PATTERNS IN DISTRIBUTION AND ABUNDANCE OF A NONCOEVOLVED ASSEMBLAGE OF ESTUARINE FISHES IN CALIFORNIA

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ABSTRACT

The patterns of distribution and abundance of the fishes of Suisun Marsh, a portion of the Sacramento-San Joaquin estuary in central California, were studied over a 54-month period. Total fish abundance in the marsh exhibited strong seasonality; numbers and biomass were lowest in winter and spring and highest in late summer. Freshwater inflow was highest in the winter and lowest in late summer, when salinities and temperatures were highest. Twenty-one species were collected on a regular basis; the 10 most abundant were *Morone saxatilis, Pogonichthys macrolepidotus, Gasterosteus aculeatus, Hysterocarpus traski, Cottus asper, Spirinchus thaleichthys, Acanthogobius flavimanus, Catostomus occidentalis, Leptocottus armatus,* and *Platichthys stellatus.* Another 21 species occurred in small numbers on an irregular basis. Twenty of the 42 species had been introduced to California since 1879. Of the 21 common species, 14 were residents, 4 were winter seasonals, and 3 were spring/summer seasonals. The resident species fell into two groups: a group of native species that were concentrated in small dead-end sloughs and a group of native and introduced species that were most abundant in the larger sloughs. The seasonal species were also a mixture of native and introduced species. Total fish abundance and species diversity declined through the study period, which seemed to be related to strong year classes of some species early in the study and the prevalance of freshwater conditions late in the study. The structure of the fish assemblage was fairly consistent over the study period but changes are expected in the near future. The structure of the Suisun Marsh fish assemblage was similar to that found in other river-dominated estuaries, despite the mixture of native and introduced species.

The Sacramento-San Joaquin Estuary system is the largest estuary on the west coast of North America. It has been highly modified by surrounding urban, industrial, and agricultural development and by extensive diversion and pollution of the freshwater that flows into it (Conomos 1979). It supports a diverse fish fauna of native and introduced species, but most previous studies have concentrated on species important to sport and commercial fisheries, especially striped bass, *Morone saxatilis*, and, to a much lesser extent, white sturgeon, *Acipenser transmontanus*; chinook salmon, *Oncorhynchus tshawytscha*; American shad, *Alosa sapidissima*; and white catfish, *Ictalurus catus* (Skinner 1972; Moyle 1976). Studies of other species have been few (Ganssle 1966; Turner and Kelley 1966; Baltz and Moyle 1982; Stevens and Miller 1983; Daniels and Moyle 1983), and there have been no community-level analyses equivalent to those conducted on estuarine fish communities in other parts of the world (e.g., Dahlberg and Odum 1970; Livingston 1976; Sheridan and Livingston 1979; Meeter et al. 1979; Blaber and Blaber 1980; Quinn 1980; Thorman 1982). The fish assemblage of the Sacramento-San Joaquin Estuary system is unusual because few of its component species are likely to have evolved together; it is composed of a mixture of introduced and native freshwater, estuarine, and euryhaline marine species (Table 1). The introduced species come from a number of geographic areas, while most of the native species have their centers of abundance in either the rivers upstream or the saltwater bays downstream from the estuary. There are no really comparable estuaries on the California coast, although some of the much smaller and more saline estuaries south of the Sacramento-San Joaquin Estuary do have fish assemblages composed in part of introduced species (Allen 1982).

We began in January 1979 systematic sampling of the fishes in Suisun Marsh on a monthly basis. Suisun Marsh was chosen as a study site because of its central location on the estuary, its proximity to the University of California, Davis campus, and the availability of earlier data from sporadic sampling by the California Department of Fish and Game. The data indicated that the fish fauna was typical of the

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TABLE 1.—Fishes collected in Suisun Marsh, Solono County, CA, in decreasing order of numerical abundance in our trawls. The principal environment of each species is coded as follows: A = anadromous, E = estuarine, F = freshwater, M = marine.

Species	Numbers	Origin
Striped bass, *Morone saxatilis*	24,154	E. North America (E)
Splittail, *Pogonichthys macrolepidotus*	11,250	Native (E)
Threespine stickleback, *Gasterosteus aculeatus*	9,956	Native (F-E)
Tule perch, *Hysterocarpus traski*	7,693	Native (F-E)
Prickly sculpin, *Cottus asper*	4,639	Native (F-E)
Yellowfin goby, *Acanthogobius flavimanus*	1,786	Japan (E-M)
Sacramento sucker, *Catostomus occidentalis*	1,703	Native (F)
Common carp, *Cyprinus carpio*	1,573	Asia (F)
Threadfin shad, *Dorosoma petenense*	1,088	E. North America (E)
Staghorn sculpin, *Leptocottus armatus*	985	Native (M)
Starry flounder, *Platichthys stellatus*	849	Native (M)
Longfin smelt, *Spirinchus thaleichthys*	650	Native (E)
Delta smelt, *Hypomesus transpacificus*	450	Native (E)
American shad, *Alosa spadissima*	218	E. North America (A)
Sacramento squawfish, *Ptychocheilus grandis*	140	Native (F)
Chinook salmon, *Oncorhynchus tshawytscha*	96	Native (A)
Hitch, *Lavinia exilicauda*	56	Native (F)
Inland silverside, *Menidia beryllina*	50	E. North America (F-E)
Goldfish, *Carassius auratus*	45	Asia (F)
Northern anchovy, *Engraulis mordax*	34	Native (M)
Sacramento blackfish, *Orthodon microlepidotus*	25	Native (F)
Pacific herring, *Clupea harengeus*	24	Native (M)
White catfish, *Ictalurus catus*	23	E. North America (F)
Bluegill, *Lepomis macrochirus*	16	E. North America (F)
Mosquitofish, *Gambusia affinis*	15	E. North America (F)
Black crappie, *Pomoxis nigromaculatus*	14	E. North America (F)
Bigscale logperch, *Percina macrolepida*	10	Texas (F)
White sturgeon, *Acipenser transmontanus*	10	Native (E)
Fathead minnow, *Pimephales promelas*	9	E. North America (F)
Brown bullhead, *Ictalurus nebulosus*	6	E. North America (F)
Rainwater killifish, *Lucania parva*	5	E. North America (E)
Green sunfish, *Lepomis cyanellus*	4	E. North America (F)
Pacific sanddab, *Citharichthys sordidus*	4	Native (M)
Pacific lamprey, *Lampetra tridentata*	4	Native (A)
Surf smelt, *Hypomesus pretiosus*	3	Native (M)
Channel catfish, *Ictalurus punctatus*	3	E. North America (F)
Black bullhead, *Ictalurus melas*	3	E. North America (F)
Shiner perch, *Cymatogaster aggregata*	3	Native (M)
Golden shiner, *Notemigonus crysoleucus*	3	E. North America (F)
Warmouth, *Lepomis gulosus*	1	E. North America (F)
Rainbow trout, *Salmo gairdneri*	1	Native (A)
Longjaw mudsucker, *Gillichthys mirabilis*	1	Native (M)

freshwater dominated portions of the estuary. The marsh is also of considerable interest because it is the largest brackish-water marsh in California. It is managed primarily as a wintering area for migratory waterfowl, but its importance as a nursery area for striped bass, salmon, and other fishes is being increasingly recognized (Baracco 1980). The purpose of this paper is to analyze the distribution and abundance of the fishes of the marsh in relation to each other, major environmental factors, and major crustacean species, during a 54-mo period.

STUDY AREA

Suisun Marsh is a large (ca 34,000 ha) tidal marsh located just downstream of the confluence of the Sacramento and San Joaquin rivers (Fig. 1). About 11,000 ha of the marsh consist of sloughs that are influenced by tidal action. The remainder consists of diked wetlands managed to attract wintering waterfowl (Baracco 1980) and for pasturage. The sloughs are shallow (most are <2 m deep) and may fluctuate in depth as much as 1 m during extreme tides. Salinities have ranged from 0 to nearly 17 ppt in recent years, with the highest salinities occurring in late summer of drought years and the lowest salinities occurring annually in winter and spring when river outflows are highest (Baracco 1980). Because increased upstream diversion of water is threatening water quality in the marsh, major modifications to the water distribution system within the marsh are being made to ensure that salinites do not become too high for production of the plants that attract waterfowl.

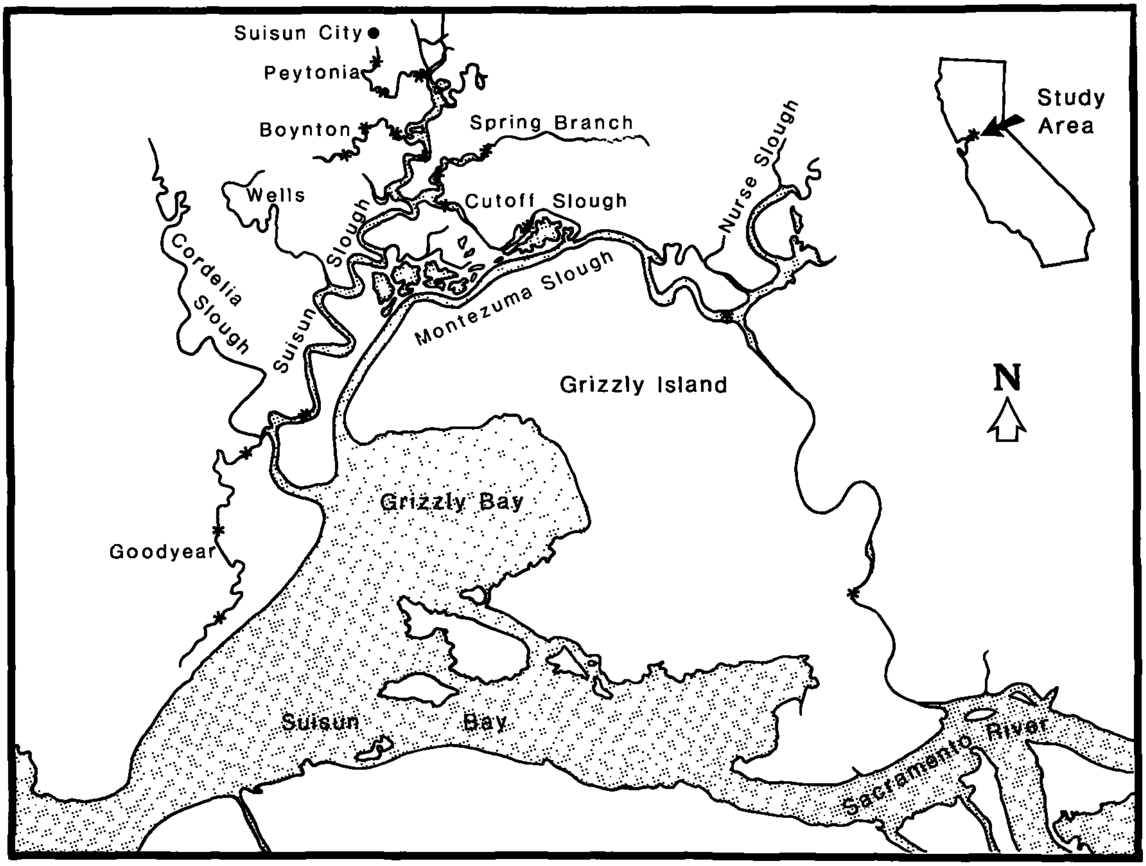


FIGURE 1.—Locations of sample sites (*) in Suisun Marsh, Sacramento-San Joaquin Estuary, CA.

During this study, two major habitat types were sampled: 1) small dead-end sloughs that were 7-10 m wide and 1-2 m deep and 2) Suisun Slough, which connected all the dead-end sloughs and was 100-150 m wide and 2-4 m deep. A third habitat, Montezuma Slough, was also sampled, but the data were not used here because our methods did not sample it adequately. This slough is deep (3-4 m), wide, and riverlike; it is the marsh's main source of freshwater.

METHODS

Sampling was conducted monthly at seven locations throughout the marsh (Fig. 1), from January 1979 through June 1983, with the exception of December 1979 and October 1980. Four of the locations were in dead-end sloughs (Peytonia, Boynton, Mallard, and Goodyear), one was a small slough open at both ends (Cutoff), and two were in Suisun Slough. Sampling was conducted biweekly from January 1980 through June 1981, but the samples for each month were lumped together for analysis, as the samples within months were comparable. All samples were taken during the day, as 24-h studies conducted in April 1979 and 1980 did not exhibit any significant differences between day and night samples.

The principal means of sampling was a four-seam otter trawl with a 1 × 2.5 m opening, a length of 5.3 m, and mesh sizes that tapered down to 6 mm stretch in the bag. At each location, the trawl was towed for either 5 min (small sloughs) or 10 min (Suisun Slough) at about 4 km/h. The longer periods were necessary in large sloughs because of the small catches that prevailed there. Each location was sampled at least twice on each date. This method of sampling was biased because large fishes probably avoided the trawl, and fishes that favor the emergent vegetation were undersampled, as were fishes in the upper part of the water column (Kjelson and Colby 1977). However, these problems were minimized by the narrowness and shallowness of most of the sampling sites; in any case such biases were consistent across the course of this study, so that comparisons should be unaffected. In addition, two locations on the marsh were sampled with a 10 × 1 m, 6 mm mesh, seine, on an irregular basis. An effort was made to seine every month but it was often not possible, as the sites were difficult to seine at extreme high or low tides.

Fishes from each trawl were placed in washtubs of water to minimize mortality and then identified, measured to the nearest millimeter (standard length), and returned to the water as quickly as possible. If more than 100 fish of any one size class of a species were captured, only the first 100 were measured; the rest were counted. Early in the study, samples of all fishes were weighed (wet weight, in gram), and a length/weight relationship developed for each species. This was later used to estimate the biomass of fish in each trawl. The shrimps *Crangon franciscorum* and *Palaemon macrodactylus* in each trawl were also counted. For the oppossum shrimp, *Neomysis mercedis*, an index of abundance was used, based on a 1-to-5 scale, where "1" represented <3 individuals; "2", 3-50 shrimp; "3", 50-200, "4", 200-500, and "5", >500. The index was necessary because most *N. mercedis* probably passed through the net due to their small size (3-5 mm). Nevertheless, they were present seasonally in most hauls, at times in enormous numbers.

At each location, salinity and temperature were taken with a YSI S-C-T meter and transparency was measured with a Secchi disk. Tidal height was determined from a tide table. An index of monthly freshwater outflow from the combined Sacramento and San Joaquin Rivers at Chipps Island was obtained from the California Department of Water Resources (unpubl. data).

For analysis, all the data were summarized by site and month. A Spearman rank correlation analysis using data ranked by month (N = 52) was used for the initial analysis because many of the variables did not conform to a normal distribution. Because no single transformation could be applied to all the variables, nonparametric statistics were used as the most conservative method. We used 13 variables for the analysis (Table 2). In addition, rank abundance (by numbers) by month for the following species categories was used: 1) total striped bass, 2) yearling and older striped bass, 3) young-of-year striped bass, 4) total splittail, 5) yearling and older splittail, 6) young-of-year splittail, 7) total tule perch, 8) tule perch adults, 9) tule perch young-of-year, 10) total prickly sculpin, 11) yearling and older prickly sculpin, 12) prickly sculpin young-of-year, 13) carp, 14) longfin smelt, 15) delta smelt, 16) staghorn sculpin, 17) starry flounder, 18) threadfin shad, 19) Sacramento sucker, 20) yellowfin goby, and 21) threespine stickleback. Because only minor differences were found among the correlations associated with adult and juvenile striped bass, tule perch, splittail, and prickly sculpin, only the results for the totals for these species will be presented.

Analyses were also run using the data from each trawl separately. Species were analyzed using both numbers and grams. Because these data were all of species abundances, a log-normal transformation was used to normalize them. The results were similar in most respects to the analyses using ranks so are not presented here. However, because we were uncertain as to the validity of using ranked data for principal components analysis (PCA), we based our discussion on cautious inspection of the correlation matrix as generated. A principal components analysis was run using the correlation matrix (Dixon and Brown 1977) of l_n numbers of fish per trawl (N = 1,238), to produce groups of species that presumably were responding to the environment in the same general ways.

TABLE 2.—Environmental variables used in the correlation analyses.

Variable	Units	Notes
Month series	1-54	January 1979 to June 1983
Water year	1-5	Begins in October of each year
Salinity	ppt	
Temperature	°C	
Secchi depth	cm	
Neomysis mercedis abundance	1-5 index	
Mean monthly outflow	0-11 index	California Department of Water Resources
Crangon franciscorum	No./trawl	
Palaemon macrodacytlus	No./trawl	
Fish species	No./trawl	
Total fish numbers	No./trawl	
Total fish biomass	Biomass/trawl	Wet weight
Species diversity	Index	Shannon-Weiner (H)

RESULTS

Environmental Variables

Salinity and temperature were negatively correlated with river outflows (Table 3, Fig. 2). Salinity had a strong ($P < 0.01$) positive correlation only with Secchi depth. River outflows generally peaked in February, March, or April, as the result of run-off from melting snow in the Sierra Nevada. Lowest

TABLE 3.—Spearman rank correlation coefficients between fish species ranked by month by numbers and other variables ranked by month. Underlined values are significant at $P > 0.05$.

	Striped bass	Splittail	Tule perch	Sacramento sucker	Yellowfin goby	Carp	Prickly sculpin	Stickleback	Delta smelt	Longfin smelt	Threadfin shad	Staghorn sculpin	Starry flounder
Month series	−0.42	−0.72	−0.51	−0.38	−0.53	−0.58	0.16	−0.10	−0.29	−0.09	−0.26	−0.15	−0.21
Temperature	0.54	0.28	0.08	0.21	0.49	0.49	0.41	−0.33	−0.41	−0.28	−0.55	−0.03	0.01
Salinity	0.62	0.24	0.53	0.14	0.43	0.38	−0.36	−0.14	0.18	0.17	0.24	0.13	−0.06
Secchi depth	0.09	−0.09	0.29	−0.18	−0.08	−0.04	−0.54	−0.09	0.33	0.31	0.52	0.06	−0.28
Outflow	−0.74	−0.36	−0.49	−0.27	−0.62	−0.44	0.06	0.04	0.07	−0.12	0.16	−0.06	0.14
Neomysis mercedis	−0.42	−0.02	−0.24	0.09	−0.45	−0.05	0.28	0.23	0.07	−0.25	−0.10	0.07	0.08
Crangon franciscorum	0.27	−0.01	0.05	0.06	0.46	−0.18	−0.03	−0.10	0.01	−0.59	−0.15	0.29	−0.23
Palaemon macrodactylus	0.43	−0.10	0.06	−0.10	0.34	0.20	0.16	−0.18	−0.30	−0.21	−0.32	0.14	0.23
No./trawl	0.67	0.64	0.72	0.53	0.46	0.45	0.07	0.21	0.16	−0.07	0.06	−0.18	−0.10
g/trawl	0.39	0.71	0.53	0.57	0.39	0.81	−0.06	−0.13	0.04	−0.24	0.13	0.04	0.04
Species/trawl	0.42	0.74	0.48	0.56	0.60	0.52	0.24	0.10	0.21	0.15	0.00	0.21	0.43
Diversity (H′)	−0.10	0.45	0.23	0.45	0.28	0.35	0.31	0.21	0.26	0.09	0.12	0.36	0.43

flows occurred from August through October. Salinity, temperature, and Secchi depth were generally lowest (0-1 ppt, 8°-11°C, and 17-18 cm, respectively) when outflows were highest, and highest (4-9 ppt, 19°-23°C, and 25-40 cm, respectively when outflows were lowest. There is, however, considerable year-to-year variation in these cycles. When outflows were comparatively low (1979, 1981), salinities, temperatures, and turbidities peaked at higher levels than they did in high outflow years. Because 1982 and 1983 were exceptionally wet years, virtual freshwater conditions prevailed throughout both years.

Invertebrates

Neomysis mercedis became very abundant in the marsh from April to June, but the population declined rapidly through the summer, reaching a low in October (Fig. 2). This pattern fits with previous studies of this species, which showed that its populations generally followed the mixing zone up and down the estuary and were reduced at temperatures higher then 22°C and salinities >7 ppt (Orsi and Knutson 1979). In this study, *N. mercedis* abundance showed a significant positive correlation with outflows and significant negative correlations with temperature, salinity, and turbidity (Table 4). It also showed a significant negative correlation (Table 3) with two of its major predators in the marsh, striped bass and yellowfin goby (Herbold 1985[4]).

Palaemon macrodactylus and *Crangon franciscorum* also showed seasonal patterns of abundance (Sigfreid 1980), but the patterns were much less marked than those of *N. mercedis*. *Palaemon macrodactylus* were most abundant during July through October and least abundant during January and February, while *C. franciscorum* were most abundant in November and December and least abundant in January through March. *Palaemon macrodactylus* abundance therefore showed strong positive correlation with temperature and salinity and a negative correlation with outflows. *Crangon franciscorum* abundance was also negatively correlated with outflows, but had a positive correlation only with salinity.

Fishes

A total of 42 species, represented by about 67,000 individuals, were collected in the 1,238 trawl hauls made during the study. The four measures of overall fish abundance and diversity showed negative correlations with month series and with years, indicating a general decline through the study period (Table 4, Fig. 3). Numbers, biomass, and number of species had positive correlations with temperature and/or salinity and negative correlations with out-

[4]Herbold, B. 1985. Resource partitioning within a non-coevolved assemblage of fishes. Unpubl. Ph.D. Thesis, Univ. California, Davis.

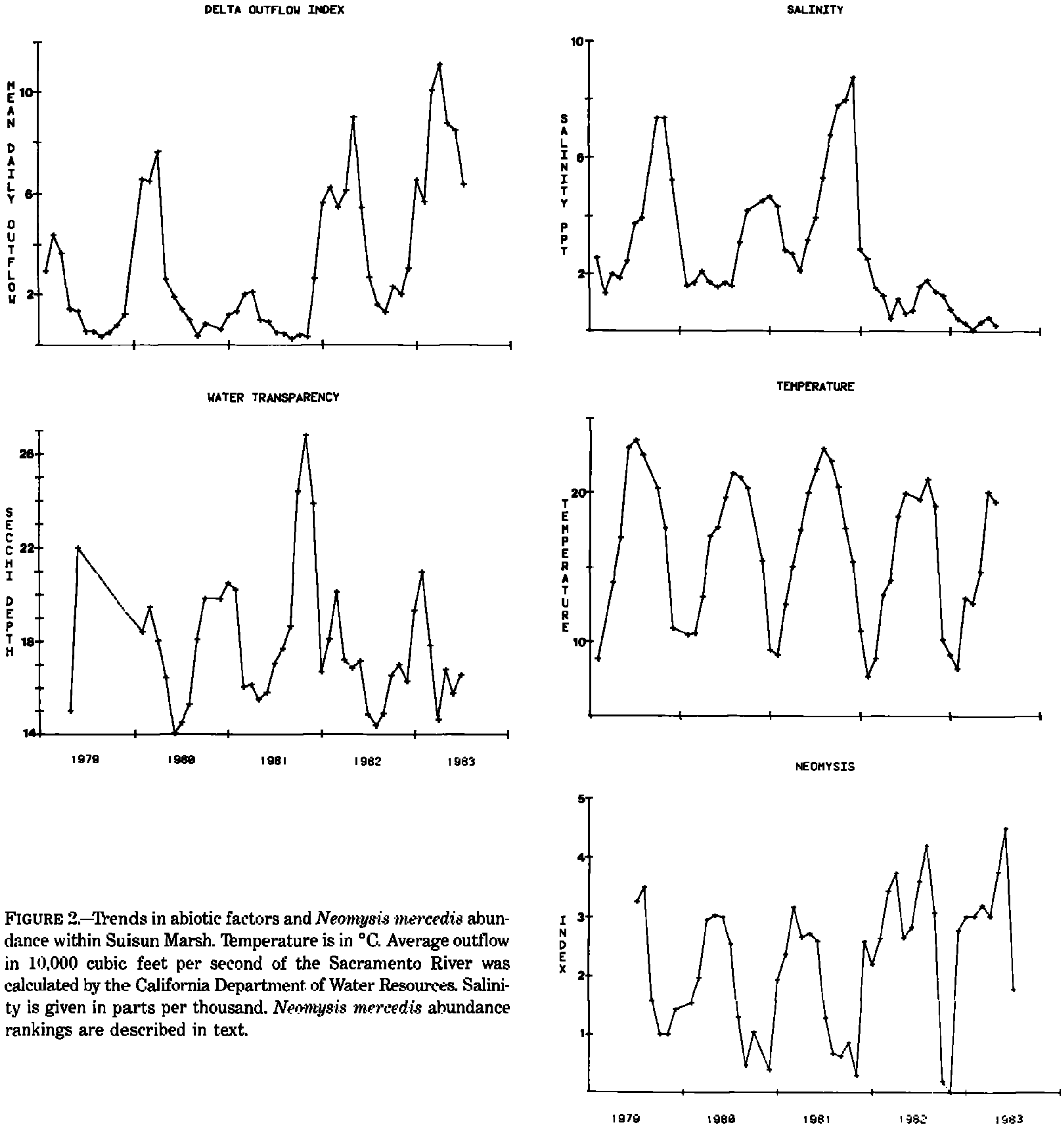


FIGURE 2.—Trends in abiotic factors and *Neomysis mercedis* abundance within Suisun Marsh. Temperature is in °C. Average outflow in 10,000 cubic feet per second of the Sacramento River was calculated by the California Department of Water Resources. Salinity is given in parts per thousand. *Neomysis mercedis* abundance rankings are described in text.

flow, indicating that catches were highest in late summer and lowest in early spring. However, when the patterns of occurrence of the 12 most abundant species were examined, three groups appeared: resident species, winter seasonals, and spring/summer seasonals.

The "resident species" included the native splittail, tule perch, Sacramento sucker, prickly sculpin, and threespine stickleback as well as the introduced striped bass, carp, and yellowfin goby. Two additional species, native white sturgeon and introduced American shad, probably also belonged in this category, as they were caught at all times of the year but too infrequently to draw any firm conclusions. Splittail, striped bass, tule perch, Sacramento sucker, carp, and yellowfin goby had similar patterns of abundance (Figs. 4, 5) and were correlated ($P < 0.05$) with each other and with total biomass, numbers, and species (Tables 3, 4). All six species usually became more abundant in our catches as the sum-

TABLE 4.—Spearman rank correlation among species ranked by month (lower matrix) by numbers and among environmental and other variables ranked by month (upper matrix). Underlined values are significant at $P > 0.05$.

	1	2	3	4	5	6	7	8	9	10	11	12	
13. Striped bass		−0.15	−0.54	−0.10	0.43	0.14	−0.04	−0.04	−0.51	−0.79	−0.80	−0.64	1. Month series
14. Splittail	0.50		0.27	0.19	−0.62	−0.29	0.19	0.44	0.33	0.30	0.37	0.05	2. Temperature
15. Tule perch	0.44	0.38		0.46	−0.78	−0.55	0.42	0.32	0.48	0.37	0.39	0.07	3. Salinity
16. Sacramento sucker	0.19	0.51	0.54		−0.13	−0.43	0.04	−0.24	0.01	0.01	−0.11	−0.19	4. Secchi depth
17. Yellowfin goby	0.68	0.58	0.32	0.22		0.51	−0.52	−0.41	−0.58	−0.34	−0.51	−0.06	5. Outflow
18. Carp	0.46	0.53	0.38	0.46	0.35		−0.56	−0.32	−0.14	−0.03	−0.10	0.16	6. *Neomysis*
19. Prickly sculpin	−0.14	0.13	−0.13	0.34	0.06	0.11		0.34	0.09	−0.19	0.25	0.01	7. *Crangon*
20. Stickleback	−0.41	−0.09	0.05	0.07	−0.22	−0.17	0.09		0.12	0.04	0.15	−0.05	8. *Palaemon*
21. Delta smelt	−0.11	0.08	0.21	0.03	−0.05	−0.15	−0.15	0.40		0.55	0.56	−0.08	9. Numbers/ trawl
22. Longfin smelt	−0.07	−0.01	−0.09	−0.12	0.21	−0.38	−0.15	−0.04	0.43		0.69	0.51	10. Grams/trawl
23. Threadfin shad	−0.17	−0.02	0.38	0.00	−0.24	−0.11	−0.47	0.42	0.36	0.21		0.74	11. Species/trawl
24. Staghorn sculpin	−0.24	−0.13	−0.05	0.06	−0.06	−0.02	0.20	0.18	0.17	0.30	0.01		12. Diversity (H′)
25. Starry flounder	−0.09	0.30	0.03	0.30	0.18	−0.14	0.25	0.22	0.10	0.37	0.00	0.07	
	13	14	15	16	17	18	19	20	21	22	23	24	

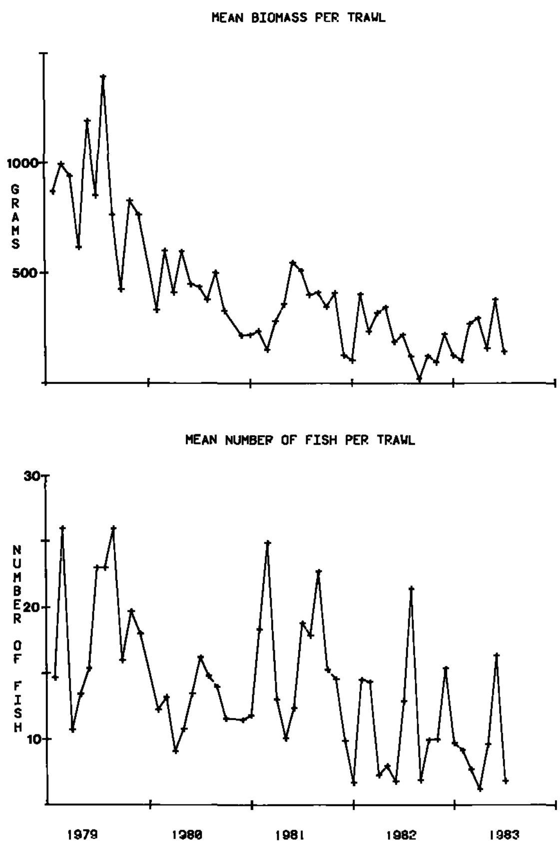


FIGURE 3.—Trends in mean numbers and grams of fish per trawl.

mer progressed although the two introduced species, striped bass and yellowfin goby, tended to peak later than the other species. Consequently, they all showed significant ($P < 0.05$) negative correlations with outflow. All except Sacramento sucker and tule perch had significant positive correlations with salinity and temperature. There was a general decline in fish abundance throughout the 5-yr period. This was reflected in that four of the six species showed a positive correlation with species diversity, and all had a negative correlation with month series.

Prickly sculpin seemed to peak in abundance earlier in the year than the first six species (Fig. 4) but the pattern was obscured by the considerable year-to-year variation in abundance of young-of-year fish. Adults were resident in the marsh but appeared in the trawls on an irregular basis because of their tendency to hide under logs and other objects (Moyle 1976). Overall, prickly sculpin had negative correlations with salinity and Secchi depth, but positive correlations with temperature, *N. mercedis* abundance, and species diversity (Table 3). Threespine stickleback abundance had a negative correlation only with temperature, presumably because their reproductive behavior obscured our ability to catch them. They were most abundant in the trawls in February through May, and the catch consisted primarily of gravid females and schools of young-of-year fish. The males were apparently defending their nesting territories in emergent vegetation. By late summer sticklebacks were rare in the trawls but could be taken in seine hauls made through weedy areas.

The "winter seasonals" were three plankton-

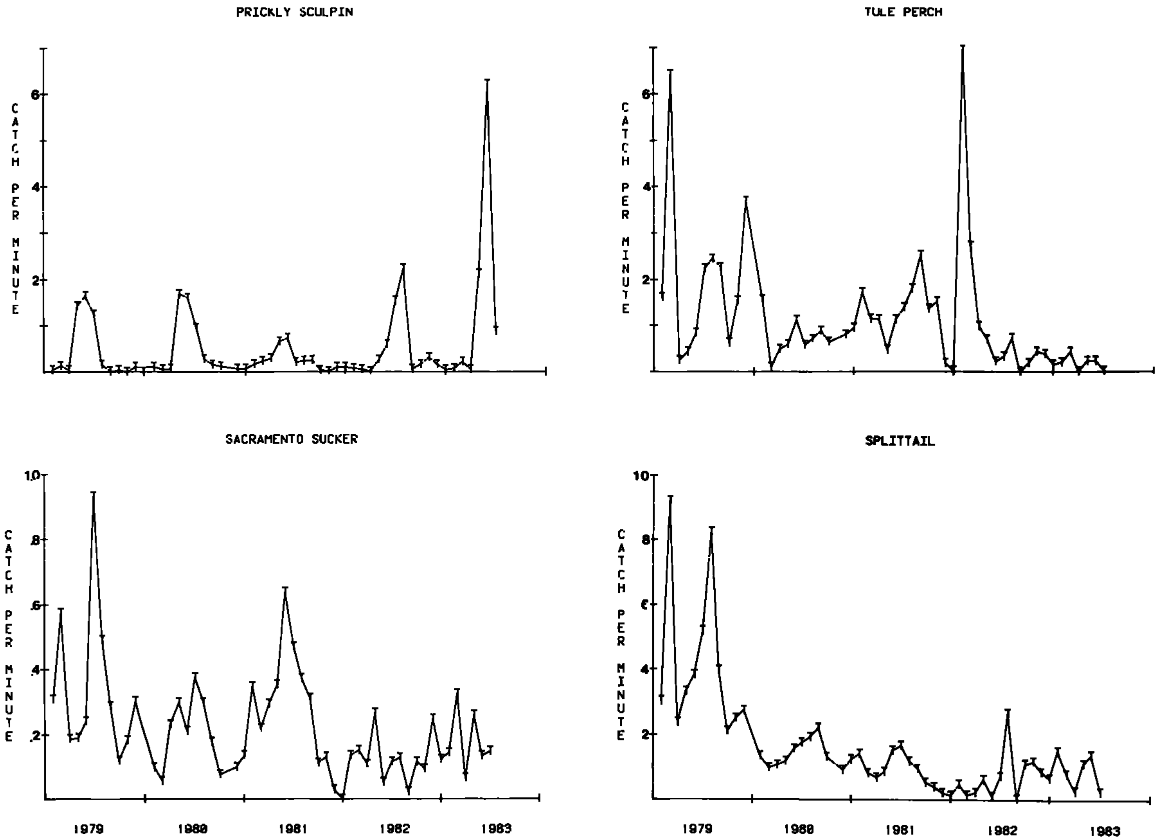


FIGURE 4.—Capture rates of native resident species within Suisun Marsh. Mean catch per effort is described as percent of the total catch for each species.

feeding species, delta smelt (native), longfin smelt (native), and threadfin shad (introduced). All three species tended to be most abundant in November through January, although the pattern was not always consistent (Fig. 6). Threadfin shad were the most erratic of the three species in abundance; they were especially abundant in the summer of 1981. Longfin smelt were largely absent from our samples in 1979 and 1981. Delta smelt abundance was positively correlated ($P < 0.05$) with that of the other two species, although the correlation between longfin smelt and threadfin shad was not significant. All three species had negative correlations with temperature, and positive correlations with Secchi depth.

The "spring/summer seasonals" were staghorn sculpin and starry flounder, both euryhaline marine species that were represented mainly by young-of-year. Their patterns of abundance were not consistent (Fig. 6) and the peaks occurred anytime from March through September. Consequently, staghorn sculpin did not show any significant correlations with the environmental variables, although starry flounder did show negative correlation with Secchi depth. Both species had a positive correlation with species diversity, presumably because they were rare in our samples during the last 2 years when the marsh was dominated by freshwater.

In addition to the 12 species that appeared regularly in our trawls, there were a number of other species of potential importance to the fish community that were either not sampled adequately by the trawl or were absent because of the effects of the 1976-77 drought. Five species that were not sampled adequately were inland silverside, chinook salmon, Sacramento squawfish, mosquitofish, and rainwater killifish. The silversides were abundant year around in the shallow, sandy or weedy areas found in some sloughs. Silversides appeared in seine hauls in 20 of the 22 mo in which seining was done; they were generally the most abundant fish in these hauls. Juvenile chinook salmon and squawfish were common in the marsh in February, March, and April (times of high outflows) and were taken mainly in seines. The tendency of the salmon to remain close to the banks and vegetation and to get sucked into diversions of marsh water consequently has led to the screening of one major diversion in the marsh. Squawfish were abundant in the Sacramento River and juveniles are known to disperse widely during high flows (Smith 1982). Mosquitofish and rainwater killifish were present in ponds adjacent to the sloughs, along with silversides and sticklebacks; mosquitofish were planted in some areas for mosquito control.

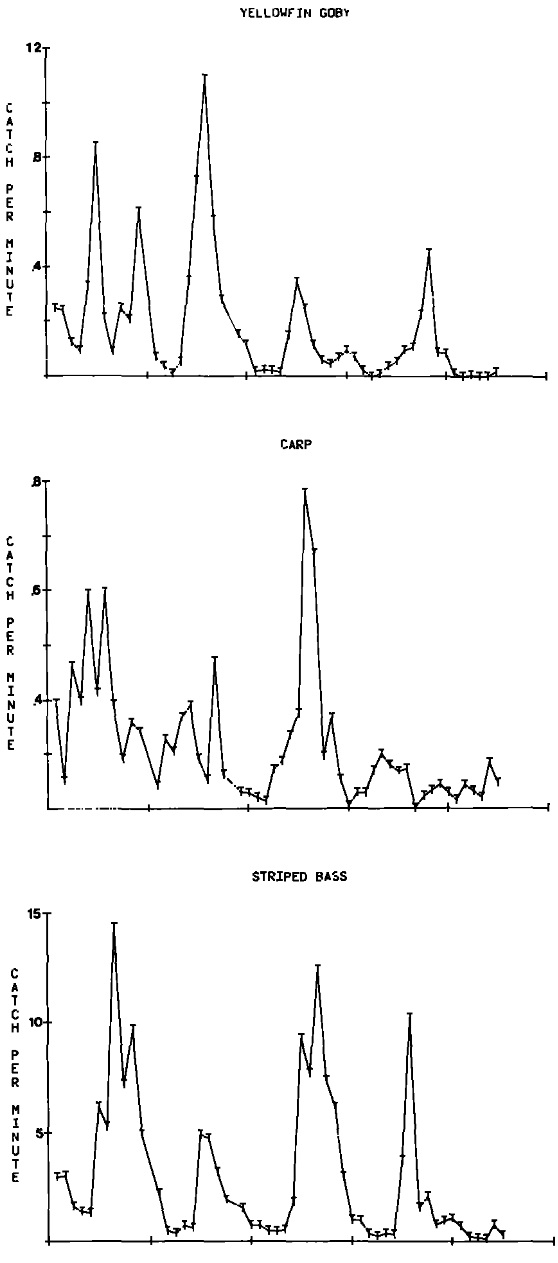


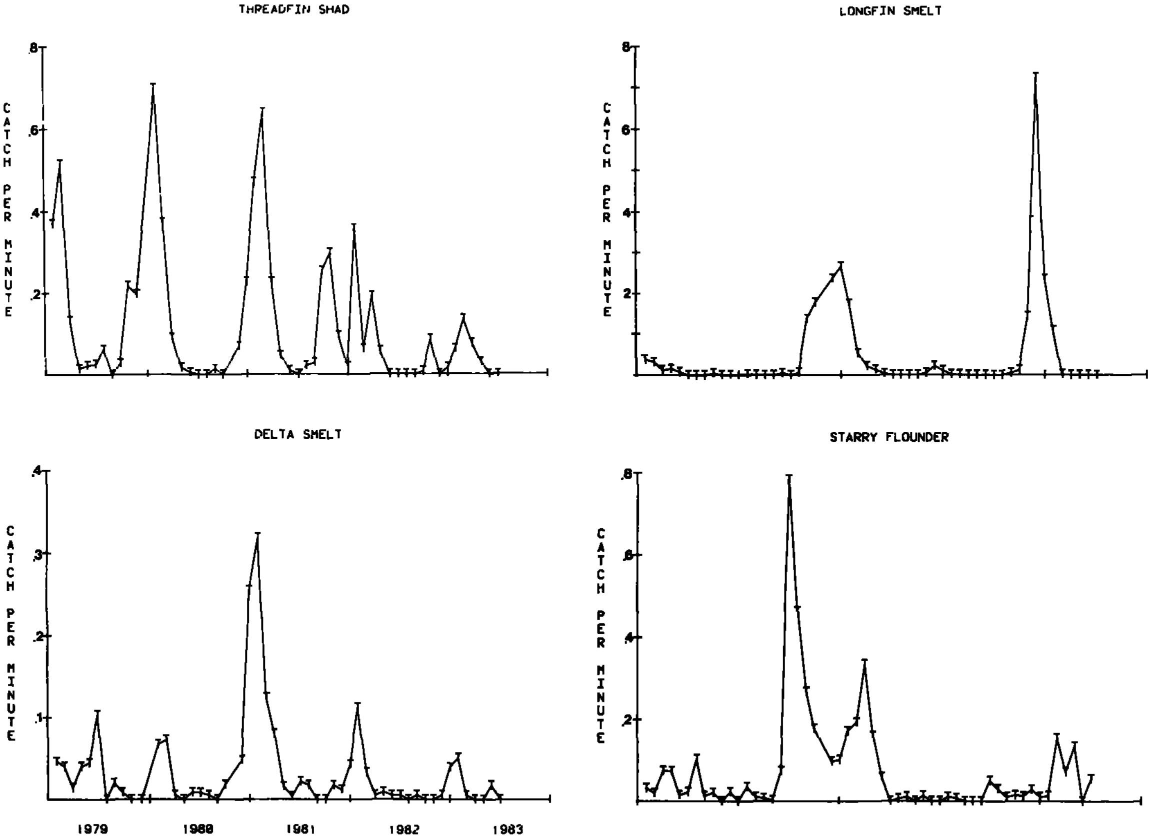
FIGURE 5.—Capture rates of introduced species within Suisun Marsh. Mean catch per effort is described as percent of the total catch for each species.

Principal Components' Analysis

The PCA using the numbers per trawl matrix resulted in four components that explained 47% of the variance in the matrix (Table 5). The first component loaded most heavily on tule perch, Sacramento sucker, and splittail, native resident species most abundant in dead-end sloughs, and to a lesser extent on carp and threadfin shad, introduced species common in such sloughs. The second component loaded heavily on striped bass, yellowfin goby, and carp, three introduced species resident throughout the marsh but most frequently captured in the main sloughs; all reached peaks of abundance in late summer. The third component loaded most heavily on prickly and staghorn sculpins, two benthic species that peaked in abundance during the summer months but were relatively scarce during the last 2

TABLE 5.—Loadings (rotated) of major fish species on four components produced by a principal components analysis of numbers of fish per trawl (n = 1,238). Values over 0.500 are underlined.

	Component 1	Component 2	Component 3	Component 4
Splittail adults	0.487	0.300	−0.024	−0.149
Splittail juveniles	<u>0.549</u>	0.100	0.318	0.149
Striped bass adults	0.058	<u>0.701</u>	0.078	−0.073
Striped bass juveniles	0.183	<u>0.631</u>	−0.157	0.046
Longfin smelt	−0.124	0.029	−0.032	<u>0.747</u>
Delta smelt	0.022	−0.061	−0.027	<u>0.734</u>
Threadfin shad	0.447	−0.286	−0.121	0.319
Common carp	0.403	0.403	0.166	−0.084
Yellowfin goby	−0.011	<u>0.660</u>	0.023	0.016
Tule perch adults	<u>0.827</u>	0.049	0.085	−0.102
Tule perch juveniles	<u>0.833</u>	−0.036	−0.045	−0.017
Sculpin adults	0.254	−0.038	0.377	−0.263
Sculpin juveniles	0.090	0.043	<u>0.780</u>	−0.077
Starry flounder	0.117	0.256	0.107	−0.030
Staghorn sculpin	0.043	0.047	<u>0.727</u>	0.118
Sacramento sucker	<u>0.637</u>	0.197	0.341	0.102
Threespine stickleback	0.039	−0.296	0.486	−0.147
Eigenvalue	2.826	1.874	1.829	1.391
Cumulative proportion of variance explained	0.200	0.304	0.396	0.472



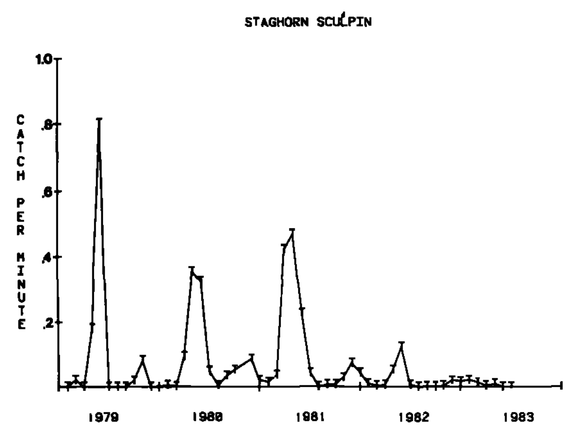


FIGURE 6.—Capture rates of seasonal species within Suisun Marsh. Mean catch per effort for each month described as percent of total for each species.

years of the study. A similar pattern was shown by threespine stickleback, which also had a relatively large positive loading on this component. The fourth component loaded heavily on delta and longfin smelt, and to a lesser extent on threadfin shad. This is the winter seasonal group identified in the previous analysis.

DISCUSSION

During the 5-yr study period, the fish assemblage of Suisun Marsh had the following characteristics:

1. There was a strong seasonal pattern of total fish

abundance with numbers and biomass lowest in winter and spring and highest in late summer. Fishes were least abundant when river outflows were highest and most abundant when salinities and temperatures were highest.

2. There was an overall decline in fish abundance and species diversity through the study period.

3. Of the 21 species that occurred in the marsh on a regular basis, 14 were residents, 4 were winter seasonals, and 3 were spring/summer seasonals. Another 21 species occurred sporadically, in small numbers. These were mainly marine and freshwater species that presumably could become established in the marsh if environmental conditions changed significantly.

4. The abundant resident species fell into two groups, one made up of native species that concentrated in the small dead-end sloughs and the other a mixture of introduced and native species that were widely distributed in the marsh, but most abundant in the larger sloughs.

5. The structure of the fish assemblage (i.e., the pattern of distribution and abundance) was fairly consistent over the 54-mo period.

The seasonal pattern of fish abundance was due to a number of factors, most importantly 1) variation in sampling efficiency, 2) influxes of young-of-year fish, 3) favorable environmental conditions for most fish species in late summer, and 4) abundance of *Neomysis mercedis*. When outflows were high, water levels in the marsh were high and showed little tidal fluctuation. Therefore trawling was less efficient because there was more water and more flooded vegetation available as cover for fish. However, even under these conditions most of the sampling areas were rarely more than 2 m deep, so our trawl covered at least half the water column, and large catches were common, especially early in the study. Therefore, variation in sampling efficiency may have exaggerated the peaks and valleys of the catch curves (Figs. 4, 5) but was unlikely to obscure the general trends in abundance. Probably the most important contributor to the seasonal patterns was the increase in young-of-year striped bass, splittail, prickly sculpin, and tule perch, in June through August. These species (and others, to a lesser extent) became vulnerable to our trawl at 30-40 mm SL, and catches of several hundred individuals in a 5-min tow were made on occasion. The rapid growth of these species during summer (Daniels and Moyle 1983; Herbold and Moyle, unpubl. data) indicated that environmental conditions, including warm temperatures and moderate salinities, were favorable for them and for other euryhaline species (e.g., staghorn sculpin, starry flounder). These same conditions also favored *N. mercedis*, a small shrimp that is an important food item in summer diets of most of the fishes (Herbold fn. 4). It is possible that the summer peak in fish abundance may be due also in part to fishes moving in to take advantage of an abundant food resource. The decline in *N. mercedis* abundance in late summer may be related in part to fish predation, although it is presumably related mainly to their seasonal movements within the entire estuary (Orsi and Knutson 1979).

The overall decline in fish abundance over the study period seemed to be due to two factors: variation in reproductive success of major species and the fact that 1982 and 1983 were years of unusually high precipitation and runoff, so freshwater conditions prevailed throughout the summer months of both years. Splittail showed an unusually strong year class in 1978, which dominated the 1979, and, to a lesser extent, 1980 samples (Daniels and Moyle 1983). Catches of splittail in 1979 were typically 2-5 times greater than in subsequent years. Striped bass, tule perch, and carp also showed peaks of abundance in 1979 and had low abundances in 1982-83, with one or two peaks of abundance in between. Except for carp, the peaks were largely due to influxes of young-of-year fish. The reason for the abundance of the 1978 year class of fish was presumably related to 1978 being a year of high, but not excessive, outflows. Increased reproductive success during high outflow years has been documented for striped bass (Stevens 1977), splittail (Daniels and Moyle 1983), American shad, chinook salmon, and longfin smelt (Stevens and Miller 1983). However, under extreme outflow conditions (such as existed in 1982 and 1983), young-of-year fish are apparently carried downstream to areas below the marsh (San Francisco and San Pablo Bay) where chances of survival may be less (Stevens 1977).

Drought also contributed to the variation in the fish fauna. During 1976 and 1977, severe drought reduced freshwater inflows to the marsh, resulting in sustained high salinities. Freshwater fishes declined dramatically during the drought period (Herrgesell et al. 1981) and the fishery for catfish (mainly white catfish and black bullhead) was greatly reduced (Baracco 1980). The catfish populations did not recover during the study period, but the regular appearance of young-of-year white catfish in our trawls in late 1983 indicated a recovery may be in progress. Other freshwater fishes found in the marsh (Table 1) showed no signs of increasing. Most were represented in our samples by <10 individuals that had presumably been washed into the marsh from freshwater habitats upstream. However, black crappie and perhaps other centrarchids contributed to the local fishery prior to the drought, mainly in the upper ends of the larger sloughs, so a recovery can be expected.

Despite the decline in freshwater fishes during the drought, there was no corresponding major increase in the abundance of euryhaline marine species characteristic of nearby San Francisco Bay (Herrgesell et al. 1981). Marine species (such as northern anchovy, Pacific herring, and shiner perch) generally appeared in our samples in late summer when salinities were highest, in parts of the marsh closest to Suisun Bay.

Considering the annual and long-term variations in fish abundances and the fact that the fish assemblage is made up of a mixture of native and introduced species, the consistency of the assemblage structure during the study is surprising. Coevolution has obviously little role in an assemblage in which the most abundant species (striped bass) entered in 1879 and other abundant species entered in the 1960's (yellowfin goby) and 1970's (inland silversides) (Moyle 1976). The apparent consistency in structure seemed to be the result of 1) two introduced species, striped bass and carp, that were consistently abundant in the marsh, 2) the group of native resident fishes that was persistent in deadend sloughs, and 3) the native fishes that moved in and out of the marsh on a seasonal basis.

This does not mean that the structure observed during this study will persist indefinitely. A number of changes in the fish fauna may already be occurring. For example, the presence of young-of-year white catfish in 1983 and 1984 may signify a shift of the assemblage towards catfishes and centrarchids, such as existed before the 1976-77 drought. Striped bass are presently in a long-term decline in abundance, a trend which seems to be continuing (Kelley et al. 1982). Past history indicates that new introductions of fishes into the system are likely: specifically, the white bass, *Morone chrysops*, has recently become established in part of the San Joaquin drainage and may become a major new predator in the Sacramento-San Joaquin Estuary if planned eradication attempts fail (California Department of Fish and Game unpubl. data). Furthermore, additional diversions of freshwater from the estuary are planned (Herrgesell et al. 1981), and major modifications to the marsh channels are planned or underway (Baracco 1980), so the environment, especially in the dead-end sloughs, may change significantly. It is difficult to predict what the combined effects of all these changes will be on the present fish assemblage, but extinctions of both native and introduced species in the estuary have occurred in the past (Moyle 1976) and could occur again in the future.

The structure of the fish assemblage of Suisun Marsh is similar in may respects to the structure of the fish assemblages of other large estuaries (e.g., Markle 1976; Meeter et al. 1979), despite the importance of recently introduced species and the stabilizing influence humanity has had on the pattern and amount of freshwater inflow (Kahrl 1978). In most such estuaries, as in the Sacramento-San Joaquin, the assemblages are dominated by juvenile fishes, and most species have substantial populations outside the estuary. As in Suisun Marsh, the fish assemblages of such estuaries are made up of a relatively small number of the species available in nearby marine and freshwater environments. Presumably, the species composition of an estuarine assemblage is determined in large part by the ability of the species to tolerate the particular set of environmental conditions that exist there. Since these conditions may change with short-term climatological changes, the fish assemblages may change as well (Meeter et al. 1979; Marais 1982). Thus coevolution is given little chance to operate in estuarine systems in general. In this context, it is not surprising that the fish assemblage of the Suisun Marsh behaves ecologically in a way similar to fish assemblages in most other estuarine systems. Because resource partitioning is commonly observed among estuarine fishes (Sheridan and Livingston 1979; Whitfield 1980), competition may be an important process in determining the structure of estuarine fish assemblages (Thorman 1982), a hypothesis we are currently investigating in the Suisun Marsh.

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