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Ecological Patterns of Early Life Stages of Fishes in a Large River-Floodplain of the San Francisco Estuary

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Abstract.—We examined assemblage patterns of early life stages of fishes for two major tributaries of the upper San Francisco Estuary: (1) Sacramento River channel, and (2) Yolo Bypass, the river's seasonal floodplain. Over four hydrologically diverse years (1999–2002), we collected 15 species in Yolo Bypass egg and larval samples, 18 species in Yolo Bypass rotary screw trap samples, and 10 species in Sacramento River egg and larval samples. Fishes captured included federally listed species (delta smelt *Hypomesus transpacificus* and splittail *Pogonichthys macrolepidotus*) and several game species (American shad *Alosa sapidissima*, striped bass *Morone saxatilis*, crappie *Pomoxis* spp., and Chinook salmon *Oncorhynchus tshawytscha*). As in other regions of the estuary, alien fish comprised a large portion of the individuals collected in Yolo Bypass (40–93% for egg and larval net samples; 84–98% for rotary screw trap samples) and Sacramento River (80–99% for egg and larval net samples). Overall ranks of species abundances were significantly correlated for Yolo Bypass and Sacramento River, suggesting that each assemblage was controlled by similar major environmental factors. However, species diversity and richness were higher in Yolo Bypass, likely because of a wider variety of habitat types and greater hydrologic variation in the floodplain. In both landscapes, we found evidence that timing of occurrence of native fishes was earlier than aliens, consistent with their life history and our data on adult migration patterns. We hypothesize that Yolo Bypass favors native fishes because the inundation of seasonal floodplain typically occurs early in the calendar year, providing access to vast areas of spawning and rearing habitat with an enhanced food web. Conclusions from this analysis have implications for the management of aquatic biodiversity of tributaries to the San Francisco Estuary and perhaps to other lowland rivers.

Introduction

Data from relatively undisturbed large rivers indicate that the structure and function of different trophic levels are determined by interactions between the river channel and its floodplain (Junk et al. 1989). Floodplains can provide higher biotic diversity and increased production of fish (Bayley 1991; Gutreuter et al. 2000) and invertebrates (Gladden and Smock 1990; Sommer et al. 2001a). Potential mechanisms for floodplain effects include increased habitat area and diversity (Junk et al. 1989), terrestrial carbon subsidies to food webs (Thorpe et al. 1998), and decreased predation or competition (Corti et al. 1997). For fishes, floodplain may function as spawning habitat (Penaz et al. 1992; Killgore and Baker 1996), as rearing habitat (Sabo and Kelso 1991; Gehrke 1992; Turner et al. 1994), and as migration corridors (authors' unpublished data). Unfortunately, there is relatively little information from large, regulated rivers, particularly in temperate areas, where floodplain connectivity has typically been compromised by river channelization and the construction of dams and levees (Michener and Haeuber 1998).

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In this study, we examined assemblage trends in the early life stages of fishes in two major tributaries of the San Francisco Estuary: (1) Sacramento River channel, and (2) Yolo Bypass, the river's seasonal floodplain (Figure 1). Several attributes of this system made it attractive for study. The floodplain is mostly separated from the adjacent river channel by a levee, allowing us to differentiate between fish assemblage responses in each landscape. Like most other regions in North America, much of the historical floodplain habitat of large rivers in California has been lost due to channelization and levee and dam construction (Rasmussen 1996). However, the fact that Yolo Bypass is one of the largest contiguous areas of floodplain habitat on the West Coast of the United States may greatly enhance its biological significance. In addition, the region is the focus of a major habitat restoration effort (CALFED 2000). Landscape scale data on trends in assemblages of early life stages of fishes in river and floodplain habitat could be relevant for resource management in the San Francisco Estuary and perhaps other regions. Our study was designed to address the following specific questions for early life stages of fishes: (1) does species composition and diversity differ for the two landscapes? and (2) what are the temporal dynamics of the assemblages in each landscape?

Study Area

The San Francisco Estuary is one of the largest estuaries on the West Coast (Figure 1). The system includes extensive downstream bays (Suisun, San Pablo, and San Francisco) and a delta, a network of tidal channels that receive inflow from the Sacramento and San Joaquin rivers. The delta drains about 40% of California (Atwater et al. 1979). The estuary has been substantially altered by a variety of anthropogenic factors, including levees, dams, land reclamation activities, water diversions, and contaminants. The primary floodplain of the Sacramento River is the Yolo Bypass, a 24,000-ha, partially leveed basin (Sommer et al. 2001a). The 61-km floodplain floods in winter and spring in about 60% of years, typically when Sacramento basin flows exceed approximately 2,000 m^3/s. During these flood events, water spills into Yolo Bypass over Fremont Weir, inundating the floodplain to a mean depth of generally less than 2 m. In low-flow periods, water is confined to a tidal perennial channel along the eastern edge of the floodplain. Although agriculture has been one of the primary land uses in the floodplain for the past three decades, the majority of the floodplain is presently (or soon to be) managed for wildlife in "natural" habitats, including riparian and upland areas, emergent marsh, and permanent ponds. The reach of the Sacramento River adjacent to Yolo Bypass is a deep (>5 m) channel with minimal emergent vegetation and has steep, rock-covered banks with a narrow riparian corridor; the lower half of this reach is a tidal freshwater channel. Outflow from Sacramento River and Yolo Bypass rejoin near Rio Vista, where the combined discharge enters the brackish regions of the estuary.

In addition to changes in physical habitat, the biota of the estuary has been altered by a large number of species introductions (Cohen and Carlton 1998). Phytoplankton, zooplankton, and macroinvertebrates have declined substantially following the introduction of the alien bivalve *Potamocorbula amurensis* (Kimmerer and Orsi 1996; Orsi and Mecum 1996; Jassby and Cloern 2000). Native fishes have shown population decreases due to multiple factors (Bennett and Moyle 1996), leading to the listing under the Federal Endangered Species Act of two races of Chinook salmon *Oncorhynchus tshawytscha*, steelhead *Oncorhynchus mykiss*, delta smelt *Hypomesus transpacificus*, and splittail *Pogonichthys macrolepidotus*.

Methods

Our overall approach was to collect comparative physical and biological data in the Sacramento River channel and adjacent Yolo Bypass floodplain. Field data were collected during winter through early summer for 4 years (1999–2002). Flow in Yolo Bypass and the adjacent stretch of Sacramento River during 1999–2002 was recorded at gauges operated by U.S. Geological Survey. Daily water temperatures for each site were obtained from temperature recorders (Onset Corp.) installed in tidal channels of Yolo Bypass and Sacra-

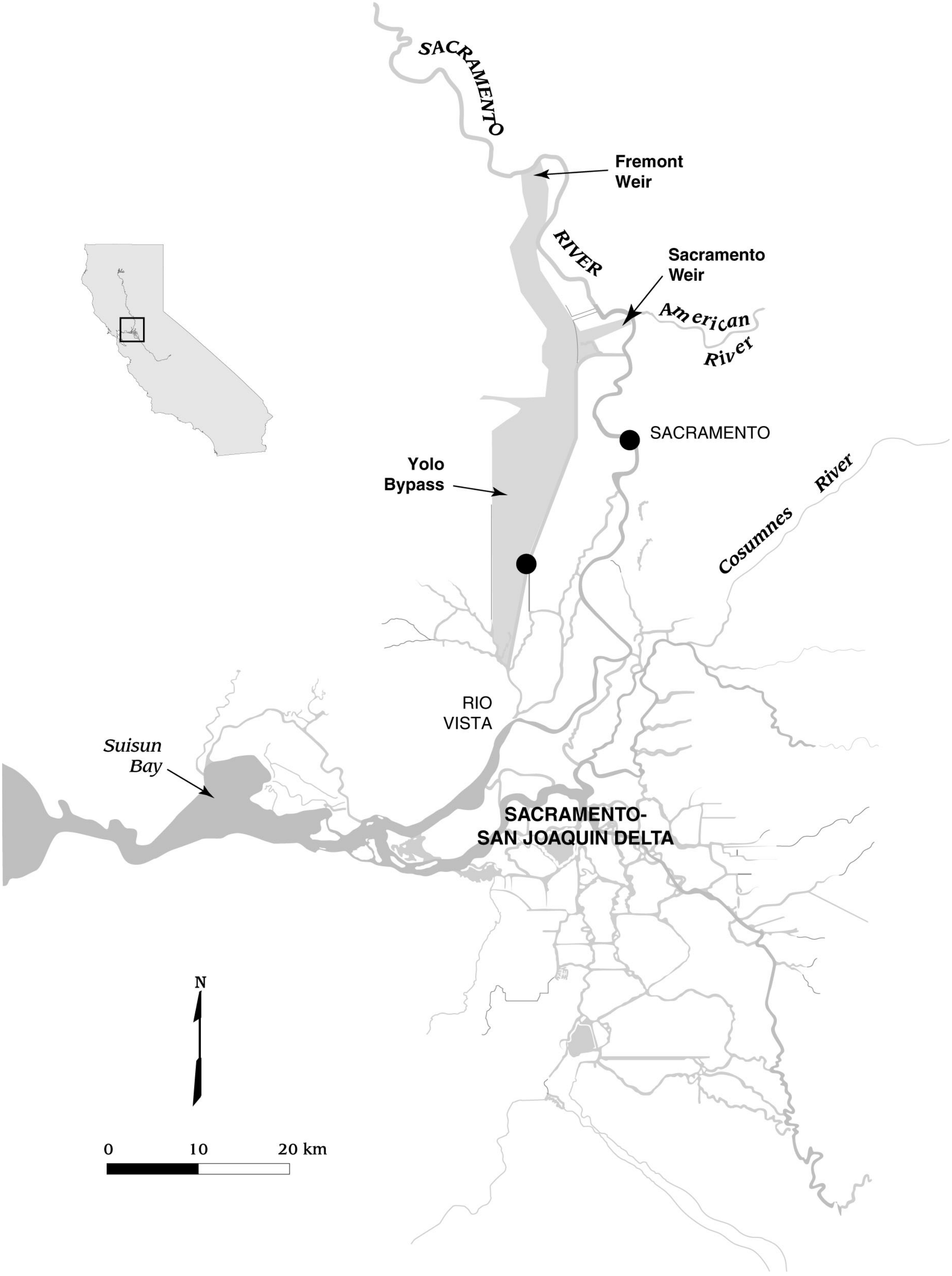

FIGURE 1. Location of Yolo Bypass and sampling stations identified with solid circles.

mento River (Figure 1). We sampled early life stages of age-0 fishes during winter and spring of 1999–2002 by egg and larval nets and rotary screw trap.

The egg and larval net sampling was designed to examine the general composition and timing of fish assemblages in each habitat, not to identify fine scale spatial variation. Sampling was generally conducted weekly during flood periods and monthly during low flow periods. Paired samples were usually collected at each location, except in 1999, when an extra 11 samples were collected in Yolo Bypass, and in 2000, when very few samples were collected in either Sacramento River ($N = 1$) or Yolo Bypass ($N = 4$). We used fixed sampling sites (Figure 1) located away from overhanging vegetation and bank eddies, in water velocities of approximately 15–60 cm/s, depending on flow. The 500-μm-mesh net was 4 m in length with a 0.65-m-diameter mouth. The net was fished passively in current near the surface for approximately 10 min during mid-morning (0900–1100 hours). The only exception was during May and June 1999, when the net was towed behind a small boat for 10 min because of low water velocities in Yolo Bypass. Sample volume was calculated using a flowmeter (General Oceanics Model 2030R) and net dimensions. Fishes were stored in formalin before being enumerated to species using a dissecting microscope.

Rotary screw trap sampling was used as an independent approach to collect data on the fish assemblage in the Yolo Bypass. In January–June of each study year, we operated a 2.4-m-diameter rotary screw trap (EG Solutions, Corvallis, Oregon) at the same location where larval samples were taken. We operated the trap 5–7 d each week, with daily effort varying from 1 to 24 h, depending on debris load and safety considerations. Fish in each sample were identified to the lowest practicable taxon and counted.

The egg and larval net data were summarized as total catch or catch per effort (volume), then examined using graphical and tabular methods. Statistical analyses on the egg and larval sampling data were performed on all years except 2000, when there were insufficient samples. Only dates in which samples were taken at both locations (i.e., paired data) were used for analysis. The degree to which species assemblages differed between the two habitats was examined in three ways. First, species ranks were compared between Sacramento River and Yolo Bypass by calculating a Spearman coefficient of rank correlation for the combined data for 1999, 2001, and 2002. Second, species richness was calculated based on the combined data for all 3 years. In addition, Shannon indices (H′) were calculated for each location based on the sum of the species collected over the same time period. The Shannon indices were then compared between Yolo Bypass and Sacramento River using a *t*-test designed especially for the comparison of two diversity indices (Zar 1999).

For rotary screw trap data, we summarized the number of fishes, less than or equal to 40 mm fork length (FL), that were clearly age-0 based on inspection of length-frequency data. Although this size range was somewhat arbitrary, initial data review suggested that the rotary screw trap adequately sampled early life stages of most species at this size threshold. Western mosquitofish *Gambusia affinis*, fathead minnow *Pimephales promelas*, golden shiner *Notemigonus crysoleucas*, and red shiner *Cyprinella lutrensis* were deleted from the dataset because their young of year were too small to be efficiently captured by our trap or because we could not clearly identify young of year in the length-frequency data. As was done for the egg and larval net data, rotary screw trap results were summarized as either total catch or catch per effort (time), then examined using graphical and tabular methods. A Friedman's analysis of variance (ANOVA) and Kendall's coefficient of concordance was used to examine variation in rank abundance among different years (1999–2002). Note that insufficient egg and larval net samples were available in each year to perform a similar analysis on that dataset.

Results

Flow varied considerably among the sampling years (Figure 2). Total flow was higher in Sacramento River than Yolo Bypass throughout the study. In 1999 and 2000, the hydrology was moderately wet, resulting in peak flood events in Yolo Bypass at the 1.7- and 2.2-year

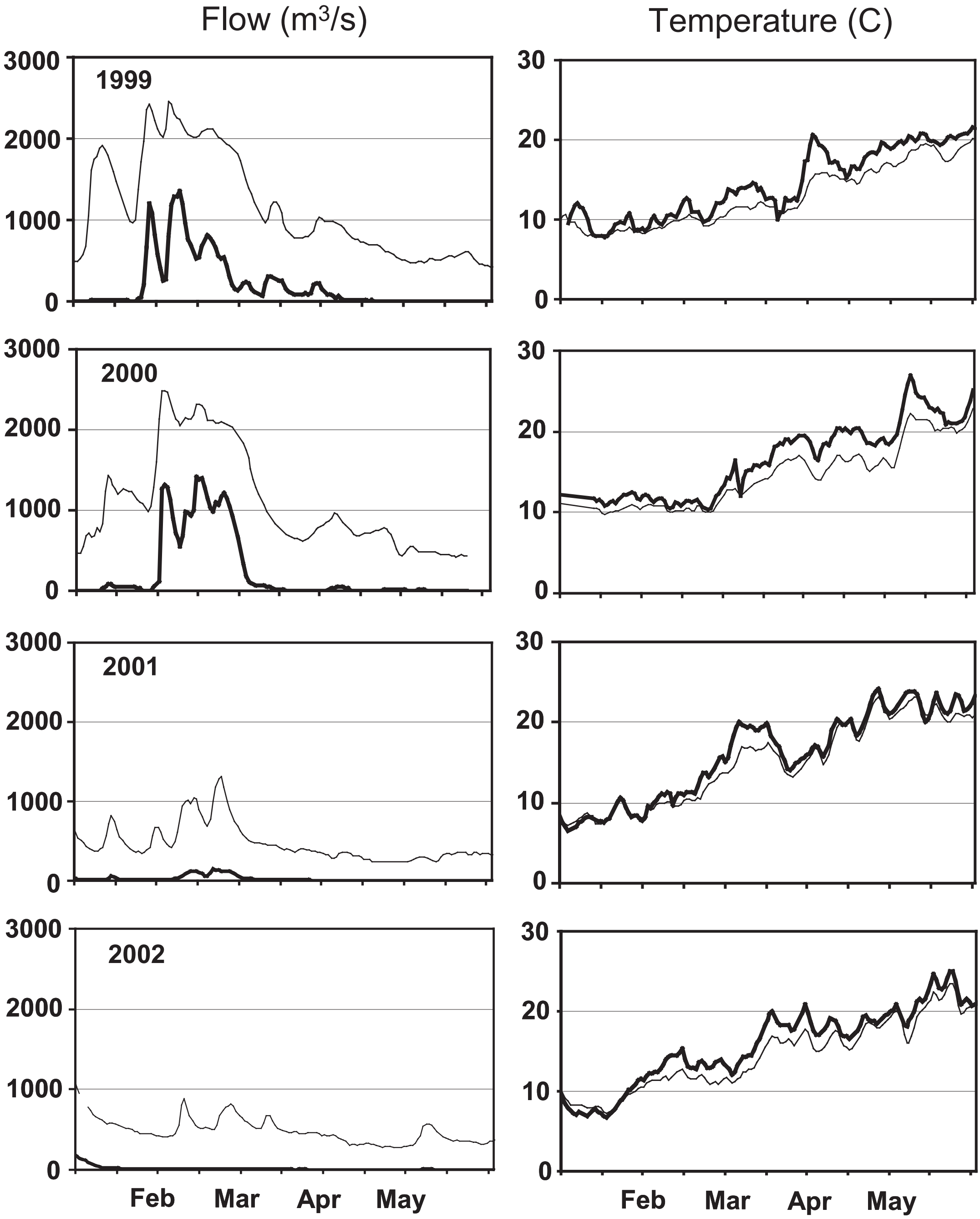

FIGURE 2. Trends in mean daily flow (m^3/s) and water temperature in Yolo Bypass (heavy line) and Sacramento River (fine line) during 1999–2002.

recurrence level, respectively. In 2001, the driest year of study, peak Sacramento River flows were insufficient to inundate the floodplain; all of the observed flooding in Yolo Bypass originated from a 1.4-year recurrence event generated by small stream tributaries to the basin. During the 2002 water year, a relatively short high flow event (1.8-year recurrence level) inundated Yolo Bypass from the Sacramento River for 1 week. Each year, water temperature gradually increased across months, although the Yolo Bypass floodplain was generally warmer than the Sacramento River.

We collected 15 taxa in Yolo Bypass egg and larval net samples, 18 taxa in Yolo Bypass rotary screw trap samples, and 10 taxa in Sacramento River egg and larval net samples (Tables 1 and 2). The range of species included two federally listed native fishes, delta smelt and splittail, and several alien sport fishes, American shad *Alosa sapidissima*, striped bass *Morone saxatilis*, largemouth bass *Micropterus salmoides*, white catfish *Ameiurus catus*, and crappie *Pomoxis* spp. In both Yolo Bypass and Sacramento River, we collected Chinook salmon fry that, based upon length

TABLE 1. Species captured during egg and larval sampling for each year. The relative ranks within each year and location are shown based on total counts (shown in parentheses). Unidentified minnows were placed into the "Other" category because the family includes both native and alien species.

	Yolo Bypass				Sacramento River			
Species	1999	2000	2001	2002	1999	2000	2001	2002
Native								
Chinook salmon	12 (1)				5 (1)		3 (2)	
Delta smelt		9 (1)		4 (7)				
Prickly sculpin *Cottus asper*	3 (78)	3 (97)	1 (57)	3 (21)	2 (10)	2 (1)	2 (4)	3 (5)
Sacramento blackfish *Orthodon microlepidotus*					5 (1)			
Splittail	5 (21)	6 (19)		7 (1)		1 (2)		4 (2)
Sacramento sucker *Catostomus occidentalis*	7(12)							
Alien								
American shad		2 (262)		3 (23)	1 (41)			
Common carp *Cyprinus carpio*	1 (119)							
Crappie	10 (3)							
Inland silverside *Menidia beryllina*	4 (74)	5 (21)		5 (6)	3 (3)			
Bigscale logperch *Percina macrolepida*	6(21)	9 (1)	3 (5)	7 (1)	5 (1)		4 (1)	
Shimofuri goby *Tridentiger bifasciatus*	11 (2)	7 (10)	4 (1)	7 (1)				
Striped bass	8 (6)	4 (37)	2 (31)	1 (200)	4 (2)		1 (173)	1 (665)
Sunfish *Lepomis* spp.	12(1)	9 (1)		7 (1)	5 (1)			5 (1)
Threadfin shad *Dorosoma petenense*	2 (113)	1 (1054)	4 (1)	2 (160)	5 (1)			2 (14)
Wakasagi *Hypomesus nipponensis*	9 (5)	9 (1)						
Other								
Unidentified minnows Cyprinidae		8 (5)	4 (1)	6 (2)				5 (1)
Total native species	4	3	1	3	3	2	2	2
Total alien species	9	8	4	7	6	0	2	3
Total fish	456	1509	96	423	61	3	180	688
Samples collected	18	4	7	12	7	1	9	12

TABLE 2. Species captured during Yolo Bypass rotary screw trap sampling for each year. The relative ranks within each year shown based on total counts (shown in parentheses) of young-of-year fishes less than or equal to 40 mm FL.

Species		1999	2000	2001	2002
Native					
Chinook salmon		3(477)	10(16)		4(19)
Delta smelt				8(3)	8(5)
Longfin smelt	*Spirinchus thaleichthys*				3(59)
Prickly sculpin		7(4)	10(16)		11(1)
Splittail		4(220)	3(1406)	3(97)	7(8)
Sacramento sucker		9(1)			
Threespine stickleback	*Gasterosteus aculeatus*	6(19)	9(22)	5(23)	6(13)
Alien					
American shad		2(970)	1(4323)	2(1512)	2(525)
Channel catfish	*Ictalurus punctatus*		12(1)		
Common carp		7(4)	8(26)		10(2)
Inland silverside		8(3)	6(142)	6(16)	9(3)
Bigscale logperch			12(1)		
Goldfish	*Carassius auratus*	8(3)		9(1)	
Largemouth bass			7(31)		11(1)
Striped bass		1(3380)	2(2524)	1(4561)	1(1085)
Sunfish			11(9)		
Threadfin shad			5(151)		
White catfish				7(11)	
Yellowfin goby	*Acanthogobius flavimanus*	5(21)	4(250)	4(66)	5(15)
Total native species		5	4	3	6
Total alien species		6	10	6	6
Total fish		5102	8918	6290	1736

criteria, were likely fall-run, although it is possible that some of the fish were federally listed spring-run. Over the entire study period, prickly sculpin and splittail were the most abundant native species collected based on ranks in egg and larval net samples; American shad, common carp, striped bass, and threadfin shad were the most abundant alien species in egg and larval net samples. Catch in Yolo Bypass rotary screw trap was reasonably similar to the egg and larval results, with splittail the most abundant native species in most years, and striped bass and American shad the most abundant alien species. There were, however, some notable differences; the egg and larval nets did not catch native threespine stickleback or alien yellowfin goby and caught few Chinook salmon. Each of these species was relatively abundant in the screw trap samples.

Species ranks in Yolo Bypass and Sacramento River were significantly correlated for fish collected in 1999, 2001, and 2002 egg and larval net sampling (Spearman $R = 0.60$; $N = 16$; $P = 0.014$; Table 1). Species diversity was significantly higher in Yolo Bypass (H′ = 0.68) than Sacramento River (H′ = 0.20) for the 3 years when sufficient data were available ($t = 21.3$; df = 1622; $P << 0.001$). During the same 3 years, species richness was higher in Yolo Bypass (14 species) than Sacramento River (10 species). For Yolo Bypass rotary screw trap data, there was significant concordance in species ranks among years (Friedman's ANOVA; $P = 0.022$; $N = 20$; df = 3; Kendall coefficient of concordance = 0.16).

Alien fish comprised a substantial portion of the total catch in each year. In Yolo Bypass egg and larval net samples, the percentage of alien fish was 75% in 1999, 92% in 2000, 40% in 2001, and 93% in 2002. The percentage of alien fish was slightly higher in Sacramento River than Yolo Bypass in all years for which there were an adequate number of egg and larval net samples: 80% in 1999, 97% in 2001, and 99% in 2002. No alien fish were collected in Sacramento River in 2000; however, the total number of fish collected was very low (*N* = 3). Yolo Bypass rotary screw trap samples also revealed a high percentage of alien fishes: 86% in 1999, 84% in 2000, 98% in 2001, and 94% in 2002.

We found evidence that there were differences in timing of occurrence of native and alien species. Except for the Yolo Bypass 1999 egg and larval net results, abundance of native fishes increased earlier than alien fishes (Figure 3). The slightly faster increase in alien fish abundance in 1999 for Yolo Bypass was caused by a single April egg and larval net sample in which 104 common carp were captured. In addition, native fishes were typically first observed at earlier dates than alien species (Tables 3 and 4). Native fishes were first observed primarily during February through early May, whereas alien larval fishes mostly appeared during March–June. The mean first date of capture (all species combined) was at least a month earlier for native fishes than alien fishes in all years of egg and larval sampling, and in all but one year (2001) of rotary screw trap sampling (Tables 3 and 4). In Yolo Bypass, native fishes also appeared at least a month earlier than alien fishes based on the median date of capture (Table 4).

Discussion

The presence of early life stages of different fishes strongly suggests that many taxa spawned in each landscape. Adult stages of the species captured in the present study have been collected in the Yolo Bypass (authors' unpublished data) and Sacramento River (California Department of Fish and Game, unpublished data) during the sampling period; many probably spawned in each landscape. Our data suggesting spawning in Yolo Bypass is consistent with many other studies demonstrating the importance of floodplain to fish reproduction (Turner et al. 1994; Killgore and Baker 1996; Molls 1999). The results indicate that Yolo Bypass provides spawning and rearing habitat to a wide range of species, including two federally listed fishes, delta smelt and splittail, and at least five sport fishes, American shad, striped bass, largemouth bass, white catfish, white crappie *Pomoxis annularis*, and black crappie *P. nigromaculatus*. The presence of larval splittail is consistent with the results of Sommer et al. (1997), who concluded that Yolo Bypass was a primary area in the estuary for spawning and rearing. Splittail are apparently attracted to spawn and forage on inundated terrestrial vegetation. Delta smelt are primarily a pelagic species (Moyle 2002) and had not previously been known to occur in floodplain habitat of the Sacramento–San Joaquin Delta. We believe that they probably spawned in the tidal channels of Yolo Bypass rather than seasonally inundated floodplain habitat. The same is likely true for American shad, striped bass, and crappie because in each year they were not captured until at least a month or two after the flood pulse had subsided. However, successful spawning of American shad in Yolo Bypass was surprising because this region is functionally a tidal slough during their late spring spawning period, quite unlike higher flow channels thought to be preferred spawning habitat of this species (Moyle 2002). Note, however, that our sampling design was not comprehensive enough to rule out the possibility that some of the early life stages of fishes from Yolo Bypass and Sacramento River originated from tributaries. This was certainly likely for Chinook salmon, which are produced in tributaries of Yolo Bypass and Sacramento River (Moyle 2002).

Catches of early life stages of fishes were highly variable over the course of the study and some sample sizes were relatively low in the egg and larval nets, making it difficult to fully explain assemblage patterns of each landscape. With these limitations in mind, we believe that there are some apparent trends in species composition and timing. Significant correlation between species ranks in Yolo Bypass and Sacramento River suggest that fish assemblages in each habitat were ultimately controlled by similar factors. However, the fact that Yolo Bypass exhibited higher species richness and diversity than the Sacramento River indicates that the floodplain had a more diverse assemblage. We attribute the more diverse fauna in Yolo Bypass to substantially

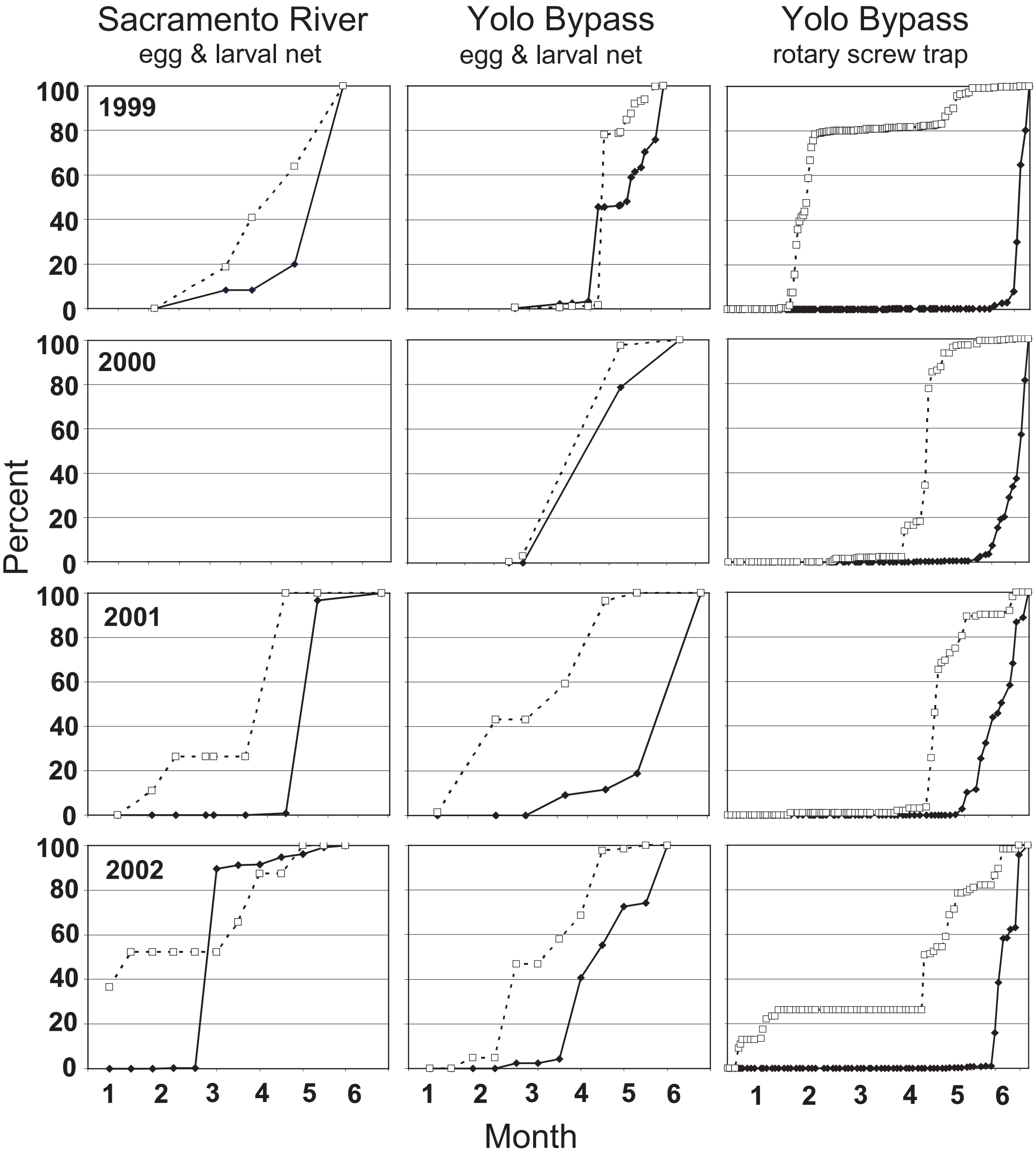

FIGURE 3. Percent of total cumulative catch for native (dotted line) and alien species (heavy line) during 1999–2002 in Yolo Bypass and Sacramento River. Values for each date have been standardized by calculating catch per volume for egg and larval net data and catch per day for rotary screw trap data.

higher habitat diversity and hydrologic variability. The floodplain has a broad suite of habitat types, including seasonal floodplain, perennial ponds, wetlands, and tidal channels, while the Sacramento River has a fairly homogenous, hydrologically stable channel with sparse riparian vegetation (Sommer et al. 2001a). Although environmental variation such as hydrology commonly affects young fish assemblages (Brown and Coon 1994; Turner et al. 1994; Gadomski and Barfoot 1998; Lazzari 2001), our finding that there was significant concordance in species ranks for Yolo Bypass rotary screw trap catch among

TABLE 3. First date (month/day) that each fish species was captured during egg and larval sampling for each year (1999–2002). Note that median capture dates were not calculated as for Table 4 because of low sample sizes.

	Yolo Bypass				Sacramento River			
Species	1999	2000	2001	2002	1999	2000	2001	2002
Native								
Chinook salmon	2/24				2/16		2/28	
Delta smelt		5/5		5/2				
Prickly sculpin	3/9	3/8	1/30	4/3	4/6	3/20	2/16	3/6
Sacramento blackfish					5/21			
Splittail	5/3	5/5		5/24		3/20		5/24
Sacramento sucker	3/9							
Alien								
American shad		6/5		6/5	5/21			
Common carp	3/31							
Crappie	3/31							
Inland silverside	5/10	5/5		5/16	6/7			
Bigscale logperch	3/9	5/5	4/24	5/24	3/24		2/28	
Shimofuri goby	6/1	5/5	5/10	5/16				
Striped bass	5/21	6/5	5/10	5/2	4/27		4/24	4/18
Sunfish	6/7	6/5		5/24	6/7			5/8
Threadfin shad	5/5	5/5	5/10	5/16	6/7			5/8
Wakasagi	5/17	5/5						
Native mean date	3/19	4/15	1/30	4/29	4/4	N/A	2/22	4/14
Alien mean date	5/1	5/13	5/6	5/16	5/14	N/A	3/27	5/1

the four different years was not consistent with our hypothesis that hydrology had a major effect on fish diversity. One possibility is that the concordance analysis was heavily influenced by several high ranking species that were not strongly affected by annual variation in floodplain inundation. These included striped bass, American shad, and inland silverside *Menidia beryllina*, fishes that spawn primarily in perennial channels, not seasonal habitat (Moyle 2002). Another possibility is that the range of flooding over the 4 years (i.e., 1.4–2.4 recurrence interval floods) was not sufficient to generate differences detectable by the concordance analysis. However, the fact that several species were captured in just one year of rotary screw trap sampling (threadfin shad in 2000, longfin smelt *Spirinchus thaleichthys* in 2002, and sunfish *Lepomis* spp. in 2002), and that another high ranking species (Chinook salmon) was completely absent in 2001, indicates that there was at least modest annual variation in the floodplain assemblages.

As found for the Cosumnes River (Crain et al. 2004, this volume), another seasonal floodplain in the San Francisco Estuary watershed, alien fish comprised a large portion of the assemblage of early life stages in Yolo Bypass. This finding is also similar to other perennial habitats of the estuary for larval fishes (Meng and Matern 2001; Feyrer 2004; Grimaldo et al. 2004; both this volume). Nonetheless, we hypothesize that seasonal floodplain offers special advantages to native fishes that are not available in perennial habitat. Our study was not designed specifically to test this hypothesis; however, the timing of the hydrological cycle seems well suited to the native fish we captured. Specifically, floodplain is typically inundated in winter and early spring, when many native fishes spawn and rear (Sommer et al. 2001a). Most of alien fishes of the estuary are warm water species and do not spawn until late spring or early summer (Moyle 2002), when floodwaters have receded and fish are confined to perennial channels and ponds. In other words, floodplain habitat

TABLE 4. First and median dates (in parentheses; month/day) that young-of-year fishes (≤ 40 mm FL) were captured during Yolo Bypass rotary screw trap sampling for each year (1999–2002). As discussed in the text, several species were excluded from the analysis because we could not clearly identify young of year in the data. We did not calculate a median date for species collected on fewer than three sampling dates.

Species	1999	2000	2001	2002
Native				
Chinook salmon	1/29(2/19)	2/11(3/2)		1/9(1/25)
Delta smelt			5/24	5/24(6/10)
Longfin smelt				4/26(5/8)
Prickly sculpin	5/17(4/24)	3/28(4/25)		5/1
Splittail	5/10(5/18)	4/19(5/3)	4/30(5/5)	6/5(6/10)
Sacramento sucker	5/21			
Threespine stickleback	4/27(5/29)	5/3(5/18)	4/13(5/24)	5/8(6/6)
Alien				
American shad	6/10(6/25)	5/31(6/25)	5/17(6/22)	5/22(6/19)
Bigscale logperch		5/31		
Common carp	5/10(5/14)	4/21(5/2)		5/24
Channel catfish		6/19		
Goldfish	4/9		4/16	
Inland silverside	5/28(6/28)	5/31(6/28)	6/1(6/26)	6/10
Largemouth bass		5/12(5/31)		6/10
Striped bass	6/10(6/24)	6/2(6/26)	5/17(6/8)	5/15(6/10)
Sunfish		5/12		
Threadfin shad		6/26(6/30)		
White catfish			6/26	
Yellowfin goby	6/14(6/21)	5/26(6/28)	4/11(6/4)	5/10(5/22)
Native mean date	4/20(4/22)	3/31(4/20)	5/2(5/14)	4/22(5/6)
Alien mean date	5/23(6/18)	5/27(6/9)	5/15(6/17)	5/25(6/6)

may favor native over alien fishes because the timing of inundation is better suited to their life history; the temporary nature of the habitat helps keep populations of alien fishes from increasing and dominating the floodplain fish assemblage. This hypothesis is consistent with our observation that native larval fishes were observed earlier each year than alien species. Differences in reproductive timing are also expected based on our observations (authors' unpublished data) that most native adult fish were most abundant during flow pulses in winter or early spring, while alien adult fishes showed fall or spring abundance peaks. Moreover, floodplain inundation substantially increases the total habitat availability, particularly shallow water area. For example, Sommer et al. (2001b) calculated that complete inundation of Yolo Bypass creates a wetted area approximately 10 times larger than the adjacent Sacramento River channel. Unlike the steep trapezoidal river channel of the Sacramento River and other Sacramento–San Joaquin Delta tributaries, the flooded Yolo Bypass contains large areas of shallow (typically <2 m), inundated vegetation, a habitat type preferred by native fishes such as young Sacramento splittail and Chinook salmon (Moyle 2002). In addition to increased habitat area, inundated floodplain provides an enhanced food supply. Sommer et al. (2001a) reported that multiple trophic levels are stimulated by floodplain inundation, increasing the availability of invertebrates to young fish.

Although our study was based on a single region and had small sample sizes for one of the survey methods, we believe that the results may be relevant for the design of habitat restoration of large rivers. Yolo Bypass and perennial habitats of the San Francisco Estuary all support native and alien fishes, but we hypothesize that the timing of floodplain inundation and its temporary nature may favor native fishes. Because river-floodplain connectivity remains poor throughout much of the estuary, we believe that floodplain restoration may provide an especially valuable tool to sustain native fishes in the San Francisco Estuary. The degree to which floodplain restoration would benefit native fishes in other lowland rivers is unclear. Nonetheless, the fact that floodplain provides enhanced productivity in many areas of the world (Junk et al. 1989) suggests that improving river floodplain connectivity could be an effective approach to help maintain biodiversity of native aquatic species in other areas.

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