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Ecological Segregation of Native and Alien Larval Fish Assemblages in the Southern Sacramento–San Joaquin Delta

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Abstract.—Fish larvae were sampled at multiple fixed sites from late winter to early summer over 6 years (1990–1995) in the southern Sacramento–San Joaquin Delta. A total of 394,797 fish larvae representing 15 species or taxonomic groups was collected. The assemblage was numerically dominated by three species that represented 98% of the total catch: alien shimofuri goby *Tridentiger bifasciatus* (71%), threadfin shad *Dorosoma petenense* (15%), and native prickly sculpin *Cottus asper* (12%). The abundance of native and alien species differentially clustered along environmental gradients of water temperature and river flow. Each native species (prickly sculpin, splittail *Pogonichthys macrolepidotus*, delta smelt *Hypomesus transpacificus*, longfin smelt *Spirinchus thaleichthys*, and Sacramento sucker *Catostomus occidentalis*) and one alien species (bigscale logperch *Percina macrolepida*) were associated with the early season conditions of cool water temperature and high river flow. Alien species (especially shimofuri goby, threadfin shad, and ictalurid catfishes) were associated with late season conditions of relatively warm water temperature and low river flow. Accordingly, native species dominated the assemblage February–March, while alien species dominated May–July. However, peak seasonal abundance of alien species was typically five times greater than that of native species. Seasonal succession of assemblage structure was persistent among years and was highly correlated with water temperature, a likely result of the differential spawning requirements of adult fishes. Interannually, the assemblage remained consistent over the study period despite considerable variability in delta inflow. I hypothesize, given the consistent temporal segregation between native and alien larval fish assemblages, that direct interactions such as competition between the two groups may not be a major factor influencing poor native fish recruitment in the south delta.

Introduction

Larval fish assemblages often exhibit temporal stability (i.e., consistent phenological appearances of species) typically because of differing environmental requirements for the spawning of adult fishes or due to environmental conditions that influence recruitment of larvae in certain geographic locations (Powles et al. 1984; Yoklavich et al. 1992; Keller et al. 1999; Witting et al. 1999; Lazzari 2001). Such chronology in appearance of larval fishes can influence the partitioning of resources and interactions among species. Given the threats associated with alien species and the desire to maintain native fish assemblages, understanding the ecological interactions between native and alien fishes is a rapidly growing area of interest (Moyle 1986; Ross 1991). Within the San Francisco Estuary, recent studies in an upstream tributary (Marchetti and Moyle 2000) and a downstream marsh (Meng and Matern 2001) have demonstrated a phenological separation between assemblages of native and alien larval fishes; native larvae typically appear earlier in the year than aliens. The princi-

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pal factors believed to be driving these observations were the influence of water temperature and river flow on timing of adult fish spawning (Marchetti and Moyle 2000; Meng and Matern 2001).

Poor recruitment of native fishes during early life stages has been identified as one potential mechanism limiting their abundance in the Sacramento–San Joaquin Delta (Bennett and Moyle 1996). Recruitment success is dependent upon survival rates, which can be influenced by biotic and abiotic factors (Houde 1987; Harvey 1991; Letcher et al. 1996). If the seasonal succession of native and alien fish larvae in the south delta is similarly segregated, as has been observed in other regions of the system, then potential for direct interactions, such as competition between the two groups, may be limited in time and thus may not strongly influence recruitment of native fishes.

In this paper, I present results of a 6-year ichthyoplankton study conducted in the southern delta. The study was initiated to describe larval fish assemblages in the south delta and to evaluate impacts of large-scale water diversions by the State Water Project (SWP) and Central Valley Project (CVP), state and federal facilities that divert water from the system for agricultural and municipal consumption. The present analysis focused on describing larval fish assemblages of the south delta with an emphasis on the ecological associations of native and alien species. My goals were to evaluate the status of native fish reproduction in the south delta, as determined by the presence of larvae, and to evaluate the extent of spatial and temporal co-occurrence between native and alien species. I addressed the following specific questions: (1) what species comprise the larval fish assemblage in the south delta? (2) are there associations among species and environmental variables? and (3) are there persistent temporal and spatial patterns of assemblage structure?

Study Area

The Sacramento–San Joaquin Delta (Figure 1), located upstream of the confluence of the Sacramento and San Joaquin rivers, consists of more than 1,000 km of waterways with a drainage area encompassing approximately 40% of California's surface area (Nichols et al. 1986). During peak diversions, up to 65% of the delta's natural discharge is diverted for agricultural and municipal consumption (Nichols et al. 1986). The majority of this water (up to 73×10^8 m^3/year) is diverted at large pumping facilities in the south delta by the SWP and CVP. The south delta is arguably the most degraded region of the system due to altered physical habitat, hydrodynamics, and water quality associated with the water project facilities and flood control projects (Arthur et al. 1996). Similar to other locations with highly altered habitats (Ross 1991), the adult fish fauna of the south delta is numerically dominated by alien species (Feyrer and Healey 2003).

Fish larvae were sampled at seven sites in the south delta: four sites in Old River and one site each in Grant Line Canal, Salmon Slough, and Victoria Canal (Figure 1). These waterways, referred to locally as sloughs, are approximately 1–5 m in depth, tidally influenced, and are constricted within flood control levees. Rock-reinforced banks (riprap) dominate riparian habitats, and alien submerged aquatic vegetation, primarily Brazilian waterweed *Egeria densa*, is prevalent in the shallow littoral zone; only remnants of natural wetland riparian habitats exist. The primary source of freshwater for the south delta is the San Joaquin River. Agriculture is the dominant land use activity beyond channel levees, and hundreds of small local agricultural diversion facilities are scattered throughout the region.

Methods

Data collection

Fish larvae were sampled during daylight hours approximately 3 d per week from April to July 1990 and 5 d per week from February to July 1991–1995. A 10-min oblique tow with a 505-μm-mesh net mounted on a towing sled was conducted at each site. The net measured 1.5 m in length and had a 0.4-m mouth diameter. A 1,000-mL plastic collecting jar, screened with 470-μm-mesh bolting cloth, was attached to the net to collect samples. A flowmeter was attached to the net frame to measure the volume of water filtered during a tow. After each tow, samples were rinsed into the collecting

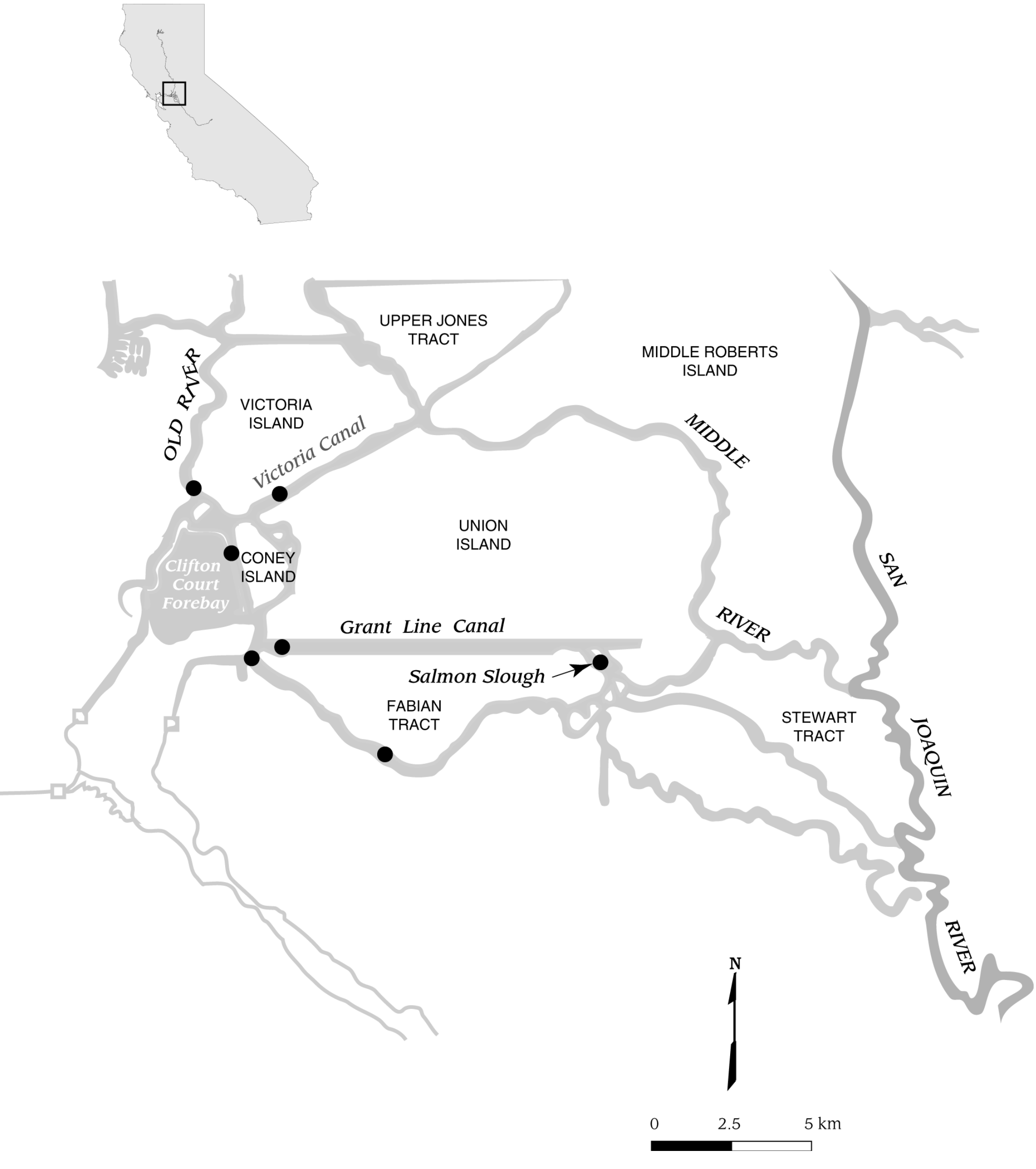

FIGURE 1. Larval fish sampling sites in the southern Sacramento–San Joaquin Delta.

jar, preserved in 5% formalin, and stained with rose-bengal dye. In the laboratory, samples were rinsed with water through a 300-mm-mesh sieve and sorted under a magnifying illuminator, and all fish larvae were identified to species or species groupings (Table 1) following the keys in Wang (1986).

Three environmental variables were measured at the time of sampling: specific conductance (μS) was estimated using a portable conductivity meter, water temperature (°C) was measured with a mercury thermometer, and water transparency (cm) was measured with a Secchi disk. Estimates of tidally averaged daily flow (m^3/s) at each site were obtained from the California Department of Water Resources' CALSIM Hydrology Model. Raw data from this study are available online from the

TABLE 1. Species (asterisk indicates native status) or taxonomic groupings, code, total number, percent number (if greater than 1%), and percent occurrence in samples of larval fishes captured in the south delta.

Taxa	Code	Number (%)	% samples
Shimofuri goby *Tridentiger bifasciatus*	SG	280,461 (71)	65
Threadfin shad *Dorosoma petenense*	TS	60,994 (15)	54
Prickly sculpin *Cottus asper**	PS	46,926 (12)	53
Striped bass *Morone saxatilis*	SB	3,153 (1)	36
Centrarchidae	CNT	979	18
Cyprinidae (other than splittail)	CYP	703	16
Bigscale logperch *Percina macrolepida*	BL	568	17
Ictaluridae	ICT	320	5
Inland silverside *Menidia beryllina*	IS	260	7
Splittail *Pogonichthys macrolepidotus**	ST	201	5
Delta smelt *Hypomesus transpacificus**	DS	74	4
American shad *Alosa sapidissima*	AS	65	<1
Sacramento sucker *Catostomus occidentalis**	SS	47	2
Longfin smelt *Spirinchus thaleichthys**	LS	31	2
Yellowfin goby *Acanthogobius flavimanus*	YG	15	<1

Interagency Ecological Program website at http://iep.water.ca.gov.

Data analysis

I used canonical correspondence analysis (CCA) to examine the association of larval fish densities ($\log_{10}[x/m^3 + 1]$) with environmental variables (Legendre and Legendre 2000). CCA is a multivariate direct ordination technique that extracts synthetic environmental gradients that maximize niche separation within species assemblages, thereby facilitating the interpretation of how species abundances relate to environmental variables. CCA was conducted with CANOCO software program (ter Braak and Smilauer 1998). I excluded two species, American shad and yellowfin goby, from this analysis because they occurred in less than 1% of the total samples (N = 1,436 samples with fish larvae). The final model was constrained to only include environmental variables significant at $P < 0.05$, as estimated by the forward selection procedure with Monte Carlo simulations (199 permutations) provided by CANOCO (ter Braak and Smilauer 1998).

I used detrended correspondence analysis (DCA) to investigate spatial and temporal variation in assemblage structure, with the same species matrix used in the CCA. DCA is an indirect eigenvector ordination technique based upon reciprocal averaging that corrects for the "arch effect" observed in reciprocal averaging (Gauch 1982; Legendre and Le-gendre 2000). Inferred primary gradients within assemblages are effectively displayed by DCA (Gauch 1982). Sample and species scores were generated with CANOCO software program (ter Braak and Smilauer 1998). DCA sample scores were subjected to an analysis of variance (ANOVA) procedure with site, month, year, and their interactions as factors. This procedure was used to partition the amount of variance accounted for by each of these variables, not to test for significant differences because replicate samples were not obtained at each site. Factor variance components were derived from expected mean squares based on a fixed effects ANOVA. This procedure allowed me to evaluate whether the spatial (site) or temporal (month and year) effects on assemblage structure were important alone or if they interacted. DCA sample scores were also sorted in numerous ways, and resulting plots were visually inspected for patterns. Detrending by segments was incorporated, and therefore only scores along axis I of the plots were interpreted as ecologically meaningful (Legendre and Legendre 2000). I used Pearson product-moment correlations to examine the relationship between DCA axis I sample scores and environmental variables.

Results

Environmental conditions

Among the environmental variables, river flow varied most among sites (Figure 2). Lowest flows occurred at the southernmost Old River site, Middle River, and Salmon Slough, while highest flows occurred at Grant Line Canal and the other Old River sites. Seasonally, river flows were highest February–April and lowest May–July. Only the southernmost Old River site exhibited almost no seasonal variation in river flow. Specific conductance was seasonally consistent, but slightly higher at the southernmost Old River, Grant Line Canal, and Salmon Slough sites (800–1,000 mS) than at Victoria Canal and the other Old River sites (400–600mS). Water temperature increased with month and was very consistent among sites, ranging from approximately 12°C in February to 22°C in July. Secchi depth consistently ranged between 40 and 80 cm across months and sites.

Catch summary

Over the study period, 394,797 fish larvae representing 15 species or taxonomic groups were collected (Table 1). The assemblage was numerically dominated by three species that represented 98% of the total catch: alien shimofuri goby (71%), threadfin shad (15%), and native prickly sculpin (12%). Alien striped bass was

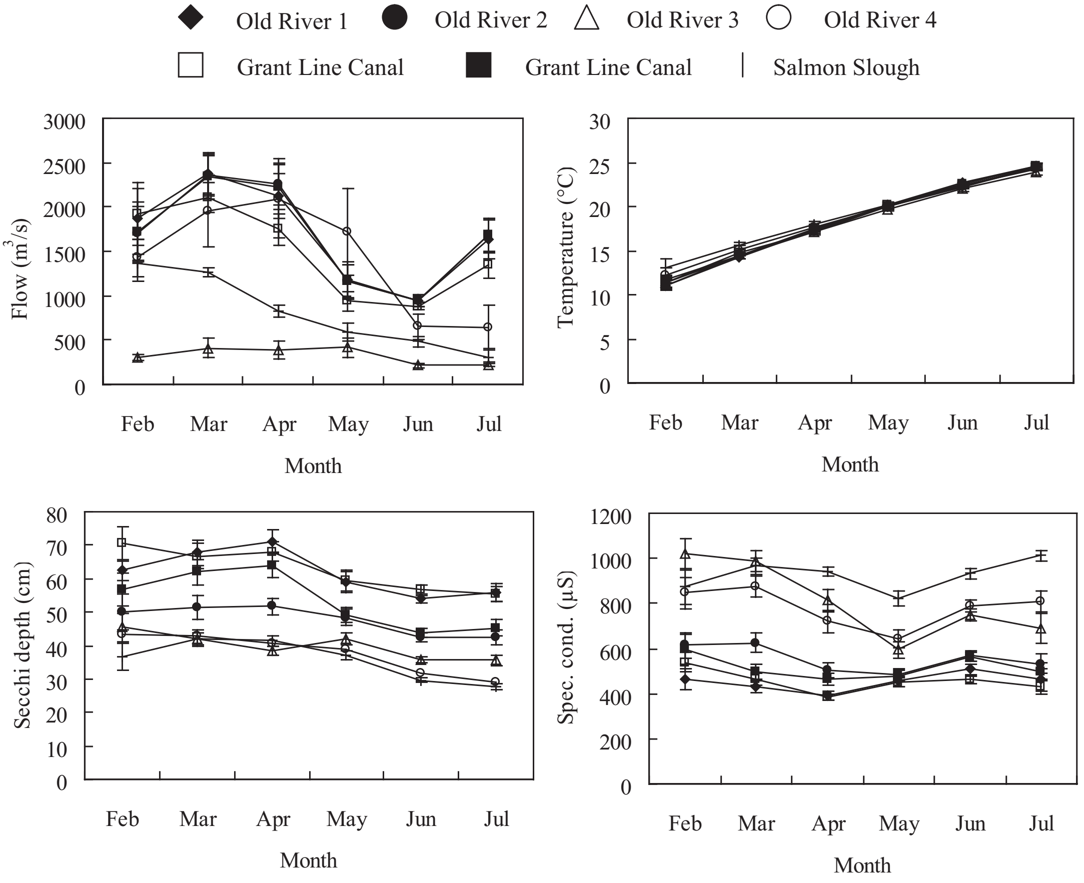

FIGURE 2. Mean monthly values (±SE) for environmental variables at each site in the south delta, 1990–1995. Old River sites are are numbered from north to south.

the only other species that represented at least 1% of the total catch. Seasonally, native species dominated the assemblage early in the year (February–April) while alien species dominated late in the year (May–July; Figure 3). However, peak seasonal abundance of native species was typically five times lower than that of alien species.

Associations among species and environmental variables

The forward selection procedure retained all four environmental variables in the final CCA model. The first two CCA axes explained 20% of the variation in species abundance (19% and 1%, respectively; Table 2). The influence of all four environmental variables on species abundances was depicted in a CCA ordination diagram (Figure 4). Native and alien species differentially clustered along environmental gradients of water temperature and river flow. Each native species (prickly sculpin, splittail, delta smelt, longfin smelt, and Sacramento sucker) and one alien species (bigscale logperch) were associated with the early season conditions of cool water temperature and high river flow. Alien species (especially

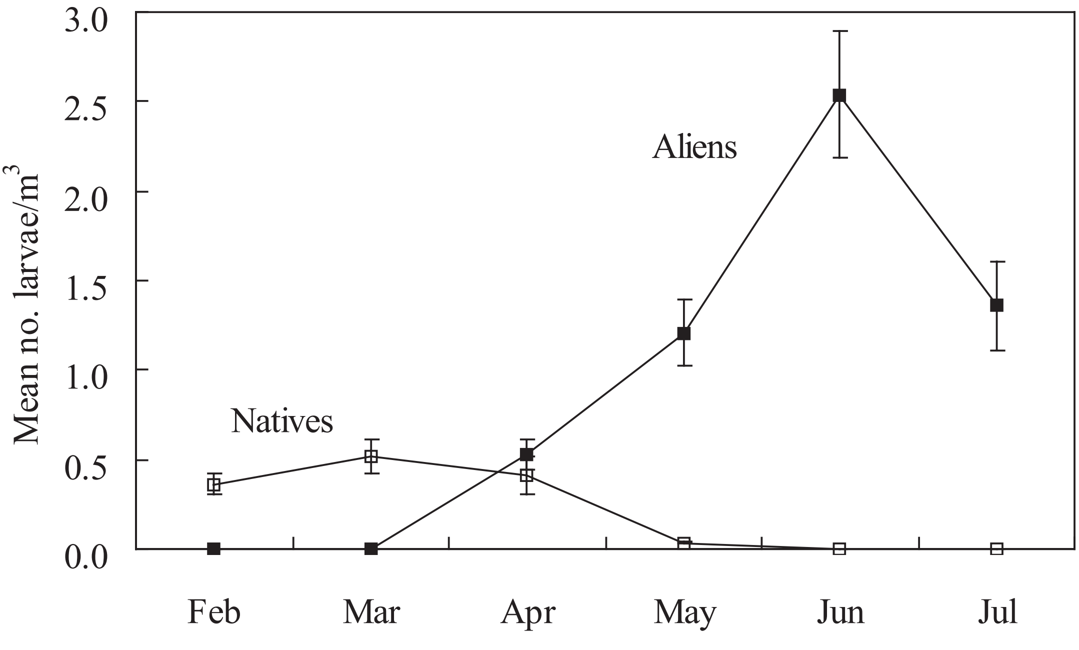

FIGURE 3. Mean monthly densities (±SE) of native and alien fish larvae in the south delta, 1990–1995.

TABLE 2. Results of a canonical correspondence analysis relating larval fish densitities to environmental variables in the south delta. Total inertia = 3.07.

	Axis 1	Axis 2
Eigenvalue	0.594	0.033
Species-environment correlation	0.838	0.308
Cumulative percentage of variance explained		
Species	19.4	20.4
Species-environment relation	91.1	96.2

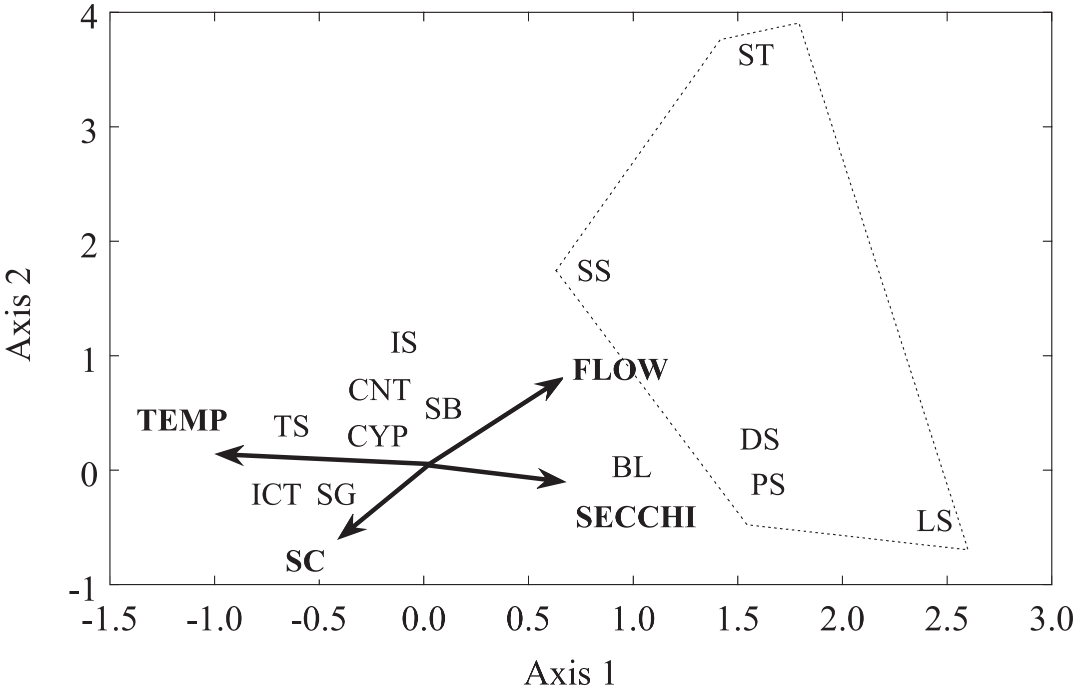

FIGURE 4. Ordination diagram showing results of canonical correspondence analysis depicting how larval fish abundances related to environmental variables in the south delta. Species codes are presented in Table 1. Environmental variables are given in bold: TEMP = water temperature, SC = specific conductance, FLOW = river flow, SECCHI = Secchi depth. Native species are enclosed by the polygon.

shimofuri goby, threadfin shad, and ictalurid catfishes) were associated with late season conditions of relatively warm water temperature and low river flow.

Spatial and temporal variation in assemblage structure

The first DCA axis explained 27.8% of the variance (eigenvalue = 0.85) in the larval fish assemblage matrix (Figure 5). Results of the ANOVA variance partitioning technique suggested that month accounted for the greatest proportion of variance (80%) in assemblage structure (Table 3). None of the other combinations of variables accounted for greater than 3.5% of the variance. This result was clearly demonstrated when DCA sample scores were sorted by month in an ordination diagram (Figure 6). Sample scores clustered tightly by month with a clear phenological progression from February to July. DCA axis I scores were highly correlated with water temperature (r = 0.82; P = 0.002), suggesting it was the most important environmental variable structuring the larval fish assemblage (river flow, r = –0.73, P = 0.37; Secchi depth, r = –0.36, P = 0.022; specific conductance, r = 0.11, P = 0.017). This result was consistent with the CCA, which indicated that species abundances clustered primarily along a water temperature gradient. Native species were associated with samples taken during early months (high axis I scores), while the alien species were associated with samples taken during later months (low axis I scores; Figure 5). These results also were consistent with the CCA, which demonstrated an ecological segregation between native and alien species based primarily on water temperature.

Discussion

The south delta larval fish assemblage is numerically dominated by alien species. This

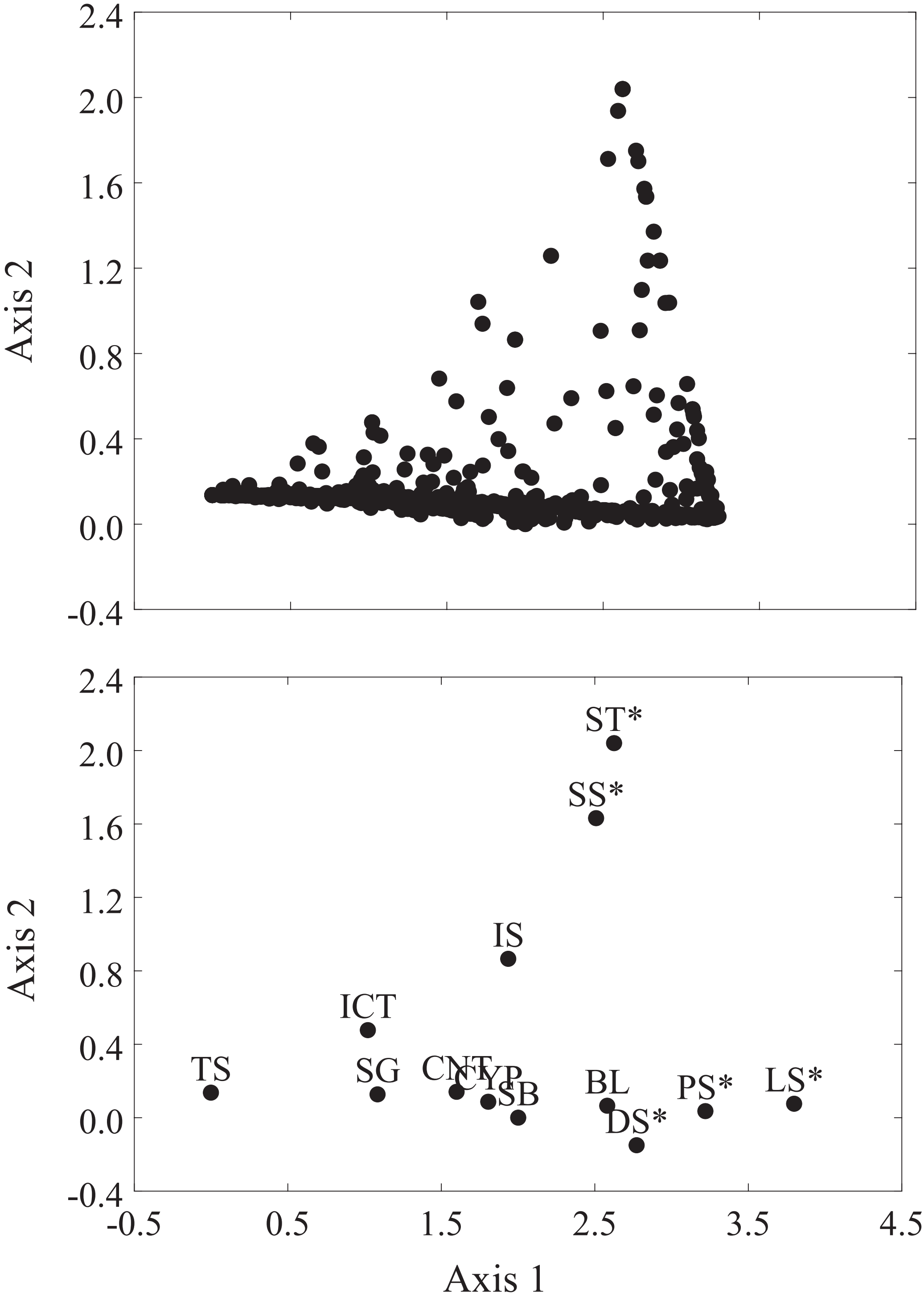

FIGURE 5. Ordination diagrams showing sample scores (top) and species scores (bottom) of a detrended correspondence analysis on larval fish samples collected in the south delta. Axis I is scaled the same on each chart and native species are indicated by an asterisk.

TABLE 3. Analysis of three main effects and their interactions on assemblage structure obtained from an ANOVA on detrended correspondence analysis axis I scores. Factor variance components were derived from expected mean squares based on a fixed-effects ANOVA.

Factor	df	MS	% Variance
Month (*M*)	5	247.42	80.1
Year (*Y*)	5	8.38	1.8
Site (*S*)	6	4.42	1.3
M × Y	23	1.99	3.5
M × *S*	30	0.77	1.3
Y × *S*	29	0.21	<0.1
M × *Y* × *S*	132	0.19	0.6

observation is characteristic of other regions of the system (Meng and Matern 2001) and also of the reported juvenile and adult fish assemblage of the south delta (Feyrer and Healey 2003). Results of this study and those of juvenile and adult fish studies in the south delta (Feyrer and Healey 2003) suggest that with the sole exception of prickly sculpin larvae, native species represent approximately 1% of the sampled fish assemblage. The presence of native larvae during the spring suggests that native species may, in fact, spawn in the south delta or at nearby locations when environmental conditions are optimal. However, again with the possible exception of prickly sculpin, such spawning appears to be uncommon for native species because their larval abundances are so low. A likely scenario is that highest abundance of native species occurs during the spring of extremely wet years when larval and juvenile native fishes either migrate or are washed into the south delta after being produced in other locations. The major components of the south delta larval fish assemblage (shimofuri goby, threadfin shad, prickly sculpin, and striped bass) were also shown to be the dominant species downstream in Suisun Marsh (Meng and Matern 2001). However, Suisun Marsh exhibited a greater proportion of native species, especially longfin smelt, a likely result of the marsh's relatively undisturbed habitat and its proximity

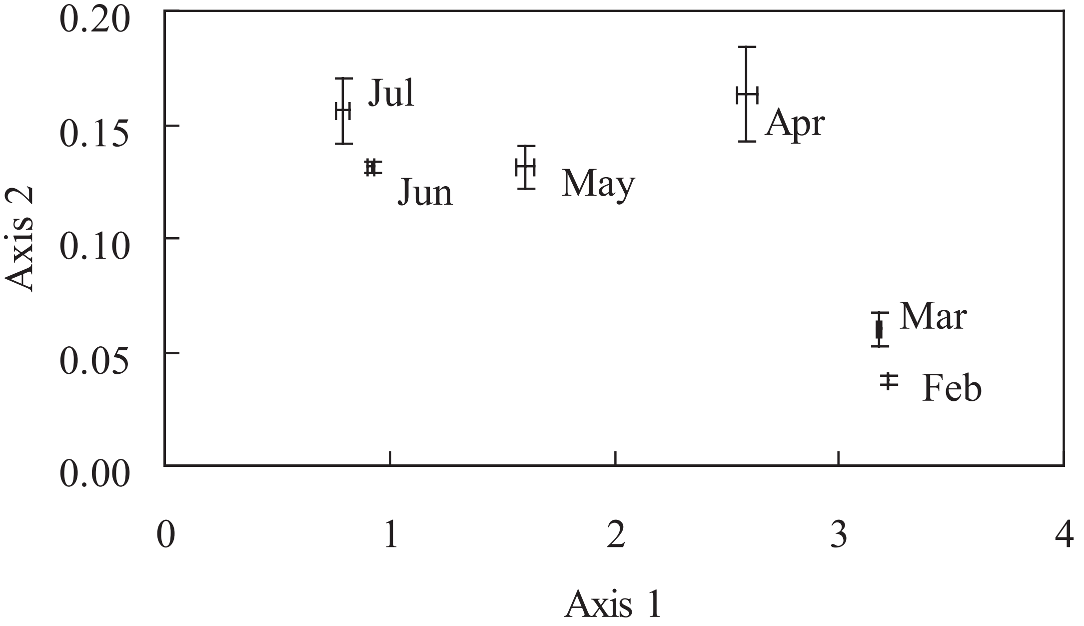

FIGURE 6. Ordination diagram showing results of detrended correspondence analysis on larval fish samples collected in the south delta. Sample scores are sorted by month with mean values (±SE) given for each axis.

to brackish water (Meng and Matern 2001). Gadomski and Barfoot (1998) documented a similar regional separation of native and alien larval fish assemblages in relatively undisturbed and disturbed habitats in the Columbia River basin. Together, these observations support the hypothesis that alien species most commonly become established in highly altered habitats (Ross 1991).

There was a striking temporal separation between the occurrence of native and alien fish larvae in the south delta. Similar to what has been reported in other regions of the system (Marchetti and Moyle 2001; Meng and Matern 2001; Grimaldo et al. 2004; Sommer et al. 2004; both this volume), abundance of native species peaked early in the season, while abundance of alien species peaked later. Results of both multivariate methods were consistent with this observation. CCA showed that native species were associated with cool water temperatures and high river flows, while DCA showed that native species were associated with samples taken early in the year, the time period when such environmental conditions exist. The same methods showed an opposite pattern for the majority of alien species. The temporal segregation of native and alien fish reproductive periods that exists in the Sacramento–San Joaquin Delta system is similar to that observed in the San Juan River, New Mexico and Utah (Gido et al. 1997)

Larval fish assemblages in the south delta exhibited substantial monthly variation within years, but little variation was exhibited spatially among sampling sites. Similarity of assemblages among sites suggests that either the available spawning habitat was equally favorable among sites or they were close enough together in space to allow tidal excursion flows to distribute larvae equally among sites. This observation is consistent with results of Meng and Matern (2001) who found similar assemblages among most sites within Suisun Marsh. Seasonal variation in assemblage structure was persistent among years and was primarily associated with the seasonal occurrence of native and alien species. Water temperature and river flow were the most important environmental variables influencing this pattern. Low water temperatures and high river flows early in the season provide spawning cues for native adult fishes, while high water temperatures and low river flows late in the season favor alien species (Moyle 2002). Of the two variables, water temperature was the most important explaining fish catches. It exhibited the highest importance on the first CCA axis and the strongest correlation with the DCA axis I scores. Additionally, temporal patterns of assemblage structure were persistent over the study period despite the fact that total delta inflow among years differed by as much as 600%, or put in a different context, nearly five standard deviations of the 40-year running average from 1955 to 1995 (not shown; flow data are available online from the California Department of Water Resources' Dayflow Database at http://iep.water.ca.gov/dayflow). This suggests that the majority of spawning by both fish groups will take place only when optimal temperatures are achieved regardless of flow conditions. However, the overall importance of river flow, especially total delta inflow, should not be underemphasized because it is known to influence the availability of spawning and rearing habitat and is positively correlated with the abundance of numerous native and commercially important species (Jassby et al. 1995; Sommer et al. 1997; Kimmerer 2002). It seems likely that there is a certain interaction between temperature, river flow, and other associated variables that produce optimal conditions that drive recruitment of native fishes in the delta.

Interactions with alien species are mechanism that may influence the abundance of native species in the delta (Bennett and Moyle 1996). Given the consistent temporal segregation between the native and alien larval fish assemblages, the opportunity for direct interactions, such as competition, between the two groups is probably relatively small and may not significantly influence native fish recruitment. Other factors that may be important include limited suitable habitat for spawning or rearing caused by anthropogenic disturbances, altered flow regimes or hydrodynamics caused by water exports and flood control facilities, limited food supply caused by food web changes, and predation by other life stages of fishes (Kimmerer et al. 1994; Bennett and Moyle 1996). Other studies have found that predation or competition by alien species on natives can be significant (Lemly 1985; Meffe 1985; Scoppettone 1993; Marsh and Douglas 1997). A combination of these factors are probably responsible for the poor recruitment of native fishes in the south delta.

The results of this study provide useful and challenging information for resource managers and water project operations in the delta. Because the native larvae are consistently present early in the year and their abundance is tightly correlated with water temperature, water project exports can be scheduled around this time period to minimize direct impacts such as entrainment. The environmental associations among native species and environmental variables described here are consistent with results of other studies on native fishes (Marchetti and Moyle 2000, 2001; Meng and Matern 2001; Feyrer and Healey 2003; Grimaldo et al. 2004). These observations highlight the importance of maintaining flow regimes that resemble natural conditions. Proper flow regimes in California's Central Valley streams benefit native species and probably keep alien species at bay (Marchetti and Moyle 2001; Brown and Ford 2002). Natural flow regimes have also been demonstrated to benefit native fish assemblages in other regions. Travnichek et al. (1995) observed an increase in fish abundance and diversity following enhanced flow regimes in the Tallapoosa River, Alabama. Meffe (1991) noted that a natural flow regime prevented the establishment of alien bluegill *Lepomis macrochirus* in a South Carolina blackwater stream. Additionally, natural flow regimes, such as seasonal flooding, are important in maintaining native fish assemblages in the southwestern United States (Minckley and Meffe 1987; Gido et al. 1997). Although these examples suggest that there is promise in restoring native fishes with natural flow regimes, results of this study suggest that manipulations in flow regimes alone will probably not result in substantial changes in the overall south delta fish assemblage. This conclusion stems from the fact that high assemblage similarity was observed among years in which inflow varied tremendously. Although a natural flow regime will probably enhance the production of native fishes during the spring flow pulse, the production of alien species will also be maintained during summer once the natural spring flow pulse has receded. Therefore, although there may be management options which have the opportunity to enhance production of native species, decreasing the production of alien species in the delta remains a considerable problem.

Acknowledgments

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