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Littoral Fish Assemblages of the Alien-dominated Sacramento–San Joaquin Delta, California, 1980–1983 and 2001–2003

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ABSTRACT: We analyzed monthly boat electrofishing data to characterize the littoral fish assemblages of five regions of the Sacramento–San Joaquin Delta (northern, southern, eastern, western, and central), California, during two sampling periods, 1980–1983 (1980s) and 2001–2003 (2000s), to provide information pertinent to the restoration of fish populations in this highly altered estuary. During the 1980s, almost 11,000 fish were captured, including 13 native species and 24 alien species. During the 2000s, just over 39,000 fish were captured, including 15 native species and 24 alien species. Catch per unit effort (CPUE) of total fish, alien fish, and centrarchid fish were greater in the 2000s compared with the 1980s, largely because of increased centrarchid fish CPUE. These differences in CPUE were associated with the spread of submerged aquatic vegetation (SAV), particularly an alien aquatic macrophyte *Egeria densa*. Native fish CPUE declined from the 1980s to the 2000s, but there was no single factor that could explain the decline. Native fish were most abundant in the northern region during both sampling periods. Nonmetric multidimensional scaling indicated similar patterns of fish assemblage composition during the two sampling periods, with the northern and western regions characterized by the presence of native species. The separation of the northern and western regions from the other regions was most distinct in the 2000s. Our results suggest that native fish restoration efforts will be most successful in the northern portion of the Delta. Management decisions on the Delta should include consideration of possible effects on SAV in littoral habitats and the associated fish assemblages and ecological processes.

Introduction

Humans depend on terrestrial and aquatic ecosystems for a variety of economically valuable services (Costanza et al. 1997). River systems provide a wide range of such services including fresh water, transportation, waste disposal, food, esthetic enjoyment, and recreational opportunities (Petts and Calow 1996). Of these services, fresh water is one of the most critical requirements of human populations. Supplying water for drinking, agricultural, and industrial purposes without damaging the ecological health of aquatic ecosystems is one of the great challenges facing water resource managers (Covich 1993; Postel 1996, 2000; Postel and Carpenter 1997). Major efforts are underway to restore aquatic ecosystems that have been affected by current patterns of human land and water use, including major programs in the Everglades (Comprehensive Everglades Restoration Plan 2005), Chesapeake Bay (Chesapeake Bay Program 2005), and the San Francisco Estuary (SFE, California Bay-Delta Authority 2005) of the United States.

The SFE is the largest estuary on the west coast of North America and drains about 40% of the surface area of California. During the 150 years since the beginning of large-scale European settlement, landscapes in the watershed have changed dramatically from natural settings to agricultural and urban areas with consequent changes in physical and ecological processes (Conomos 1979; Cloern and Nichols 1985; Hollibaugh 1996) and native fish populations (Bennett and Moyle 1996; Moyle 2002). The Sacramento–San Joaquin Delta (Delta; Fig. 1), the landward, freshwater portion of the SFE, has been largely re-engineered to divert as much as 60% of the natural inflow into San Francisco Bay for agricultural, urban, or industrial uses (Jacobs et al. 2003). The CALFED Bay-Delta (CALFED) Program is an ambitious effort to restore ecosystems in the SFE and its watershed, while improving the quantity and reliability of other beneficial services, primarily freshwater supply (Jacobs et al. 2003; California Bay–Delta Authority 2005; Kimmerer et al. 2005). The challenges in restoring SFE watershed ecosystems are considerable. Kimmerer et al. (2005) noted that the Ecosystem Restoration Program of the CALFED Program includes possible conflicting goals, e.g., recovering at-risk native species, rehabilitating natural processes and natural biotic communities, and reducing the effects of nonnative species, while maintaining harvestable populations of selected biota (including some nonnative species). These goals conflict because the harvestable nonnative species include possible predators and competitors of native species, including largemouth bass *Micropterus salmoides* and striped bass *Morone*

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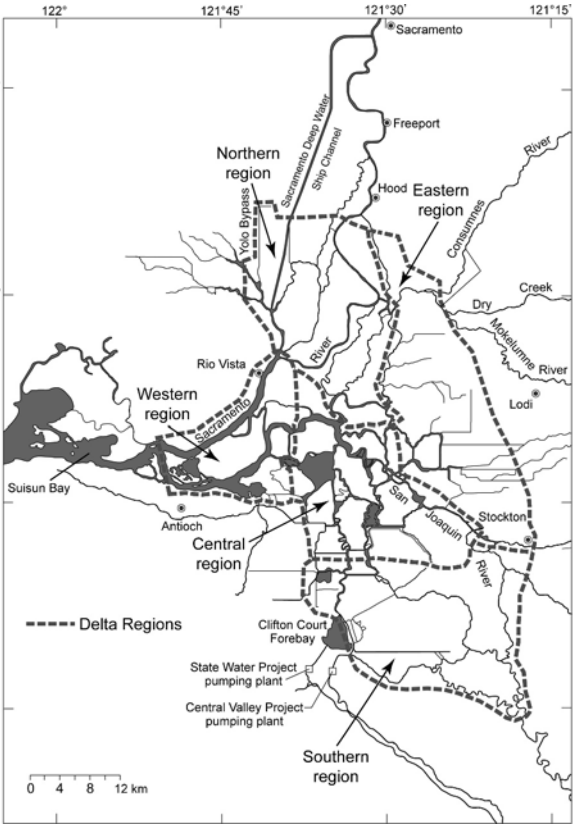

Fig. 1. Map of the Sacramento–San Joaquin Delta, California, and the regions within the Delta used for sampling and data analysis.

saxatilis (Brown 2003a; Lindley and Mohr 2003). Given the difficulties in addressing possible conflicting goals, resource managers need to develop appropriate conceptual models that are based on the best available data to help reduce uncertainty related to management decisions (Kimmerer et al. 2005).

We focus on the littoral fish assemblages of the tidal, freshwater Delta. Recent work in the Delta suggests that alien fish populations, particularly centrarchids, have expanded and native fish populations declined concurrent with the expansion of *Egeria densa*, an alien aquatic macrophyte that grows in dense monospecific beds (see Brown 2003a for a review) and now covers large portions of the littoral area of Delta waterways (California Department of Boating and Waterways 2001). The expansion of submerged aquatic vegetation (SAV) in the Delta (primarily *E. densa*; California Department of Boating and Waterways 2001) was reported in the mid 1980s, but that time period and the extent of the expansion have not been thoroughly documented. Recent studies and analyses of littoral fish assemblages in the Delta have focused on relatively few sites or particular regions within the Delta (Feyrer and Healey 2003; Grimaldo et al. 2004a,b; Feyrer 2004); managers lack a Delta-wide perspective on littoral fish assemblages. Without such a perspective, anticipating the regional effects of management actions is difficult at best. We analyze boat electrofishing data and habitat data collected as part of a baseline monitoring program by the California Department of Fish and Game from May 1980 to April 1983 (1980s) and from April 2001 to April 2003 (2000s) to address the following objectives on a Delta-wide geographic scale: to determine if the extent of SAV increased markedly between the 1980s and 2000s, to determine if catch per unit effort (CPUE) of native or alien fishes, particularly centrarchids, changed between the 1980s and 2000s, to determine if fish assemblage composition changed between the 1980s and 2000s, and to determine if changes in CPUE or fish assemblage composition were correlated with changes in SAV or other habitat or environmental variables.

STUDY AREA

The Delta is formed by the confluence of the Sacramento and San Joaquin rivers in central California (Fig. 1). The Mokelumne and Cosumnes rivers also flow into the Delta from the east, as do a number of smaller streams. The Delta drains into Suisun Bay and San Francisco Bay and then the Pacific Ocean. The Delta includes about 1,100 km of tidal channels of various sizes ranging from major rivers with large deep shipping channels maintained by dredging to small dead-end sloughs (Turner and Kelley 1966). There are also several large areas of open water, which are actually flooded agricultural islands that were never reclaimed. Littoral habitats include SAV, emergent vegetation (primarily *Scirpus* spp. and *Typha* spp.), large woody debris, overhanging riparian vegetation, and extensive riprap on levees that protect agricultural land and other human land use areas. Brazilian waterweed *E. densa* dominates SAV habitat with smaller amounts of both native (*Ceratophyllum demersum*, *Potamogeton nodusus*, and *P. pectinatus*) and alien (*Myriophyllum aquaticum*, *M. spicatum*, and *P. crispus*) species (California Department of Boating and Waterways 2001). The floating water hyacinth *Eichhornia crassipes*, also an alien species, can be locally abundant.

The Delta is a tidal, freshwater system that has been engineered and operated to supply freshwater to the federal Central Valley Project and State Water Project pumping plants located in the southern Delta (Kimmerer 2004, Fig. 1). Upstream reservoirs and various Delta facilities are operated to prevent intrusion of brackish water from Suisun Bay into the Delta where it might be entrained by the state or federal pumping plants or numerous other smaller drinking water or irrigation diversion points in the Delta. There is particular emphasis on preventing the intrusion of bromide because the high organic carbon content of Delta waters makes the formation of trihalomethanes and other disinfection byproducts likely in drinking water treatment plants (Brown 2003b). Salinity is generally low throughout the Delta, even during the summers of drought years when salinity may have intruded far inland under natural conditions. Despite this high degree of alteration, tidal flows rather than river inflows largely determine water velocities in Delta channels (Kimmerer 2004).

Materials and Methods

SITE SELECTION

The Delta was arbitrarily subdivided into five regions (Fig. 1) to reflect relatively homogenous ecological conditions. Sampling was conducted monthly in the 1980s and 2000s, except for a few months when boat malfunction precluded sampling. Sampling reaches consisted of 1,000 m of shoreline in the 1980s and 500 m of shoreline in the 2000s.

In the 1980s, each of the five regions of the Delta was divided into a series of numbered cells, each containing some portion of littoral habitat. A random number generator was then used to pick a number of cells for sampling. In the 1980s, 10 reaches were sampled each month: 3 in the eastern region, 1 in the northern region, 1 in the western region, 3 in the central region, and 2 in the southern region. The number of reaches sampled per region was roughly in proportion to the percentage of the total length of Delta waterways in each region.

In the 2000s, the entire shoreline of the Delta was divided into 500-m reaches. The reaches actually sampled each month in each region were randomly chosen from the population of available reaches. Between April 2001 and December 2002, 15 reaches were sampled each month: 4 in the eastern region, 2 in the northern region, 2 in the western region, 4 in the central region, and 3 in the southern region. Starting in January 2003, the number of reaches sampled each month was increased to 20 with 5 in the eastern region, 3 in the northern region, 3 in the western region, 5 in the central region, and 4 in the southern region.

ENVIRONMENTAL VARIABLES

Delta outflow data were obtained from the DAYFLOW database (http://iep.water.ca.gov/dayflow/index.html). Water temperature (°C), Secchi depth (cm), and specific conductance (μS cm^{-1}) were measured at each reach sampled. Several habitat characteristics were also measured including the number of snags (logs or fallen trees), vegetation type, and bank type. Vegetation type and bank type were characterized differently in the 1980s and 2000s. In the 1980s, the percentages of each vegetation type (bare, floating, submerged, emergent, and riparian) and bank type (riprap, mud bank, sand beach, mud flats, and docks) were scored using categories of visually estimated percentages (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100%) within the 1,000-m sampling reach. In the 2000s, the 500-m sampling reaches were assigned to a single vegetation or bank type category (e.g., riprap bank and SAV). In rare cases when more than one type of vegetation or bank type was present in a reach, the reach was divided into two subreaches, which were then characterized. Splitting was only necessary for 40 of 349 sampling reaches. For analysis, each subreach was treated as a separate reach with respect to fish sampling and environmental measurements.

FISH SAMPLING

In the 1980s, fish sampling was conducted using a 16-foot Smith Root electrofishing boat with a VI-A shocking unit. In the 2000s, fish sampling was conducted using an SR-18EH Smith Root electrofishing boat with a GPP 5.0 shocking unit. Sampling bias associated with the use of different boats during the two periods was likely minimal because the boats had a similar physical deployment of electrodes and were operated in a similar manner. Pulse width was always 60 pulses per second. Voltage was set at 50–500 volts, depending on specific conductance at a reach, with amperage adjusted to 6 ± 1 amps. The reach was shocked in the downcurrent direction. Stunned fish were collected with long-handled dipnets and placed in a live well before being identified to the lowest possible taxon, primarily species, except for lamprey ammocoetes *Lampetra* spp. and very small individuals. Fish were then measured (fork length, mm) and released.

DATA ANALYSIS

Delta outflow, water temperature, specific conductance, and Secchi depth were compared graphically between the two sampling periods. We focused our habitat analyses on SAV because of our interest in expansion of this habitat type between sampling periods and on riprap banks because this bank type has replaced natural banks in many areas of the Delta. Comparisons of SAV and riprap were complicated by the different methods used to record those data during the two sampling periods. We compared the frequency of 2000s sampling reaches designated as having SAV habitat (100% SAV) with the frequencies of 1980s reaches in each of the following categories: any percentage of SAV, greater than 50% SAV, and greater than 75% SAV. We followed a similar strategy for comparing the frequency of riprap banks between sampling periods. Statistical comparisons were made with χ^2.

Preliminary analysis indicated that the catches of some species differed between day and night sampling in the 1980s data; only day samples were analyzed to be most comparable with the 2000s data, which were all from day samples. This resulted in a reduction in 1980s sampling reaches from 360 to 205. The deletion of night samples from the data set also resulted in less than monthly data for less extensively sampled regions, but the omissions were not biased toward a particular month or season. The main effect of the deletions was to reduce sample size for each region during the 1980s, which consequently decreased the power of the statistical tests. Although effort varied between sampling periods in terms of number and length of reaches, total effort (total distance of littoral habitat sampled) was similar with 20,500 m sampled in the 1980s and 17,450 m sampled in the 2000s.

To account for differences in reach length between sampling periods, abundances at each sampling reach were converted to CPUE (fish km^{-1}) by dividing the number of fish captured by the reach length (km). CPUE was calculated for total catch, catch of alien fish, catch of centrarchid fish, and catch of native fish. All CPUE variables were analyzed using two-way analysis of variance (ANOVA; SYSTAT 2002) with sampling period and region as factors. CPUE data were $\log_{10}(x + 1)$ transformed before analysis based on examination of normal probability plots. We recognize that several of the CPUE variables are not independent, which affects interpretation of p values. For example total catch is the sum of CPUE of alien fish and CPUE of native fish and CPUE of centrarchid fish is included in CPUE of alien fish; we believe the results for the different variables aid in interpreting the patterns observed.

We explored fish assemblage composition using PRIMER software (Clarke and Warwick 2001; PRIMER-E 2005). We used nonmetric multidimensional scaling (NMS; Kruskal 1964a,b; Mather 1976) to ordinate samples on the basis of species CPUEs. NMS is similar in concept to other ordination techniques but does not assume linear relationships among variables, uses ranked distances, and allows for the use of any data transformation or distance measure (McCune and Grace 2002). The fit of the ordination is assessed by the stress value with values < 0.20 indicating a useful ordination (Clarke and Warwick 2001). Conceptually, stress compares the original distances between samples calculated from the full data matrix with the distances in the lower dimension ordination space.

Species CPUEs were square-root transformed to reduce the influence of common species and Bray-Curtis similarities were then calculated and used in the ordination. The greater reach length in the 1980s results in a higher probability of capturing rare species compared to the shorter reach lengths in the 2000s; this should only slightly bias the results of the analysis. Bray-Curtis similarities are much more influenced by abundant species (Clarke and Warwick 2001). The purpose of the square-root transformation is to down-weight the influence of the most abundant species so moderately abundant species have more importance in the analysis. To aid in the interpretation of NMS axes, we correlated NMS axes scores with $\log_{10}$-transformed CPUE of total catch, CPUE of alien fish, CPUE of centrarchid fish, and CPUE of native fish.

We used the ANOSIM procedure in PRIMER to compare fish assemblage similarity between periods for each region. ANOSIM is a permutation (randomization) test analogous to ANOVA (Clarke and Warwick 2001). Each ANOSIM test was based on 1,000 permutations of the sample data. The ANOSIM test statistic R varies from 0 to 1. An R value of 0 indicates no difference between groups. An R value of 1 indicates that all samples within a group are more similar to each other than to any sample from another group.

We used the BVSTEP procedure in PRIMER to select a subset of influential species that summarize the patterns evident in the full data set (Clarke and Warwick 2001). This permutation test is somewhat analogous to stepwise regression. We selected species included in the model most often resulting from 100 permutations of the sample data. The reduced model was required to have a Spearman rank correlation of > 0.95 with the original data.

We tested the correlation of fish assemblage composition with environmental factors using the BIO-ENV procedure in PRIMER (Clarke and Warwick 2001). This multivariate permutation test compares a distance matrix that is based on environmental measurements with the species similarity matrix. A high correlation indicates a strong association of the species assemblage with the measured environmental variables. This analysis also proceeds in a stepwise manner and tests all combinations of environmental variables to determine the best model. This test was based on 100 permutations of the sample data. We did not test for an effect of SAV with this test because there was so little SAV present in the 1980s (see Results) and because of the different methods of measurement

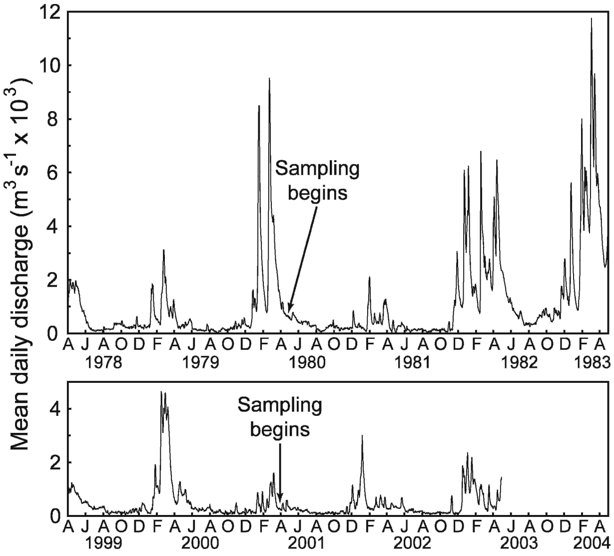

Fig. 2. Delta outflow (DAYFLOW, http://iep.water.ca.gov/dayflow/index.html) for the two years preceding fish sampling and during fish sampling from May 1980 to April 1983 and from April 2001 to April 2003. (Dates shown are month/day/year).

used during the two sampling periods. We conducted a two-way ANOVA for each of the CPUE variables from the 2000s data with region and presence of SAV as factors. This analysis is not affected by the different methods for characterizing SAV during the 2 periods because only data from one period is analyzed. We did not conduct a similar analysis for riprap banks because there was no clear evidence of differences between sampling periods (see Results).

Results

Environmental Variables

Delta outflow was generally greater during the 1980s sampling period compared with the 2000s (Fig. 2). Outflow was similar for the 2 yr before sampling began, except for the final 4 mo with the 1980s having much greater outflow. Flows were comparable for about the first 20 mo after sampling began. Subsequently, the outflows during the 1980s were greater than during the 2000s.

Water temperature exhibited a clear seasonal pattern during both sampling periods (Fig. 3). Mean monthly temperatures were lowest (near or below 10°C) in December or January. During both periods, temperatures warmed through July and August, with mean monthly temperatures between 20°C and 25°C from June to September.

Mean monthly Secchi depth did not show a strong seasonal pattern (Fig. 3). During the 1980s, mean monthly Secchi depth varied from a minimum of 33 cm in February to a maximum of 61 cm in October. During the 2000s, mean monthly Secchi depth varied from a minimum of 39 cm in January to a maximum of 87 cm in November.

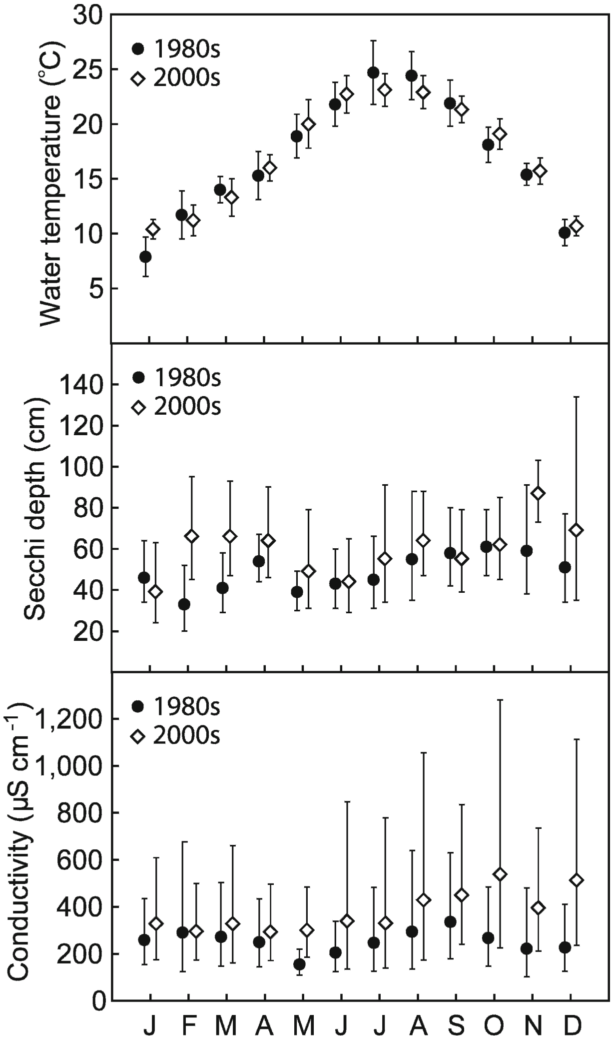

Fig. 3. Mean monthly temperature from January (J) to December (D), Secchi depth, and specific conductance (± SD) during fish sampling from May 1980 to April 1983 (1980s) and from April 2001 to April 2003 (2000s). Values for Secchi depth and specific conductance were back-transformed from $\log_{10}$-transformed values.

Mean monthly specific conductance did not show a strong seasonal pattern (Fig. 3). During the 1980s, mean monthly specific conductance varied from a minimum of 156 µS cm^{-1} in May to a maximum of 336 µS cm^{-1} in September. During the 2000s, mean monthly specific conductance varied from a minimum of 293 µS cm^{-1} in April to a maximum of 538 µS cm^{-1} in October.

The mean number of snags per sampling reach was low in both periods. During the 1980s there was a mean of 2 snags per reach with a 95% confidence

TABLE 1. Percentage of sample reaches with various levels of submerged aquatic vegetation coverage (SAV) for the Delta as a whole and for five regions within the Delta from May 1980 to April 1983 (1980s) and from April 2001 to April 2003 (2000s). During the 1980s, percent cover was visually estimated for each 1,000 m sampling reach. During the 2000s, sampling reaches were characterized as having SAV if SAV was present throughout the reach.

		1980s			2000s	
Region	n	Greater than 0% coverage	Greater than 50% coverage	Greater than 75% coverage	n	Complete coverage
Delta	204	11.3	4.4	1.5	389	34.2
Eastern	62	6.4	1.6	0	105	46.7
Central	56	28.6	12.5	5.4	96	41.7
Southern	43	4.7	0	0	83	25
Western	19	5.3	5.3	0	49	32.7
Northern	24	0	0	0	56	5.4

interval of 0–5 snags. During the 2000s, there was a mean of 3 snags per reach with a 95% confidence interval of 1–8 snags.

Reaches with SAV were much more frequent in the 2000s compared with the 1980s (Table 1). For the whole Delta, the frequency of reaches with SAV in the 2000s (100% coverage) was greater than the frequency of sampling reaches with any occurrence of SAV in the 1980s (Pearson $\chi^2 = 36.2$, df = 1, $p < 0.001$). This is the most conservative test possible and suggests that, despite differences in data collection between periods, the data indicate expansion of SAV habitat between the 1980s and 2000s. This result is consistent with qualitative observations of SAV expansion in the mid-1980s (California Department of Boating and Waterways 2001). In the 2000s, 25% or more of all reaches sampled in each region were characterized as having SAV, except for the northern region where only 5% of the reaches had SAV. In the 1980s, reaches in the central region always had the highest frequency of sites with SAV no matter what cutoff value was used to define SAV sites (i.e., sites with > 0%, > 50%, or > 75%; Table 1). SAV was not present in any of the northern region sampling reaches in the 1980s. There were significant regional differences in the 1980s (Pearson $\chi^2 = 31.0$, df = 4, $p < 0.001$, for > 0% coverage data) and the 2000s (Pearson $\chi^2 = 23.8$, df = 4, $p < 0.001$). These regional comparisons are not affected by the differences in sampling methodology because the comparisons were within periods.

The results for riprap coverage of the banks of sampling reaches were less clear (Table 2). The frequency of sampling reaches with riprap banks in the 2000s (100%) was higher than the frequency of reaches with greater than 75% riprap in the 1980s (Pearson $\chi^2 = 5.6$, df = 1, $p < 0.05$), was not different from the frequency of reaches with greater than 50% riprap in the 1980s (Pearson $\chi^2 = 5.6$, df = 1, $p < 0.05$), and was lower than the frequency of reaches with any occurrence of riprap in the 1980s (Pearson $\chi^2 = 5.6$, df = 1, $p < 0.05$). Differences among regions were statistically significant in the 2000s (Pearson $\chi^2 = 11.5$, df = 4, $p < 0.05$) with the western region having the lowest occurrence of riprap banks. In the 1980s, there was not a statistically significant difference among regions for the frequency of reaches with greater than 75% riprap (Pearson $\chi^2 = 2.7$, df = 4, $p > 0.05$), the frequency of reaches with greater than 50% riprap (Pearson $\chi^2 = 4.6$, df = 4, $p > 0.05$), or the frequency of reaches with any occurrence of riprap (Pearson $\chi^2 = 8.0$, df = 4, $p > 0.05$). The differences in reach length and methods may contribute to the inability to find consistent differences between periods, although it is clear that riprap banks were frequently encountered during both periods (Table 2). There is not a Delta-wide database available regarding the extent and location of riprap banks that we could use to

TABLE 2. Percentage of sample reaches with riprap bank for the Delta as a whole and for five regions within the Delta from May 1980 to April 1983 (1980s) and from April 2001 to April 2003 (2000s). During the 1980s, percent riprap bank was visually estimated for each 1,000 m sampling reach. During the 2000s, sampling reaches were characterized as having riprap if riprap was present throughout the reach.

		1980s			2000s	
Region	n	Greater than 0% of bank	Greater than 50% of bank	Greater than 75% of bank	n	Complete bank
Delta	204	55.9	40.7	33.8	389	42.9
Eastern	62	58.1	40.3	33.9	105	44.8
Central	56	44.6	33.9	26.8	96	40.6
Southern	43	72.1	53.5	41.9	83	54.2
Western	19	52.6	31.6	31.6	49	24.5
Northern	24	50	41.7	37.5	56	42.9

TABLE 3. Common name, scientific name, native status, and percentage of total catch for all fishes captured during Delta fish sampling from May 1980 to April 1983 (1980s) and from April 2001 to April 2003 (2000s). N = no; Y = yes. Anadromous species are not expected to occur in the Delta during all months because of migration.

Common name	Scientific name	Native	1980s	2000s
Anadromous:				
American shad	*Alosa sapidissima*	N	0.9	0.3
Chinook salmon	*Oncorhynchus tshawytscha*	Y	0.9	0.7
Steelhead rainbow trout	*Oncorhynchus mykiss*	Y	0.1	0.1
Resident:				
White catfish	*Ameiurus catus*	N	15.6	1.4
Bluegill	*Lepomis macrochirus*	N	14.7	29.9
Threadfin shad	*Dorosoma petenense*	N	10.7	22.2
Largemouth bass	*Micropterus salmoides*	N	8.0	13.1
Redear sunfish	*Lepomis microlophus*	N	8.0	14.9
Tule perch	*Hysterocarpus traskii*	Y	6.3	1.1
Striped bass	*Morone saxatilis*	N	5.1	1.2
Common carp	*Cyprinus carpio*	N	4.7	1.8
Golden shiner	*Notemigonus crysoleucas*	N	4.5	3.2
Inland silverside	*Menidia beryllina*	N	4.2	3.0
Goldfish	*Carassius auratus*	N	2.3	0.1
Sacramento blackfish	*Orthodon microlepidotus*	Y	1.9	0.1
Yellowfin goby	*Acanthogobius flavimanus*	N	1.8	0.9
Black crappie	*Pomoxis nigromaculatus*	N	1.7	0.3
Warmouth	*Lepomis gulosus*	N	1.4	2.2
Green sunfish	*Lepomis cyanellus*	N	1.3	0.3
Sacramento pikeminnow	*Ptychocheilus grandis*	Y	1.3	0.4
Sacramento sucker	*Catostomus occidentalis*	Y	1.1	0.6
Bigscale logperch	*Percina macrolepida*	N	1.0	0.4
Prickly sculpin	*Cottus asper*	Y	0.7	0.2
Channel catfish	*Ictalurus punctatus*	N	0.6	0.5
White crappie	*Pomoxis annularis*	N	0.3	< 0.1
Brown bullhead	*Ameiurus nebulosus*	N	0.3	0.2
Spittail	*Pogonichthys macrolepidotus*	Y	0.3	0.1
Smallmouth bass	*Micropterus dolomieu*	N	0.2	0.3
Black bullhead	*Ameiurus melas*	N	0.1	0.0
Delta smelt	*Hypomesus transpacificus*	Y	0.1	0.1
Hitch	*Lavinia exilicauda*	Y	0.1	0.1
Lampreys	*Lampetra* sp.	Y	< 0.1	< 0.1
Pumpkinseed	*Lepomis gibbosus*	N	< 0.1	0.0
Spotted bass	*Micropterus punctulatus*	N	< 0.1	< 0.1
Staghorn sculpin	*Leptocottus armatus*	Y	< 0.1	< 0.1
Sunfish hybrids	*Lepomis* sp.	N	< 0.1	0.0
Threespine stickleback	*Gasterosteus aculeatus*	Y	< 0.1	< 0.1
Western mosquitofish	*Gambusia affinis*	N	< 0.1	< 0.1
California roach	*Hesperoleucus symmetricus*	Y	0.0	< 0.1
Hardhead	*Mylopharodon conocephalus*	Y	0.0	< 0.1
Red shiner	*Cyprinella lutrensis*	N	0.0	< 0.1
Shimofuri goby	*Tridentiger bifasciatus*	N	0.0	< 0.1

clarify these results, but it is unlikely that there were large changes between periods because the existing levee system was largely in place by the 1980s (Dudas written communication). Because there was not a clear difference in the occurrence of riprap banks between the 1980s and 2000s, as there was for SAV, we did not attempt to relate riprap banks with fish abundances.

FISHES

Forty-two taxa of fishes were collected during the study (Table 3), including hybrid sunfish *Lepomis* spp. and unidentified lamprey ammoecetes. Three species are anadromous and only inhabit the Delta in large numbers during certain seasons of the year (Moyle 2002). Tule perch *Hysterocarpus traskii* was the only native species accounting for more than 2% of the catch and only during the 1980s.

During the 1980s, 37 species of fish were captured, excluding hybrids (Table 3). Thirteen (35%) were native species, and 24 (65%) were alien species. The total catch was 10,915 fish, of which 1,396 (13%) were native, and 9,519 (87%) were alien. During the 2000s, 39 species of fish were collected, including 15 (38%) native species and 24

TABLE 4. Results of two-way analysis of variance of $\log_{10}$-transformed catch per unit effort (CPUE, fish km^{-1}) for total fish, alien fish, centrarchid fish, and native fish. The main factors in the analyses include region (five regions within the Delta) and either period (1980s or 2000s) or the presence of submerged aquatic vegetation (SAV). The SAV analysis only included data from the 2000s.

Variable	Factor	df	F	p
Total CPUE	Period	1	31.2	<0.001
	Region	4	28.7	<0.001
	Interaction	4	4.7	<0.01
	Error	583		
Alien CPUE	Period	1	38.1	<0.001
	Region	4	46.2	<0.001
	Interaction	4	3.6	<0.01
	Error	583		
Centrarchid CPUE	Period	1	91.8	<0.001
	Region	4	84.2	<0.001
	Interaction	4	9.1	<0.001
	Error	583		
Native CPUE	Period	1	20.1	<0.001
	Region	4	34.9	<0.001
	Interaction	4	2.2	NS
	Error	583		
Total CPUE	SAV	1	10.7	<0.01
	Region	4	27.3	<0.001
	Interaction	1	1.7	NS
	Error	583		
Alien CPUE	SAV	1		<0.01
	Region	4		<0.001
	Interaction	1		NS
	Error	583		
Centrarchid CPUE	SAV	1		<0.001
	Region	4		<0.001
	Interaction	1		NS
	Error	583		

(62%) alien species. A total of 39,095 fish were captured, of which 1,409 (4%) were native and 37,686 (96%) were alien. Species captured during the 1980s were captured in the 2000s with the exceptions of rare taxa including black bullhead *Ameiurus melas*, pumpkinseed *Lepomis gibbosus*, and sunfish hybrids. Species captured only in 2000s included new invaders, red shiner *Cyprinella lutrensis* (Jennings and Saiki 1990) and shimofuri goby *Tridentiger bifasciatus* (Moyle 2002), or native stream fishes that are not expected to occur in a large tidal estuary (Moyle 2002), hardhead *Mylopharodon conocephalus* and California roach *Hesperoleucas symmetricus*.

Total CPUE, alien fish CPUE, and centrarchid fish CPUE were statistically different between sampling periods and among regions, all with significant interaction terms (Table 4). All three variables were greater in the 2000s compared with the 1980s (Fig. 4). The significant interactions were due to large increases in values in the eastern and southern Delta during the 2000s compared to

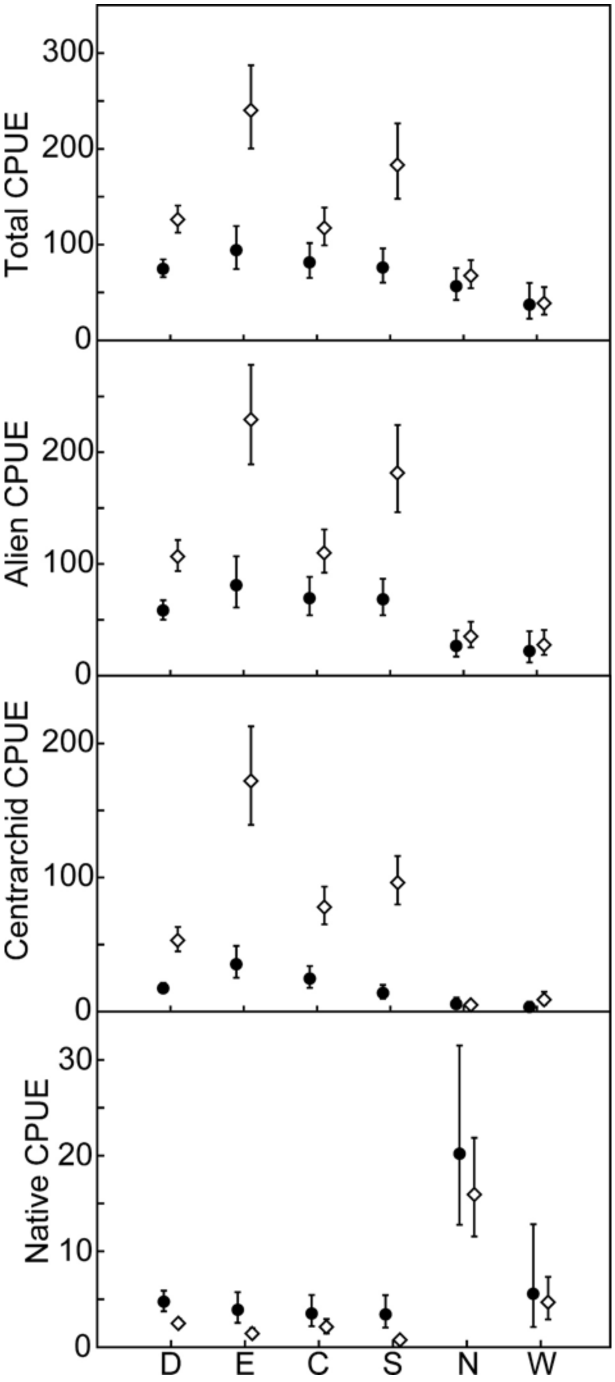

Fig. 4. Mean and 95% confidence intervals (back-transformed from $\log_{10}$-transformed values) for catch per unit effort (CPUE, fish km^{-1}) of total fish, alien fish, centrarchid fish, and native fish for fish sampling from May 1980 to April 1983 (1980s) and from April 2001 to April 2003 (2000s). Values are given for the entire Delta (D) and five regions within the Delta (C: central; E: eastern; N: northern; S: southern; W: western).

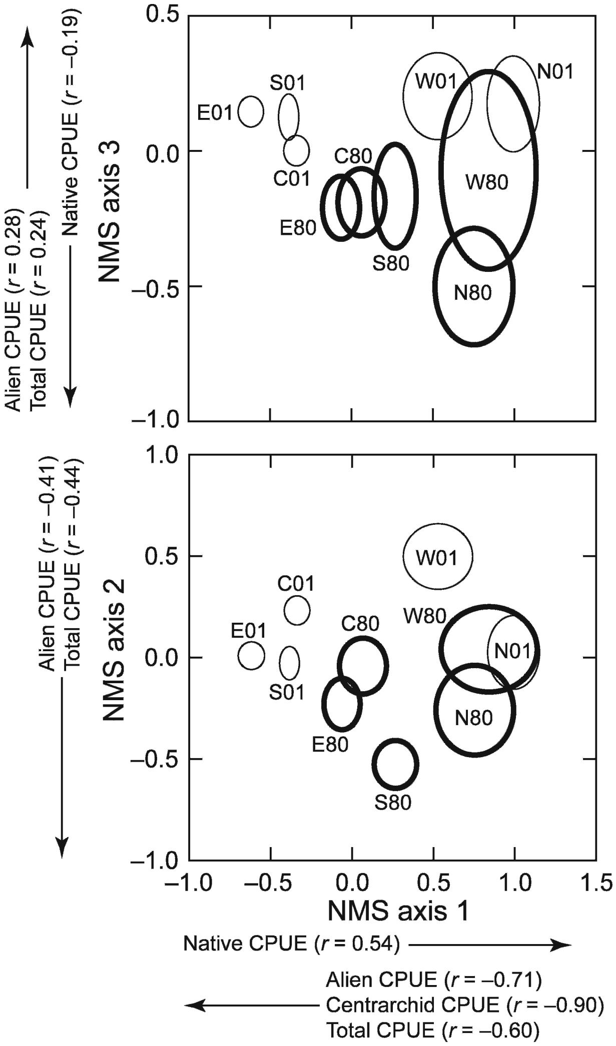

Fig. 5. Sample score 95% confidence ellipses from three-dimensional nonmetric multidimensional scaling (NMS) ordinations of fish catch per unit effort (CPUE) for five regions of the Delta, during fish sampling from May 1980 to April 1983 (heavy line) and from April 2001 to April 2003 (thin line). The first letter of the ellipse label indicates the region (C: central; E: eastern; N: northern; S: southern; W: western) and the number indicates the sampling period (80: May 1980 to April 1983; 01: April 2001 to April 2003). Pearson correlations of $\log_{10}$-transformed CPUE characteristics with NMS axis scores are also shown (all $p < 0.05$). Values for the CPUE characteristics increase in the direction of the arrow.

smaller or no change in the other regions. Total CPUE was lowest in the western region during both sampling periods. Total CPUE was much greater in the eastern and southern regions in the 2000s compared with the 1980s, while total CPUE was similar between sampling periods for the other regions. Alien fish CPUE was clearly lower in both the northern and western regions compared with the other three regions. Alien fish CPUE accounted for most of the total CPUE during both periods. Centrarchid fish CPUE was larger in the central region as well as in the eastern and southern regions in the 2000s compared with the 1980s, in contrast to alien fish CPUE and total CPUE, which were similar in the central region during the 1980s and 2000s. Centrarchid fish CPUE was lowest in the northern and western regions. The differences in alien fish CPUE between the 1980s and 2000s were largely due to differences in centrarchid fish CPUE. In the 1980s, centrarchid fish CPUE was less than 50% of the alien fish CPUE in all regions, but in the 2000s, centrarchid fish CPUE was greater than 50% of the alien fish CPUE for the Delta as a whole and for eastern, central, and southern regions.

Native fish CPUE was statistically different between the sampling periods (Table 4) with lower values in the 2000s compared with the 1980s (Fig. 4). Native fish CPUE was also statistically different among regions (Table 4). The greatest catches of native fishes occurred in the northern region (Fig. 4). The mean native fish CPUE in the western region tended to be slightly higher than in the central, eastern, and southern regions, and the variability tended to be high. Native fish CPUE was lower in the 2000s compared with the 1980s in the eastern and southern regions; these differences in regional response were not great enough to result in a statistically significant interaction term (Table 4).

A three-dimensional NMS solution was selected as the best representation of the data (stress = 0.16; Fig. 5). NMS axis 1 largely separated the western and northern regions from the other regions. Samples from the 2000s covered a wider range of values than during the 1980s. NMS axis 2 provided some separation of 1980s samples from 2000s samples, with the greatest difference between the southern region in the 1980s and the western region in the 1980s. NMS axis 3 also provided some separation of 1980s samples from 2000s samples, with the greatest difference between the northern region in the 1980s and 2000s samples.

The ANOSIM comparisons indicate that there are statistically significant differences in fish assemblage composition between sampling periods ($R = 0.34$, $p \leq 0.001$) and among regions ($R = 0.34$, $p \leq 0.001$). For the specific regions, only the central ($R = 0.31$), eastern ($R = 0.38$), and southern ($R = 0.54$) regions are significantly different between sampling periods (all $p \leq 0.001$). The southern region exhibited the largest difference. The northern ($R = 0.06$, $p > 0.05$) and western ($R = 0.06$, $p > 0.05$) regions were very similar between sampling periods.

Correlations of the $\log_{10}$-transformed CPUE characteristics with NMS axis 1 scores (Fig. 5) indicate that native fishes were most abundant in

TABLE 5. Back-transformed mean catch per unit effort (CPUE, fish km^{-1}) and frequency of occurrence (in parentheses) for selected fishes in five regions of the Delta during fish sampling from May 1980 to April 1983 (1980s) and from April 2001 to April 2003 (2000s).

	Central		Eastern		Southern		Northern		Western	
	1980s n = 57	2000s n = 96	1980s n = 62	2000s n = 105	1980s n = 43	2000s n = 83	1980s n = 24	2000s n = 56	1980s n = 19	2000s n = 49
Alien species:										
Bluegill	6.92 (81)	13.56 (89)	12.88 (92)	82.83 (97)	6.65 (88)	39.11 (96)	0.07 (33)	<0.01 (16)	0.09 (37)	0.06 (22)
Common carp	0.92 (68)	0.52 (59)	1.94 (68)	0.55 (53)	1.41 (70)	1.28 (64)	0.41 (58)	0.22 (45)	0.11 (47)	0.03 (27)
Largemouth bass	8.16 (93)	32.62 (99)	6.70 (90)	28.07 (98)	0.75 (65)	31.43 (100)	0.27 (50)	0.13 (34)	0.84 (58)	4.12 (76)
Inland silverside	<0.01 (14)	0.01 (18)	0.06 (32)	0.07 (30)	0.23 (44)	0.60 (41)	0.03 (25)	1.23 (59)	0.30 (37)	0.07 (29)
Redear sunfish	0.75 (51)	16.67 (90)	3.69 (71)	44.23 (96)	0.11 (37)	13.48 (95)	0.80 (38)	0.03 (25)	<0.01 (5)	0.56 (49)
Threadfin shad	0.39 (40)	0.21 (29)	1.55 (58)	0.98 (37)	1.75 (65)	3.91 (49)	0.18 (38)	0.51 (43)	0.21 (42)	0.23 (27)
White catfish	1.51 (61)	0.01 (22)	3.32 (68)	0.01 (16)	14.45 (86)	0.30 (39)	0.54 (54)	0.02 (23)	0.12 (47)	<0.01 (6)
Native species:										
Tule perch	0.13 (35)	0.08 (33)	0.13 (35)	<0.01 (7)	0.12 (37)	<0.01 (4)	4.74 (83)	0.61 (50)	0.94 (47)	0.12 (37)

the western and northern regions compared with other areas of the Delta. Alien fishes, particularly centrarchids, were most abundant in the eastern, central, and southern regions. The wider range of NMS axis 1 scores observed during the 2000s appears to be due to increased abundances of alien fishes, particularly centrarchids, in the eastern, central, and southern regions compared with the 1980s. This change appears largest for the southern region. Correlations of the CPUE characteristics with the other two NMS axes were less strong ($r < 0.45$; Fig. 5). The correlations with NMS axis 2 indicate differences in total and alien fish CPUE independent of centrarchid CPUE. The correlations with NMS axis 3 appear to indicate minor differences in total, alien, and native fish CPUE independent of centrarchid CPUE.

The BVSTEP procedure identified a set of 8 influential species (Table 5). The model that included these 8 species was selected as the best model by the stepwise procedure in 54 cases out of 100. No other model was selected more than four times. Examination of CPUE for these species supported many of the general patterns described earlier. CPUE of the centrarchids, bluegill *Lepomis macrochirus,* largemouth bass, and redear sunfish *Lepomis microlophus* exhibited large increases from the 1980s to the 2000s in the central, eastern, and southern regions. CPUE of the native tule perch declined in all regions but particularly the northern region. The CPUE of white catfish *Ameiurus catus* declined throughout the Delta, but particularly in the southern region.

FISHES AND ENVIRONMENT

The BIO-ENV procedure indicated that little of the variance in fish community composition could be explained by the environmental variables measured. The best model included water temperature, specific conductance, Secchi depth, and water depth, but the Spearman rank correlation between these environmental variables and fish assemblage composition was only 0.21.

The greater frequency of SAV in the 2000s compared with the 1980s (Table 1) coincided with higher CPUE for total fish, alien fish, and centrarchid fish in the 2000s compared with the 1980s, especially for the eastern and central regions (Fig. 4). This suggested that the presence of SAV was affecting the abundance of fishes, although a similar increase in the occurrence of SAV in the western region was not associated with increased CPUE. Region and the presence of SAV were statistically significant factors in all three two-way ANOVAs (Table 4). The interaction term was not statistically significant in any of the analyses. The 95% confidence interval for mean CPUE in the northern region was extremely broad for all three variables because of a wide range in values for the three sampling reaches with SAV (Fig. 6). These results were not affected by differences in sampling methods between periods because only 2000s data were analyzed.

The failure of the western region to conform to the pattern of increased CPUE of alien and centrarchid fishes with increased SAV may simply be due to electrofishing efficiency. During the 2000s in the western region, specific conductance exceeded 1,000 μS cm^{-1} at 29% of the sample reaches, resulting in poorly stunned fish. The western region sampling reaches also had some of the widest, windiest, and steepest channels, resulting in the most challenging sampling conditions in the study area (Michniuk personal observation).

Discussion

The dominance of alien fishes in the littoral habitats of the Delta was not unexpected. Feyrer and Healey (2003) documented a similar dominance of alien fishes in an electrofishing study restricted to the southern region. Low abundance of native species has also been documented in a seining

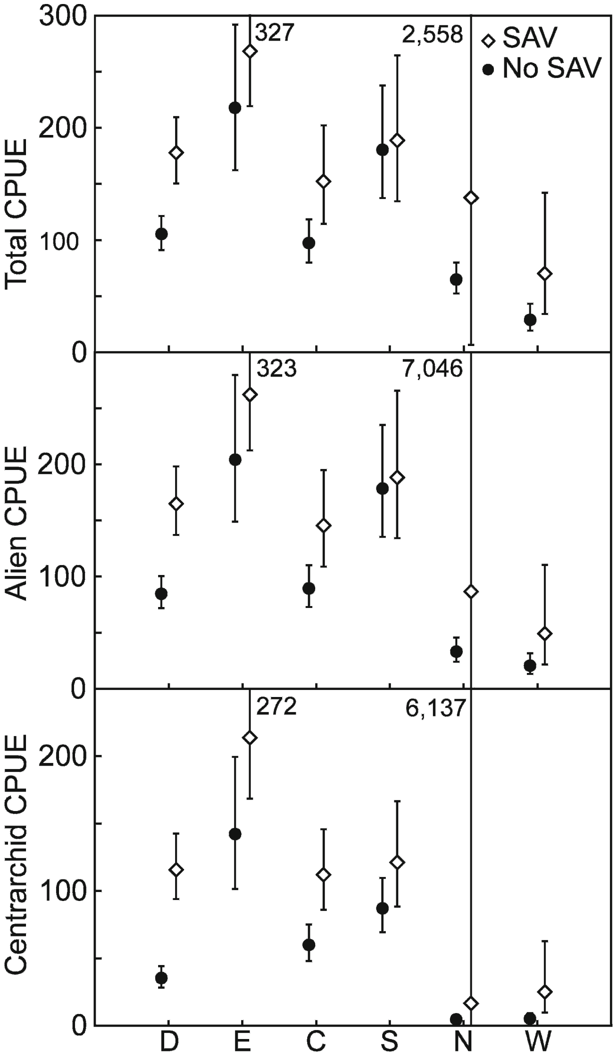

Fig. 6. Mean and 95% confidence intervals (back-transformed from $\log_{10}$-transformed values) for catch per unit effort (CPUE, fish km^{-1}) of total fish, alien fish, and centrarchid fish for sampling reaches with and without submerged aquatic vegetation (SAV) for reaches sampled between April 2001 and April 2003. Values are given for the entire Delta (D) and five regions within the Delta (C: central; E: eastern; N: northern; S: southern; W: western). Numbers next to confidence intervals indicate values outside of the range of the graph.

study at four locations within the Delta (Nobriga et al. 2005). Overall, the lists of species captured within the Delta were similar in the 1980s and 2000s (Table 3), but the presence or absence of rare species should be interpreted with caution. The greater reach length sampled in the 1980s would increase the probability of capturing rare species in a particular reach; the relatively similar total distance of littoral habitat sampled during both periods likely reduces this bias. The BVSTEP procedure also showed that 8 of the 10 most abundant species were most responsible for the patterns observed in fish assemblage composition and rare species had little influence.

Alien fishes likely dominated the littoral habitats of the Delta for many decades prior to the sampling in the 1980s. Many of the common alien species were deliberately introduced to California over 100 years ago (Dill and Cordone 1997). The recent expansion of *E. densa* appears to have allowed for greater CPUE of alien fishes, particularly centrarchids, but has not greatly altered overall fish assemblage composition. It seems likely that the littoral habitats and associated fishes will remain largely unchanged for the near future, barring major new invasions or changes in water management operations or Delta infrastructure that cause salinities lethal to *E. densa* (about 5‰, Haunstein and Ramirez 1986). The main control of SAV abundance in natural river systems appears to be high velocities related to flooding (Wilcock et al. 1999; Champion and Tanner 2000), a factor not likely to be important in a tidal system, where water velocities are more sensitive to tides than to inflow. *E. densa* now covers about 7.8% of the surface area of the Delta and dominates littoral and other shallow water habitats. Chemical control of SAV is being considered for about half of the area currently dominated by *E. densa* (California Department of Boating and Waterways 2001), which could cause shifts in CPUE back to 1980s values in treated areas.

The relationship between fish CPUE and SAV abundance is certainly not surprising from the work done by others on native habitats of the alien species. Killgore et al. (1989) documented a similar relationship in the Potomac River where expansion of SAV was associated with greater species richness and greater abundance of fish including several species commonly captured in the Delta, inland silverside *Menidia beryllina* and largemouth bass. Areas with SAV beds had seven times more fish than unvegetated areas. This relationship between aquatic vegetation and fish production has been well established in nontidal freshwater habitats and has been attributed to increased food and cover within beds of aquatic macrophytes (Conrow et al. 1990; Miranda and Pugh 1997; Grenouillet et al. 2000; Tate et al. 2003). Numerous studies have explored relationships between SAV and centrarchid abundance (e.g., Crowder and Cooper 1982; Durocher et al. 1984; Colle et al. 1987; Unmuth and Hansen 1999; Bettoli et al. 1993), predation efficiency (e.g., Savino and Stein 1982; Gocietas and Colgan 1987; Hayse and Wissing 1996), and interspecific interactions (e.g., Werner and Hall 1979; Osenberg et al. 1987; Nibbelink and Carpenter 1998). The interesting feature in the Delta is that an alien plant from South America is providing habitat for a variety of alien fishes from eastern North America with minimal integration of the native fish fauna. This new ecosystem appears to be trophically isolated from the adjacent pelagic ecosystem (Grimaldo et al. 2004b).

The lack of change between the 1980s and the 2000s in the northern region and perhaps the western region, given possible sampling efficiency problems, may be related to possible sources of immigrants as well as presence or absence of SAV. The Sacramento River is likely an important source of native fishes to the northern and western regions. Two of the native species commonly captured in the northern region—Sacramento sucker *Catostomus occidentalis* and Sacramento pikeminnow *Ptychocheilus grandis*—are riffle spawners (Moyle 2002) and cannot complete their life cycle in the Delta, which is dominated by fine substrates. These species spawn in upstream riverine areas and juveniles and adults move into the Delta (Nobriga et al. 2006; Brown and May 2006). Delta larval fish sampling supports the idea that these stream-oriented species do not spawn in the Delta (Dege and Brown 2004; Feyrer 2004; Grimaldo et al. 2004a). The Sacramento River and its tributaries still maintain healthy populations of native fishes (May and Brown 2002; Seesholtz et al. 2004), but the San Joaquin River does not (Brown 2000); so the San Joaquin River does not serve as a major source of native fishes for the southern region, except in very wet years. The native tule perch and prickly sculpin *Cottus asper* can complete their life cycle in the Delta, but may benefit from both immigration from upstream areas and reduced competition and predation from alien fishes that are not as abundant in the northern and western regions. The Sacramento River is also the major spawning river for striped bass in the system (Turner and Chadwick 1972; Stevens 1977), which may contribute to constancy of fish assemblage composition over time.

The decreased native fish CPUE in the 2000s compared with the 1980s may partially be a response to flow conditions. Native species generally have greater spawning success during higher flow years (Brown 2000; Marchetti and Moyle 2000, 2001; Brown and Ford 2002; Feyrer and Healey 2003). The greater flows throughout the 1980s sampling period, particularly in the winter of 1979 and spring of 1980 just as sampling began, likely produced strong year classes of native fishes that were sampled throughout the remainder of the 1980s. The period from 1995 to 2000, leading up to the 2000s sampling period was also quite wet (DAYFLOW database http://iep.water.ca.gov/dayflow/index.html), so the role of flow is arguable.

The primary concern regarding alien fishes, particularly centrarchids, in the Delta has been that they will prey on or compete with native fishes (Brown 2003a). The predatory role of *Micropterus* basses in California freshwater systems is well established (Moyle 2002; Moyle et al. 2003; Gard 2004). The decline of native fish CPUE concurrent with an increase in centrarchid fish CPUE is compatible with this concern, but the largest decline in native fish CPUE occurred in the northern region where centrarchid CPUE was unchanged. We conclude our data and analyses do not support any particular explanation for the decline in native fish CPUE.

Understanding the role of *E. densa* and alien fishes in the Delta has important management implications. Native fish restoration in the Delta was originally predicated on a conceptual model that assumed native fishes were habitat limited and that restoration of tidal wetland habitat would increase abundances of native species by reestablishing favored habitat and associated ecosystem processes (Kimmerer et al. 2005). This assumption seemed reasonable given that 95% of Delta tidal wetlands had been lost concurrent with the declines in native fishes (The Bay Institute 1998). That conceptual model largely ignored the role of alien species. Given the results of this study, restoration of tidal wetlands is most likely to benefit native fishes in the northern region where *E. densa* is not well established, alien fishes are relatively rare, native fishes are most abundant, and there are upstream sources of immigrants of some native species. Tidal wetland restoration in other regions of the Delta is more likely to provide additional nearshore habitat for *E. densa* and the alien fishes it favors. Recent studies suggest that floodplain restoration rather than tidal restoration may have more benefits for native fishes (Sommer 2001a,b; Crain et al. 2004).

Managing complex ecosystems is difficult at best, especially when there are multiple goals and substantial uncertainty regarding the outcome of management actions. Well-formulated conceptual models regarding important processes and sources of uncertainty can be useful tools in guiding management (Walters 1986; Kimmerer et al. 2005) and in fostering the interdisciplinary understanding necessary for successful collaborative studies of environmental problems (Benda et al. 2002). Any conceptual model addressing the Delta should include the roles of alien species in ecosystem processes and specifically the role of *E. densa.* Indeed, *E. densa* may be having additional unsuspected effects on the Delta ecosystem. Submerged aquatic macrophytes are known to affect phytoplankton production in lakes (Scheffer 1999; Mazzeo et al. 2003) and hydrodynamics and physicochemical properties of streams (Wilcock et al. 1999; Champion and Tanner 2000). It seems likely that *E. densa* is having similar but as yet undocumented effects in the Delta. Understanding such effects may be essential to the proper management and restoration of this highly altered ecosystem.

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Literature Cited

Benda, L. E., N. L. Poff, C. Tague, M. A. Palmer, J. Pizzuto, S. Cooper, E. Stanley, and G. Moglen. 2002. How to avoid train wrecks when using science in environmental problem solving. *BioScience* 52:1127–1136.

Bennett, W. A. and P. B. Moyle. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento-San Joaquin estuary, p. 519–542. *In* J. T. Hollibaugh (ed.), San Francisco Bay: The ecosystem, further investigations into the natural history of San Francisco Bay and Delta with reference to the influence of man. Pacific Division of the American Association for the Advancement of Science, San Francisco, California.

Bettoli, P. W., M. J. Maciena, R. L. Noble, and R. K. Betsill. 1993. Response of a reservoir fish community to aquatic vegetation removal. *North American Journal of Fisheries Management* 13:110–124.

Brown, L. R. 2000. Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes* 57:251–269.

Brown, L. R. 2003a. Will tidal wetland restoration enhance populations of native fishes? p. 1–42. *In* L. R. Brown (ed.), Issues in San Francisco Estuary Tidal Wetlands Restoration. *San Francisco Estuary and Watershed Science.* Volume 1, Issue 1, Article 2. http://repositories.cdlib.org/jmie/sfews/vol1/iss1/art2.

Brown, L. R. 2003b. Potential effects of organic carbon production on ecosystems and drinking water, p. 1–22. *In* L. R. Brown (ed.), Issues in San Francisco Estuary Tidal Wetlands Restoration. *San Francisco Estuary and Watershed Science.* Volume 1, Issue 1, Article 3. http://repositories.cdlib.org/jmie/sfews/vol1/iss1/art3.

Brown, L. R. and T. J. Ford. 2002. Effects of flow on the fish communities of a regulated California river: Implications for managing native fishes. *River Research and Applications* 18:331–342.

Brown, L. R. and J. T. May. 2006. Variation in Spring nearshore resident fish species composition and life histories in the lower Sacramento-San Joaquin Watershed and Delta. *San Francisco Estuary and Watershed Science.* Volume 4, Issue 2, Article 1. http://repositories.cdlib.org/jmie/sfews/vol4/iss3/art1.

Champion, P. D. and C. C. Tanner. 2000. Seasonality of macrophytes and interaction with flow in a New Zealand lowland stream. *Hydrobiologia* 441:1–12.

Clarke, K. R. and R. M. Warwick. 2001. Change in Marine Communities: An approach to statistical analysis and interpretation, 2nd edition. Primer-E, Plymouth, U.K.

Cloern, J. E. and F. H. Nichols (eds.). 1985. Temporal Dynamics of an Estuary: San Francisco Bay. Kluwer, Dordrecht, The Netherlands.

Colle, D. E., J. V. Shireman, W. T. Haller, J. C. Joyce, and D. E. Canfield, Jr. 1987. Influence of Hydrilla on harvestable sport fish populations, angler use, and angler expenditures at Orange Lake, Florida. *North American Journal of Fisheries Management* 7:410–417.

Conomos, T. J. (ed.). 1979. San Francisco Bay: The urbanized estuary, investigations into the natural history of San Francisco Bay and Delta with reference to the influence of man. American Association for the Advancement of Science, San Francisco, California.

Conrow, R., A. V. Zale, and R. W. Gregory. 1990. Distributions and abundances of early life stages of fishes in a Florida USA lake dominated by aquatic macrophytes. *Transactions of the American Fisheries Society* 119:521–528.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, and J. Paruelo. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–260.

Covich, A. 1993. Water and ecosystems, p. 40–55. *In* P. H. Gleick (ed.), Water in Crisis: A guide to the world's fresh water resources. Oxford University Press, New York.

Crain, P. K., K. Whitener, and P. B. Moyle. 2004. Use of a restored central California floodplain by larvae of native and alien fishes, p. 125–140. *In* F. Feyrer, L. R. Brown, R. L. Brown, and J. J. Orsi (eds.), Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland.

Crowder, L. B. and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813.

Dege, M. and L. R. Brown. 2004. Springtime distribution and abundance of larval and juvenile fishes in the upper San Francisco Estuary, p. 49–66. *In* F. Feyrer, L. R. Brown, R. Brown, and J. Orsi (eds.), Early Life History of Fishes in the San Francisco Estuary and Watershed, Symposium 39. American Fisheries Society, Bethesda, Maryland.

Dill, W. A. and A. J. Cordone. 1997. History and status of introduced fishes in California, 1871–1996. Fishery Bulletin 178. California Department of Fish and Game, Sacramento, California.

Durocher, P. P., W. C. Provine, and J. E. Kraai. 1984. Relationship between abundance of largemouth bass and submerged vegetation in Texas reservoirs. *North American Journal of Fisheries Management* 4:84–88.

Feyrer, F. 2004. Ecological segregation of native and alien larval fish assemblages in the southern Sacramento–San Joaquin Delta, p. 67–79. *In* F. Feyrer, L. R. Brown, R. L. Brown, and J. J. Orsi (eds.), Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland.

Feyrer, F. and M. P. Healey. 2003. Fish community structure and environmental correlates in the highly altered southern Sacramento–San Joaquin Delta. *Environmental Biology of Fishes* 66:123–132.

Gard, M. 2004. Interactions between an introduced piscivore and a native piscivore in a California stream. *Environmental Biology of Fishes* 71:287–295.

Gocietas, V. and P. Colgan. 1987. Selection between densities of artificial vegetation by young bluegills avoiding predation. *Transactions of the American Fisheries Society* 116:40–49.

Grenouillet, G., D. Pont, and J. M. Olivier. 2000. Habitat occupancy patterns of juvenile fishes in a large lowland river: Interactions with macrophytes. *Archiv Fuer Hydrobiologie* 149: 307–326.

Grimaldo, L. F., R. E. Miller, C. M. Peregrin, and Z. P. Hymanson. 2004a. Spatial and temporal distribution of native and alien ichthyoplankton in three habitat types of the Sacramento–San Joaquin Delta, p. 81–96. *In* R. Feyrer, L. R. Brown, R. L. Brown, and J. J. Orsi (eds.), Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland.

Grimaldo, L. F., W. Kimmerer, and A. R. Stewart. 2004b. Diet and carbon sources supporting fishes from open-water, edge and SAV habitats in restored freshwater wetlands of the San

Francisco Estuary. M.S. Thesis, San Francisco State University, San Francisco, California.

Haunstein, E. and C. Ramirez. 1986. The influence of salinity on the distribution of *Egeria densa* in the Valdivia River Basin Chile. *Archiv Fuer Hydrobiologie* 107:511–520.

Hayse, J. W. and T. E. Wissing. 1996. Effects of stem density of artificial vegetation on abundance and growth of age-0 bluegills and predation by largemouth bass. *Transactions of the American Fisheries Society* 125:422–433.

Hollibaugh, J. T. (ed.). 1996. San Francisco Bay: The ecosystem, further investigations into the natural history of San Francisco Bay and Delta with reference to the influence of man. American Association for the Advancement of Science, San Francisco, California.

Jacobs, K. L., S. N. Luoma, and K. A. Taylor. 2003. CALFED: An experiment in science and decision making. *Environment* 45:30–41.

Jennings, M. R. and M. K. Saiki. 1990. Establishment of red shiner, *Notropis lutrensis*, in the San Joaquin Valley, California. *California Fish and Game* 76:46–57.

Killgore, K. J., R. P. Morgan, II, and N. B. Rybicki. 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac River. *North American Journal of Fisheries Management* 9:101–111.

Kimmerer, W. J. 2004. Open water processes of the San Francisco Estuary: From physical forcing to biological response. *San Francisco Estuary and Watershed Science*. Volume 2, Issue 1 (February 2004), Article 1. Available: http://repositories.cdlib.org/jmie/sfews/vol2/iss1/art1. (27 May 2005).

Kimmerer, W. J., D. D. Murphy, and P. L. Angermeier. 2005. A landscape-level model for ecosystem restoration in the San Francisco Estuary and watershed. *San Francisco Estuary and Watershed Science*. Volume 3, Issue 1 (March 2005), Article 2. Available: http://repositories.cdlib.org/jmie/sfews/vol3/iss1/art2. (27 May 2005).

Kruskal, J. B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1–27.

Kruskal, J. B. 1964b. Nonmetric multidimensional scaling: A numerical method. *Psychometrika* 29:115–129.

Lindley, S. T. and M. S. Mohr. 2003. Modeling the effect of striped bass (*Morone saxatilis*) on the population viability of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*). *Fishery Bulletin* 101:321–331.

Marchetti, M. P. and P. B. Moyle. 2000. Spatial and temporal ecology of native and introduced larval fish in lower Putah Creek (Yolo Co. CA). *Environmental Biology of Fishes* 58:75–87.

Marchetti, M. P. and P. B. Moyle. 2001. Keeping alien fishes at bay: Effects of flow regime and habitat structure on fish assemblages in a regulated California stream. *Ecological Applications* 11:75–87.

Mather, P. M. 1976. Computational Methods of Multivariate Analysis in Physical Geography. John Wiley and Sons, London, England.

May, J. T. and L. R. Brown. 2002. Fish community structure in relation to environmental variation within the Sacramento River Basin and implications for streams of the Central Valley, California. *Environmental Biology of Fishes* 63:373–388.

Mazzeo, N., L. Rodriguez-Gallego, C. Kruk, M. Meerhoff, J. Gorga, G. Lacerot, F. Quintans, M. Loureiro, D. Larrea, and F. Garcia-Rodriguez. 2003. Effects of *Egeria densa* Planch beds on a shallow lake without piscivorous fish. *Hydrobiologia* 506–509:591–602.

McCune, B. and J. B. Grace. 2002. PC-ORD. Analysis of Ecological Communities. MjM Software Design, Gleneden Brach, Oregon.

Miranda, L. E. and L. L. Pugh. 1997. Relationship between vegetation coverage and abundance, size, and diet of juvenile largemouth bass during winter. *North American Journal of Fisheries Management* 17:601–610.

Moyle, P. B. 2002. Inland Fishes of California, revised and expanded. University of California Press, Berkeley, California.

Moyle, P. B., P. K. Crain, K. Whitener, and J. F. Mount. 2003. Alien fishes in natural streams: Fish distribution, assemblage structure, and conservation in the Cosumnes River, California, U.S.A. *Environmental Biology of Fishes* 68:143–162.

Nibbelink, N. P. and S. R. Carpenter. 1998. Interlake variation in growth and size structure of bluegill (*Lepomis macrochirus*): Inverse analysis of an individual-based model. *Canadian Journal of Fisheries and Aquatic Sciences* 55:387–396.

Nobriga, M. L., F. Feyrer, and R. D. Baxter. 2006. Aspects of Sacramento pikeminnow biology in nearshore habitats of the Sacramento–San Joaquin Delta, California. *Western North American Naturalist* 66:106–114.

Nobriga, M. L., F. Feyrer, R. D. Baxter, and M. Chotkowski. 2005. Fish community ecology in an altered river delta: Spatial patterns in species composition, life history strategies, and biomass. *Estuaries* 28:776–785.

Osenberg, C. W., E. E. Werner, G. G. Mittlebach, and D. J. Hall. 1987. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*Lepomis gibbosus*) sunfish: Environmental variation and the importance of ontogenetic niche shifts. *Canadian Journal of Fisheries and Aquatic Sciences* 45:17–26.

Petts, G. and P. Calow (eds.). 1996. River Biota Diversity and Dynamics. Blackwell Science, Oxford, U.K.

Postel, S. L. 1996. Dividing the Waters: Food security, ecosystem health, and the new politics of scarcity. Worldwatch Institute, Washington, D.C.

Postel, S. L. 2000. Entering an era of water scarcity: The challenges ahead. *Ecological Applications* 10:941–948.

Postel, S. L. and S. Carpenter. 1997. Freshwater ecosystem services, p. 195–214. *In* G. C. Daily (ed.), Nature's Services: Societal dependence on natural ecosystems. Island Press, Washington D.C.

PRIMER-E. 2005. PRIMER 6 (beta version 10). PRIMER-E, Plymouth, UK.

Savino, J. F. and R. A. Stein. 1982. Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Transactions of the American Fisheries Society* 111:255–265.

Scheffer, M. 1999. The effect of aquatic vegetation on turbidity: How important are the filter feeders? *Hydrobiologia* 408–409: 307–316.

Seesholtz, A., B. J. Cavallo, J. Kindopp, and R. Kurth. 2004. Juvenile fishes of the lower Feather River: Distribution, emigration patterns, and associations with environmental variables, p. 141–166. *In* F. Feyrer, L. R. Brown, R. L. Brown, and J. J. Orsi (eds.), Early Life History of Fishes in the San Francisco Estuary and Watershed. American Fisheries Society, Symposium 39, Bethesda, Maryland.

Sommer, T., B. Harrell, M. Nobriga, R. Brown, P. Moyle, W. Kimmerer, and L. Schemel. 2001a. California's Yolo Bypass: Evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. *Fisheries* 26:6–16.

Sommer, T., M. L. Nobriga, W. C. Harrell, W. Batham, and W. Kimmerer. 2001b. Floodplain rearing of juvenile chinook salmon: Evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58:325–333.

Stevens, D. E. 1977. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento–San Joaquin Estuary, California. *Transactions of the American Fisheries Society* 106:34–42.

SYSTAT. 2002. SYSTAT 10.2 Statistics I. SYSTAT Software, Richmond, California.

Tate, W. B., M. S. Allan, R. A. Meyers, E. J. Nagid, and J. R. Estes. 2003. Relation of age-0 largemouth bass abundance to Hydrilla coverage and water level at Lochloosa and Orange Lakes, Florida. *North American Journal of Fisheries Management* 23:251–257.

The Bay Institute. 1998. From the Sierra to the Sea. The Bay Institute, San Rafael, California.

TURNER, J. L. AND H. K. CHADWICK. 1972. Distribution and abundance of young-of-the-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento–San Joaquin Estuary. *Transactions of the American Fisheries Society* 101:442–452.

TURNER, J. L. AND D. W. KELLEY. 1966. Ecological studies of the Sacramento–San Joaquin Delta, Part II, fishes of the Delta. California Department of Fish and Game, Fish Bulletin 136, Sacramento, California.

UNMUTH, J. M. L. AND M. J. HANSEN. 1999. Effects of mechanical harvesting of Eurasian watermilfoil on largemouth bass and bluegill populations in Fish Lake, Wisconsin. *North American Journal of Fisheries Management* 19:1089–1098.

WALTERS, C. J. 1986. Adaptive Management of Renewable Resources. MacMillan, New York.

WERNER, E. E. AND D. J. HALL. 1979. Foraging efficiency and habitat switching in competing sunfishes. *Ecology* 60:256–264.

WILCOCK, R. J., P. D. CHAMPION, J. W. NAGELS, AND G. F. CROKER. 1999. The influence of aquatic macrophytes on the hydraulic and physico-chemical properties of a New Zealand lowland stream. *Hydrobiologia* 416:203–214.

SOURCES OF UNPUBLISHED MATERIALS

CALIFORNIA BAY–DELTA AUTHORITY. 2005. Sacramento, California, Available: http://calwater.ca.gov/ (3 May 2005).

CALIFORNIA DEPARTMENT OF BOATING AND WATERWAYS. 2001. Environmental impact report, *Egeria densa* control program. California Department of Boating and Waterways, Sacramento, California. Available: http://dbw.ca.gov/PDF/EIR/eir.pdf (12 May 2005).

CHESAPEAKE BAY PROGRAM. 2005. Annapolis, Maryland, Available: http://www.chesapeakebay.net/index_cbp.cfm (3 May 2005).

COMPREHENSIVE EVERGLADES RESTORATION PLAN. 2005. West Palm Beach, Florida, Available: http://www.evergladesplan.org/index.cfm (3 May 2005).

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