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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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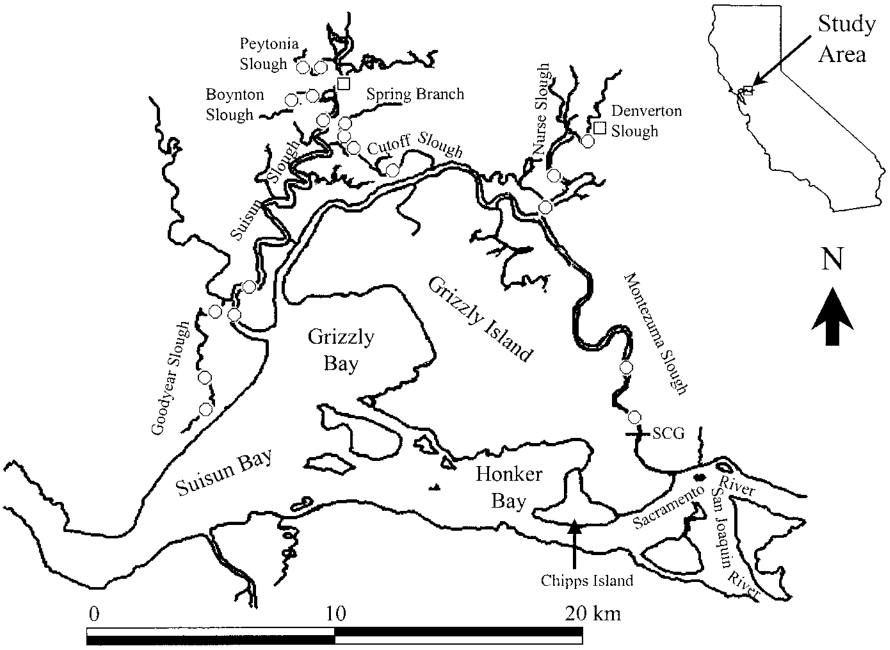

FIGURE 1.—Suisun Marsh, San Francisco Estuary, California. Circles represent sites where trawling was conducted, squares sites where both trawling and beach seining were conducted. The salinity control gates (SCG) in Montezuma Slough began operating in 1988.

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

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TABLE 1.—Physical characteristics and catch data for the nine sloughs in Suisun Marsh, California, sampled during 1979–1999. Temperature (°C), salinity (‰), and transparency (Secchi depth in cm) are for all years sampled. Diversion area refers to the total cross-sectional area of the diversion opening. Common lowercase letters denote means that are 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'' ($<$150 mm) or ''adult'' ($\geq$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	Slough				
	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

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

Species	Code	Otter trawl		Beach seine		Principal environment
		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

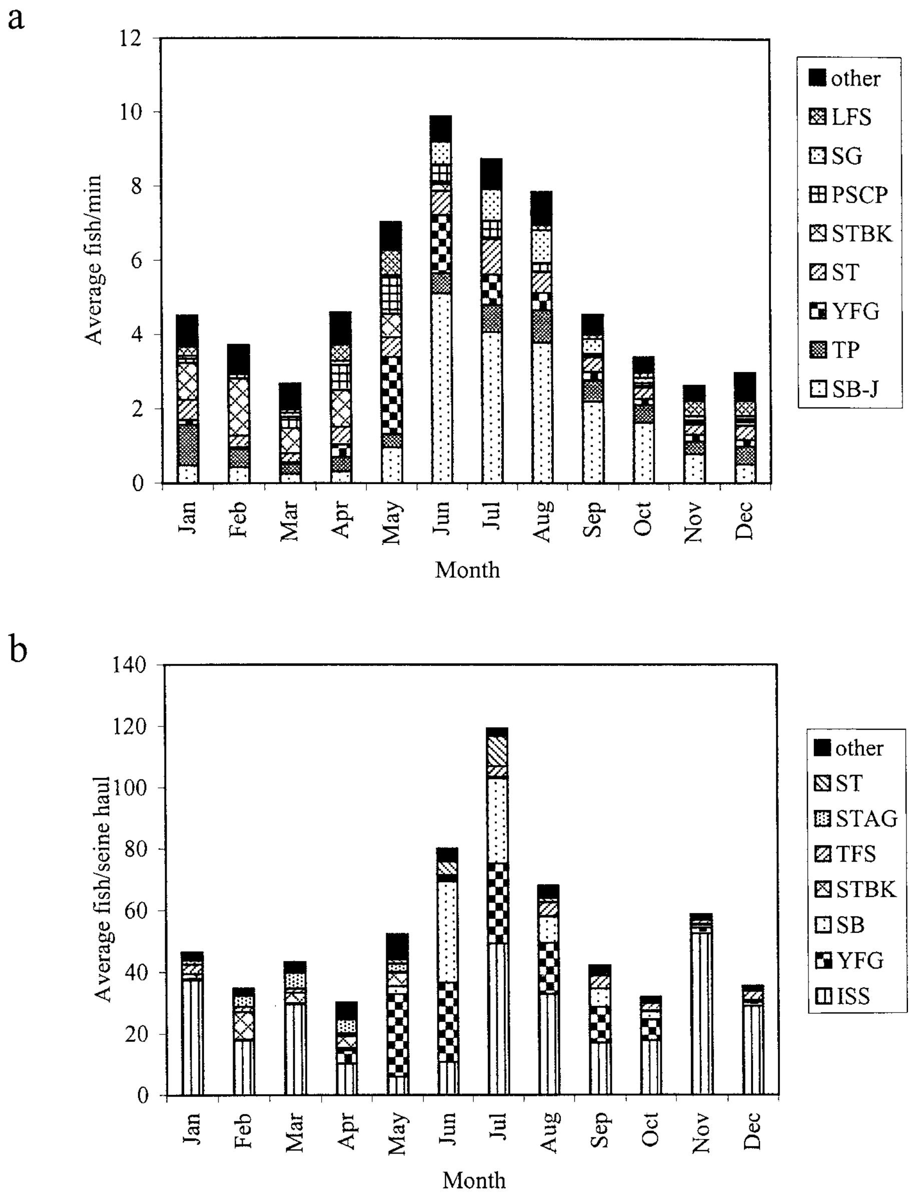

FIGURE 2.—Average monthly catch in Suisun Marsh as measured by **(a)** fish per minute of trawling and **(b)** fish per seine haul. Species comprising less than 4% of the overall trawling catch or less than 2% of the overall seine catch are not shown. Species codes are listed in Table 2.

threespine sticklebacks peaked in January–April and prickly sculpins in April–July (Figure 2). The seasonal species used the marsh at different times of the year. Longfin smelt were collected in November and December as adults and in April and May as juveniles (Figure 2). Juvenile Pacific staghorn sculpin entered the marsh in March–May, delta smelt peaked in November–February, and threadfin shad peaked in December–February. Juvenile starry flounder were present year-round but were classified as a seasonal species to remain consistent with Moyle et al. (1986) and Meng et al. (1994).

The beach seining data showed similar seasonal trends (e.g., striped bass and yellowfin goby peaks; Figure 2). However, there were some important differences. Young-of-the-year chinook salmon, which were too rare in the trawls to warrant anal-

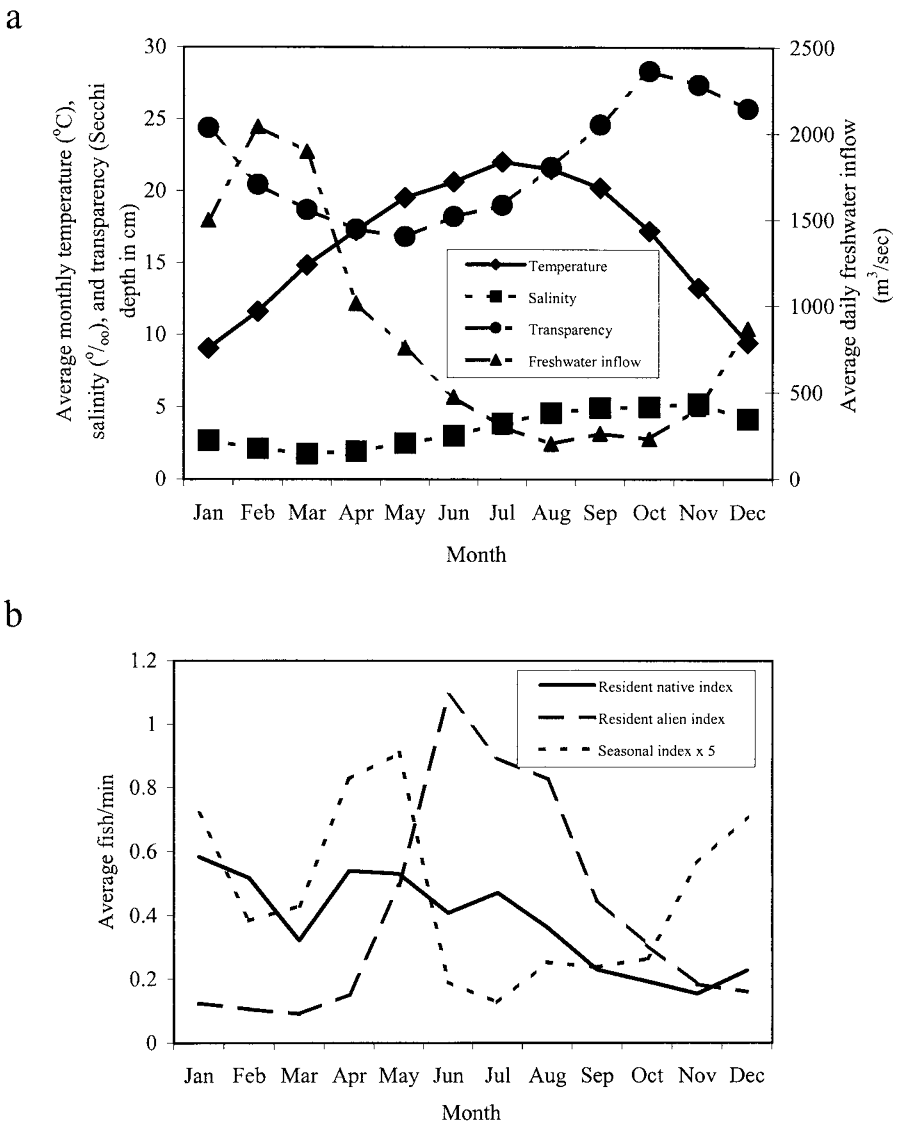

FIGURE 3.—Average monthly values for 1979–1999 of **(a)** temperature, salinity, and transparency (all left scale) at Suisun Marsh and the daily index of freshwater inflow (net delta outflow at Chipps Island; right scale) and **(b)** indices for resident native fishes, resident alien fishes, and seasonal fishes. The seasonal species index was multiplied by 5 to make it comparable to the other indices.

ysis (Table 2), were collected from January to March in the beach seines. Pacific staghorn sculpin were collected about 1 month earlier (and at a smaller size) in the seines (Figure 2) than they were in the trawls. Splittails of all sizes were collected fairly evenly across months in the trawls, but in the beach seines we caught mainly young of the year in large numbers from June to September (Figure 2).

Long-Term Patterns in Resident Native Species, Resident Alien Species, and Seasonal Species Abundance

Spearman rank correlation tests were used to identify long-term trends in species abundance as indicated by the correlations between catch data and year. Shimofuri goby, white catfish, and yellowfin goby all showed positive correlations, but only that of shimofuri goby was significant ($P <$

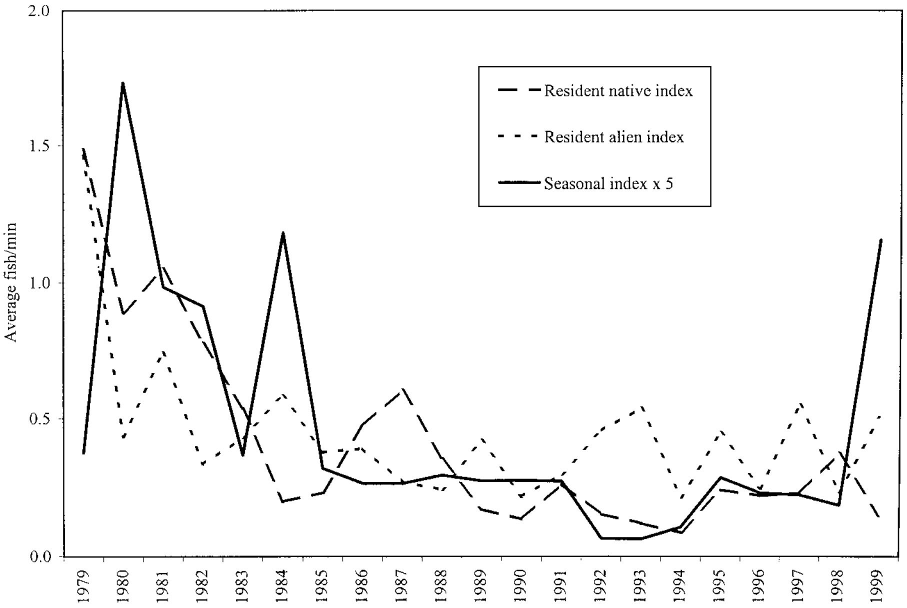

FIGURE 4.—Average yearly indices for resident native fishes, resident alien fishes, and seasonal fishes in Suisun Marsh, 1979–1999.

0.05). Common carp, longfin smelt, Sacramento sucker, splittail, striped bass juveniles, threadfin shad, threespine stickleback, and tule perch showed significant negative correlations.

Spearman rank correlation analysis by years showed significant ($P < 0.05$) long-term declines in the indices for seasonal and resident native species but no significant correlations among the indices. The seasonal species index had the largest relative fluctuations and indicated a long period of very low abundance (Figure 4). Resident native species declined and then fluctuated at lower levels (Figure 4), a trend that was partially obscured by extremely high catches of threespine sticklebacks in some years (Figure 5). Resident alien species did not show a clear trend in long-term abundance (Figure 4). This was due to large and widely fluctuating populations of yellowfin and shimofuri gobies in the later years of our study (Figure 5). The abundance of shimofuri goby was positively correlated with that of threespine stickleback, but the catches of yellowfin goby, shimofuri goby, and the two species combined showed no other significant correlations with the 10 most abundant species. Despite exceptionally wet conditions, which provided good spawning conditions for many species (e.g., splittail) in the last 5 years of our study, there was little change in total catch (Figure 5).

Effects of Environmental Variables on Patterns of Abundance and Co-occurrence

In the CCA conducted on the full database, the environmental variables included in the final model were temperature, salinity, transparency, 365-d inflow, and the standard deviation of 60-d inflow. The first four ordination axes explained only 10% of the variance in catch (Table 3). The ordination diagram (Figure 6) showed three loose groups of species: (1) alien species that were most abundant in summer (striped bass adults and juveniles, shimofuri goby, yellowfin goby, and white catfish); (2) plankton-feeding fishes associated with cool water (inland silverside, delta smelt, threadfin shad, and longfin smelt); and (3) resident species that centered on mean conditions.

When the database was subdivided into high-inflow years (1980, 1982–1984, 1986, 1995, and 1997–1999) and low-inflow years (1981, 1985, 1987–1992, and 1994), the CCAs explained 11% of the variation in catch for high-inflow years and 12% for low-inflow years. Although the relationships between temperature and the inflow variables changed with the amount of inflow, most species had the same general responses to environmental variables in high-inflow years as they did in low-inflow years. These analyses had several results in common: (1) shimofuri goby, yellowfin goby,

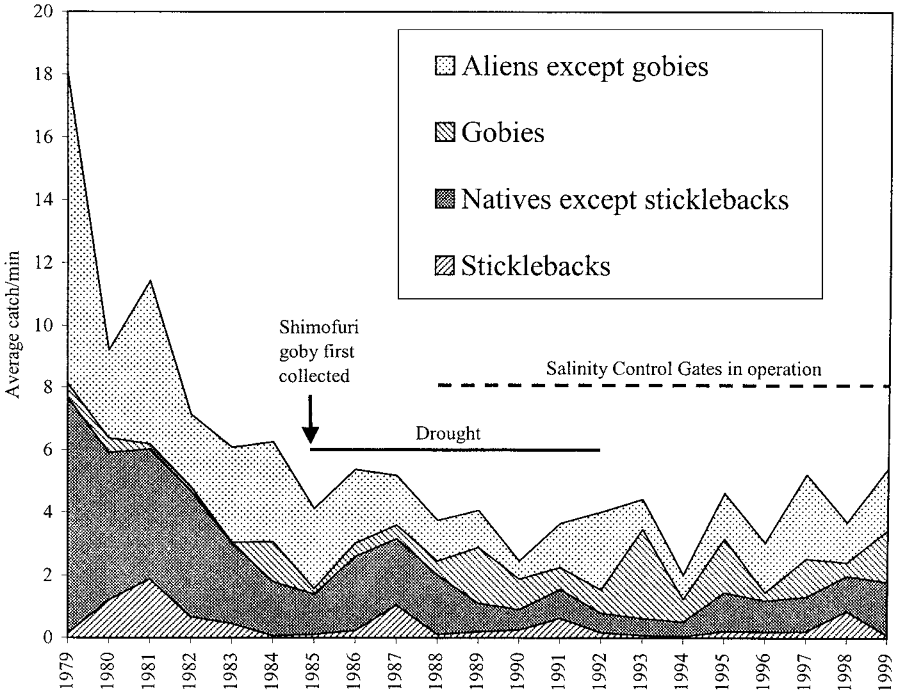

FIGURE 5.—Average yearly catch per minute of (1) alien fishes excluding yellowfin and shimofuri gobies, (2) yellowfin and shimofuri gobies, (3) native fishes excluding threespine sticklebacks, and (4) threespine sticklebacks in Suisun Marsh, 1979–1999. The timing of some major events is indicated.

white catfish, and striped bass adults and juveniles were associated with warm temperatures and high salinity; (2) delta smelt and threadfin shad were associated with cool temperatures; (3) threespine stickleback and Pacific staghorn sculpin were associated with high variation in inflow; and (4) Sacramento sucker, splittail, tule perch, common carp, and starry flounder showed no strong variation in numbers with seasonal changes in conditions. These results were generally similar to those for all years combined (Figure 6). However, one species showed different responses in high- and low-inflow years, namely, the longfin smelt, catches of which were correlated mainly with (1) salinity, (2) transparency, and (3) low 365-d inflow in high-inflow years but high 365-d inflow in low-inflow years.

Other factors that could affect the species' responses to environmental variables were also investigated using CCA. When the year was divided into four seasons based on temperature patterns, CCAs conducted on each season failed to explain additional variation or yield new insights (S. A. Matern, unpublished analyses). Similarly, there were no obvious effects of the salinity control gates (which began operating in 1988) on our catches. An investigation of species' responses to environmental variables before and after the gates began operation also revealed no clear patterns (Matern, unpublished analysis).

TABLE 3.—Summary of the first four ordination axes for canonical correspondence analysis conducted on environmental variable and fish catch data collected in Suisun Marsh from May 1979 to December 1999.

	Ordination axis			
	1	2	3	4
Eigenvalues	0.070	0.050	0.029	0.013
Species–environment correlations	0.605	0.613	0.447	0.313
Cumulative percentage variance				
Species data	4.4	7.4	9.3	10.1
Species–environment relationship	42.0	71.8	89.3	97.0

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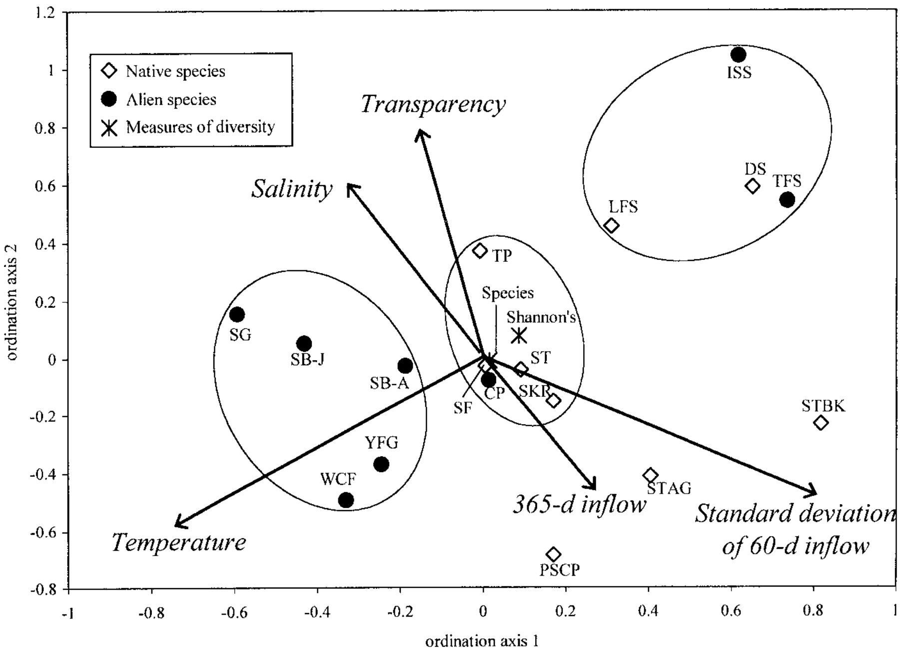

FIGURE 6.—Ordination diagram depicting the results of a canonical correspondence analysis on catch and environmental data collected in Suisun Marsh, 1979–1999. Species codes are listed in Table 2; Shannon's = Shannon's diversity index and species = the total number of species caught per minute.

Differences among Sloughs

Sloughs differed in physical and environmental characteristics (Table 1). The intensity of water diversion activity ranged from none in Spring Branch to 3.1 diversions/km in Goodyear and Suisun. The SS−STP analysis showed how site-specific environmental variables differed among sloughs. Temperature did not vary significantly among sloughs. Salinity was lowest in the sloughs close to the Sacramento River or other freshwater inputs and highest in the sloughs close to Grizzly Bay. Transparency was generally similar among sloughs but was higher in lower Suisun and upper Montezuma, the sloughs that receive the most marine water and freshwater, respectively (Table 1). The SS−STP analyses showed that catches were generally high (species and fish per minute) and relatively diverse (Shannon's diversity index) in small sloughs with few diversions (Cutoff and Spring Branch) and low in the largest sloughs (upper Montezuma, upper and lower Suisun, and Nurse; Table 1).

Because temperature did not vary significantly among sloughs (Table 1) and inflow data were identical, the locations of the 95% confidence ellipses of mean slough scores on the CCA ordination diagram (Figure 7) are primarily reflections of catch differences among sloughs. Goodyear Slough is distinguished from the others by very high catches of threespine sticklebacks and very low catches of shimofuri gobies (Figure 8). Denverton and Nurse sloughs are isolated from the others owing to high catches of white catfish in both sloughs and high catches of shimofuri gobies in Denverton Slough (Figure 8). Montezuma and upper Suisun sloughs were both characterized by small catches of low diversity (Table 1), but they differed in that shimofuri gobies were rare in Montezuma Slough but common in upper Suisun Slough (Figure 8), which resulted in the latter's placement closer to Denverton Slough (Figure 7). The remaining five sloughs (Boynton, Cutoff, lower Suisun, Peytonia, and Spring Branch) were located closer to the origin (Figure 7), indicating less obvious differences in catch and a lack of unusually high catches of any one species.

In the seine hauls, several species were more abundant in one of the two sloughs. Suisun Slough had significantly higher catches of yellowfin goby, Pacific staghorn sculpin, starry flounder, Sacramento sucker, and longfin smelt. Denverton Slough had higher catches of shimofuri goby, common carp, chinook salmon, and black crappie (Table 2).

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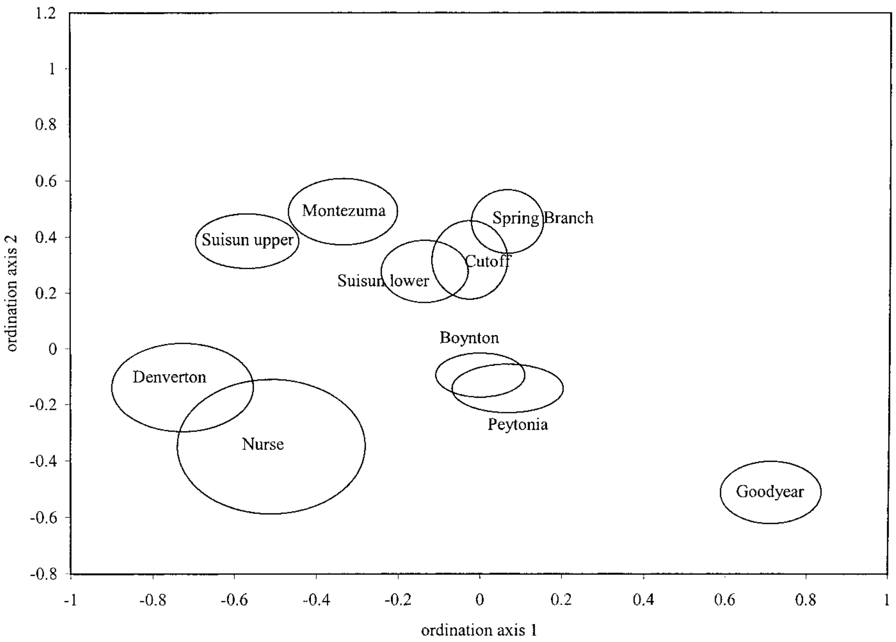

FIGURE 7.—Ordination diagram depicting the results of a canonical correspondence analysis on catch and environmental data collected in Suisun Marsh, 1979–1999. Ellipses represent the 95% confidence intervals of mean slough scores.

Discussion

Seasonal Patterns of Abundance, Diversity, and Environmental Variables

Our catches were dominated by young of the year and small species with short life cycles (e.g., inland silverside and shimofuri goby), as is the case in most estuaries worldwide (Moyle and Cech 2000). Thus, the seasonal patterns that we observed are probably functions of the reproductive programming of the abundant fishes. In Suisun Marsh, the larvae of many of the abundant native fishes appeared sequentially during winter and early spring, while those of the abundant alien species appeared later in the spring and summer (Meng and Matern 2001). Overall, we caught the fewest fish during winter and the most fish during summer.

Just as catch had a seasonal periodicity, so did the environmental variables. It is tempting, therefore, to assign a causative role to these variables, as is apparently the case in other systems (e.g., Loneragan et al. 1987; Cyrus and Blaber 1992; Rakocinski et al. 1992; Thiel et al. 1995; Able et al. 2001). However, our data indicate that, at least in Suisun Marsh, the relationship between environmental variables and catch is correlative rather than causative.

The results from the CCAs suggest that each species' response to environmental change within the range found in Suisun Marsh is limited. Basically, the range of environmental variation experienced over the course of a year by the young of the year is well within their physiological limits (e.g., splittail, Young and Cech 1996; striped bass, Turner and Chadwick 1972; shimofuri goby, Matern 2001). The intermediate position of Suisun Marsh in the estuary and its relatively low variability in salinity and temperature suggest that it should be a good (i.e., entailing low physiological stress) environment for euryhaline fishes, providing rearing habitat for young of the year spawned in both upstream (e.g., splittail and striped bass) and downstream (e.g., Pacific staghorn sculpin and starry flounder) areas, as well as for fish spawning in the marsh itself (e.g., shimofuri goby, yellowfin goby, and tule perch).

Long-Term Patterns in Resident Native Species, Resident Alien Species, and Seasonal Species Abundance

Most of the fishes in Suisun Marsh that were abundant enough for us to detect trends have declined in abundance. This phenomenon has been documented elsewhere in the estuary for striped bass (Turner and Chadwick 1972; Stevens et

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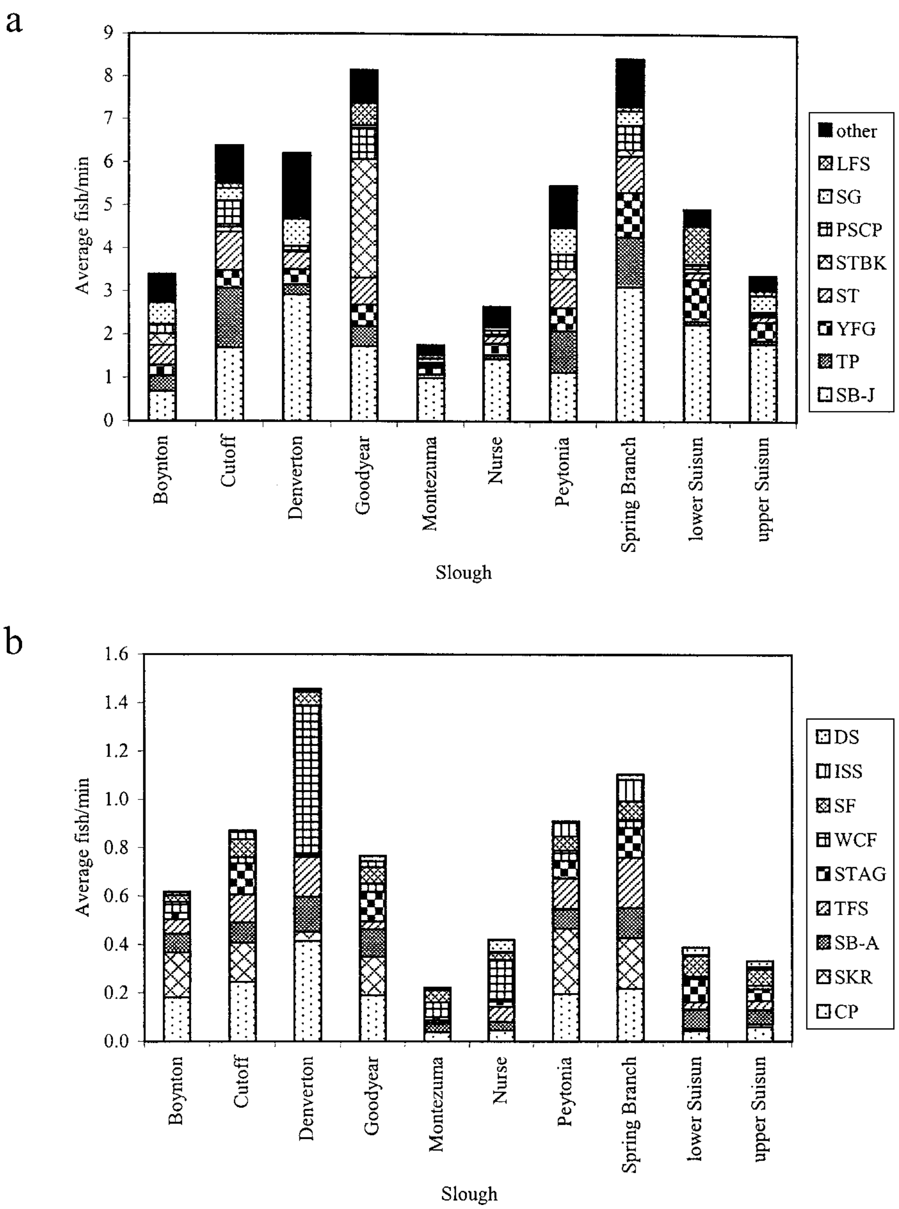

FIGURE 8.—Average number of fish caught per minute of trawling in Suisun Marsh, by slough. Panel **(a)** shows values for species comprising more than 4% of the overall catch, panel **(b)** values for species comprising 0.25–4% of the overall catch. Species codes are listed in Table 2.

al.1985; Kohlhorst 1999), delta smelt (Herbold et al. 1992; Moyle et al. 1992), longfin smelt (Herbold et al. 1992; Meng and Moyle 1995), and other species, particularly planktivorous species that spend a substantial portion of their life in the delta or Suisun Bay (Herbold et al. 1992). The splittail is unusual in that its decline in Suisun Marsh was not mirrored strongly elsewhere in the estuary (Sommer et al. 1997). Discrepancies in the strength of recent splittail year-classes between the marsh and upstream sites probably result from localized spawning in areas other than the marsh during some years and widespread spawning in others (Sommer et al. 1997; P. B. Moyle, unpublished data). The steepest decline of splittail and other native fishes coincided with a period of increased diversion of water from the estuary followed by a severe drought (1986–1992), which suggests that fish populations are affected by a combination of natural and anthropogenic factors.

Three alien species in Suisun Marsh showed increases in yearly abundance. The shimofuri goby is a recent invader that quickly became one of the most abundant fishes in the marsh (Matern and Fleming 1995). The white catfish is not a recent invader, but its abundance increased dramatically when we added sampling sites in Denverton Slough late in the study. The yellowfin goby avoided a negative correlation with year by virtue of three very successful spawning events in the 1990s.

Our analyses support the conclusion of Meng et al. (1994) that, considered as a group, the resident native species are in serious decline, although there has been an apparent stabilization in overall abundance in the recent wet years. The decline is further supported by negative correlations with year for several abundant native species.

Species that use the marsh on a seasonal basis showed large fluctuations in catch, in part because of the predominance of short-lived species for which strong cohorts only affect the catch for 1 year (Meng et al. 1994). Our analyses show some seasonal species (delta and longfin smelt) to be in sharp decline.

The alien species index did not show a significant decline over time and included the only species with significant increases in abundance. Given the frequency with which new species invade the estuary (Cohen and Carlton 1998), it is certain that such invasions will continue for some time. Thus, while the pool of potential resident native species can only decline, the pool of potential resident alien species continues to grow. For example, the shimofuri goby is a new invader to North America (Matern and Fleming 1995) that did not occur in the estuary until 1985. By 1987, when it began to appear regularly in our catches, over one-half of the fish in our study had already been collected. Nevertheless, it became so abundant that it was the eighth most common species collected over the entire study. In 1999 we collected a closely related Asian species, the shokihaze goby, in Suisun Marsh for the first time. This goby appears to be rapidly increasing its population in the estuary (S. Slater, California Department of Fish and Game, personal communication).

Despite the contrast between increasing populations of some alien species and decreasing populations of many native species, we found no significant correlations between the species group indices. We were also unable to detect significant negative correlations between the abundances of alien gobies and those of the other abundant species. Because gobies were some of the most abundant species in the marsh, our findings support the conclusions of other studies (e.g., Weinstein 1979; Weinstein et al. 1980; Peterson and Ross 1991) suggesting that biological interactions among fish species usually play a relatively minor role in determining patterns of abundance in estuaries. Interactions are apparently overshadowed by the physiological demands of an estuarine lifestyle (Moyle and Cech 2000) and differences in the timing of reproduction or are undetectable in the San Francisco Estuary due to overall low population sizes. More important may be the interactions with ecosystem-altering invertebrates such as the overbite clam, which has decimated the zooplankton community (Alpine and Cloern 1992; Kimmerer and Orsi 1996; Orsi and Mecum 1996), shifting the food web from a pelagic toward a benthic base (Kimmerer et al. 1994) and forcing fish to find alternative prey. Herbold (1987) and Feyrer (1999) have shown that native species are more successful at switching to alternative prey when their preferred prey undergo periods of low abundance. On the other hand, analyses showed a decrease in the growth rate of splittail after the introduction of the overbite clam (Matern, unpublished data). Furthermore, the alien shimofuri goby (which was not present during Herbold's study) has been shown to utilize seasonally abundant prey and exploit novel food sources, including alien hydroids and barnacle cirri (Matern 1999). Additional interactions between fish and alien invertebrates may be revealed as the impacts of alien mysid shrimp (Modlin and Orsi 1997), copepods (Orsi et al. 1983), crabs (Cohen and Carlton 1997), and even cnidarians (Mills and Sommer 1995) are studied.

Effects of Environmental Variables on Patterns of Abundance and Co-occurrence

The CCAs indicated that species' responses to environmental variables were weak overall and changed little between years with high and low freshwater inflows. Although young of the year dominated our catches and spawning success for many species depends on freshwater inflow (Jassby et al. 1995), there was apparently enough survival between years to dampen annual inflow effects. The effect of freshwater inflow may have also been masked by the general downward trend in the abundance of most species with time (for reasons unrelated to inflow). Thus, while the relationships among temperature and the inflow variables changed, most species maintained the same general associations and positions relative to one another. Shimofuri goby, white catfish, yellowfin goby, and striped bass were associated with high temperature, delta smelt and threadfin shad were associated with cool water, and threespine stickleback and Pacific staghorn sculpin were associated with high variation in inflow. All of these associations can be related to species' spawning times. One species showing a distinctly different pattern was the longfin smelt, which was correlated with high salinity, transparency, and low 365-d inflow in high-inflow years but high 365-d inflow in low-inflow years. More than any other species, this species uses the entire estuary and the ocean off the estuary (the Gulf of the Farallones) to complete its life history. The factors regulating its abundance, however, are still poorly understood (Moyle 2002).

We do not mean to imply that the environment plays a minor role in determining fish abundance. We believe that environmental variables act mainly on very young life stages and not on the larger juveniles and adults that we primarily capture in our trawls and seines. This hypothesis is supported by similar analyses of larval fish collected in Suisun Marsh in 1994–1999 (Meng and Matern 2001), which found that environmental variables (particularly freshwater inflow) played an important role in determining species abundance. Similarly, Kimmerer et al. (2001) found that the survival of striped bass in the San Francisco Estuary was strongly affected by freshwater inflow, but only during the first few weeks of life. Thus, we suggest that environmental variables determine which species spawn and recruit successfully and that subsequent minor fluctuations in those variables do not have a large enough effect on fish abundances to be detected in our sampling. The importance attributed to environmental variables in the literature varies, but most studies showing that such variables are highly important were conducted over areas encompassing much of the estuary (e.g., Weinstein et al. 1980; Allen 1982; Thiel and Potter 2001) and thus over a wide range of salinities and temperatures. Studies like ours that were conducted on a smaller portion of the estuary (e.g., Rozas and Hackney 1984; Loneragan et al. 1987) typically attribute less importance to these variables. However, the scale of our study is more likely to detect interaction effects among species than those at larger scales (Jackson et al. 2001).

Differences among Sloughs

After examining the first 13 years of catch data from this study, Meng et al. (1994) found that native fishes were more abundant in smaller sloughs and that seasonal species were more common in larger sloughs. They found alien species in both slough types but noticed that these species were becoming more abundant in the small sloughs over time, partly because of the increasing abundance of the shimofuri goby (Meng et al. 1994). Because the present analysis was based on a larger set of data, we were able to make comparisons among individual sloughs.

We found that sloughs differed from one another physically and chemically and that these differences helped to explain the differences in catch among sloughs. The biggest differences were related to overall slough size, with the largest sloughs having the lowest total catches and least diversity. This inverse relationship is partially due to decreased sampling efficiency in the larger sloughs. One anomaly was Boynton Slough, which had a high amount of flocculent substrate and in which catches were unusually low for a small slough. A difference between Boynton Slough and the others is that a local sewer district releases tertiary treated water into it.

Other small sloughs differed primarily in salinity and diversion density, but catches of most species were most likely related to local physical or chemical conditions that were not measured during our study. For example, on occasion we made large catches (>500) of threespine sticklebacks in a single otter trawl. These catches always occurred during January–May (usually February) in Goodyear Slough near duck pond drains. The habitat within duck ponds is likely conducive to threespine stickleback spawning, and our exceptionally large catches corresponded closely with the seasonal patterns of duck pond draining (S. Chappell, Suisun Resources Conservation District, personal communication). Denverton Slough was distinguished by large numbers of shimofuri goby, a species known to prefer hard substrates (Akihito and Sakamoto 1989; Matern 1999), which are absent from most sloughs. In contrast, yellowfin gobies are burrowers that require soft substrate (Dotu and Mito 1955); they were rare in the rocky habitat of Denverton Slough but abundant elsewhere in the marsh. We have no explanation for the high relative abundance of white catfish in Denverton Slough. They were abundant throughout the marsh at the beginning of our study (Moyle et al. 1986) but became rare during the extended drought (1985–1992). Although they were predicted to return to previous levels of abundance (Moyle et al. 1986), they have thus far failed to do so except in Denverton Slough.

Our seining data also showed differences in catch between the two sloughs sampled. Denverton Slough was distinguished by higher catches of chinook salmon. These fish were typically 30–50 mm SL and may have resulted from spawning upstream in Denverton Creek. Suisun Slough was subject to more marine influence and had high catches of seasonal species, including Pacific staghorn sculpin, starry flounder, and longfin smelt. At this location we also collected more yellowfin goby (probably because of the substrate differences mentioned above) and more Sacramento sucker (which spawn in upstream tributaries of the western marsh).

Synthesis: Factors Structuring Fish Assemblages in Suisun Marsh

The species composition in Suisun Marsh follows the model of Moyle and Light (1996), in which the potential species pool of over 200 marine, estuarine, and freshwater species is filtered by their ability to adapt to the local abiotic conditions, with biotic factors playing relatively minor roles. As in all estuaries, the pool of potential species contains not only ‘‘true’’ estuarine species but also those present in nearby freshwater and marine environments. In the San Francisco Estuary, this species pool is supplemented by frequent introductions, mainly from ballast water (Cohen and Carlton 1998). Which species colonize and become established in Suisun Marsh depends largely on the physiological tolerances of those species to the marsh environment, particularly its low salinity and fluctuating temperature. ‘‘Marine stragglers’’ (e.g., plainfin midshipman, white croaker, bay pipefish, speckled sanddab, Pacific sanddab, California halibut, surf smelt, and shiner perch; Loneragan et al. 1989) occasionally enter the marsh when salinity is high but do not establish persistent populations. Similarly, when freshwater conditions prevail, upstream colonists (e.g., centrarchids and bigscale logperch) temporarily move into the marsh. This pattern is similar to that of other altered estuaries (e.g., Thiel and Potter 2001).

We did not find convincing evidence of important interactions among fish species, possibly because most population sizes were relatively low. It is likely that biotic interactions among fishes and invertebrates play a secondary role in structuring the assemblage even during times of abundance. The recent invasion of the overbite clam has resulted in the depletion of zooplankton and increased the potential for competitive interactions among fishes (Feyrer 1999). This deserves further investigation.

While species' presence in the marsh reflects both opportunity and physiology, their abundance and distribution are a result of several other interacting factors. Clearly, the most important of these is the timing of reproduction of the abundant resident species. In probable order of importance, the abundance and distribution of most species can be related to (1) spawning habits within the marsh (e.g., yellowfin goby, shimofuri goby, and occasionally splittail), (2) the recruitment of young of the year to the marsh from upstream (e.g., striped bass, Sacramento sucker, and splittail), (3) the recruitment of young of the year to the marsh from downstream (e.g., starry flounder and Pacific staghorn sculpin), (4) the passage of young of the year through the marsh during their downstream migrations (e.g., chinook salmon and Pacific lamprey), and (5) the passage of adults through the marsh to spawn upstream (e.g., longfin smelt).

After seasonal patterns of reproduction, the most useful predictor of species abundance is past reproductive success, which may be determined by environmental conditions (Meng and Matern 2001). Because the young of the year of many species recruit to the marsh, it is often possible to follow a particular successful cohort over many consecutive months. With apparent disregard for changing environmental conditions in the marsh, abundant cohorts of splittail, striped bass, and yellowfin goby continued to appear in our trawls for many months.

Catches also vary by location within the marsh. We have documented differences due to slough size (small versus large) and substrate (rocky versus muddy). It is also apparent that proximity to sources of freshwater, saline water, and even duck pond drainage water affects catch in certain sloughs.

All of the major trends in abundance were explained by the above factors. Only after they are taken into account do the minor fluctuations in the environmental variables that we measured play a role in structuring the juvenile and adult fish assemblages. While we found no evidence of important interactions among species, such interactions may become more important as the assemblage continues to change as a result of alien invasions or environmental conditions stabilize in ways that cause dramatic increases in fish populations.

Conclusions

The fishes of Suisun Marsh consist of groups of co-occurring species, but the composition and relative abundance of species within these groups shift in major ways through time and space, suggesting a lack of real structure (the result of species interactions). The longer the fishes are studied, the less apparent fish assemblages become. Differences among species within groups in feeding habits and habitat use are presumably more attributable to intrinsic differences in morphology and physiology than to interspecific interactions. Indeed, it appears that the major driving force for the relative abundances of species is reproductive success both inside and outside the marsh; species that regularly co-occur have similar spawning times and requirements for larvae and juveniles.

The lack of assemblage structure is not surprising considering (1) the natural fluctuating conditions of estuaries in general, especially in the brackish regions where species come and go according to changes in temperature and salinity; (2) the general decline in fish abundance in the brackish and freshwater portions of the estuary, which suggests a high level of anthropogenic disturbance; and (3) the frequent invasions of alien species of both fish and invertebrates.

The environment of the marsh nevertheless selects for a distinct subset of the species available. Even given the biases in our sampling, only about one-third of the species we have collected over the years have been abundant enough to be important players in the ecosystem. Furthermore, the total species list for the marsh is less than one-third of that for the entire estuary when stenohaline marine and freshwater species are counted. Thus, it seems possible to create predictable, persistent, interacting subsets of species (fish communities) in the marsh if the stochastic factors of human disturbance and alien invasions are reduced.

We think that these conclusions apply not just to Suisun Marsh but to the San Francisco Estuary as a whole and, in general, to temperate estuaries with a high degree of human-caused disturbance and frequent invasions by alien species. They suggest that there will be a high degree of unpredictability in fish abundances and assemblage composition until estuarine processes return to some semblance of their historic variability and invasions by alien species are halted. In the short run, management strategies for desirable fish species (especially threatened native species) should focus on the reproductive requirements of those species because returning the estuary to a more predictable condition (as much as estuaries are ever predictable) is unlikely in the immediate future. Fortunately, the tendency of native fishes to exhibit some degree of concordance in their abundances suggests that actions that benefit one species are likely to benefit others as well.

Acknowledgments

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