding such restoration is how to physically restore connectivity between rivers and floodplains. It is well established that the physical characteristics of perennial floodplain habitats (e.g., ponds and lakes) and their hydrologic connectivity to the adjacent river influence fish communities within them (e.g., Rodriguez and Lewis 1997; Winemiller et

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al. 2000; Feyrer et al. 2004; Miranda and Lucas 2004; Zeug et al. 2005); thus, intrinsic physical habitat can be as important as flood pulse dynamics in structuring river–floodplain fish communities. An understanding of how connectivity and intrinsic physical habitat interact to influence fish communities is needed to help guide the design and construction of restoration projects at both a regional and site-specific basis.

The objective of our study was to examine the factors structuring fish communities at two longitudinally adjacent floodplain systems of the Sacramento River, California: Yolo and Sutter bypasses (Figure 1). The two large systems are historical floodplains that were modified for flood control. They represent the primary facilities used to protect agricultural activities and residential communities, including the greater Sacramento region, from flooding during peak flow events in the lower Sacramento River. The two floodplain systems are similar in that they are immediately adjacent to each other, have similar flood cycles, are isolated from the main-stem Sacramento River by levees except when water overtops isolated weirs during high-flow events, and have shallow perennial channels that flank the floodplain perimeter.

An important difference is the source of water for the perennial channels. In Yolo Bypass, the source originates downstream and the channel is tidal for most of its length except during high-flow events. In Sutter Bypass, the source originates upstream and the primary channel remains lotic for much of the year. We hypothesized that this fundamental physical difference would be important in structuring fish communities at the two locations, despite the highly dynamic seasonal flooding that occurs at each location. Explicit in our hypothesis is that if flood dynamics are the primary mechanism structuring fish communities, the two systems will be indistinguishable and comprised primarily of similar groups of “floodplain-dependent” species. However, if flood dynamics are of lesser importance, the communities could be differentiated based upon the presence of species associated with the underlying physical habitat associated with the perennial channels, as well as other unidentified features, at each location. Thus, our overall goal was to assess the relative importance of seasonal flood dynamics versus intrinsic physical habitat features in structuring fish communities at these two immediately adjacent floodplain systems. To test our hypothesis, we examined 2 years (2002 and 2004) of intensive fish monitoring data in which the overall timing and magnitude of flooding differed substantially. We specifically sought to determine (1) how fish communities varied across the floodplain systems, seasons, and years, and (2) what large-scale environmental factors were important in explaining variation in the abundance of selected fishes.

Study Area

The Sacramento River is California’s largest river (Figure 1). It drains the northern portion of California’s Central Valley, captures approximately 1/3 of the state’s total runoff, is 526 km long, and has a mean annual discharge of about 8,000 m³/s per day. California’s Mediterranean climate constrains rainfall primarily to the winter–spring wet season and causes Sacramento River flow to vary seasonally by about tenfold. The river has been highly modified for flood control and a variety of water reclamation activities, including storage, conveyance, and diversion. These modifications have included straightening and leveeing long segments of the river—often by means of rock reinforcement (riprap)—which have reduced habitat complexity and greatly diminished natural floodplain inundation. The result is that the natural historic floodplain inundation that occurred in the lower valley is now confined primarily to two relatively large leveed basins, the Sutter and Yolo bypasses.

Sutter Bypass runs along the east side of the

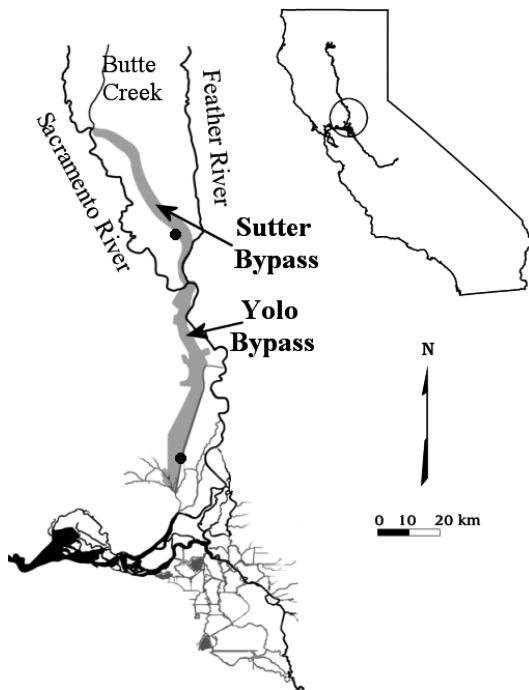


FIGURE 1.—Map depicting the study area in California (Sutter and Yolo bypasses) and sampling sites (circles) at which the factors influencing fish community structure were evaluated.

Sacramento River and is situated between the points where Butte Creek and the Feather River join the Sacramento River. The basin is 51 km long and has a surface area of 6,300 ha. Water enters Sutter Bypass in at least three ways. First, Butte Creek, a small tributary of the Sacramento River, spills into Sutter Bypass via Butte Slough. As it enters Sutter Bypass, Butte Slough splits into two shallow perennial channels that flank either side of the floodplain. The channel that runs along the west side of the floodplain carries most of the flow, while the eastern channel remains perennially inundated but can become lentic during dry periods. Opposite the floodplain, the channels are bordered by levees that delineate the area of Sutter Bypass. Water spills onto the floodplain when flows overtop the channel banks; we are uncertain of the required flow but believe it is similar to that of Yolo Bypass ($\sim 100 \text{ m}^3/\text{s}$; see below). A second mechanism for floodplain inundation is that relatively small flow events in the Sacramento River create water surface elevations that inundate the lower portion of Sutter Bypass. Finally, water also enters Sutter Bypass at weirs along the Sacramento River during high-flow events; water enters Sutter Bypass at Tisdale Weir when Sacramento River flow exceeds $595 \text{ m}^3/\text{s}$, at Moulton Weir when flow exceeds $1,274 \text{ m}^3/\text{s}$, and at Colusa Weir when flow exceeds $1,841 \text{ m}^3/\text{s}$. Land use on the floodplain during the dry season includes agriculture and a mosaic of "natural" habitats, such as mixed riparian forest, seasonal marsh, permanent ponds, and upland, including over 1,300 ha dedicated to state and federal wildlife refuges (Table 1).

Yolo Bypass is located immediately downstream of Sutter Bypass, along the west side of Sacramento River. The basin is 61 km long and has a surface area of 24,000 ha (Sommer et al. 2001b). Like Sutter Bypass, the hydrology is complex and inundation originates from multiple sources. The major difference is that tidal effects control Yolo Bypass hydrology for much of the year; however, like Sutter Bypass, the system is completely composed of freshwater. The very base of the Yolo Bypass is low-elevation, open-water habitat, and the inundated area is approximately 1,920 ha. A perennial channel, locally referred to as the "Toe Drain," flanks the east side of the floodplain. During low-flow periods, the Toe Drain is tidal and the amplitude exceeds 1 m. Water also enters Yolo Bypass at weirs along the Sacramento River during high-flow events; water enters Yolo Bypass at Fremont Weir when Sacramento River flow exceeds $2,000 \text{ m}^3/\text{s}$ and at Sacramento Weir when flow exceeds $5,000 \text{ m}^3/\text{s}$. Water also enters Yolo Bypass from the west via high-flow events in small west-side tributaries. All of these water sources join the Toe Drain, and water spills onto

TABLE 1.—Land use coverage (percent of total area) in Yolo and Sutter bypasses, California, summarized from data obtained by geographical information systems software from digitized aerial photographs (California Department of Water Resources, Land and Water Use Survey Program). Original land use data are publicly available from <http://www.landwateruse.water.ca.gov>. Aerial photographs of Yolo and Sutter bypasses were taken in 1997 and 1998, respectively.

| Land use category | Yolo Bypass | Sutter Bypass |
|-------------------|-------------|---------------|
| Water surface | 4 | 3 |
| Native vegetation | | |
| Terrestrial | 10 | 45 |
| Riparian | 2 | 8 |
| Agriculture | | |
| General | 23 | 19 |
| Rice | 4 | 10 |
| Field crops | 13 | 8 |
| Fallow | 1 | 1 |
| Grain and hay | 1 | <1 |
| Tomato | 2 | <1 |
| Pasture | 3 | <1 |
| Other | <1 | <1 |
| Other | <1 | <1 |
| Unknown | 37 | 7 |

the Yolo Bypass floodplain when the Toe Drain flow exceeds approximately $100 \text{ m}^3/\text{s}$. Land use on the floodplain during the dry season is generally similar to that of Sutter Bypass except that native terrestrial and riparian vegetation is much less common, and over 7,640 ha are dedicated to state and federal wildlife refuges (Table 1). Sommer et al. (2001b) provide additional details on Yolo Bypass.

Methods

We sampled fishes in each floodplain with a 2.4-m-diameter rotary screw trap (EG Solutions, Corvallis, Oregon). As part of different monitoring programs, Sutter bypass sampling was implemented by the California Department of Fish and Game and Yolo bypass sampling was implemented by the California Department of Water Resources. Sampling was conducted during January–June in 2002 and 2004 (Sommer et al. 2004a). Sampling also occurred in additional years in both floodplains, but we limited our analyses to these 2 years because Sutter Bypass effort and sites were not consistent during other years. We operated the traps for up to 7 d each week, and daily effort varied from 1 to 24 h depending on debris load and safety considerations. The traps were located in the downstream region of each floodplain (Figure 1). The Sutter Bypass trap was located in the western perennial channel, and the Yolo Bypass trap was located in the Toe Drain. All fishes collected in the traps were identified to species, counted, and measured for fork length (mm), except during instances of extremely large catches, when we only measured a representative

subsample. We used Moyle (2002) to classify fishes as native or alien and as either freshwater, estuarine, or anadromous.

Like any technique, rotary screw trap sampling has inherent biases (Roper and Scarnecchia 1996). Because our sampling method and effort were consistent across years and locations, any associated biases should also be consistent. Thus, we assumed that our sampling provided a fairly consistent representation of fishes that were susceptible to the traps. As with any field study utilizing a single sampling gear, we acknowledge that rotary screw trap sampling may provide a somewhat biased characterization of the fish communities. However, several other data sources from Yolo Bypass—including our unpublished beach seine data, beach seine and gill-net data from Nobriga et al. (2005), large fyke trap data from Harrell and Sommer (2003), and larval fish sampling from Sommer et al. (2004b)—suggest that our rotary screw trap sampling provided a good overall representation of the fish community. We summarized our fish catches as proportional abundances because we assumed that more direct measures of abundance (e.g., catch per unit effort) would be biased, as catch efficiency would probably fluctuate with stage. We examined the full data set ($N = 371$ samples) for patterns in fish community structure by use of nonmetric multidimensional scaling (NMDS) performed with the Primer version 5.0 software package (Clarke and Gorley 2001). Nonmetric multidimensional scaling is a particularly useful indirect gradient analysis because it provides operational flexibility in defining similarity among samples and converting it to distance that is accurately portrayed in low-dimension ordination space (Legendre and Legendre 2000). We chose the Bray–Curtis coefficient to construct the similarity matrices used in the NMDS ordination so that joint absences would not influence similarity. The fit of an NMDS ordination, quantified by a value termed stress, is determined by how well the among-sample distances in the ordination preserve the actual sample dissimilarities. Stress values did not change from that of the original run when we repeated the analysis several times and increased the number of random restarts (default value = 10), indicating that the ordination provided a good representation of sample dissimilarities (Clarke and Gorley 2001). To assist our interpretation of the NMDS ordination, we performed a variance partitioning technique (Lewis 1978) on the NMDS sample scores that allowed us to quantitatively evaluate whether spatial (site) or temporal (month and year) effects on community structure were important and whether they interacted. The NMDS sample scores were subjected to an analysis of variance (ANOVA)

procedure that employed site, month, year, and their interactions as factors. Factor variance components were derived from expected mean squares based on a fixed-effects factorial design ANOVA.

We used an information-theoretic approach to examine the importance of physical habitat features on the abundance of selected fishes (Burnham and Anderson 1998). This technique allows for a comparison of models with varying numbers of parameters and is based upon a strength-of-evidence context rather than traditional statistical tests of null hypotheses. We used least-squares regression to model relationships between environmental parameters and the abundance of selected fishes, and we identified the “best-fitting” models based upon Akaike’s information criterion (AIC). Candidate models were evaluated based upon three criteria: (Burnham and Anderson 1998): (1) the AIC adjusted for small sample size (AIC_c); (2) the AIC_c difference (Δ_i), which provides a level of empirical support for each model and is evaluated in relative rather than absolute terms (values of 0–2 provide substantial support for a given model [0 is best], values of 4–7 provide considerably less support, and values greater than 10 give virtually no support); and (3) Akaike weight (w_i), which provides a relative weight of evidence in support of a given model wherein the largest value is the best. We modeled $\log(x + 1)$ transformed abundances in relation to log-transformed independent variables of flow (m^3/s), water temperature ($^{\circ}C$), and site (Sutter Bypass or Yolo Bypass), all summarized as weekly averages. Flow was the total amount of water passing through the bypasses measured at permanent gauging stations; water temperature was obtained from daily measurements made by continuous recorders (Onset Computer Corp.) or discrete measurements at the sampling sites (Sommer et al. 2001a, 2004b). Because we had no a priori justification for excluding any of the independent variables, we developed candidate regression models for each independent variable by itself (simple regressions) and also for each possible combination of multiple variables (multiple regressions). We developed candidate regression models for all species that occurred at both sites, except for the ubiquitous common carp *Cyprinus carpio* and western mosquitofish *Gambusia affinis*.

Results

Physical conditions were generally similar between sites but differed between years (Figure 2). Peak flows that fully inundated floodplains occurred in early January during 2002 and in March during 2004. The March 2004 flow pulse was nearly three times as large and slightly longer in duration than that of January

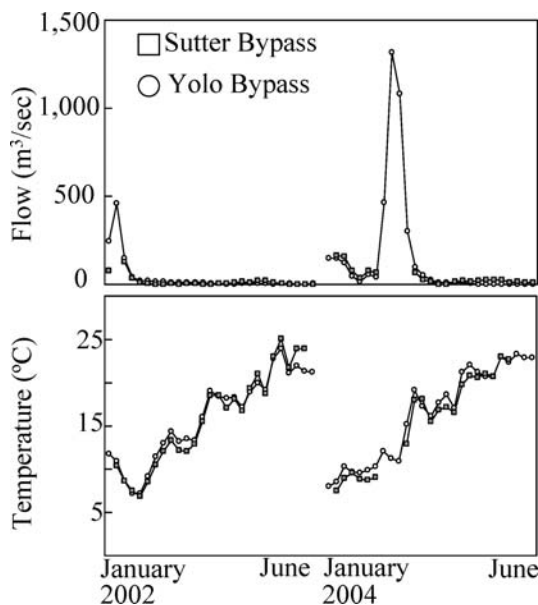


FIGURE 2.—Mean daily flow (m^3/s) and water temperature ($^{\circ}\text{C}$) in Yolo and Sutter bypasses, California, during January–June of 2002 and 2004.

2002. Water temperature exhibited typical winter–summer seasonality; lows of about 9°C occurred in January, and the temperature climbed to about 24°C in June. During 2002, water temperature exhibited an initial drop of about 4°C before steadily increasing through summer.

We collected a total of 126,635 fish represented by 29 species of primarily age-0 individuals (Table 2). A native floodplain-spawning cyprinid, the splittail, represented 67% of the total catch. Chinook salmon, which use the floodplains as both migration corridors and rearing habitat, represented 12% of the total catch. Overall, Yolo Bypass had more species and a greater proportion of native species than did Sutter Bypass. Sutter Bypass had a greater proportion of species classified as freshwater, while Yolo Bypass had a greater proportion of species classified as either estuarine or anadromous.

The NMDS ordination provided a three-dimensional solution, and the stress level (0.10) indicated that community structure was substantially different from random. The extraction of variance components from the NMDS sample scores (Table 3) demonstrated that site accounted for the overwhelming majority of variance (88%) of NMDS axis 1, indicating a strong spatial gradient in community structure that persisted throughout the study (Figure 3). An interaction between site and year—such that, imbedded within

the site differences, 2004 data were more similar overall than 2002 data—accounted for the majority of variance (50%) extracted from NMDS axis 2. Month accounted for the majority of the variance (46%) extracted from axis 3, indicating a persistent temporal component of community structure. Sites remained distinct along the seasonal gradient but converged slightly during the months of March and June (Figure 3). These periods of convergence appeared to be influenced primarily by variation in the catch of Chinook salmon, which represented a substantial portion of the fish community in Sutter Bypass until June and occurred in Yolo Bypass primarily in March (Figure 4). Several other species also exhibited strong seasonality (Figure 4). Splittail and threadfin shad occurred at both locations but during spring and winter, respectively. An important sport fish, the striped bass, occurred only at Yolo Bypass during summer.

Among those species we examined, the splittail was the only species for which site was not included in a meaningful regression model, as evaluated with the information-theoretic approach (Table 4). Only a single model fitted with just the temperature variable produced a meaningful regression for splittails. This demonstrates that at both sites, splittails exhibited their highest abundance during summer after the spring flood flows had receded. This observation is consistent with their life history of utilizing inundated floodplains for spawning and rearing, and then emigrating to the San Francisco Estuary during summer once flows have receded and floodplains have begun to dry (Moyle et al. 2004; Feyrer et al. 2005). Of the remaining species, inland silversides and threadfin shad had significant models with site variables that included Yolo Bypass. These species also exhibited their highest abundances under contrasting conditions: high flow and low temperature for threadfin shad and low flow and warm temperature for inland silversides. The models for all remaining species included a site variable favoring Sutter Bypass and essentially segregated into groups of coolwater and warmwater species, which coincidentally were comprised exclusively of native (Chinook salmon, lampreys, Sacramento pikeminnow) and alien (channel catfish, largemouth bass) species, respectively.

Discussion

The fish communities of Yolo and Sutter bypasses appeared to be structured primarily by the habitat characteristics of each floodplain and secondarily by the flood pulse dynamics. This observation was supported by both the NMDS ordination and the regression models developed for species that occurred at both locations. Although this finding is consistent with our original hypothesis, we were surprised at the

TABLE 2.—Status (A = alien, N = native), life history characterization (AN = anadromous, ES = estuarine, FW = freshwater), and the frequency of occurrence in samples (%) for fishes collected by rotary screw trap sampling at Sutter and Yolo bypasses, California, during January–June of 2002 and 2004.

| Taxon | Status | Life history | Frequency | |
|--|--------|--------------|---------------|-------------|
| | | | Sutter Bypass | Yolo Bypass |
| Petromyzontidae | | | | |
| Lamprey <i>Lampetra</i> spp. | N | AN | 16.7 | 10.1 |
| Clupeidae | | | | |
| American shad <i>Alosa sapidissima</i> | A | AN | 18.0 | |
| Threadfin shad <i>Dorosoma petenense</i> | A | FW | 38.2 | 50.4 |
| Cyprinidae | | | | |
| Sacramento pikeminnow <i>Ptychocheilus grandis</i> | N | ES | 41.2 | 11.5 |
| Splittail <i>Pogonichthys macrolepidotus</i> | N | ES | 18.0 | 30.2 |
| Common carp <i>Cyprinus carpio</i> | A | FW | 15.0 | 8.6 |
| Fathead minnow <i>Pimephales promelas</i> | A | FW | 24.5 | |
| Goldfish <i>Carassius auratus</i> | A | FW | 5.8 | |
| Golden shiner <i>Notemigonus crysoleucas</i> | A | FW | 19.3 | |
| Red shiner <i>Cyprinella lutrensis</i> | A | FW | 6.0 | |
| Ictaluridae | | | | |
| Channel catfish <i>Ictalurus punctatus</i> | A | FW | 12.0 | 10.8 |
| White catfish <i>Ameiurus catus</i> | A | FW | | 35.3 |
| Osmeridae | | | | |
| Longfin smelt <i>Spirinchus thaleichthys</i> | N | AN | | 18.0 |
| Delta smelt <i>Hypomesus transpacificus</i> | N | ES | | 10.1 |
| Wakasagi <i>H. nipponensis</i> | A | FW | 9.9 | |
| Salmonidae | | | | |
| Chinook salmon <i>Oncorhynchus tshawytscha</i> | N | AN | 81.1 | 43.9 |
| Atherinopsidae | | | | |
| Inland silverside <i>Menidia beryllina</i> | A | ES | 37.8 | 90.6 |
| Poeciliidae | | | | |
| Western mosquitofish <i>Gambusia affinis</i> | A | FW | 17.2 | 46.8 |
| Gasterosteidae | | | | |
| Threespine stickleback <i>Gasterosteus aculeatus</i> | N | FW | | 14.4 |
| Cottidae | | | | |
| Prickly sculpin <i>Cottus asper</i> | N | FW | | 5.8 |
| Moronidae | | | | |
| Striped bass <i>Morone saxatilis</i> | A | AN | | 22.3 |
| Centrarchidae | | | | |
| Black crappie <i>Pomoxis nigromaculatus</i> | A | FW | | 20.1 |
| White crappie <i>Pomoxis annularis</i> | A | FW | | 7.2 |
| Bluegill <i>Lepomis macrochirus</i> | A | FW | 18.0 | |
| Green sunfish <i>Lepomis cyanellus</i> | A | FW | 5.6 | |
| Largemouth bass <i>Micropterus salmoides</i> | A | FW | 18.0 | 12.2 |
| Warmouth <i>Lepomis gulosus</i> | A | FW | 5.2 | |
| Gobiidae | | | | |
| Shimofuri goby <i>Tridentiger bifasciatus</i> | A | ES | | 18.0 |
| Yellowfin goby <i>Acanthogobius flavimanus</i> | A | ES | | 36.7 |
| Total species | | | 17 | 22 |
| Proportion of native species | | | 23.5 | 36.4 |
| Proportion FW species | | | 70.6 | 50.0 |
| Proportion ES species | | | 18.8 | 27.3 |
| Proportion AN species | | | 12.5 | 22.7 |

degree to which the locations remained distinct across seasonal and annual scales given that their flood dynamics and temperature regimes were similar. The two locations showed very little convergence in community structure at any time during our study, even during periods when two prominent species, juvenile Chinook salmon and splittail, were collected in high numbers at each location. These observations underscore the importance of underlying physical habitat in structuring fish communities even in hydrologically dynamic environments such as river-floodplain systems.

We believe that the physical habitat characteristics that are important in distinguishing the fish communities at Yolo and Sutter bypasses include primarily the point source of water for the perennial channels and secondarily the physical habitat within the floodplain. Consistent with the general concept of longitudinal zonation and additive change in lotic fish communities (Rahel and Hubert 1991; Moyle 2002), the upstream source of water for Sutter Bypass contributed to a community consisting primarily of fishes classified as freshwater, whereas the downstream source of water for Yolo Bypass contributed to it having a higher

TABLE 3.—Summary of spatial (site [Yolo or Sutter bypass, California]) and temporal (month and year) factor variance components (%) derived from expected mean squares based on a fixed-effects ANOVA performed on nonmetric multidimensional scaling sample scores used to describe fish community structure.

| Component | Axis | | |
|-----------|------|----|----|
| | 1 | 2 | 3 |
| Month (M) | 4 | 15 | 46 |
| Year (Y) | 3 | 14 | 19 |
| Site (S) | 88 | 9 | 18 |
| M × Y | 0 | 4 | 11 |
| Y × S | 0 | 50 | 3 |
| M × S | 4 | 7 | 0 |
| M × Y × S | 1 | 1 | 3 |

proportion of fishes classified as estuarine or anadromous. Habitat complexity is also an important factor structuring fish communities and biological diversity in streams and floodplains (Ward et al. 1998; Grift et al. 2003; Hirzinger et al. 2004). Further, May and Brown (2002) found that physical habitat was a key determinant of the relative abundance of native fishes in

the Sacramento River basin. Physical habitat in each floodplain was generally similar; however, Sutter Bypass had a much higher proportion of native terrestrial and riparian vegetation (Table 1). Additionally, littoral habitats within the perennial channels of the two floodplain systems are very different and probably contributed to structuring the fish communities. The Toe Drain in Yolo Bypass exhibits little sinuosity and little in-channel or riparian structural complexity, whereas the perennial channels within Sutter Bypass exhibit noticeable complexity in these habitat zones and substantial mixed riparian forests that are inundated under very moderate flows. There is also a substantial amount of aquatic vegetation within Sutter Bypass versus virtually none in Yolo Bypass; this factor probably contributed to the relatively high

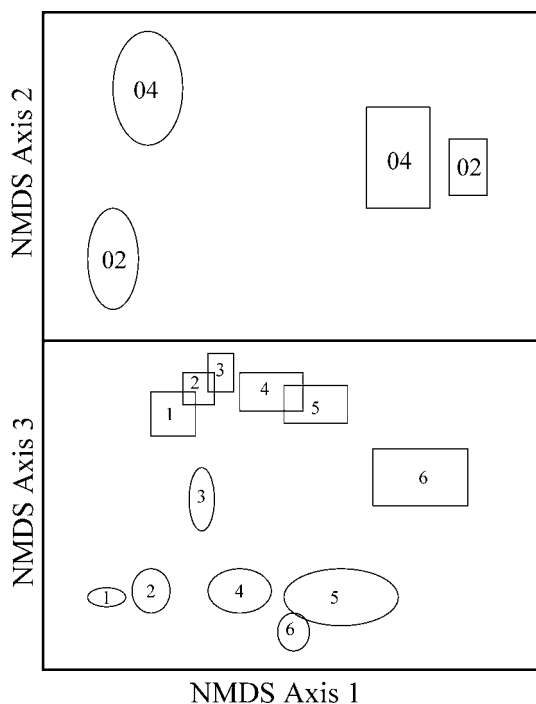


FIGURE 3.—Ordination diagram depicting the results of nonmetric multidimensional scaling (NMDS) based on fish proportional abundances in rotary screw trap samples from Yolo (ellipses) and Sutter (rectangles) bypasses, California. Numbers within the upper panel refer to years (02 = 2002; 04 = 2004). Numbers within the lower panel refer to months (1 = January, 2 = February, etc.). Ellipses and rectangles are centered on mean values for sample scores, and their dimensions reflect 95% confidence intervals.

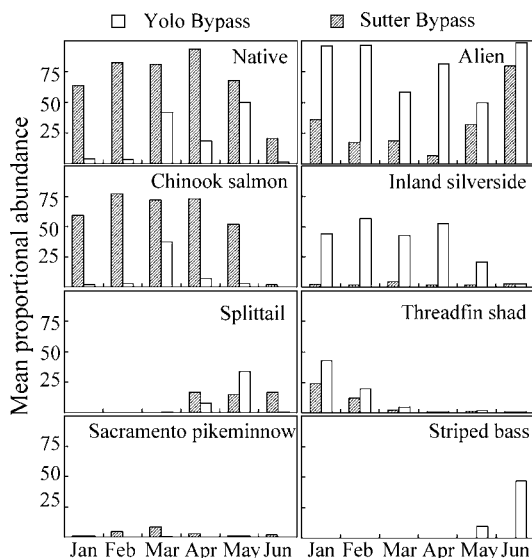


FIGURE 4.—Summary plots of proportional abundances for selected fishes collected via rotary screw trap sampling in Yolo and Sutter bypasses, California, in 2002 and 2004.

TABLE 4.—Best-fitting regression models for selected fish species, used to examine abundance related to three independent variables: site (Yolo [Y] or Sutter [S] bypass, California), water temperature (temp), and flow. Signs or symbols in parentheses indicate the influence of the variable on fish proportional abundance. The best-fitting model and any model within two units of the best adjusted Akaike information criterion (AIC_c) (given as AIC_c differences, Δ_i) are listed for each species. Adjusted r^2 values are presented for comparison.

| Species | Model | Δ_i | Adjusted r^2 |
|-----------------------|------------------------------|------------|----------------|
| Chinook salmon | Site (S), temp (–) | 0.000 | 0.55 |
| Lampreys | Temp (–), flow (+) | 0.000 | 0.14 |
| | Temp (–) | 0.442 | 0.13 |
| | Temp (–), flow (+), site (S) | 0.535 | 0.15 |
| | Temp (–), site (S) | 1.242 | 0.13 |
| Sacramento pikeminnow | Site (S), flow (–) | 0.000 | 0.24 |
| | Site (S), flow (–), temp (–) | 0.228 | 0.25 |
| Splittail | Temp (+) | 0.000 | 0.10 |
| | Site (Y), temp (+) | 0.000 | 0.50 |
| Inland silverside | Site (Y), temp (+), flow (–) | 1.196 | 0.50 |
| | Site (S), flow (+), temp (+) | 0.000 | 0.12 |
| Channel catfish | Site (S), flow (+), temp (+) | 0.000 | 0.24 |
| Largemouth bass | Site (S), flow (+), temp (+) | 0.000 | 0.24 |
| Threadfin shad | Site (Y), flow (+), temp (–) | 0.000 | 0.57 |

abundances of several alien cyprinids and centrarchids in Sutter Bypass.

Although dynamic flooding appears unable to override the underlying physical habitat differences in structuring the overall fish communities, it is an important factor controlling the abundances of two prominent native species: Chinook salmon and splittail. Juvenile Chinook salmon were abundant in Sutter Bypass in all months but June because of the direct connection with Butte Creek, which supports a substantial population of anadromous salmonids (Moyle 2002). However, in Yolo Bypass, the abundance of Chinook salmon only reaches high levels when Sacramento River flow overtops weirs and enters the floodplain. For splittails, extensive floodplain inundation is needed to attract adults to spawn and produce offspring at each location (Moyle et al. 2004). Our observation that these two native species dominated the overall catch (79% of total individuals) is consistent with the findings of May and Brown (2002) and Nobriga et al. (2005) that native fishes are still relatively more abundant in the Sacramento River basin than in other parts of the system.

The natural flow regime concept has received considerable attention with respect to the restoration and maintenance of native fish communities (Poff et al. 1997). Many studies have demonstrated that flow regimes mimicking historical natural conditions have greatly benefited native species or have limited the success of alien species (e.g., Meffe 1991; Travnicek et al. 1995; Bernardo et al. 2003). Studies in California's Central Valley have also provided support for natural flow regimes (Marchetti and Moyle 2001; Brown and Ford 2002). Although these examples provide promise in restoring native fishes with natural flow regimes, our results, similar to those of Feyrer

(2004), suggest that flow alone is not enough to appreciably manipulate some fish communities. The flow regimes in Yolo and Sutter bypasses generally reflect natural conditions in that they exhibit dynamic seasonal flooding that has been lost from much of the watershed. However, with the exception of Chinook salmon and splittail, fish communities appeared to be largely a function of the underlying physical habitat rather than the flow regimes. One important consideration, though, is that both systems exhibit relatively little, if any, flow at times during the summer and fall dry seasons. Based upon studies in Yolo Bypass, such conditions may be important in facilitating the reproductive success of alien fishes in perennial channels (Sommer et al. 2004b) and ponds (Feyrer et al. 2004) within floodplains. Moyle et al. (2003) suggested that restoring summer minimum flows in the nearby Cosumnes River basin was important for native fishes. The same might be true for Sutter and Yolo bypasses, especially with regard to limiting the reproductive success of alien fishes (Brown and Ford 2002), and should be given consideration for further study.

Our results have important implications for the restoration of river–floodplain systems. While many other studies have demonstrated the importance of flow regime, our study has illustrated that the manner in which connectivity is established and the underlying physical habitat are also critical in structuring fish communities utilizing river–floodplain systems. Because connectivity influences other taxa and productivity (Tockner et al. 1998; Sommer et al. 2004b) and because fishes can have important roles in structuring food webs and facilitating the transfer of energy within river–floodplain systems, it is important to consider physical habitat rehabilitation in the context of ecosystem restoration. Further, the design and

implementation of river–floodplain restoration is likely to be most effective within a framework of adaptive management.

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