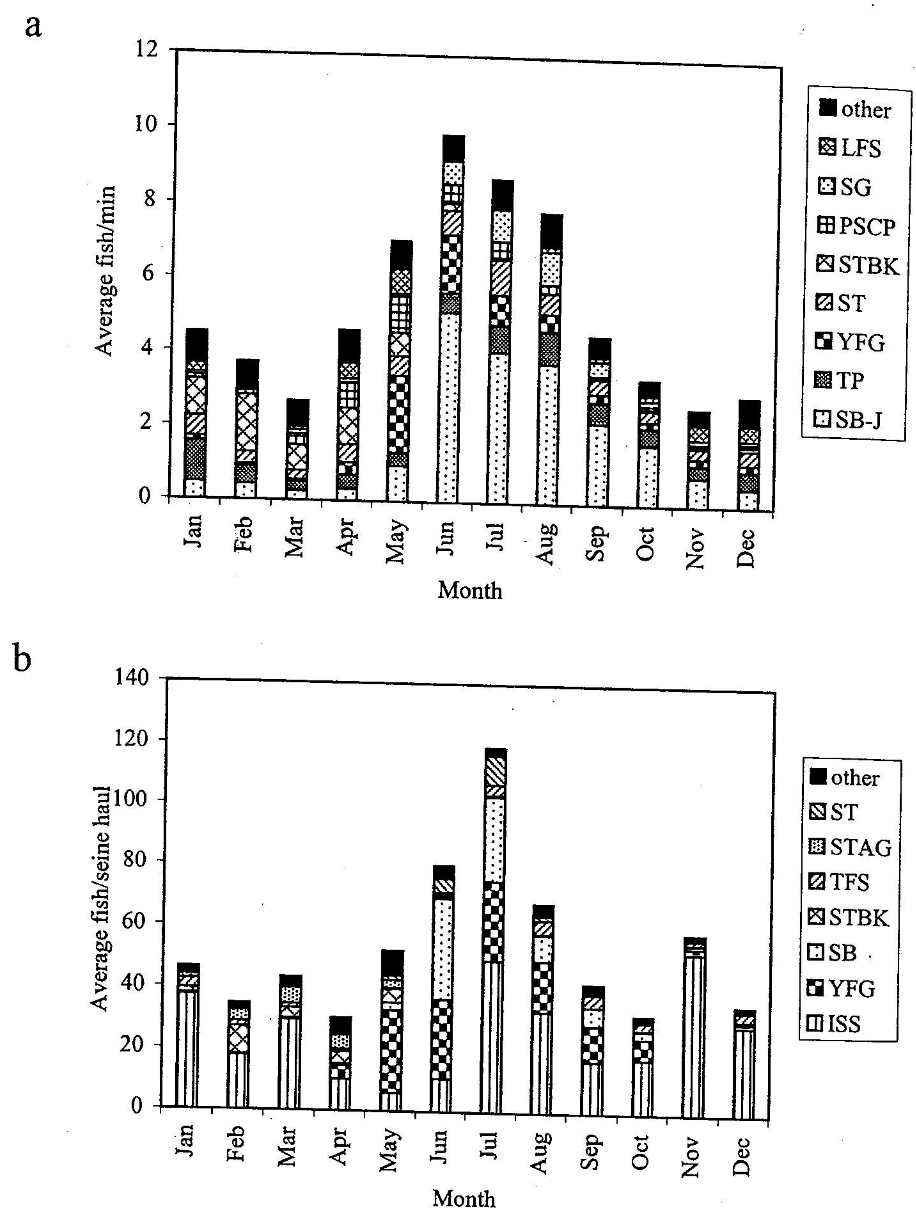

FIGURE 2.—Average monthly catch in Suisun Marsh as measured by **(a)** fish per minute of trawling and **(b)** fish per seine haul. Species comprising less than 4% of the overall trawling catch or less than 2% of the overall seine catch are not shown. Species codes are listed in Table 2.

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-

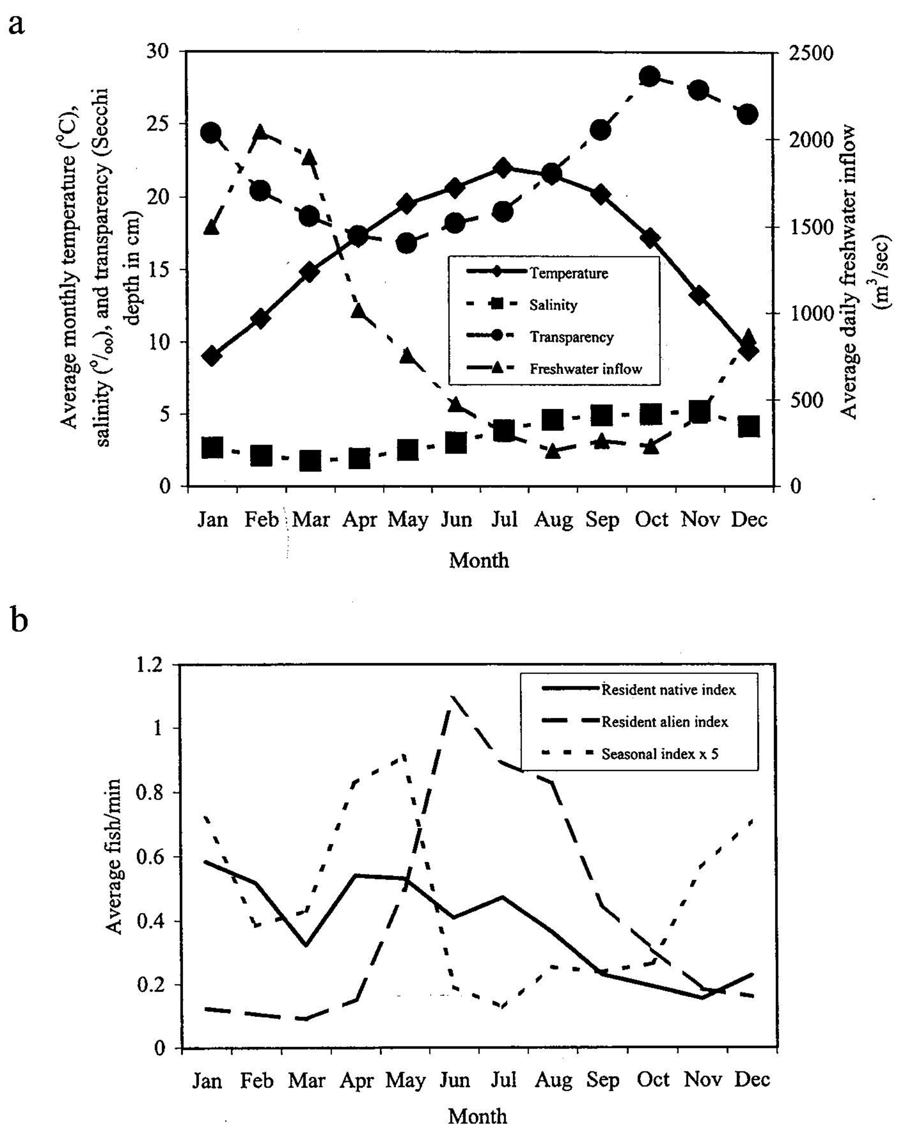

FIGURE 3.—Average monthly values for 1979–1999 of (**a**) temperature, salinity, and transparency (all left scale) at Suisun Marsh and the daily index of freshwater inflow (net delta outflow at Chipps Island; right scale) and (**b**) indices for resident native fishes, resident alien fishes, and seasonal 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 ($P <$

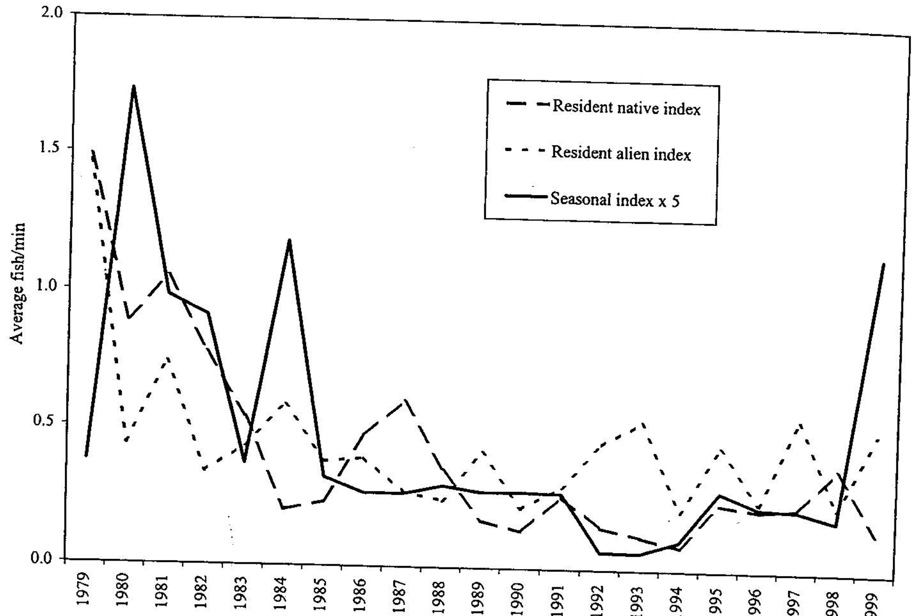

FIGURE 4.—Average yearly indices for resident native fishes, resident alien fishes, and seasonal fishes in Suisun Marsh, 1979–1999.

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,

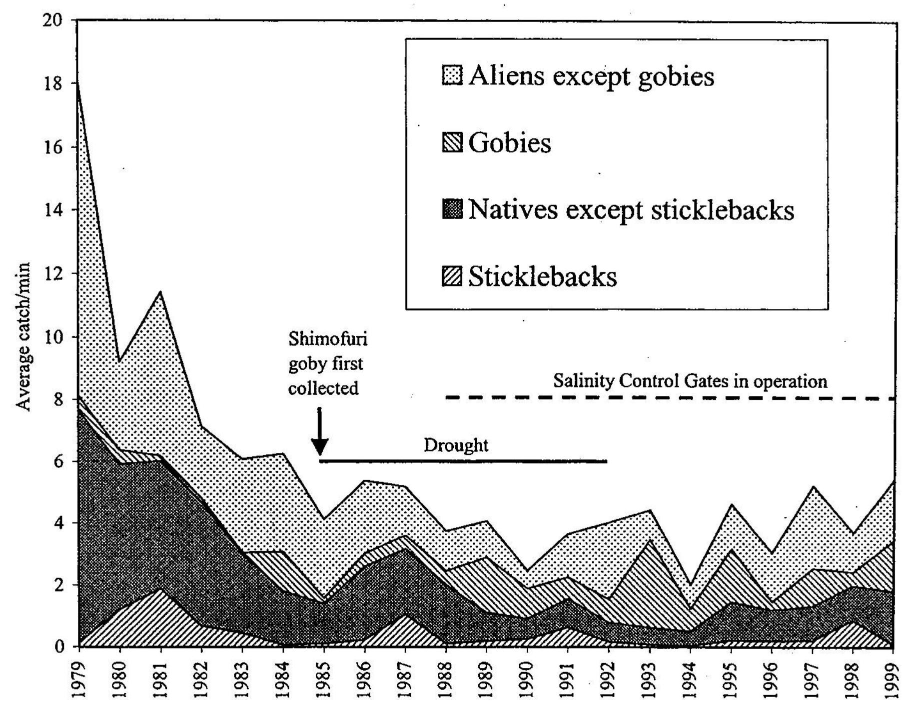

FIGURE 5.—Average yearly catch per minute of (1) alien fishes excluding yellowfin and shimofuri gobies, (2) yellowfin and shimofuri gobies, (3) native fishes excluding threespine sticklebacks, and (4) threespine sticklebacks in Suisun Marsh, 1979–1999. The timing of some major events is indicated.

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

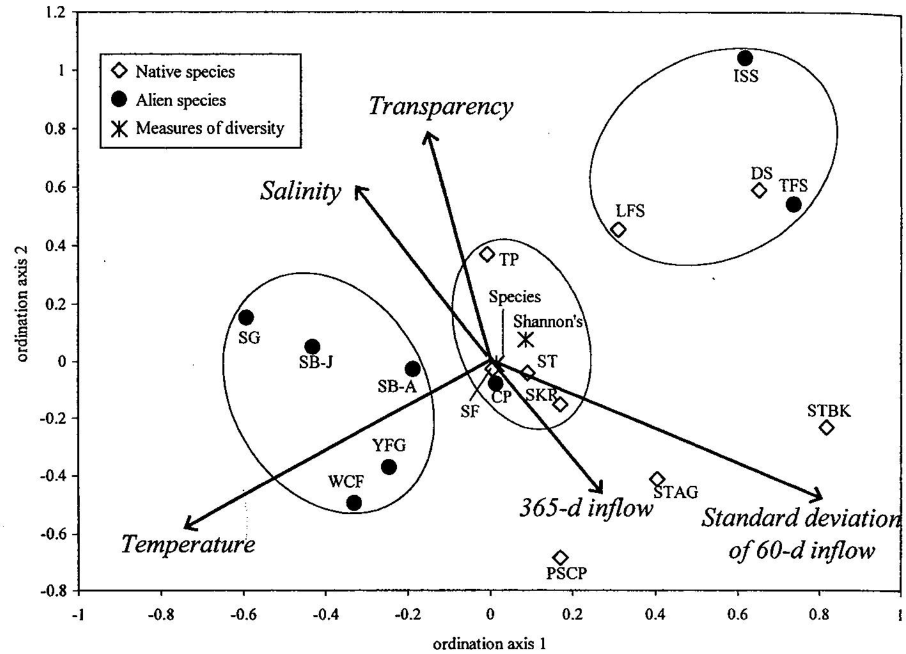

FIGURE 6.—Ordination diagram depicting the results of a canonical correspondence analysis on catch and environmental data collected in Suisun Marsh, 1979–1999. Species codes are listed in Table 2; Shannon's = Shannon's diversity index and species = the total number of species caught per minute.

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).

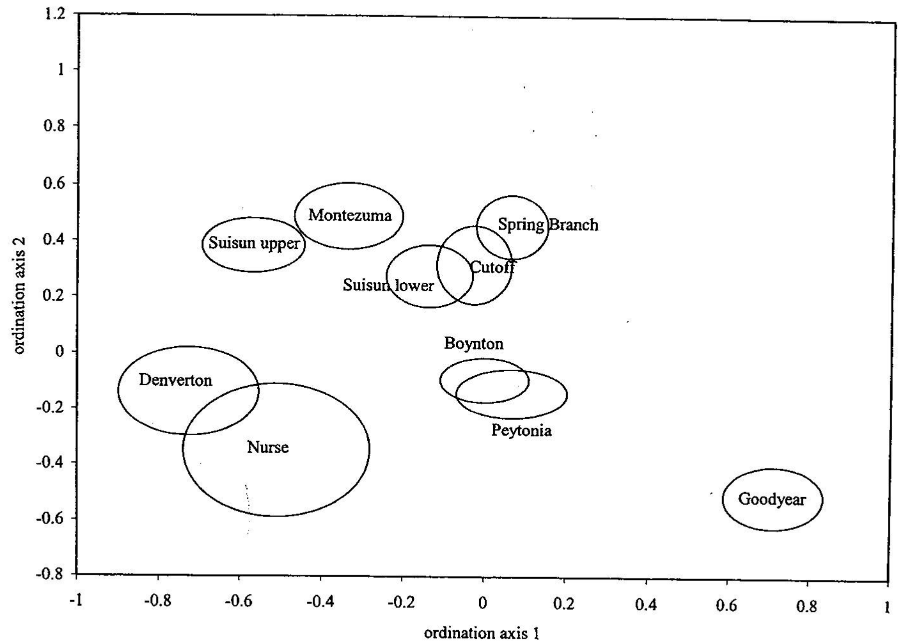

FIGURE 7.—Ordination diagram depicting the results of a canonical correspondence analysis on catch and environmental data collected in Suisun Marsh, 1979–1999. Ellipses represent the 95% confidence intervals of mean slough scores.

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

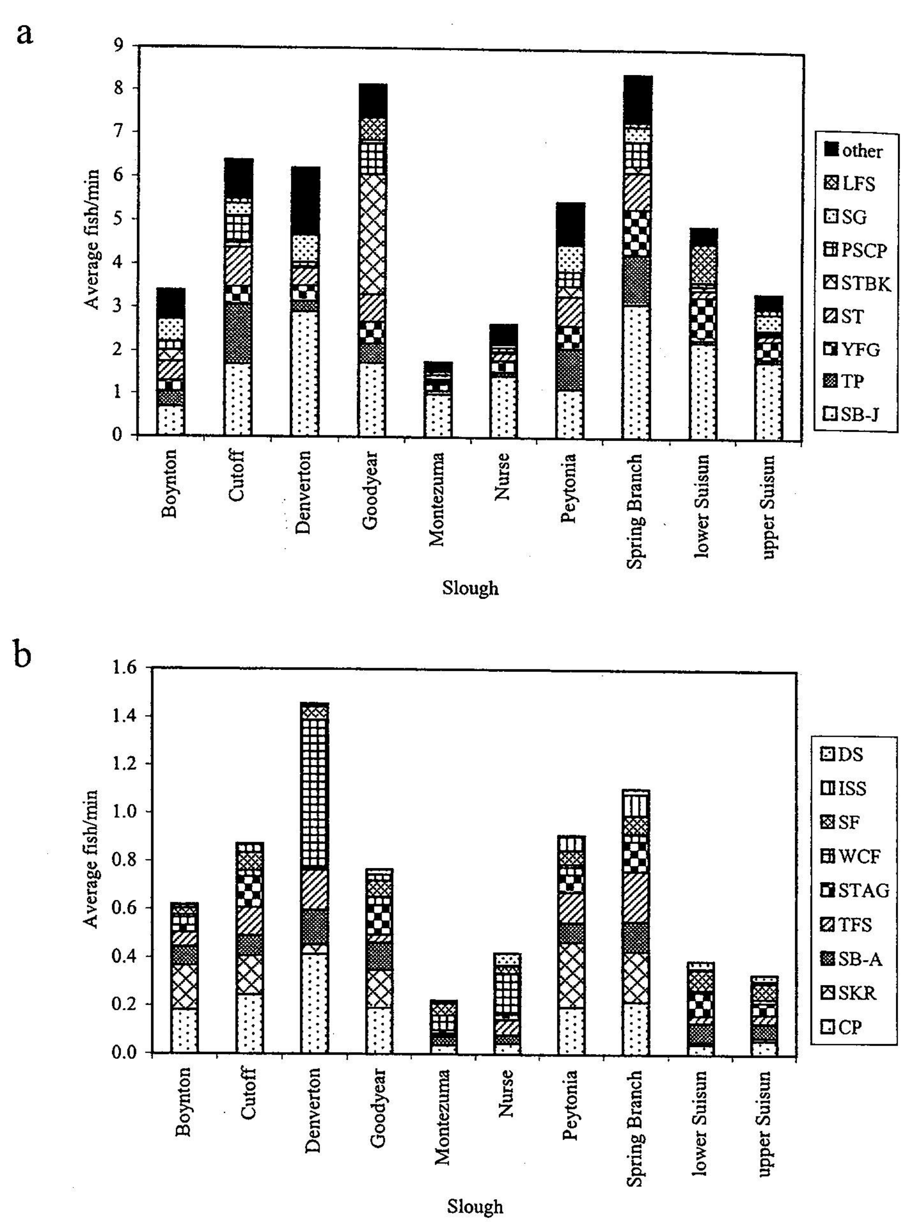

FIGURE 8.—Average number of fish caught per minute of trawling in Suisun Marsh, by slough. Panel **(a)** shows values for species comprising more than 4% of the overall catch, panel **(b)** values for species comprising 0.25–4% of the overall catch. Species codes are listed in Table 2.

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 in-