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Native and Alien Fishes in a California Estuarine Marsh: Twenty-One Years of Changing Assemblages

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Abstract.—We used monthly otter trawling and beach seining to sample the fishes of Suisun Marsh in the San Francisco Estuary from 1979 to 1999. We collected nearly 173,000 fish, mostly young of the year, representing 28 native species and 25 alien species. Catch data were related to temperature, salinity, water transparency, and several measures of freshwater inflow into the marsh. Species abundance and distribution within the marsh were the product of several interacting factors: (1) the timing and place of reproduction of the abundant resident species, (2) past reproductive success, (3) habitat differences among sloughs, and (4) physiological tolerance. We did not find consistent groups of potentially interacting species, although some native species showed weak concordance in abundance. The lack of persistent fish assemblages is related to the naturally fluctuating environmental conditions of the estuary, the overall decline in fish abundance through time, and the frequent invasions of alien fishes and invertebrates. Our results suggest that the fish assemblages in Suisun Marsh will continue to be unpredictable until estuarine processes approach their historic range of variability and alien invasions are halted.

Estuaries are geologically transient habitats with strong, fluctuating environmental gradients. Worldwide, they are highly perturbed by human activity because they are the most downstream recipients of changes in watersheds and are sites of major urban areas. As a consequence, fish distribution and abundance is considered to be largely driven by abiotic factors, especially salinity, temperature, and pollutants (e.g., Peterson and Ross 1991; Cyrus and Blaber 1992; Thiel et al. 1995). However, the regular occurrence of groups of species (assemblages) that segregate in part by diet and habitat use suggests that the assemblages have some degree of structure, presumably the result of coevolution and continued species interactions. Most of the studies showing structured, persistent assemblages (communities) have been relatively short term and have taken place in estuaries with few human-caused additions or deletions and/or low species diversity (e.g., Thorman 1982; Baltz et al. 1993; Humphries and Potter 1993; Able et al. 2001; Methven et al. 2001). However, even a 5-year study in Suisun Marsh, which is part of the highly disturbed San Francisco Estuary, California, showed distinct assemblages made up of native and alien fishes (Moyle et al. 1986) that appeared to have some structure based on habitat use and diet (Herbold 1987). After 13 years, the assemblages were arguably still present, although their structure was much less evident (Meng et al. 1994). In this paper, we report on the Suisun Marsh fish assemblages after 21 years of sampling.

The San Francisco Estuary is one of the largest and most hydrologically complex estuaries on the Pacific coast of North America. While the present estuary is only around 10,000 years old, there has been a large estuary in the region for millions of years and the upper portion once supported a complex, highly endemic fish fauna (Moyle 2002). Today it is one of the most altered estuaries in the world, and many of the endemic fishes are extinct or rare (Nichols et al. 1986). The uppermost part of the estuary, the Sacramento–San Joaquin Delta, was once a vast marshland, but it has been diked and drained to create farmland. Likewise, tidal marshes surrounding the middle (Suisun Bay and Marsh) and lower (San Francisco Bay) parts of the estuary have also been diked and drained (Nichols et al. 1986). Much of the freshwater inflow has been diverted, resulting in major changes in estuarine hydrology, especially during years of low

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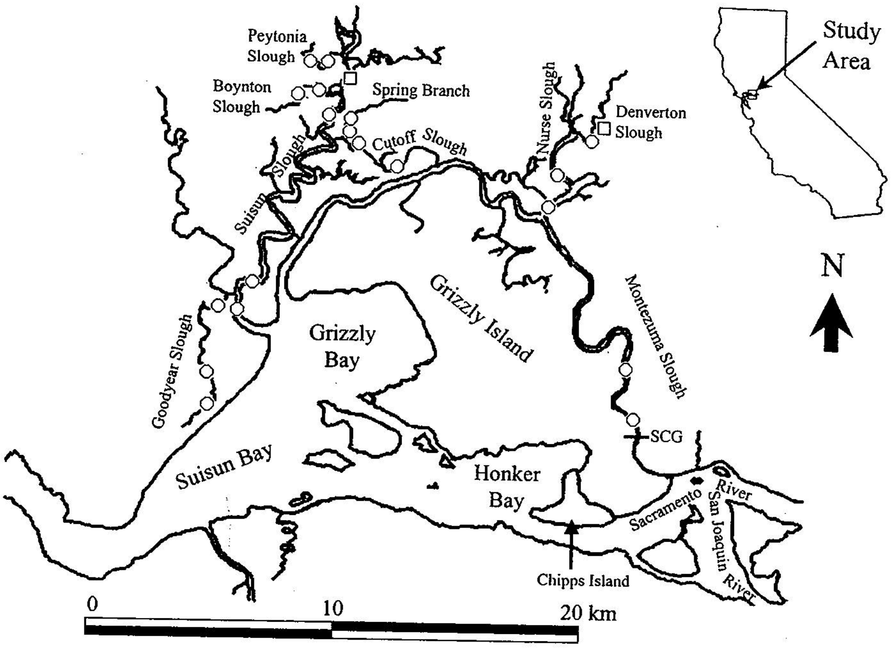

FIGURE 1.—Suisun Marsh, San Francisco Estuary, California. Circles represent sites where trawling was conducted, squares sites where both trawling and beach seining were conducted. The salinity control gates (SCG) in Montezuma Slough began operating in 1988.

precipitation (Nichols et al. 1986; Bennett and Moyle 1996). The estuary has also been characterized as one of the most invaded estuaries in the world, with new aquatic species becoming established at the rate of one every 14 weeks during the 1961–1995 period (Cohen and Carlton 1998). Some of the invaders are major factors in ecosystem dynamics. For example, striped bass *Morone saxatilis*, which were introduced in the 1870s, quickly became the dominant piscivore, replacing native piscivores (Moyle 2002). In the 1980s, the overbite clam *Potamocorbula amurensis* became enormously abundant (Alpine and Cloern 1992), severely depleting the phytoplankton and directly or indirectly affecting all lower trophic levels in Suisun and San Francisco bays (Kimmerer and Orsi 1996), major rearing areas for estuarine fish. In contrast, the invasion of the shimofuri goby *Tridentiger bifasciatus* in the 1980s appears to have had little impact on other fishes or invertebrates even though it is now one of the most common fish in the estuary (Matern and Fleming 1995; Matern 1999). Thus, the estuary provides an opportunity to explore the nature of estuarine fish assemblages by examining the role that alien invaders play in structuring them.

We analyzed 21 years of monthly otter trawl and beach seine data to answer the following questions: (1) How do seasonal patterns of fish abundance and diversity relate to environmental variation? (2) Do resident native species, resident alien species, and seasonal species show different long-term patterns in abundance? (3) Are there groups of co-occurring species with patterns of abundance that respond in similar ways to changes in temperature, salinity, and freshwater inflow? (4) Are there differences in species composition in different parts of the marsh related to local environmental characteristics?

Methods

Study area.—Suisun Marsh is a large (about 340 km^2), brackish tidal marsh in the San Francisco Estuary (Figure 1). This hydrologically complex marsh receives most of its freshwater at the eastern end of Montezuma Slough near the confluence of the Sacramento and San Joaquin rivers, but several small creeks also deliver freshwater into some sloughs. In the western portion of the marsh, tidal action forces water from Grizzly Bay into the downstream ends of Suisun and Montezuma sloughs. About two-thirds of the marsh consists primarily of diked wetlands that are managed by hunting clubs to attract wintering waterfowl; the remainder consists of tidally influenced sloughs (Meng et al. 1994). The tide's primary influence is on the volume of water present in the sloughs, with salinity being only minimally affected. Instead, salinity in Suisun Marsh varies seasonally because most rain falls during winter and early spring, creating freshwater inflows that are often 20 times higher than early fall inflows. In recent years salinities have ranged from 0‰ to 16‰, with the highest salinities occurring in early fall of drought years and the lowest salinities in early spring when freshwater inflows to the marsh are highest. In an effort to maintain historical salinity levels in the western marsh in the face of low freshwater inflow and increasing upstream water exports, salinity control gates were installed in Montezuma Slough (Figure 1) and began operating in 1988.

The sloughs in Suisun Marsh vary in salinity, water transparency, size (length, width, and depth), and the intensity of water diversion (Table 1). Suisun and Montezuma sloughs are the most prominent and are wide, deep, and heavily riprapped and have many diversions. The other major slough, Nurse Slough, which is located in the eastern part of Suisun Marsh, is short, wide, and intermediate in depth and has few diversions. These three sloughs connect with many smaller ones that are relatively narrow and shallow, are lined with tules *Scirpus* spp. and common reeds *Phragmites communis* (Meng et al. 1994), and are subjected to varying degrees of water diversion. Water depth fluctuates 1 m during spring tides, and the smallest sloughs (not sampled) can be completely dewatered during extremely low tides. However, tidal ranges are generally much less than 1 m, and none of our sample sites became dewatered at low tide.

Field methods.—We conducted monthly sampling in nine sloughs in the marsh. Because Suisun and Montezuma sloughs are so long, we distinguished upper and lower reaches for our analyses. Each slough was sampled with an otter trawl at two or three sites each month. From 1979 to 1999, we sampled in Peytonia, Boynton, upper Suisun, lower Suisun, Goodyear, Cutoff, Spring Branch, and upper Montezuma sloughs. Nurse and Denverton sloughs were sampled infrequently from 1981 to 1985, and regular monthly sampling in these sloughs began in 1994. We augmented our otter trawling effort with beach seining conducted monthly at two locations. Upper Suisun Slough was sampled from 1979 to 1999, while Denverton Slough was sampled irregularly from 1981 to 1986 and monthly from 1994 to 1999 (Figure 1).

We used a four-seam otter trawl with a 1-m × 2.5-m opening, a length of 5.3 m, and mesh sizes of 35 mm stretch in the body and 6 mm stretch in the bag. We trawled at approximately 4 km/h for 5 min in the smaller sloughs and for 10 min in upper Suisun, lower Suisun, and upper Montezuma sloughs, where catches were lower. Although insufficient to capture all species present, these relatively short trawling times were necessitated by the small size of some sloughs, our desire to conduct at least two trawls per slough, and our goal of minimizing mortality, especially of species listed as threatened by state and federal agencies. Our concerns about inadequately sampling the fishes (species–area curves) were assuaged by pooling data from multiple trawls and making broad-scale use of the data. To minimize the possible effects of diel variation (e.g., increased catch of pelagic species at night), all trawls were conducted in daylight between 0500 and 2059 hours. To increase the capture of small individuals and edge-associated species, seining was conducted with a 10-m beach seine with a stretched mesh size of 6 mm. Based on the size of the available beaches, we typically made three seine hauls perpendicular to the beach in upper Suisun Slough and two in Denverton Slough. At both beaches we made an additional seine haul along the shoreline parallel to the beach. Each haul covered approximately 200 m^2, and none of the hauls overlapped spatially. Biases due to methodology or gear efficiency (Hartman and Herke 1987; Yoklavich et al. 1991; Allen et al. 1992; Rozas and Minello 1997) were indisputably present (e.g., undersampling of large fish and pelagic species) but were consistent over the course of this study, so that comparisons should be unaffected.

The contents of each trawl or seine were placed into large containers of water. Fishes were identified, measured to the nearest millimeter standard length (SL), and returned to the site of capture. At each site we measured water transparency (Secchi depth in centimeters) and used a Yellow Springs Instruments salinity–conductivity–temperature meter to measure temperature (°C) and salinity (‰). All catch and environmental data collected as part of this study are available online from the California Department of Water Resources (DWR 2001). Slough width, length, maximum depth, and number of diversions were obtained from maps or field observations or with the help of the California Department of Water Resources and the California Department of Fish and Game. As an index of freshwater inputs to the marsh, we obtained indices

TABLE 1.—Physical characteristics and catch data for the nine sloughs in Suisun Marsh, California, sampled duri 1979–1999. Temperature (°C), salinity (‰), and transparency (Secchi depth in cm) are for all years sampled. Diversio area refers to the total cross-sectional area of the diversion opening. Common lowercase letters denote means that a not significantly different as determined by a sum of squares–simultaneous test procedure.

Variable	Slough				
	Boynton	Cutoff	Denverton	Goodyear	Lower Montezuma
			Characteristic		
Mean temperature (range)	16.8 (4.9–25.5) z	16.9 (4.9–27.0) z	16.9 (5.7–25.5) z	16.7 (4.6–27.0) z	16.1 (4.0–24.5) z
Mean salinity (range)	2.5 (0.0–11.2) z	3.6 (0.0–11.8) y	2.6 (0.0–9.5) zy	5.2 (0.0–16.0) w	2.2 (0.0–10.0) z
Mean transparency (range)	19 (8–48) z	22 (7–57) yx	22 (8–60) zyx	21 (4–52) zyx	30 (3–74)
Mean width (m)	35	39	68	25	102
Maximum depth (m)	2	1	4	4	9
Length (km)	5.1	6.4	4.9	10.7	33.9
Number of diversions	12	4	6	33	106
Diversions/km	2.4	0.6	1.2	3.1	3.1
Diversion area (m^3)	6.5	3.0	3.5	23.9	60.3
Diversion area/km	1.3	0.5	0.7	2.2	1.8
			Catch data		
Species/min	0.645 xw	0.795	0.755 wv	0.675 wv	0.242 z
Shannon's diversity index	0.531 xwv	0.553 wv	0.479 zyxw	0.608	0.406 zy
Fish/min	3.48 zyx	6.5 wv	6.4 xwv	8.27 wv	1.8 z

of daily freshwater outflow at Chipps Island (Figure 1; see the Dayflow section of DWR 2001. This index is calculated by summing surface water inflows and precipitation runoff estimates and then subtracting gross channel depletion (consumptive use) and total exports, diversions, and transfers (for details see the Dayflow documentation section of DWR 2001). Although this index is a measure of net outflow from the largely tidal Sacramento–San Joaquin Delta, it is also a useful indicator of net inflow to Suisun Marsh because both Chipps Island and Suisun Marsh are located downstream from the confluence of the Sacramento and San Joaquin rivers as well as from the major water diversions. In this paper, the variable is called "freshwater inflow" or "inflow" because outflow from the upper estuary results in inflow to the marsh.

Database organization.—Because striped bass adopt a piscivorous lifestyle as they approach 150 mm SL (Stevens 1966; Feyrer 1999), we classified them as "juvenile" (<150 mm) or "adult" (≥150 mm) and treated these life stages as separate species in our analyses. We then calculated the total number of species collected in each trawl and summarized the data by computing the mean catch per minute of each species, total species per minute, temperature, salinity, and transparency for every slough sampled per month and year for all months in which sampling occurred in a slough. Less than 3% of the values for temperature (28 occurrences), salinity (44 occurrences), and transparency (90 occurrences) were missing. The omissions were distributed evenly across months and sloughs but occurred more frequently in the early years of our study. When analyses required complete data sets, the missing values for temperature, salinity, or transparency were replaced with the 21-year average for that slough and month. Ten freshwater inflow variables were based on the average date of sampling in each slough and month. We calculated average daily inflow for five intervals (14, 30, 60, 180, and 365 d) and standard deviations of daily inflow for those same intervals. To measure the evenness of species composition in our catches, we calculated Shannon's diversity index (Krebs 1999),

$$H = -\sum_{i=1}^{s} P_i \log_{10} P_i,$$

where P_i is the proportion of a species in relation to the total catch. Aside from their inclusion in the calculations of total species and Shannon's diversity index, species comprising less than 0.25% of the total trawl catch (<300 fish) were not considered. This simplified the analysis so that it included only the 16 most abundant and frequently occurring species. The data from this subset of species were summarized by year, month, and slough. To facilitate comparisons with the previous analyses by Meng et al. (1994), we created yearly and monthly indices of resident native species, resident alien species, and seasonal species by summing the average catch per minute for all species in a particular group and dividing by the number of

TABLE 1.—Extended.

Variable	Nurse	Peytonia	Spring Branch	Lower Suisun	Upper Suisun
	Characteristic				
Mean temperature (range)	16.7 (6.0–23.8) z	16.1 (4.8–26.5) z	16.7 (4.1–29.5) z	16.7 (5.0–26.8) z	16.5 (4.8–25.4) z
Mean salinity (range)	2.1 (0.0–8.6) z	2.6 (0.0–10.5) z	3.6 (0.0–13.1) yx	4.7 (0–14.8) xw	3.4 (0–12.7) y
Mean transparency (range)	23 (7–52) x	19 (8–55) zy	20 (8–54) zyx	25 (4–75)	20 (5–46) zyx
Mean width (m)	120	37	30	205	161
Maximum depth (m)	5	2	1	6	5
Length (km)	6.2	3.6	1.9	22.6	
Number of diversions	3	7	0	31	
Diversions/km	0.5	1.9	0.0	1.4	
Diversion area (m^3)	1.4	7.1	0.0	23.3	
Diversion area/km	0.2	2.0	0.0	1.0	
	Catch data				
Species/min	0.457 yx	0.785 v	0.931	0.375 y	0.337 zy
Shannon's diversity index	0.386 z	0.574 v	0.606	0.493 yxwv	0.449 zyx
Fish/min	2.7 zy	5.67 yxw	8.67 v	5.06 zyx	3.43 zyx

species in the group. Because catches of seasonal species were relatively small, the seasonal species index was multiplied by 5 to make the indices comparable. Prior to statistical analyses, all environmental variables and catch data except total species per minute and Shannon's diversity index were $\log_{10}(x + 1)$ transformed to reduce the influence of extreme values and compensate for the effects of the different measurement units of the environmental variables, thus improving normality. The environmental data were then standardized to a mean of 0 and standard deviation of 1 to ensure that these variables were equally weighted in the analyses.

Beach seining data were used to examine trends in species and size-classes that occurred mainly in edge habitat and were inadequately sampled by the otter trawl (Table 2). These data were standardized to the mean number of fish per haul for each slough, month, and year.

Data analyses.—To examine the relationships among the environmental variables and between these variables and the catch data, we conducted canonical correspondence analyses (CCAs) using the Canoco (ter Braak and Smilauer 1998) software package. For all CCAs, data on 13 environmental variables (temperature, salinity, transparency, and the 10 inflow variables) were used to explain the variation in trawl catch data, which consisted of the average catch per minute for each of the abundant species. Because many measures of inflow were highly correlated and thus unlikely to explain additional variation in catch data (ter Braak and Verdonschot 1995), and to make the resulting ordination diagrams comparable, we imposed constraints on the selection of the environmental variables included in the final model. Using forward selection, environmental variables were ordered by their ability to explain the variation in the catch data. Each variable was tested for significance before being included in the final model, and then the remaining variables were reordered by their ability to explain additional variation in the catch data. This procedure was repeated until we had included temperature, salinity, transparency, one measure of average daily freshwater inflow, and one measure of the standard deviation of daily inflow.

We addressed question 1 (how seasonal patterns of fish abundance and diversity relate to environmental variation) by graphing and visually comparing the mean catches per month, the diversity indices, and selected environmental variables.

To answer question 2 (whether resident native species, resident alien species, and seasonal species show different long-term patterns in abundance), we began by computing Spearman rank correlations with year (1980–1999) for each of the species and species group indices and graphing each species group index by year. We then used Spearman rank correlations to compare trends over time for each pair of indices because of the nonlinear nature of many of the variables (see Meng et al. 1994). All years for which we had complete data (i.e., 1980–1999) were included in this analysis. To visually compare long-term trends in the

TABLE 2.—Fishes collected from May 1979 to December 1999 using an otter trawl and beach seine in Suisun Mar listed in decreasing order of abundance in the trawl. The principal environment of each species is coded as follows: = anadromous, E = estuarine, F = freshwater, and M = marine. Asterisks denote native species. Species assigned code were used in the analysis.

Species	Code	Otter trawl		Beach seine		Principal environmen
		Number	%	Number	%	
Striped bass *Morone saxatilis*[a]	SB	46,125	36	5,497	12	E
*Threespine stickleback *Gasterosteus aculeatus*[a]	STBK	13,128	10	1,955	4	F, E
Yellowfin goby *Acanthogobius flavimanus*[a,c]	YFG	12,470	10	8,551	19	E, M
*Tule perch *Hysterocarpus traski*[a]	TP	11,069	9	817	2	F, E
*Splittail *Pogonichthys macrolepidotus*[a]	ST	10,770	8	1,358	3	E
*Longfin smelt *Spirinchus thaleichthys*[a,c]	LFS	7,514	6	20	<1	E
*Prickly sculpin *Cottus asper*[a]	PSCP	7,017	6	311	1	F, E
Shimofuri goby *Tridentiger bifasciatus*[a,b,d]	SG	6,044	5	698	2	E
Common carp *Cyprinus carpio*[a,d]	CP	2,732	2	250	1	F
*Sacramento sucker *Catostomus occidentalis*[c]	SKR	2,114	2	72	<1	F
*Pacific staghorn sculpin *Leptocottus armatus*[a,c]	STAG	1,630	1	1,704	4	M
Threadfin shad *Dorosoma petenense*[a]	TFS	1,369	1	1,180	4	F
*Starry flounder *Platichthys stellatus*[a,c]	SF	1,302	1	213	<1	M
White catfish *Ameiurus catus*[a]	WCF	1,038	1	71	<1	F
*Delta smelt *Hypomesus transpacificus*[a]	DS	442	<1	69	<1	E
Inland silverside *Menidia beryllina*	ISS	335	<1	21,843	47	F, E
American shad *Alosa sapidissima*[a]		263	<1	24	<1	A
Black crappie *Pomoxis nigromaculatus*[d]		235	<1	10	<1	F
*Northern anchovy *Engraulis mordax*		224	<1	0	0	M
*Pacific herring *Clupea harengus*		208	<1	54	<1	M
Goldfish *Carassius auratus*		162	<1	11	<1	F
Channel catfish *Ictalurus punctatus*[a]		123	<1	6	<1	F
*Hitch *Lavinia exilicauda*		99	<1	13	<1	F
*Sacramento pikeminnow *Ptychocheilus grandis*		96	<1	85	<1	F
Black bullhead *Ameiurus melas*		90	<1	2	<1	F
White crappie *Pomoxis annularis*		88	<1	0	0	F
*White sturgeon *Acipenser transmontanus*		43	<1	0	0	A
*Pacific lamprey *Lampetra tridentata*		38	<1	0	0	A
*Chinook salmon *Oncorhynchus tshawytscha*[d]		34	<1	183	<1	A
Brown bullhead *Ameiurus nebulosus*		19	<1	0	0	F
Fathead minnow *Pimephales promelas*		16	<1	23	<1	F
Bigscale logperch *Percina macrolepida*		15	<1	5	<1	F
Western mosquitofish *Gambusia affinis*		15	<1	215	<1	F
Rainwater killifish *Lucania parva*		15	<1	24	<1	E
*Sacramento blackfish *Orthodon microlepidotus*		15	<1	78	<1	F
*Shiner perch *Cymatogaster aggregata*		14	<1	0	0	M
Bluegill *Lepomis macrochirus*		11	<1	12	<1	F
*Plainfin midshipman *Porichthys notatus*		10	<1	0	0	M
*California halibut *Paralichthys californicus*		3	<1	0	0	M
Green sunfish *Lepomis cyanellus*		3	<1	2	<1	F
Golden shiner *Notemigonus crysoleucas*		3	<1	2	<1	F
*Green sturgeon *Acipenser medirostris*		3	<1	0	0	A
*Rainbow trout *Oncorhynchus mykiss*		3	<1	2	<1	A
*Speckled sanddab *Citharichthys stigmaeus*		3	<1	0	0	M
*Bay pipefish *Syngnathus leptorhynchus*		2	<1	0	0	M
Redear sunfish *Lepomis microlophus*		2	<1	0	0	F
*Surf smelt *Hypomesus pretiosus*		2	<1	0	0	M
Shokihaze goby *Tridentiger barbatus*		1	<1	0	0	E
*Longjaw mudsucker *Gillichthys mirabilis*		1	<1	0	0	E, M
*Pacific sanddab *Citharichthys sordidus*		1	<1	0	0	M
Wakasagi *Hypomesus nipponensis*		1	<1	1	<1	F, E
*White croaker *Genyonemus lineatus*		1	<1	0	0	M
Warmouth *Lepomis gulosus*		1	<1	0	0	F
Largemouth bass *Micropterus salmoides*		0	0	2	<1	F

[a] Species collected in all 10 sloughs.

[b] Identified as chameleon goby *Tridentiger trigonocephalus* in Meng et al. (1994) but later shown to be shimofuri goby (Matern and Fleming 1995).

[c] Collected in significantly greater abundance in Suisun Slough seines.

[d] Collected in significantly greater abundance in Denverton Slough seines.

relative abundance of native versus alien fishes and to examine the degree to which fluctuations in these groups were due to a few sporadically very abundant species (threespine stickleback, yellowfin goby, and shimofuri goby) we graphed the abundance of native fishes (excluding threespine stickleback), threespine stickleback, alien fishes (excluding gobies), and gobies. Finally, we used Spearman rank correlation analyses to examine the potential impacts of two recent abundant invaders, shimofuri goby and yellowfin goby. The yearly abundances of each goby and both gobies combined and the combined abundance of both gobies for the previous year were compared with the abundances of the other most common species.

To answer question 3 (whether there are groups of co-occurring species with patterns of abundance that respond in similar ways to changes in temperature, salinity, and freshwater inflow) we took a multivariate approach because these factors do not operate independently; examining the effects of each one separately can lead to erroneous conclusions (Matthews et al. 1992). Therefore, we conducted CCAs on all years to examine the overall effect of the environmental variables on catch. We then conducted CCAs on subsets of our data to compare the relative importance and effects of environmental variables between water years (which begin 1 October and end 30 September) having above-average inflow ("high inflow") and those having below-average inflow ("low inflow").

We addressed question 4 (whether there are differences in species composition in different parts of the marsh that are related to local environmental characteristics) by using sum of squares–simultaneous test procedures (SS–STP; Sokal and Rohlf 1995). This test was used to compare means and distinguish groups of sloughs based on temperature, salinity, transparency, species caught per minute, Shannon's diversity index, and total fish caught per minute. Denverton and Nurse sloughs were included in these comparisons despite the potentially important effects resulting from the later (1994) onset of regular monthly sampling in those sloughs. Next, in an effort to describe catch differences among sloughs, we plotted 95% confidence ellipses for mean slough scores on the ordination diagram generated by the CCA conducted on the full database. Species caught more frequently in the seines at Denverton or Suisun sloughs were identified by comparing monthly average catch per haul in each slough using a two-tailed *t*-test with unequal variances (significance, $P < 0.05$).

Results

We trawled during 233 out of 245 months from May 1979 to December 1999, conducting over 4,400 trawls and collecting nearly 127,000 fish, most of which were juveniles. Twenty-eight native fish species and 25 alien species were captured (Table 2). Most species were widespread in the marsh. We collected 31–39 species from each slough, with the exceptions of Nurse Slough (24 species) and Denverton Slough (25 species), the two sloughs in which we began regular sampling in 1994. The 16 most abundant species accounted for 99% of the total catch and were grouped as follows to calculate indices: native residents (threespine stickleback, tule perch, splittail, prickly sculpin, and Sacramento sucker); alien residents (striped bass juveniles, striped bass adults, yellowfin goby, shimofuri goby, common carp, white catfish, and inland silverside); and seasonal species (longfin smelt, Pacific staghorn sculpin, threadfin shad, starry flounder, and delta smelt). Among the seasonal species only threadfin shad were not native.

We also conducted over 900 seine hauls, collecting nearly 46,000 fish. Thirty-six fish species were represented, including 15 natives and 21 aliens (Table 2). Rank abundance differed markedly from our trawling survey, most notably for species or size-classes that were inadequately sampled by our otter trawl; the smaller mesh of the beach seine allowed us to more regularly capture smaller fish. We also collected greater numbers of species that were littoral (e.g., inland silverside, western mosquitofish, and chinook salmon) or found high in the water column (threadfin shad).

Seasonal Patterns of Abundance, Diversity, and Environmental Variables

The catches of most species were low from October to March (Figure 2), when water temperatures were coolest (Figure 3). The highest catches occurred from June to August (Figure 2), when water temperatures were warmest. This peak was mainly the result of the increased abundance of alien species (Figure 3), particularly striped bass juveniles, yellowfin gobies, and shimofuri gobies (Figure 2). In comparison with alien species, natives peaked earlier in the year and were more evenly abundant throughout the year (Figure 3). This relative stability resulted from consistent monthly catches of splittails and tule perch, while