Spatial and Temporal Distribution of Native and Alien Ichthyoplankton in Three Habitat Types of the Sacramento–San Joaquin Delta

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Abstract.—We examined the spatial and temporal variability of native and alien ichthyoplankton in three habitat types (marsh edge, shallow open-water, and river channel) in one reference and three restored marshes in the Sacramento–San Joaquin Delta, California, during 1998 and 1999. More than 6,700 fish embryos and 25,000 larvae represented by 10 families were collected in 240 tows during the 2-year study. Overall, the assemblage was dominated by alien fishes, but natives were more abundant during winter and spring, whereas aliens were more abundant during summer. Overall abundance was highest in marsh edge habitats, suggesting that this habitat provides favorable larval rearing habitats for many fishes. The reference marsh was dominated by alien species making it difficult to assess whether it had attributes that promoted use by native fish. Ichthyoplankton abundance varied comparably at restored sites of similar configuration. The restored site, with minimal tidal exchange and greater lower trophic productivity, supported the highest densities of alien fish. We conclude that restoration projects in this region of the estuary must consider the potential impacts of alien fishes on natives and evaluate strategies designed to improve recruitment success of native fishes. Specifically, we suggest that restored wetlands that offer only winter and spring inundation periods may provide maximum benefits to natives while limiting access by many alien fishes regardless of specific habitat-use requirements.

Introduction

Many researchers have described how ichthyoplankton populations can vary in composition and abundance along geographic axes in estuaries, mostly with respect to salinity (Houde and Alpern-Lovdal 1985; Dodson et al. 1989; Meng et al. 1994; Rakocinski et al. 1996) or distance from embayment openings (Laprise and Dodson 1989a). Though these studies have yielded valuable information on the range of various taxa within estuaries, microscale distributions of fish larvae have been overlooked (Houde and Rutherford 1993). Even within localized regions of estuaries, there are frequent strong physical and biological gradients (Jassby et al. 1995; Lucas et al. 2002). These gradients are often responsible for the inherent patchiness of larval fish populations (Cushing 1983; Houde and Alpern-Lovdal 1985). Because larval survival can hinge upon the microhabitat conditions within a system (Houde 1987; Houde and Rutherford 1993), identifying spatial distributions of larvae among habitats could yield valuable insights into processes influencing recruitment variability.

Many estuarine organisms exhibit dis-

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tinct vertical distributions to aid migration or position maintenance in specific regions of estuaries (Laprise and Dodson 1989b; Kimmerer et al. 1998; Bennett et al. 2002). To date, there has been little research to determine if ichthyoplankton abundance varies across gradients from nearshore to offshore habitats (Paller 1987; Dewey and Jennings 1992; Cardinale et al. 1998; Gadomski and Barfoot 1998). The purpose of our study was to examine the temporal and spatial distribution of ichthyoplankton along three subtidal habitat zones parallel to shore in one natural (reference) and three restored marshes. The three habitat zones were marsh edge, shallow open-water, and main river channel. We simultaneously measured physical variables and zooplankton densities to determine how characteristics of each habitat type may have influenced ichthyoplankton abundance and distribution.

Study Area

The Sacramento–San Joaquin Delta is formed by the Sacramento and San Joaquin rivers, which drain into San Francisco Bay (Figure 1). The delta is characterized by a myriad of channel and slough networks primarily under tidal freshwater influence. The delta has been highly modified by human activities, including extensive dredging, contaminant pollution, and water diversions (Conomos et al. 1985). At the turn of the 20th century, many historic delta marshes were drained and isolated with rock-reinforced (riprap) levees. These and the remaining natural marshes are patchily distributed throughout the delta. Besides extensive marshland loss, numerous alien plants and animals have successfully invaded and colonized the delta (Meng et al. 1994; Bennett and Moyle 1996; Meng and Matern 2001). The San Francisco Estuary is considered the most highly invaded in the United States (Cohen and Carlton 1998).

Our four study sites were located in the central delta (Figure 1). We selected upper Mandeville Tip (UM) as a natural marsh because it was never leveed or directly altered by human activities; therefore, we assumed that habitat features (e.g., vegetation composi-

tion, hydrology) would represent relatively natural conditions. We selected three restored marshes that were previously leveed for varying time periods (15–62 years) but were breached by natural (i.e., levee failure) or human actions during the last 7 decades. These sites are Mildred Island (MI; breached 16 years), lower Mandeville Tip (LM; breached 65 years), and Venice Cut (VC; breached 67 years). Breached marshes in the delta are typically termed flooded islands because they are below sea level and often still have remnants, if not all, of the constructed levees around them. Historically, these flooded islands would have been dominated by marsh plains drained by small intertidal sloughs and channels (Atwater et al. 1979). The subsidence is primarily due to soil decomposition caused by agricultural activity and wind erosion during the leveed period; subsidence is proportional to the number of years the island was leveed prior to being breached.

The subtidal interiors of the selected restored sites were characterized by different physical attributes, including shallow areas dominated with submerged aquatic vegetation (SAV), unvegetated shoals, and large open embayments. Subtidal regions at the natural site (UM) were confined to a narrow region between the intertidal and main river channel interface, and most of these habitats were colonized by SAV. The main difference among the restored sites was that MI still had much of the constructed levee surrounding its deep interior (~4 m), whereas the interior portions of VC and LM were generally shallower (~2 m) and more exposed to the main river channel. Tidal exchange at MI was largely restricted to a large breach opening (~8 m wide, 20 m deep) located at the northern end of the site (Lucas et al. 2002). The SAV beds at MI were largely confined to an approximately 5-m-wide band along the inner rim of the site. In contrast, the SAV beds at LM, VC, and UM were far more extensive, at times extending as far as 25 m from the shoreline during summer. The dominant SAV at all study sites was Brazilian waterweed *Egeria densa* and Eurasian milfoil *Myriophyllum spicatum*, both alien macrophytes.
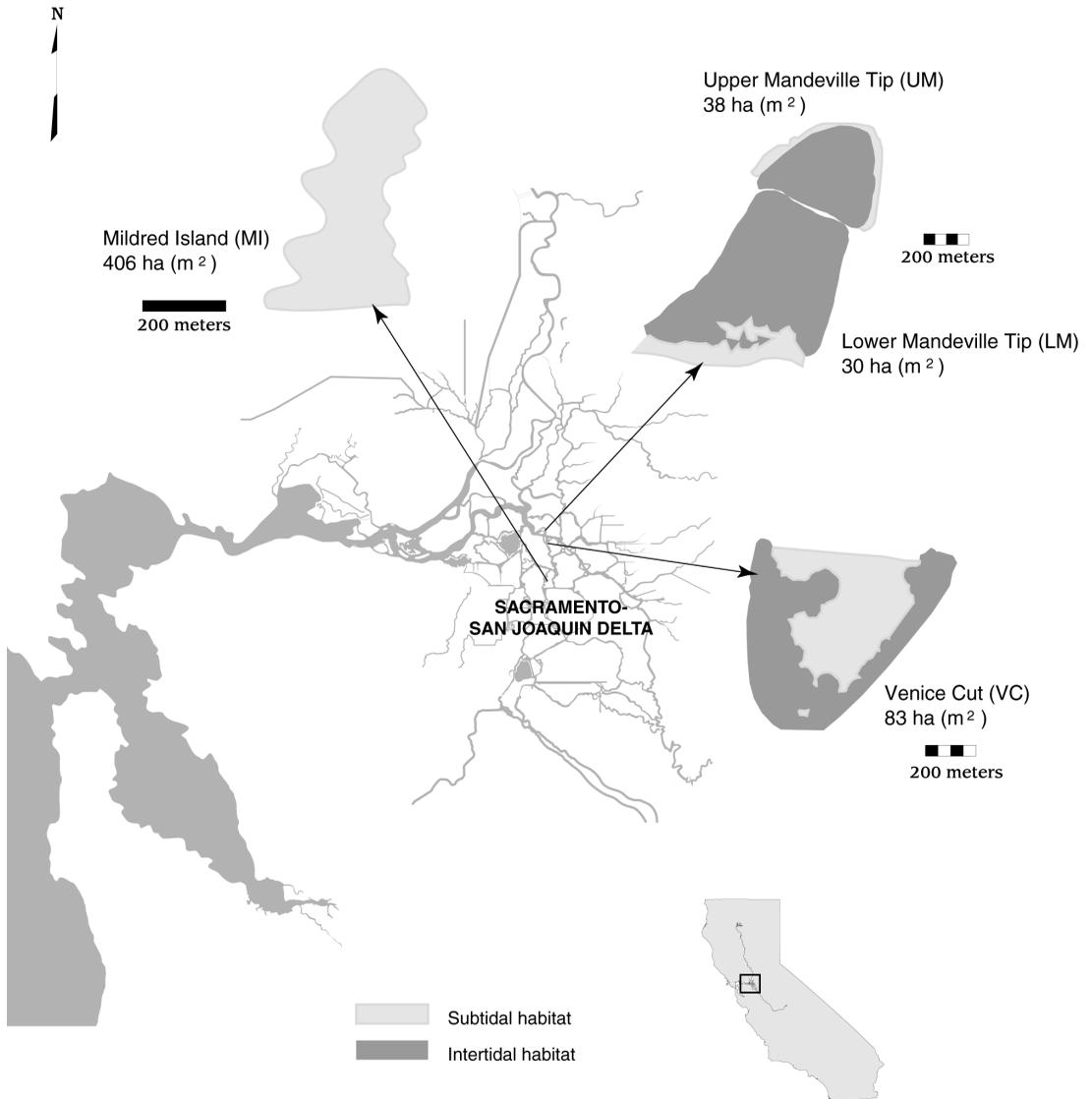
FIGURE 1. San Francisco Estuary and the four study sites located in the central Sacramento–San Joaquin Delta.

Methods

Field methods

Sampling planktonic organisms in shallow water can be challenging when using traditional stern-mounted towed nets because of submerged structures that can impair, clog, or foul the gear during tows (Cole and MacMillan 1984). To overcome this problem, we bridled a 4-m-long × 0.65-m-mouth-diameter ichthyo-plankton net (505 μm mesh) to a 2.5-m boom (aluminum rod). We deployed the net off the side of a boat using a bow-anchored rope for leverage (Figure 2). A zooplankton net (110 mm mesh), 1 m long with 1.5-m mouth opening, was attached directly to the outside frame of the ichthyoplankton net. Flowmeters were mounted across the opening of each net to determine the volume of water sampled per tow. The net was towed just below the water surface, and submerged objects were avoided by
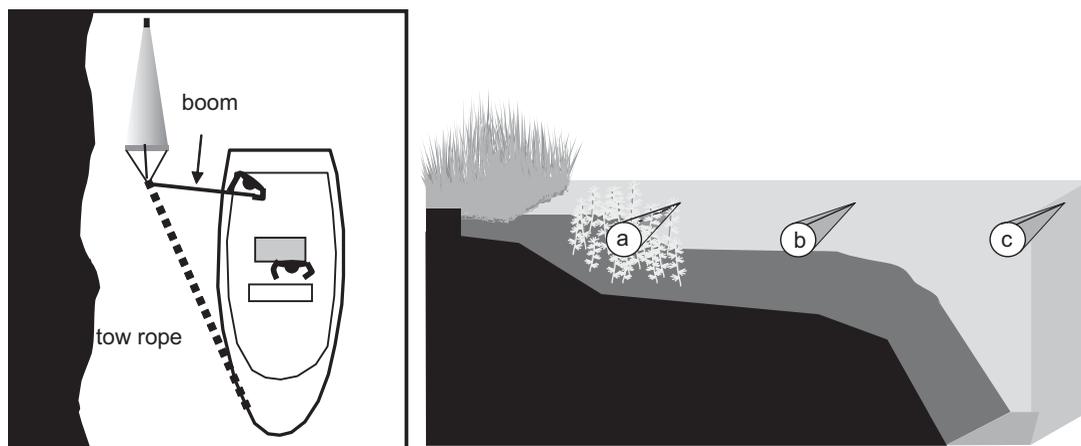
FIGURE 2. Diagram of side-towed ichthyoplankton net (505 mm mesh) and stylized cross-sectional diagram of subtidal sampling locations: (a) marsh edge, (b) shallow open-water, and (c) river channel.

manually maneuvering the boom. Ten-minute tows were conducted in each available habitat transect (marsh edge, shallow open-water, and river channel) per study site. Ichthyoplankton were sampled about one neap tide per month during April–August 1998 and two neap tides per month during January–July 1999. Zooplankton were sampled only one neap tide per month during May–June 1998 and March–June 1999. Water quality data were measured either before or after each tow. Water temperature (°C) and specific conductance (µS/cm) were measured just below the surface (~0.5 m) using a YSI 85. Water clarity (cm) was estimated using a Secchi disk. We estimated water depth (m) as the average of discrete measurements by a boat-mounted fatho-meter. Tows were done irrespective of tidal stage or time of day. All samples were individually preserved in a 10% formalin solution and transferred to the laboratory for identification to the lowest taxonomic level and life stage. The densities of larval fish and zooplankton were calculated as the number of organisms per volume (m^3) of water sampled.

We did not do any shallow open-water tows at UM because the marsh edge abruptly transitioned to the main channel. Further, we did not sample any of the channels surrounding MI because the site was almost entirely enclosed by a levee. We assumed that any substantial exchange of ichthyoplankton or zooplankton between MI and outside channels would occur mainly at the large northern breach and would affect only a small portion of the site. Rather, we focused our examination of ichthyoplankton and zooplankton variability within MI habitats and its northern and southern regions because these two areas had different hydrological and biological properties (Lucas et al. 2002).

Data analysis

Intercorrelations among physical variables were examined using Pearson product-moment correlation tests to potentially reduce the number of highly correlated predicator variables to a smaller number of uncorrelated variables. This analytical step ensures a more concise comparison of spatial and temporal dynamics between taxa and environmental data (Turner et al. 1994). One-way analysis of variance (ANOVA) was used to determine water column depth difference by habitat transect. Intersite and intermonth variation of each water quality variable (water temperature, specific conductance, and water clarity) was examined using two-way ANOVA tests. Intrayear trends between each variable and consecutive sample month were examined using Pearson product-moment correlation tests.

Multivariate analysis of covariance (MANCOVA) was used to test for significant

differences between the most abundant ichthyoplankton species (dependent variable) and three predicator variables: site, habitat type, and year. Water temperature (ºC), specific conductance (mS/cm), and water clarity (cm) were included in the model as covariates to test if ichthyoplankton abundance was influenced by water quality conditions at each habitat type. Interannual abundance differences were tested by including interaction terms in the MANCOVA model: (1) year × site, and (2) year × habitat type.

Monthly densities of native and alien fishes were plotted and visually examined for patterns. Ichthyoplankton and zooplankton densities were compared between north and south MI using parametric t-tests. Only fish species that contributed to 1% or more of the total relative abundance and occurred in 5% or more of the samples were used in statistical analyses. Since we did not sample zooplankton at the same frequency as fish larvae, we only analyzed the five dominant taxa of adult zooplankton to provide a general description of how potential prey abundances varied by habitat, site, and season (three-way ANOVA). Fish and zooplankton densities were natural log-transformed ($x + 1$) prior to all statistical tests to reduce heteroscedasticity in the data.

To examine taxa-specific densities in relation to water quality variables, the most abundant ichthyoplankton species were also subjected to canonical correspondence analysis (CCA) with the CANOCO software program (ter Braak and Smilauer 1998). Canonical correspondence analysis is a direct gradient analysis that is used to determine a taxon niche center (e.g., time and space) through calculation of weighted-average algorithms of abundance with environmental data (ter Braak and Verdonschot 1995). Niche separation among taxa is evaluated through examination of biplots, which depict extracted synthetic gradients (ordination axes) of species abundances and environmental variables (ter Braak and Verdonschot 1995). The environmental variables included in this analysis were habitat type, water temperature, specific conductance, Secchi depth, tide stage, and time of day.

Results

Environmental variables

Mean water column depths of marsh edge (1.60 m ± 0.50 SD), shallow open-water (3.11 m ± 1.20 SD), and river channel (10.17 m ± 3.11 SD) habitat types were significantly different ($P < 0.01$). Water temperature and Secchi disk depth varied significantly by month, but did not vary among habitat types (Figure 3). In 1999, specific conductance varied among habitat types and sample month. Both water temperature and specific conductance were significantly correlated with each consecutive sample month, $r^2 = 0.79$ ($P < 0.001$) and $r^2 = 0.45$ ($P < 0.001$), respectively. Secchi disk depth was not significantly correlated with consecutive sample month ($r^2 = 0.02$; $P > 0.05$). Water temperature and specific conductance were the only two variables significantly correlated with each other ($r^2 = 0.21$; $P < 0.01$). Since these variables were only weakly correlated and could both independently affect larval fish distribution, both were included in statistical models as potential predicator variables.

Ichthyoplankton

We collected 25,863 individual fish larvae in 240 tows (Table 1). Only six tows did not capture larvae, suggesting that the gear methodology provided high capture rates and adequate characterization of ichthyoplankton distributions. Most larvae were identified to species, except for centrarchids, which were identified to genus and pooled for statistical analyses. A few fish (78) could only be identified to the family Cyprinidae, while 9 other larvae could not be identified due to mutilation. Prickly sculpin *Cottus asper*, threadfin shad *Dorosoma petenense*, inland silverside *Menidia beryllina*, delta smelt *Hypomesus transpacificus*, bigscale logperch *Percina macrolepida*, striped bass *Morone saxatilis*, golden shiner *Notemigonus crysoleucas*, and centrarchid larvae accounted for 99% of the total number of fish larvae collected; these species and one family group were analyzed in MANCOVA and CCA analyses. All are alien species except for prickly sculpin and delta smelt. Approximately 6,700 embryos repre-
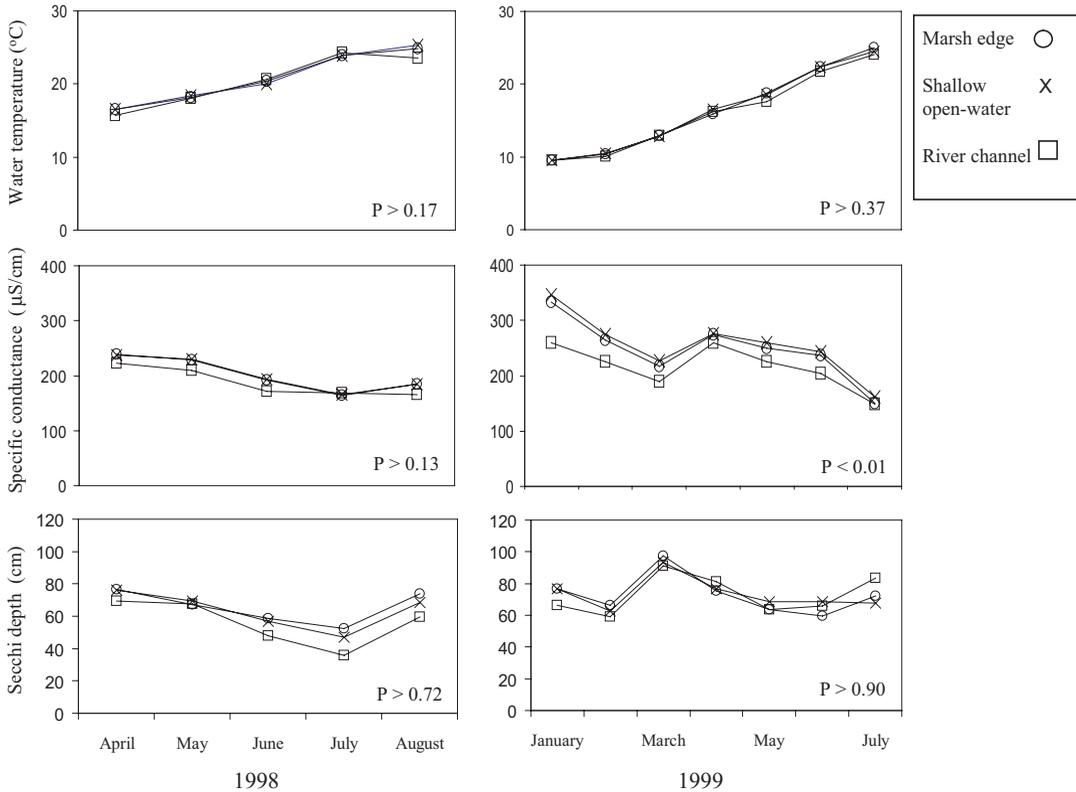
FIGURE 3. Mean values of physical variables by habitat type and month for each year. Significant differences among transects were tested using ANOVA models.

senting at least five species were collected during the study (Table 2); most of these embryos were threadfin shad collected at MI.

The MANCOVA model indicated that ichthyoplankton abundance varied significantly by habitat type ($P < 0.001$), site ($P < 0.001$), year ($P < 0.05$), and water temperature ($P < 0.001$). We did not detect a significant interaction effect between year and site ($P > 0.34$) or year and habitat type ($P > 0.46$), indicating consistent habitat-use by ichthyoplankton. Overall ichthyoplankton abundances varied between years, but this was expected given that we did not sample the same months each year. Although water temperature was indicated to have an effect on ichthyoplankton abundance, we interpret this effect to indicate intra-annual differences with respect to season, given that water temperature differed by month but not habitat type. Total ichthyoplankton abundance was highest in marsh edge habitat (Figure 4). Among sites, total abundance was highest at MI (Table 3). Within MI, the abundance of ichthyoplankton was significantly higher ($P < 0.05$) in the south (Figure 5). Seasonal abundance trends in ichthyoplankton were strongly patterned by recruitment peaks of native and alien fishes through the year (Figure 6). Generally, native fishes were more abundant during winter and spring, whereas alien fishes were generally more abundant during late summer. Golden shiner and bigscale logperch were the exception to this pattern, as they were most abundant during spring of both years.

The CCA indicated water temperature and habitat type were important variables influencing fish abundance (Figure 7). Early season recruits (prickly sculpin, delta smelt, golden shiner, and bigscale logperch) were located on the right side of canonical space, corresponding with low water temperatures and

TABLE 1. Frequency of occurrence (FO) and ranked summary of ichthyoplankton by total collected (*N*) during 240 tows between April 1998 and July 1999 in the Sacramento–San Joaquin Delta. Origin: A = Alien; N = native.

Taxa		Origin	FO (%)	*N*
Threadfin shad		A	43	11,822
Prickly sculpin		N	73	9,516
Centrarchidae[a]		A	32	2,260
Inland silversides		A	18	1,590
Delta smelt		N	24	216
Bigscale logperch		A	20	151
Striped bass		A	12	88
Cyprinidae		Unknown	9	78
Golden shiner		A	11	50
American shad	*Alosa sapidissima*	A	5	34
White catfish	*Ameiurus catus*	A	2	12
Sacramento blackfish	*Orthodon microlepidotus*	N	3	10
Unidentified			3	9
Splittail	*Pogonichthys macrolepidotus*	N	5	8
Shimofuri goby	*Tridentiger bifasciatus*	A	3	6
Wakasagi	*Hypomesus nipponensis*	A	5	4
Common carp	*Cyprinus carpio*	A	<1	3
Longfin smelt	*Spirinchus thaleichthys*	N	<2	1
Staghorn sculpin	*Leptocottus armatus*	N	<1	1
Goldfish	*Carassius auratus*	A	<1	1
Sacramento sucker	*Catostomus occidentalis*	N	<1	1
Total				25,863

[a] includes *Lepomis* spp., *Pomoxis* spp., and *Micropterus* spp.

high specific conductance. In contrast, summer recruits (inland silverside, threadfin shad, striped bass, and centrarchids) grouped in the opposite side of canonical space corresponding with high water temperatures and low specific conductance. Delta smelt was centered in the upper portion of the biplot corresponding with deep channel habitats. Inland silver-

TABLE 2. Summary of embryos collected between 1998 and 1999 in the Sacramento–San Joaquin Delta. Substrate codes indicate if embryos were unattached (U) or attached to either emergent vegetation (EV) or submerged aquatic vegetation (SAV). Site codes are VC = Venice Cut; UM = upper Mandeville Tip; LM = lower Mandeville Tip; and MI = Mildred Island.

| Common name	Months collected	Site	Habitat	Substrate	*N*
Common carp	June	VC	Shallow open water	U	11
Threadfin shad	late April–June	UM, MI	Marsh edge	EV, SAV	6,785
Inland silverside	May–June	MI, VC	Marsh edge	EV	30
Striped bass	May	LM	River channel	U	1
Unidentified cyprinidae	April	VC	Marsh edge	SAV	23
Unidentified	May–July	UM, MI, LM, VC	Marsh edge, shallow open water	EV, U	115
				Total	6,966
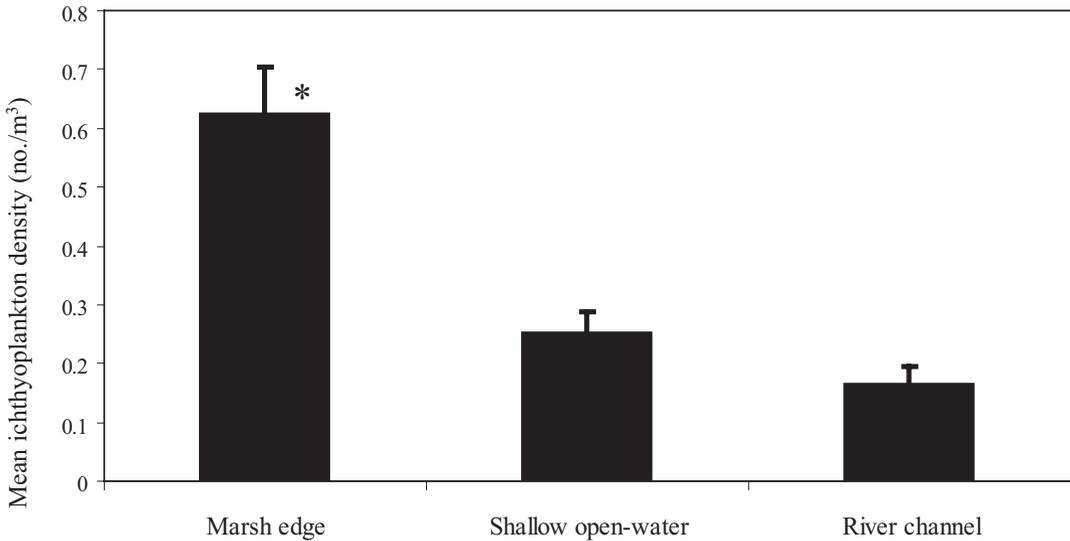
FIGURE 4. Mean ichthyoplankton abundance (±SE) by habitat type. Data were averaged from all sites sampled during 1998 and 1999. Asterisk indicates significant difference from other groups by one-way ANOVA ($P < 0.05$).

side, centrarchids, prickly sculpin, threadfin shad, and bigscale logperch were centered more towards the lower region of the biplot corresponding to nearshore transects (edge and shallow open-water habitats).

Zooplankton

The most common zooplankton groups collected were calanoid copepods and cladocerans. Of the calanoids collected, adult *Eurytemora affinis* was significantly ($P < 0.001$) more abundant in marsh edge habitat and during late spring (i.e., April and May). Abundance of adult *Pseudodiaptomus forbesi* did not vary significantly among habitat types ($P > 0.40$) but was significantly more abundant during June ($P < 0.001$; Figure 8). Another calanoid, *Sinocalanus doerrii*, did not vary by habitat type ($P > 0.23$) or month ($P > 0.21$). Of the cladocerans, *Daphnia* spp. were more abundant in channel habitat and during late spring. *Bosmina* spp. abundance did not vary among habitats, but they were higher during late spring as well. Overall, zooplankton abundance did not differ among habitat types ($P > 0.30$) but was highest at MI compared to the other study sites ($P < 0.05$). Abundance in MI did not differ be-

tween the northern and southern regions (Figure 5).

Discussion

Although estuarine environments are complex, many researchers have documented estuarine organisms aggregating within plume fronts (Govoni et al. 1989), during certain tidal stages (Melville-Smith et al. 1981; Drake and Arias 1991; Joyeux 1999), and vertically throughout the water column (Laprise and Dodson 1989b; Kimmerer et al. 1998; Bennett et al. 2002). In this study, we found that ichthyoplankton abundance and composition differed among subtidal horizontal transects. Specifically, we found that marsh edge habitats supported higher abundances of most fishes, suggesting that they provided favorable rearing conditions. Because the habitat use results were consistent between years, we believe that the results are robust and reflect strategic life history traits. For example, marsh edge habitats potentially are favorable rearing habitats because they typically support high prey abundances (Cardinale et al. 1998) and provide cover from predators (Crowder and Cooper 1982; Rozas and Odum 1988).

TABLE 3. Mean densities of the eight most abundant ichthyoplankton taxa by site and habitat transect between April 1998 and July 1999. Mean densities (no./m^3 * 100). Individual ichthyoplankton densities were significantly different by wetland site and habitat type (MANCOVA; $P < 0.05$). The average density for all eight fishes by wetland site were examined using one-way ANOVA.

	Upper Mandeville Tip		Venice Cut			Lower Mandeville Tip			Mildred Island		P-value
	Marsh edge	River channel	Marsh edge	Shallow open-water	River channel	Marsh edge	Shallow open-water	River channel	Marsh edge	Shallow open-water	
Bigscale logperch	0.53	0.03	2.73	0.02	0.04	0.81	0.05	0.00	0.75	0.08	
Centrarchidae	0.44	0.09	4.78	0.59	0.00	0.93	0.26	0.16	17.12	1.33	
Delta smelt	0.40	0.20	0.50	0.91	1.08	0.32	0.34	2.37	0.18	0.09	
Golden shiner	0.22	0.14	0.91	0.03	0.24	0.76	0.23	0.15	0.07	0.00	
Inland silverside	4.15	0.08	15.14	0.02	0.10	1.63	0.00	0.04	9.50	0.05	
Prickly sculpin	6.32	3.82	30.68	15.41	17.71	21.90	11.93	10.76	28.77	10.55	
Striped bass	0.02	0.00	0.11	0.49	0.21	0.23	0.38	0.50	0.08	0.17	
Threadfin shad	12.82	9.24	7.56	8.62	2.00	13.33	4.03	1.64	48.41	18.47	
Average density per site	19.62		39.40			26.05			68.98		<0.001

Mildred Island

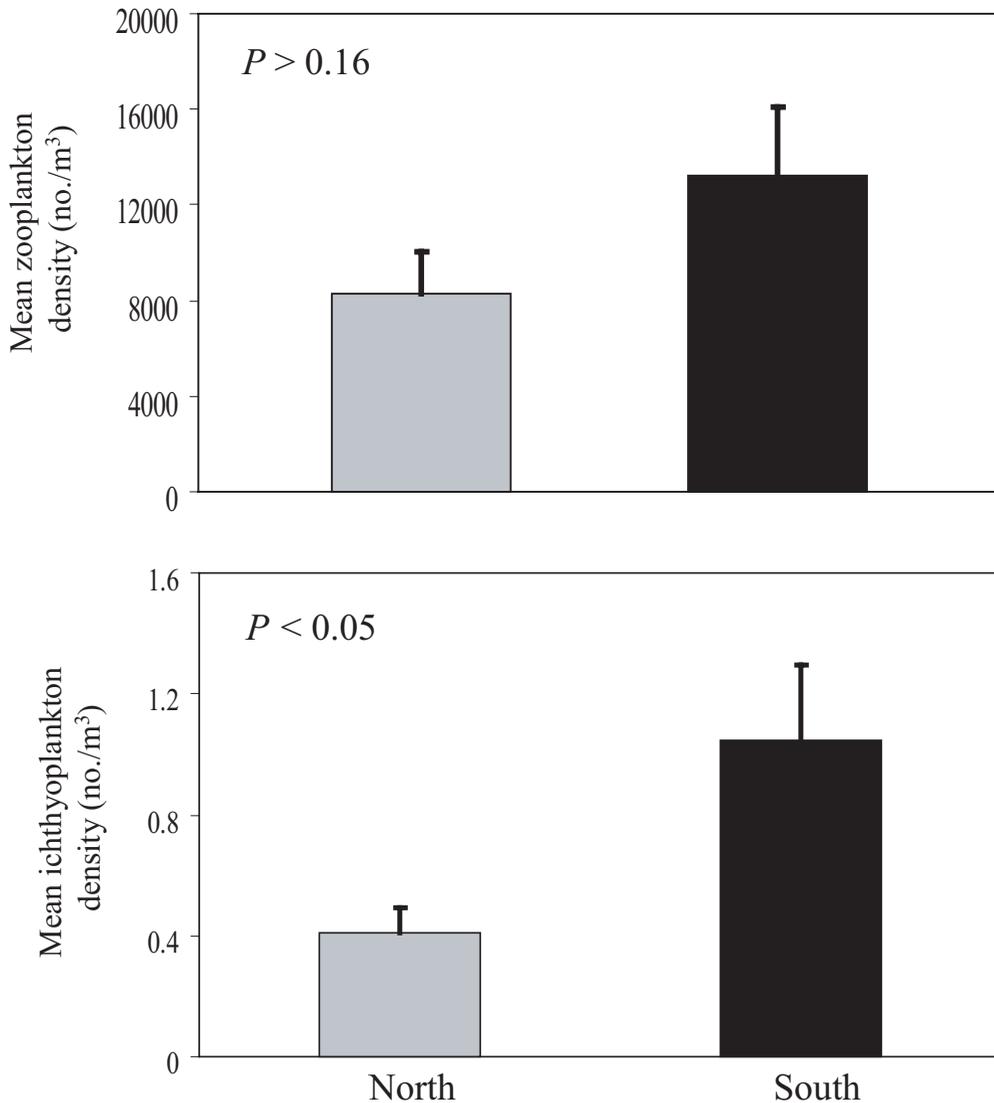

FIGURE 5. Comparisons between mean densities (±SE) of zooplankton (top) and ichthyoplankton (bottom) in southern and northern Mildred Island combined from 1998 and 1999. Significance ($P < 0.05$) was determined using Student's t-tests.

Others have documented the importance of edge habitats for larval fishes in other ecosystems (Paller 1987; Dewey and Jennings 1992).

We found a strong parallel between ichthyoplankton distributions documented in this study with distribution of juvenile and adult fishes observed in a companion inshore–offshore investigation (authors' unpublished data). Specifically, we found that the marsh edge supported a distinct group of resident larvae belonging to many of the same species that were observed in these habitats as juveniles and adults. The most prominent members of this marsh edge assemblage were centrarchids, which are often key members of edge habitats in other aquatic ecosystems
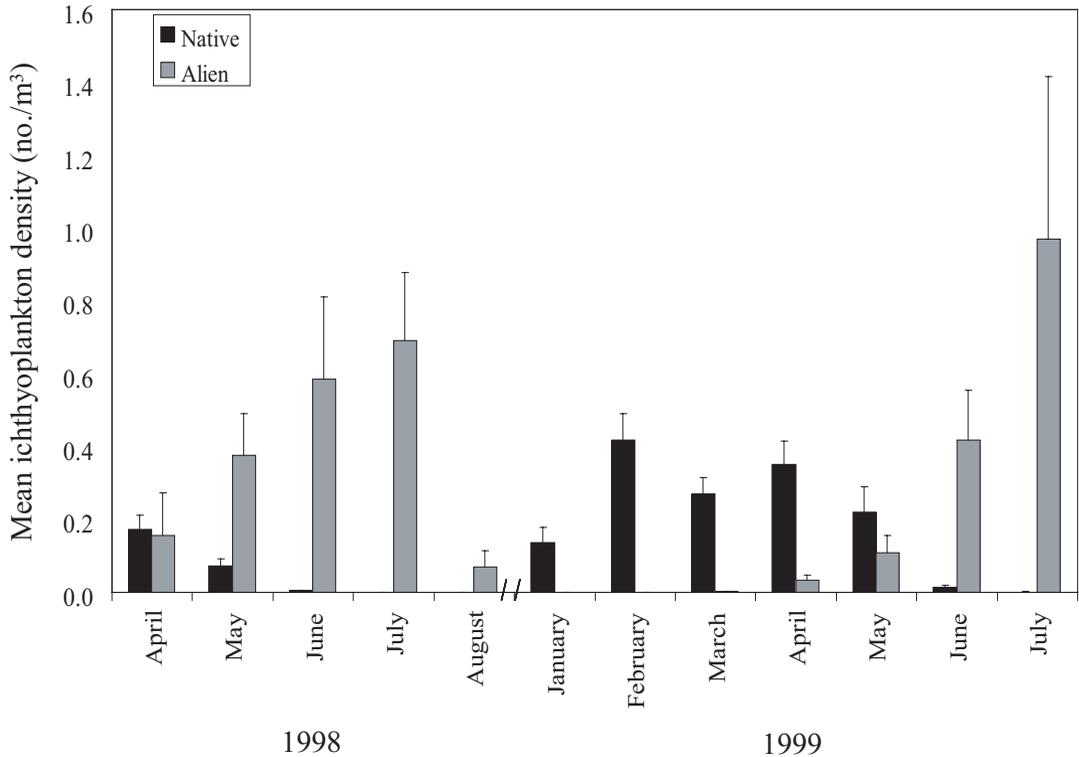
FIGURE 6. Mean densities (±SE) of native and alien fishes by month during the study period.

(Crowder and Cooper 1982; Paller 1987; Rozas and Odum 1987; Killgore et al. 1989; Dewey and Jennings 1992; Cardinale et al. 1998; Johnson and Jennings 1998). Larvae of resident fishes, such as bigscale logperch, golden shiner, and inland silverside, were also very abundant in marsh edge habitat, but the juvenile stages of these fishes were most often found in nearshore unvegetated habitats. In contrast, juvenile centrarchids were mostly found within dense SAV beds (authors' unpublished data). We could not examine the question as to whether the interior of dense SAV exhibited higher or lower densities of this edge-associated fauna. Paller (1987) found that centrarchids were more abundant in SAV compared to the edge ecotone.

The marsh edge may also serve as important transitional habitat for many pelagic and demersal fishes. For example, we found that high larval threadfin shad densities and many of their embryos attached to vegetation in the edge transects. As juveniles and adults, threadfin shad are most abundant in offshore areas

(authors' unpublished data), indicating they move from nearshore to offshore habitats during the larval–juvenile transition phase. This observed ontogenetic shift indicates a strong dependence on marsh edge habitats, which provide both spawning substrate and rearing habitat for threadfin shad. Benthic fishes, such as native prickly sculpin larvae, were also more abundant in marsh edge compared to open shallow-water and river channel. This finding could indicate a sampling bias, particularly in the river channel areas where a smaller proportion of the water column was sampled (i.e., only the surface) compared to open shallow-water and marsh edge habitats. However, because prickly sculpin larvae are planktonic (Wang 1986) and juveniles are found in SAV (authors' unpublished data), our results suggest that marsh edge habitats are important presettlement aggregation zones for this species.

The abundance of native migratory larval fishes (delta smelt and splittail) varied between years. This was expected given that
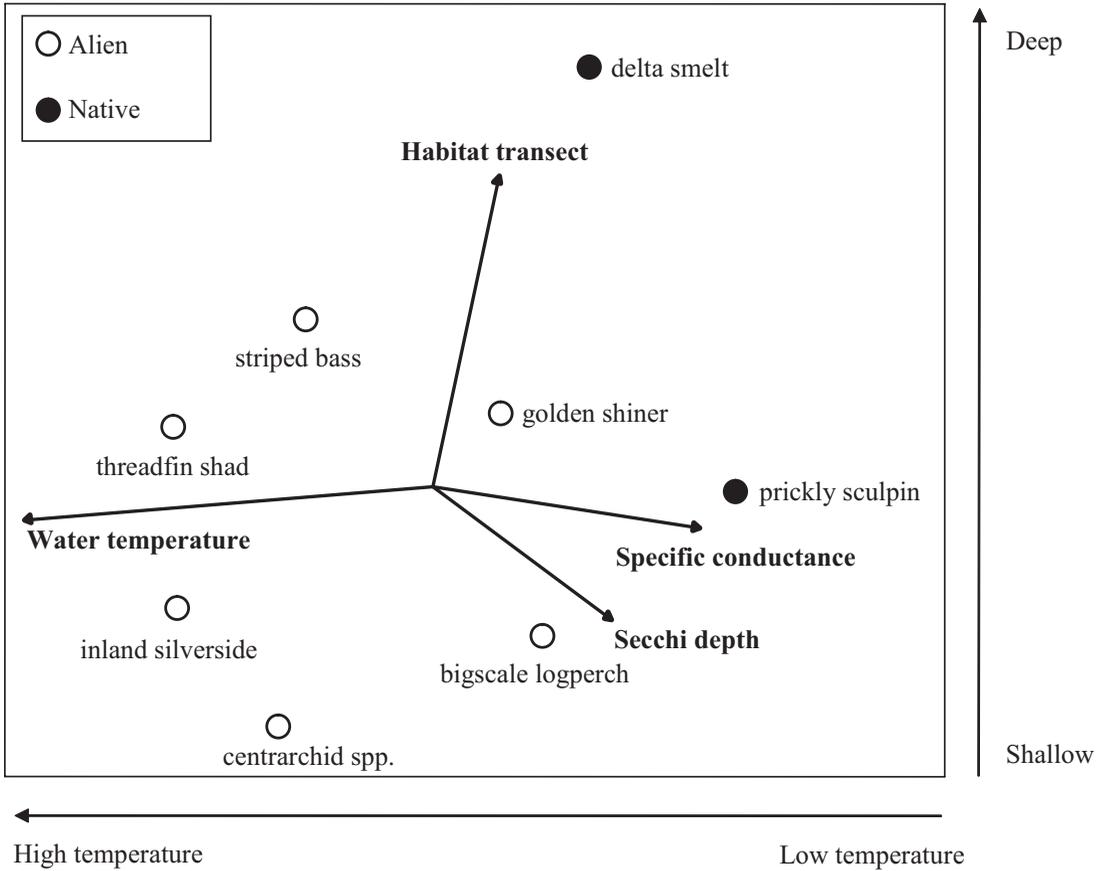
FIGURE 7. Canonical correspondence analysis (CCA) plot of important environmental correlation vectors and species scores in the first two CCA dimensions for the eight most abundant fish species collected.

mechanisms influencing recruitment of these fishes have been found to vary inter-annually and with upstream conditions (Sommer et al. 1997). Splittail larvae, for example, was primarily observed during 1998. In contrast, delta smelt larvae were present in 52% of tows (*N* = 92) during March–May 1999 compared to only 20% of tows (*N* = 30) during the same time period in 1998. Delta smelt is primarily an annual species that spawns in tidal freshwater habitats, migrating from the lower estuary to upstream habitats during spring (Moyle et al. 1992). During 1999, California Department of Fish and Game monitoring surveys revealed that adult delta smelt spawning was concentrated in the same geographic region as our study sites (Dege and Brown 2004, this volume). We did not collect any delta smelt embryos to verify spawning

microhabitat; however, we did find that delta smelt larvae were most abundant in river channel habitat, the only fish other than striped bass to exhibit such a distribution pattern. Residing in channels and using tidal currents may be an important strategy to transport delta smelt downstream to optimal rearing habitats.

Natural and restored wetlands

Given that ichthyoplankton densities at the natural site were low and mostly dominated by alien fishes, our results suggest that the natural site offers little suitable habitat for native fishes. It was our expectation that the natural site would provide habitats with natural conditions; however, it became evident during the study that natural conditions
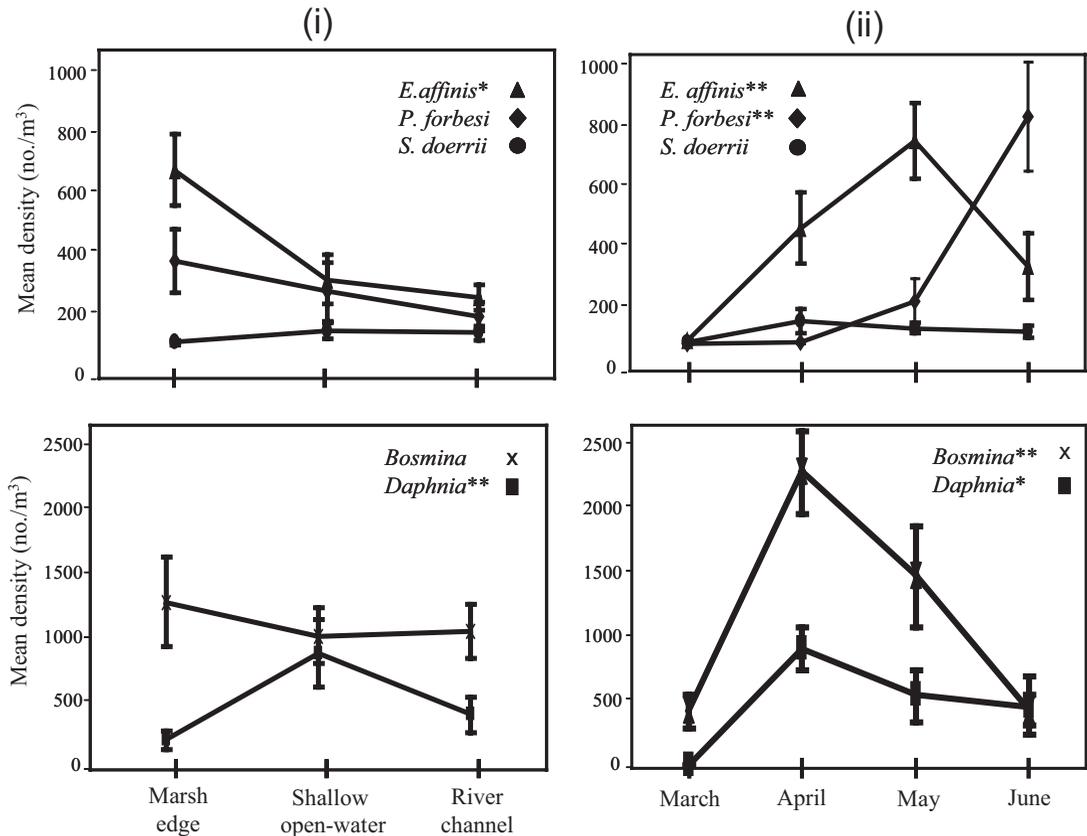
FIGURE 8. Mean densities (±SE) of adult calanoid copepods and cladocerans by habitat type (i) and month (ii). Data were averaged for 1998 and 1999. Significant differences of individual taxa by month and habitat are denoted in the figure legend: * = $P < 0.05$, ** = $P < 0.001$.

might have been altered by the extensive colonization of *E. densa* in the subtidal regions of this study site. Evidence from the juvenile fish study (authors' unpublished data) indicates that UM supports a large number of alien fishes. We suggest that centrarchids limit the number of native fish in the area, largely through predatory influences.

Among restored sites, ichthyoplankton abundances were similarly low at VC and LM and highest at MI. We suspect that two key mechanisms are responsible for these findings. First, MI supported enhanced lower trophic conditions, such as higher zooplankton abundances (this study) and high zooplankton growth rates (Mueller-Solger et al. 2002). These conditions likely promoted larval recruitment success. Second, larvae were probably more aggregated in MI compared to LM and VC because MI has only one large

breach where ichthyoplankton can be exchanged tidally with outside channels (Lucas et al. 2002). Our results provide some support of this hypothesis as we found higher ichthyoplankton abundance in the southern region of MI, which experiences minimal tidal exchange influence (Lucas et al. 2002). In contrast, VC and LM were more open to main channels (i.e., had fewer intact levees) and supported similar ichthyoplankton assemblages. Because the subtidal regions of VC and LM were much shallower than those of MI, these areas were colonized more extensively by *E. densa*. As a result, we believe that we may have underestimated the numbers and perhaps composition of larvae at these sites, particularly of some centrarchids, since they are often found at higher densities within SAV compared to the edge (Paller 1987).

Seasonal abundance patterns

The recruitment patterns exhibited by ichthyoplankton during our study period are consistent with those observed in other investigations conducted in the San Francisco Estuary (Meng and Matern 2001; Feyrer 2004, this volume) and nearby adjoining regions (Rockriver 1998; Marchetti and Moyle 2000; Sommer et al. 2004, this volume). In particular, our results substantiate the previous observations that larvae of native fishes are early season recruits compared to larvae of alien fishes, which were more common during summer. The recruitment pattern differences are likely initiated by environmental conditions meant to cue adult spawning migrations or maximize larval success after hatching. For example, splittail year-class strength has been found to be positively linked with winter and spring inundation of upstream floodplain habitats (Sommer et al. 1997). For other native fishes, increased river flows are believed to provide optimal rearing conditions (Meng et al. 1994; Jassby et al. 1995; Rockriver 1998; Marchetti and Moyle 2000; Meng and Matern 2001).

Our results suggest that the bioenergetics and agents of larval mortality (e.g., competition and predation) vary between native and alien fishes, since trends in water quality parameters and zooplankton assemblages vary seasonally. For example, we documented that *E. affinis*, the main diet item of delta smelt (Nobriga 2002), was most abundant during spring coincident with the presence of delta smelt larvae. This suggests that survival of delta smelt larvae may depend upon *E. affinis* densities and growth may depend on water temperature in spring. In contrast, recruitment of many alien fishes hinges on densities of zooplankton common in the summer, mainly *P. forbesi*, and summer conditions, such as elevated water temperatures or low flow conditions.

Restoration opportunities

Whether native fishes can benefit through habitat restoration in this region of the delta remains in doubt given that alien fishes were found among all habitat types and sites. We argue that the best restoration strategy may be to create or restore wetlands that only flood during winter and spring, the period when native fishes spawn and recruit in the estuary. This strategy may not eliminate use by alien fishes altogether, but it may limit their use on a perennial basis, thereby limiting spawning or recruit success. Clearly, the need to understand the underlying mechanisms governing both native and alien recruitment is warranted given the strong impetus to restore wetlands in the estuary (CALFED 2000).

Acknowledgments

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