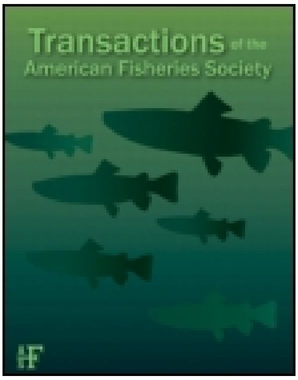
Changes in Abundance and Distribution of Native and Introduced Fishes of Suisun Marsh

Article *in* Transactions of the American Fisheries Society · July 1994

DOI: 10.1577/1548-8659(1994)123<0498:CIAADO>2.3.CO;2

Peter B Moyle
University of California, Davis

Herbold Bruce
Private Consultant



Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

Changes in Abundance and Distribution of Native and Introduced Fishes of Suisun Marsh

Lesa Meng [a] , Peter B. Moyle [a] & Bruce Herbold [b]

[a] Department of Wildlife and Fisheries Biology, University of California, Davis, California, 95616, USA

[b] U.S. Environmental Protection Agency, 75 Hawthorne Street, San Francisco, California, 94105, USA

Published online: 09 Jan 2011.

Transactions of the American Fisheries Society 123:498–507, 1994
American Fisheries Society

Changes in Abundance and Distribution of Native and Introduced Fishes of Suisun Marsh

LESA MENG AND PETER B. MOYLE

Department of Wildlife and Fisheries Biology
University of California, Davis, California 95616, USA

BRUCE HERBOLD

U.S. Environmental Protection Agency
75 Hawthorne Street, San Francisco, California 94105, USA

Abstract.—Overall fish abundance, abundance of introduced, native, and seasonal fish groups, and species diversity declined over a 14-year period in Suisun Marsh, a portion of the San Francisco Bay estuary, and were associated with decreases in freshwater outflow and increases in salinity. Fish groups showed different patterns of abundance; large fluctuations in introduced and seasonal fish groups contrasted with a steady decline in native fish. Native species were found more often in small, dead-end sloughs, seasonal species were found in larger sloughs, and introduced species were found in both habitats. Fish assemblage structure was less predictable than in an earlier (and shorter) study of the same community. Mixed groups of native and introduced species with similar freshwater and seasonal needs reflected effects of drought and increasing water diversions from the estuary. Chameleon goby *Tridentiger trigonocephalus* and yellowfin goby *Acanthogobius flavimanus*, two introduced species, fluctuated greatly in abundance in recent years, whereas other species declined steadily. Changes in fish abundance in the marsh reflect estuary-wide changes and suggest that environmental disturbances coupled with introduced species are altering fish communities and hastening native fish declines.

The San Francisco Bay estuary, at the confluence of the Sacramento and San Joaquin rivers, is the largest estuary on the west coast of North America; it carries runoff from 40% of California's surface area (Kahrl 1978). The estuary has been highly modified by human activities that include diking and filling of wetlands, pollution, reduction of freshwater inflow by more than half, and the introduction of exotic species (Conomos 1979; Nichols et al. 1986). Fish populations in the estuary have declined dramatically since the 1970s with major losses in populations of chinook salmon *Oncorhynchus tshawytscha*, striped bass *Morone saxatilis*, delta smelt *Hypomesus transpacificus*, longfin smelt *Spirinchus thaleichthys*, and splittail *Pogonichthys macrolepidotus* (Stevens 1977; Stevens and Miller 1983; Stevens et al. 1985; Moyle et al. 1992).

Environmental changes induced by human activities alter fish communities and allow successful colonization by introduced species, which further compromise community structure (Herbold and Moyle 1986; Moyle 1986). About half of the 55 fish species collected from the estuary are introduced (Herbold et al. 1992). Fishes such as striped bass and American shad *Alosa sapidissima* have been introduced intentionally into the estuary since the 1870s (Moyle 1976). Others, such as threadfin shad *Dorosoma petenense* and inland silverside *Menidia beryllina*, entered the estuary after being introduced into connecting waterways (Moyle 1976). More recently, yellowfin goby *Acanthogobius flavimanus* and chameleon goby *Tridentiger trigonocephalus* have been introduced from Asia in the ballast water from ships (Brittan et al. 1970). Approximately 100 invertebrate species have been introduced into the estuary (Carlton 1979; Nichols et al. 1986); many have altered estuarine food webs (e.g., Nichols et al. 1990; Meng and Orsi 1991).

Suisun Marsh is in the center of the estuary and is the largest contiguous estuarine marsh remaining in the United States (Moyle et al. 1986). The fish assemblage is unusual because few of its component species evolved together; it is composed of a mixture of native and introduced freshwater, estuarine, and euryhaline marine species (Moyle et al. 1986). Of species captured in the marsh, native fishes tend to be more common in small dead-end sloughs, whereas introduced fishes are found more often in larger sloughs (Moyle et al. 1986). We began systematic sampling of Suisun Marsh in January 1979. Previous analyses of Suisun Marsh data concluded that declines in fish abundance and species diversity were related to temporary conditions of exceptionally high out-

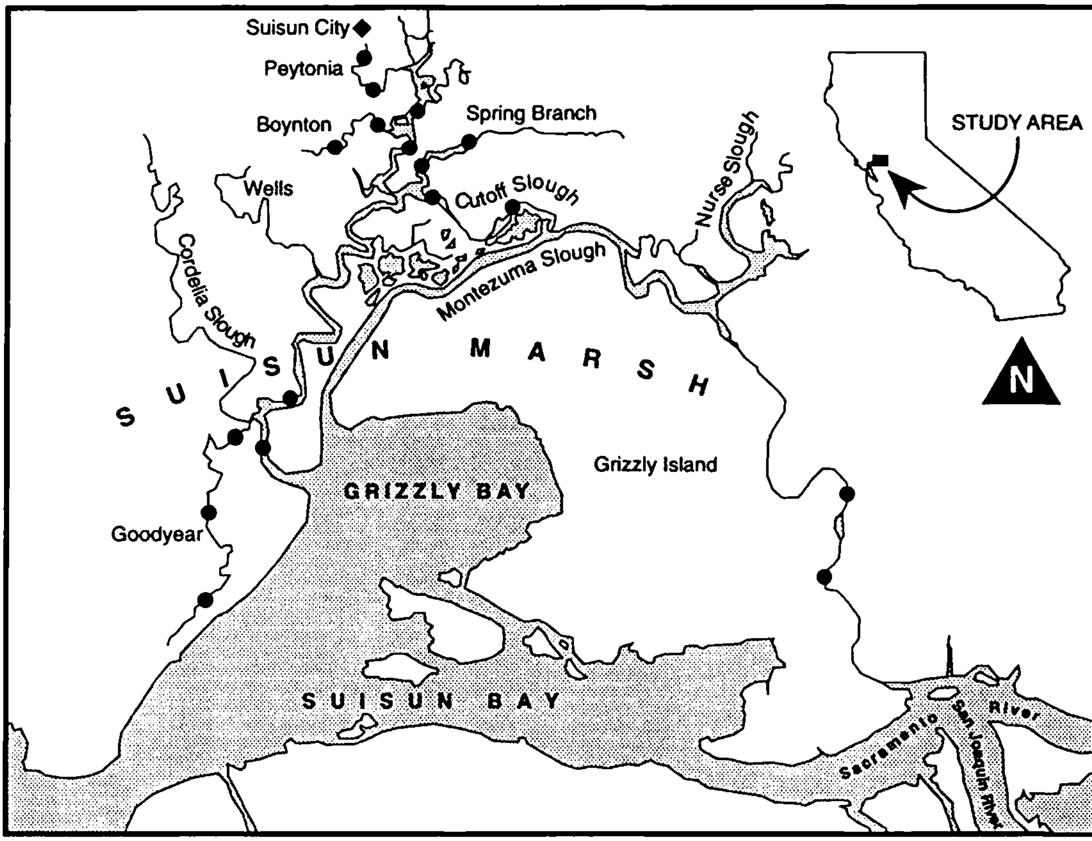


FIGURE 1.—Suisun Marsh, San Francisco Bay estuary, California. Trawling was done at sites marked with black circles.

flow and lack of strong year-classes of the more abundant species (Moyle et al. 1986). Furthermore, Moyle et al. (1986) noted that the structure of the fish assemblage was fairly consistent over the period studied.

In this paper we reexamine the conclusions of Moyle et al. (1986) and incorporate nine more years of data. We analyze data from 1979 to 1992 and ask the following questions. (1) Has fish abundance changed? (2) Do introduced, native, and seasonal fish groups show different trends in abundance? (3) Is there a difference in fish group distribution between dead-end and larger sloughs? (4) Are fish abundances and species diversity (measured here as number of species) correlated with environmental variables and macroinvertebrate abundance? (5) Is the fish assemblage consistent and comparable to patterns found by Moyle et al. (1986)? (6) How do abundances of chameleon and yellowfin gobies (recent introductions) compare with overall fish abundance?

Methods

Study area.—Suisun Marsh is a large (about 34,000-ha) tidal marsh downstream of the confluence of the Sacramento and San Joaquin rivers (Figure 1). About one-third of the marsh is sloughs influenced by tidal action; the remainder is diked wetlands managed to attract wintering waterfowl. Salinities have ranged from 0 to nearly 17‰ in recent years, highest salinities occurring in early fall of drought years and lowest salinities occurring in spring when river outflows are highest.

We sampled two major habitat types in the marsh. Small dead-end sloughs are 7–10 m wide, 1–2 m deep, and lined with tules *Scirpus* spp. and reeds *Phragmites communis*. Most of the dead-end sloughs are connected by larger sloughs that are 100–150 m wide, 2–4 m deep, and partially riprapped. Sloughs fluctuate as much as 1 m in depth during extreme tides, resulting in a 50–75% dewatering of dead-end sloughs during low tides.

TABLE 1.—Selected introduced, native, and seasonal fish species used to index abundance as derived from the "most abundant species" of Moyle et al. (1986), with the addition of chameleon goby, a recent introduction.

	Introduced
Chameleon goby	*Tridentiger trigonocephalus*
Common carp	*Cyprinus carpio*
Striped bass	*Morone saxatilis*
Yellowfin goby	*Acanthogobius flavimanus*
	Native
Prickly sculpin	*Cottus asper*
Sacramento sucker	*Catostomus occidentalis*
Splittail	*Pogonichthys macrolepidotus*
Threespine stickleback	*Gasterosteus aculeatus*
Tule perch	*Hysterocarpus traski*
	Seasonal
Delta smelt	*Hypomesus transpacificus*
Longfin smelt	*Spirinchus thaleichthys*
Pacific staghorn sculpin	*Leptocottus armatus*
Starry flouder	*Platichthys stellatus*
Threadfin shad	*Dorosoma petenense*

The major source of freshwater for the marsh is the Sacramento River.

Field methods.—We obtained fish samples monthly at seven locations throughout the marsh from January 1979 through January 1992 by trawling 2–4 times at each location (Figure 1). Five of the locations were categorized as small dead-end sloughs (Peytonia, Boynton, Spring Branch, Goodyear, and Cutoff). Cutoff is open at both ends, but similarities in size, shoreline vegetation, and configuration, including abundant backwaters, allowed it to be classified as a dead-end slough. The two larger sloughs were Suisun and Montezuma. All samples were taken during the day, because 24-h studies conducted in April 1979 and 1980 did not reveal any significant differences between day and night samples (Moyle et al. 1986).

We sampled with a four-seam otter trawl with a 1×2.5-m opening, a length of 5.3 m, and mesh size that tapered from 25 mm to 6 mm stretch in the bag. We trawled for 5 min in dead-end sloughs and 10 min in larger sloughs at about 4 km/h. Longer trawls were necessary in larger sloughs because of small catches. Any biases in sampling, gear effectiveness, and other methodology were consistent over the course of the study, so comparisons should be unaffected.

Contents of each trawl were placed in washtubs of water. Fishes were identified and then returned to the slough. We also recorded the abundance of common macroinvertebrates. The shrimps *Crangon franciscorum* and *Palaemon macrodactylus* were counted. For the opossum shrimp *Neomysis mercedis*, an index of abundance was used: 1 represented fewer than 3 individuals; 2, 3, and 4 represented 3–50, 51–200, 201–500 shrimp, respectively; and 5 represented more than 500 animals. The number of fish species per trawl was recorded as a measure of species diversity.

Environmental variables were recorded for each trawl set. We measured temperature and salinity with a YSI S-C-T meter. Water transparency was measured with a Secchi disk. An index of monthly freshwater outflow was obtained from the California Department of Water Resources. This index is calculated by summing estuarine inflows from the Sacramento and San Joaquin rivers, smaller streams, precipitation, and cropland drainage. Exports from state and federal water project facilities in the upper estuary are then subtracted from estuarine inflow to produce the freshwater outflow index.

Repeated-measures analysis.—We used a repeated-measures analysis of variance (SAS Institute 1988) with two grouping factors (fish group index and dead-end versus larger sloughs) and one within factor (yearly index of fish group abundance) to address questions 1–3 (Did fish abundance change through time? Did fish groups show similar trends in abundance? Was there a difference in distribution among the groups between dead-end and larger sloughs?). Locations served as replicates in our repeated measures. Because the test for sphericity (a test for independence) was significant ($P = 0.0004$), reported probability values for the within factor (years) are based on the Huynh–Feldt adjustment (SAS Institute 1988). For the repeated-measures analysis, all data were summarized by year and location.

Fish group indices were derived from the same group of most "abundant species" used by Moyle et al. (1986). Of the 42 species that have been captured in the marsh, the abundant species of Moyle et al. (1986) made up 98% of the total catch; we added chameleon goby, bringing the total to 14 species (Table 1). Introduced, native, and seasonal fish group indices were derived by summing the number of fish per group per trawl and then dividing by the number of species in the group. None of the fish group indices were dominated by the abundance of a single species; each species in each index contributed roughly equally to their respective index. Because catches of seasonal fish are quite small in the marsh, the seasonal species index was multiplied by 10 to make the indices comparable.

TABLE 2.—Results of repeated-measures analysis of variance with two grouping factors (fish group index and dead-end versus larger sloughs) and one within factor (yearly index of fish abundance). Probability values for the within factor (year) are based on the Huynh–Feldt adjustment.

Source	df	P^a
Between-subjects effects		
Fish group	2	0.004
Slough	1	0.75
Slough × fish group	2	0.005
Between-subjects contrasts		
Introduced versus native fish	1	0.003
Seasonal versus native fish	1	0.003
Introduced versus seasonal fish	1	0.97
Introduced fish, dead-end versus larger sloughs	1	0.16
Native fish, dead-end versus larger slough	1	0.009
Seasonal fish, dead-end versus larger slough	1	0.05
Within-subjects effects		
Year	13	0.0001
Year × fish group	26	0.0001
Year × slough	13	0.27
Year × slough × fish group	26	0.001
Within-subjects contrasts		
Year × (introduced versus native fish)	13	0.009
Year × (seasonal versus native fish)	13	0.0001
Year × (introduced versus seasonal fish)	13	0.0001
Year × introduced fish × (dead-end versus larger sloughs)	13	0.014
Year × native fish × (dead-end versus larger sloughs)	13	0.026
Year × seasonal fish × (dead-end versus larger sloughs)	13	0.10

[a] Probability of a greater F-value.

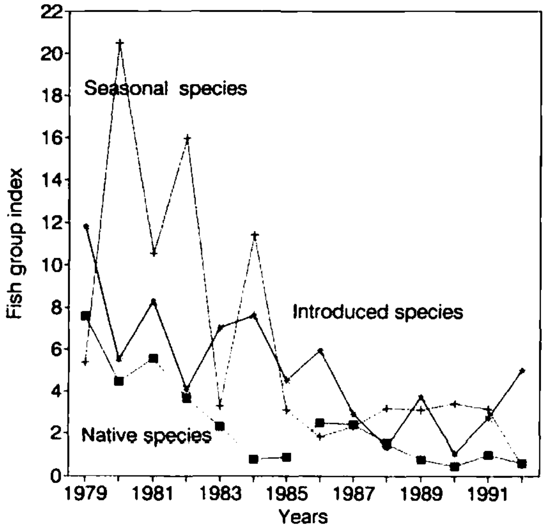


FIGURE 2.—Index of abundance of introduced, native, and seasonal fish groups versus time. Fish group indices were derived from the 14 most abundant species by summing the number of fish per trawl and then dividing by the number of species in the group.

We used a Spearman rank correlation analysis to answer question 4 (Do total fish and fish group abundances and species diversity respond differently to environmental variables and macroinvertebrate abundances across years?). We used this analysis because plots of yearly averages of environmental variables and shrimp abundances versus fish abundances and species diversity were nonlinear, and repeated-measures analyses of fish abundances with environmental variables as covariates were not significant.

Principal components analysis.—We used principal components analysis (PCA) to answer question 5 (Was the fish assemblage consistent and comparable to patterns found by Moyle et al. 1986?). Moyle et al. (1986) used data from January 1979–June 1983 in their PCA, whereas we used data from July 1983–January 1992. Data were summarized by month in order to reveal seasonal patterns among fish species similar to patterns seen by Moyle et al. (1986). We used fish abundance per month ($\log_e$-transformed) of each species in Table 1 for the analysis.

We graphed chameleon and yellowfin goby abundances to answer question 6 (How did abundances of these two recent introductions compare with overall fish abundance?).

Results

Fish Abundance and Distribution

Our repeated-measures analysis indicated that overall fish abundance and abundances of introduced, native, and seasonal fishes declined during the study (Table 2; Figure 2). Results were significant for years ($P < 0.0001$) and years × fish group ($P < 0.0001$). Each fish group declined differently through time ($P = 0.004$), and the decline of native species differed from those of introduced and seasonal species ($P < 0.003$). A graph of fish group indices versus time indicated that seasonal species fluctuated the most, followed by introduced and then by native species (Figure 2).

Introduced species showed no selection for slough type, but native species were found more often in dead-end sloughs and seasonal species were found more often in larger sloughs (Table 2). There was no overall habitat effect for introduced species, but there was an effect through time (fish group × slough × time interaction, $P < 0.014$). Introduced species became proportionally less

TABLE 3.—Spearman rank correlations between fish abundances (overall fish abundance, species diversity, fish group abundances) and environmental variables including abundance of macroinvertebrates. Temperature and Secchi depth are not included because they were not significant in all cases. Outflow is the sum of estuarine inflow from rivers, streams, precipitation, and cropland drainage minus water diverted by state and federal water projects. Values with asterisks are significant at $P < 0.05$. Data are yearly averages from January 1979 through January 1992.

Environmental variable	Fish abundance	Number of species	Introduced fish	Native fish	Seasonal fish	Years
Salinity (‰)	−0.62*	−0.55*	−0.49	−0.46	−0.55*	0.69*
Outflow	0.80*	0.64*	0.67*	0.57*	0.39	−0.70*
Neomysis mercedes	0.71*	0.69*	0.78*	0.50	0.32	−0.79*
Crangon franciscorum	0.46	0.43	0.17	0.53*	0.24	0.32
Palaemon macrodactylus	0.66*	0.78*	0.51	0.67*	0.19	−0.71*
Fish abundance		0.86*	0.83*	0.79*	0.56*	−0.90*
Species diversity			0.69*	0.88*	0.50	−0.93*

abundant in larger sloughs and more abundant in dead-end sloughs. The most consistent trend seen in the contrasts for the repeated measures was the decline of native fishes in dead-end sloughs (Table 2).

The presence of a fish group (introduced, native, or seasonal species) in dead-end or larger sloughs accounted for the difference between slough types (fish group × slough interaction, $P = 0.005$) and was significant through years (fish group × slough × year interaction, $P = 0.001$). There was no difference between dead-end and larger sloughs, either as grouping factors ($P = 0.75$) or through years ($P = 0.27$).

TABLE 4.—Spearman rank correlations between fish abundance (monthly numbers) and environmental variables (monthly averages). Flow is a composite variable of freshwater outflow, salinity, and Secchi depth derived from a principal components analysis of environmental variables. Data are from July 1983–January 1992. Fish species are grouped by results of principal components analysis according to similarities in seasonal and habitat requirements. Values with asterisks significant at $P < 0.05$. Letters in parentheses following species indicate introduced (I), native (N), and seasonal (S) fish groups.

Species	Temperature (°C)	Flow, salinity, and Secchi depth
Sacramento sucker (N)	0.02	0.48*
Splittail, young (N)	−0.08	0.36*
Prickly sculpin (N)	0.02	0.24*
Common carp (I)	0.25*	0.09
Chameleon goby (I)	0.17	−0.57*
Pacific staghorn sculpin (S)	−0.03	0.03
Longfin smelt (S)	−0.31*	0.23*
Threespine stickleback (N)	−0.35*	0.35*
Striped bass, young (I)	0.49*	−0.21*
Yellowfin goby (I)	0.43*	−0.24*
Delta smelt (S)	−0.35*	0.08
Tule perch (N)	0.14	−0.31*
Splittail, adults (N)	−0.10	0.04
Striped bass, adults (I)	0.08	−0.12
Starry flounder (S)	0.17	−0.13
Threadfin shad (S)	−0.44*	0.37*

Environmental Variables

Environmental variables and abundance of macroinvertebrates affected fish abundances and species diversity in many cases (Table 3). Fish abundances, species diversity and brackish-water invertebrates declined with time and were correlated with increases in salinity and decreases in outflow (Table 3). Seasonal fish abundances were not correlated with macroinvertebrate numbers, but resident fish abundances were. Numbers of brackish-water shrimps, *N. mercedis* and *P. macrodactylus*, were positively correlated with fish abundance and species diversity, whereas the more marine shrimp, *C. franciscorum*, did not decline over time and was associated with abundance of native species.

Fish Assemblage and Introduced Species

We used a Spearman rank correlation between two summary environmental variables (produced by a principal components analysis) and each species to aid in the interpretation of the PCA (Table 4). The first environmental component was a composite of monthly averages of salinity, Secchi depth, and freshwater outflow, and it explained 42% of the variance. The second component was temperature, which explained 30% of the variance. We used loadings from the first component to weight salinity, Secchi depth, and outflow to produce the composite variable "flow, salinity, and Secchi depth" (Table 4).

Principal components analysis identified mixed

TABLE 5.—Loadings of fish species on five components produced by a principal components analysis of numbers of fish per month. An asterisk with a loading indicates a significant correlation with the component.

Species or statistic	Component 1	2	3	4	5
		Loadings			
Sacramento sucker	0.80*	0.19	0.08	0.20	−0.10
Splittail, young	0.68*	−0.39*	−0.14	0.09	0.08
Prickly sculpin	0.59*	0.08	0.35	0.23	0.32
Common carp	0.48*	0.25	0.30	0.15	0.35
Chameleon goby	−0.82*	−0.12	−0.01	0.10	0.20
Pacific staghorn sculpin	−0.04	0.83*	0.04	−0.09	0.14
Longfin smelt	0.22	0.66*	0.01	0.12	−0.33
Threespine stickleback	0.34	0.48*	−0.35	0.07	0.02
Striped bass, young	0.20	−0.58*	0.45*	0.16	0.20
Yellowfin goby	−0.04	−0.08	0.79*	0.09	0.12
Delta smelt	−0.08	−0.05	−0.73*	−0.02	0.20
Tule perch	−0.15	−0.17	0.16	0.81*	0.10
Splittail, adults	0.21	0.01	−0.09	0.68*	−0.06
Striped bass, adults	0.01	0.48*	0.18	0.53*	0.13
Starry flounder	0.11	−0.12	−0.16	0.10	0.66*
Threadfin shad	0.45*	−0.13	−0.16	0.11	−0.64*
		Eigenvalue or explained variance			
Eigenvalue	2.86	2.26	1.83	1.62	1.38
Cumulative proportion of variance explained	0.18	0.32	0.43	0.53	0.62

groups of native and introduced species, apparently structured by seasonal or freshwater needs (Tables 4, 5). About 62% of the variance was explained by five principal components. The first component described species (Sacramento sucker, splittail young, prickly sculpin, common carp, and threadfin shad) that were most abundant when the marsh was dominated by freshwater; this group was negatively correlated with chameleon goby. The second component described species that were most abundant in early spring (Pacific staghorn sculpin, longfin smelt, and threespine stickleback); this group was negatively correlated with splittail young and striped bass young. Yellowfin goby and striped bass young, introduced species most common in summer, made up the third group and were negatively correlated with delta smelt. Tule perch, splittail adults, and striped bass adults, a group captured year around and in sharp decline since 1983, loaded heavily on the fourth component. Starry flounder was negatively correlated with threadfin shad on the fifth component; these seasonal species are abundant in summer and winter, respectively.

Chameleon goby and yellowfin goby exhibited large fluctuations in numbers (Figure 3). The first yellowfin goby was caught in Suisun Marsh in 1967 (Brittan et al. 1970); in 1980–1982 it was the third most abundant fish in our catches. We caught our first chameleon goby in 1985, but we did not catch large numbers until 1988; by 1989 chameleon goby was the most abundant fish in our catch. This pattern contrasted with overall fish abundance, which showed a steady decline over the years (Figure 3).

Discussion

The decline in fish abundance in Suisun Marsh can be attributed to interacting factors. From 1986 to 1992, California experienced a severe drought. The effects of the drought were amplified by increases in freshwater exports from state and federal water project facilities in the upper estuary. Since the previous drought of 1976–1977, the average proportion of estuarine inflow diverted by water projects has increased from an average of 30% to one of 50% and proportions diverted were even higher during the most recent drought (Moyle et al. 1992). In 1988, the amount of estuarine inflow diverted exceeded the amount flowing out to sea (Moyle et al. 1992). High pumping rates during the 1976–1977 drought resulted in major fish losses (Moyle et al. 1992). The most recent drought, however, lasted 6 years and can be expected to have a more prolonged effect on Suisun Marsh fishes. Moreover, high salinities due to low outflows have decreased the reproductive success of native species and allowed several exotic species to gain a foothold in the more saline habitat (Herbold et al. 1992).

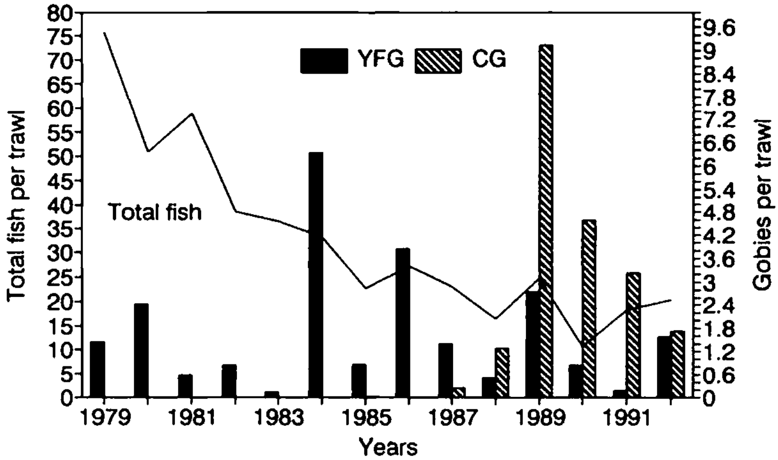


FIGURE 3.—Abundances of chameleon goby (CG), yellowfin goby (YFG), and total fish, 1979–1992. Numbers are average numbers of fish per trawl.

Changes in abundance of fish groups indicated that seasonal species fluctuated most, followed by introduced and native species. Because species in the seasonal fish group rely on freshwater for spawning, year-class abundance of these species varies markedly in relation to amount of freshwater outflow (Stevens and Miller 1983; Moyle et al. 1992). Furthermore, three species in this group, delta smelt, longfin smelt, and threadfin shad, live only 1–2 years, so spikes in abundance are not dampened by subsequent year-classes. Abundance of introduced species was also quite variable, reflecting dramatic deceases in striped bass and increases in chameleon and yellowfin gobies. Native fish showed the lowest degree of variability among the fish groups. These species are well adapted to the wet and dry cycles of California. Splittail and Sacramento sucker are long-lived, highly fecund, and able to defer spawning until conditions are favorable (Moyle 1976). Tule perch is a brackish-water species that bears live, well-developed young (Moyle 1976).

The distribution of introduced, native, and seasonal fish groups shown by the repeated measures supports the fish groupings of Moyle et al. (1986) and verifies our choice of these groups for our analysis. Moyle et al. (1986) grouped Suisun Marsh fishes on the basis of habitat preference after examining PCA results. In our repeated measures and the analysis of Moyle et al. (1986), native species were associated more often in dead-end sloughs and seasonal fish in larger sloughs; introduced species showed no habitat preference. Harsh environmental conditions (the drought) and introduced species (which were able to invade during the drought) have altered habitat preferences of the groups somewhat. Introduced species are now proportionally less abundant in larger sloughs and more abundant in dead-end sloughs. The increase in chameleon gobies, which are found more often in dead-end sloughs, may partly account for this result.

Environmental changes and changes in macroinvertebrate abundances affected fish abundance in the marsh. Increasing salinities and decreasing outflows are associated with decreasing fish abundances and species diversity and declines in brackish-water invertebrates. The more marine shrimp, *C. franciscorum*, did not decline in the marsh, although it declined overall in the estuary (Herbold et al. 1992). Increasing salinities in the marsh allowed *C. franciscorum*, which is normally found downstream, to become very abundant in the marsh. Abundance of *C. franciscorum* was associated with native fish abundance, whereas introduced fishes were associated with the brackish-water *N. mercedis*. Herbold (1987) found that introduced and native species in the marsh relied heavily on *N. mercedis* as food, but that native species had the ability to switch to other prey types in times of *N. mercedis* scarcity. He postulated that evolution had better equipped native species to cope with seasonal food shortages.

The differences between the present study and that of Moyle et al. (1986) are partly due to the way the data were summarized and length of the studies. The 1986 results were summarized by month, whereas the current repeated-measures results and correlations were summarized by year. The 1986 study examined a finer (and shorter) scale of phenomena. Correlations between fish abundance and environmental variables were based on seasonal effects: abundant young-of-year fish appeared in late spring and summer and shifted the correlation of fish abundance towards months that are correlated with higher temperatures, increased salinities, and decreased outflow. Moreover, the previous 5-year study was too short to discern long-term trends in fish abundance. Connell and Sousa (1983) have argued that the minimum time period for studies on community persistence should encompass the replacement of all adults.

The pattern we found in the structure of the fish assemblage (Table 5) differed somewhat from that found by Moyle et al. (1986). Moyle et al. (1986) found an underlying structure to the fish community with groups of (1) native resident species found mostly in dead-end sloughs (splittail, tule perch, and Sacramento sucker), (2) introduced species found throughout the marsh but captured most often in the larger sloughs (striped bass, yellowfin goby, and common carp), and (3) two benthic species (prickly and Pacific staghorn sculpins). Moyle et al. (1986) also described groups of spring–summer seasonal species (Pacific staghorn sculpin and starry flounder) and winter seasonals (delta smelt, longfin smelt, and threadfin shad). The main differences between that analysis and ours are due to environmental effects that produced some shifting among groups.

Occurrence of fish species in different groups than previously reflects changing environmental factors. The PCA reflects effects of decreasing outflow due to drought and increasing proportional diversions of freshwater from the estuary. In the earlier study, longfin smelt and delta smelt were found together as seasonals in winter, when outflows were high. In the current study, longfin smelt were most common in March and April. Longfin smelt formerly appeared in the marsh as adults in winter as they migrated upstream to spawn, but now they are found as larvae or juveniles in the spring. Before 1983, freshwater outflows were high in winter and spring (Moyle et al. 1992). As freshwater outflows decreased, longfin smelt movements changed. Adult longfin smelt no longer migrated through the marsh and juveniles were transported into the marsh, rather than being washed downstream to lower Suisun Bay by high spring outflows. Delta smelt almost disappeared from the marsh during the drought, and the PCA placed them in a group of their own, opposite two very abundant introduced species, yellowfin goby and striped bass young.

Results of the repeated-measures analysis indicate that the introduced, native, and seasonal fish groups of Moyle et al. (1986) are fairly predictable and consistent through time. In many cases, the PCA produced similar results, but shifts among groups suggest that these groupings can be affected by extreme environmental conditions, such as a 6-year drought. The shifts of species to different groups are apparently driven by changes in freshwater outflow, as discussed for longfin smelt. Prickly sculpin previously peaked in the summer with Pacific staghorn sculpin, but as the marsh became more saline, it appeared with a group that is characteristic of freshwater conditions. Changing environmental conditions can also affect predictability and consistency of the fish assemblage by creating conditions beneficial to invading species. The increasing proportion of introduced species found in dead-end sloughs may affect native species and alter predictability of the fish assemblage.

Chameleon and yellowfin gobies were introduced to the San Francisco Bay estuary around the same time in the late 1950s (Brittan et al. 1970; Carlton 1979), but they showed very different patterns of invasion. Yellowfin goby increased explosively throughout the estuary in the late 1960s and early 1970s (Brittan et al. 1970). Both gobies are native to Asia, where the yellowfin goby is found in fresh, brackish, and marine waters and the chameleon goby in brackish and marine waters (Haaker 1979). We hypothesize that increasing levels of salinity, decreasing outflows, and drought have interacted with the flushing flows of 1986 (Moyle et al. 1992) to create conditions in the marsh that allowed the chameleon goby to invade. Recently, chameleon goby numbers have plummeted, possibly due in part to predation by yellowfin gobies. Chameleon gobies spawn 3–4 months after yellowfin gobies (Wang 1986; our unpublished data). Because yellowfin goby include fish in their diets (Wang 1986), chameleon goby eggs and larvae are likely to be vulnerable to predation by yellowfin goby juveniles and adults. In any case, the chameleon goby, like the yellowfin goby before it, has shown a dramatic spike in abundance (Figure 3) typical of introduced species invading disturbed habitats (Herbold and Moyle 1986; Moyle 1986).

The decreasing abundance of Suisun Marsh fishes parallels fish losses in the estuary and is associated with increases in salinity and decreases in outflow due to drought and increasing water diversions (Stevens 1977; Stevens and Miller 1983; Stevens et al. 1985; Moyle et al. 1992). When large proportions of estuarine inflow are diverted, effects of droughts are amplified, spawning habitat decreases, flow patterns important to migratory fishes are modified, and food webs are altered (Herbold et al. 1992). Changes in the pattern of freshwater outflow alter habitat and create beneficial conditions for invading species. Introduced species colonize rapidly under favorable conditions and may disrupt the structure of fish communities by competing with or preying on native fishes (Herbold and Moyle 1986; Moyle 1986). The chameleon goby is the most recent introduction to gain a foothold in the Suisun Marsh due to altered environmental conditions. Populations of the Asiatic clam *Potamocorbula amurensis* have exploded in a similar manner and have severely reduced planktonic foods in the estuary (Nichols et al. 1990).

Populations of recently introduced species are inherently unstable, and the combined effects of introduced species and human-caused environmental changes may cause rapid, unpredictable changes in fish assemblages (Herbold and Moyle 1986; Moyle 1986). The fish assemblage of Suisun Marsh has lost some its consistency, but if normal precipitation returns and the proportion of water diverted from the estuary is reduced, Suisun Marsh fishes may regain their previous abundance and predictability. An aggressive campaign to prevent further introductions of new estuarine species is also needed.

Acknowledgments

We thank R. Brown and the Department of Water Resources for their generous support throughout the years. We thank J. Dykes for statistical advice. The manuscript was reviewed by W. Bennett, M. Gard, D. Kelley, S. Matern, M. Marchetti, and R. Yoshiyama. This study would not have been possible without the help of countless volunteers who aided us with the sampling.

References

Brittan, M. R., J. D. Hopkirk, J. D. Conners, and M. Martin. 1970. Explosive spread of the oriental goby *Acanthogobius flavimanus* in the San Francisco Bay–Delta region of California. Proceedings of the California Academy of Sciences 38:207–214.

Carlton, J. T. 1979. Introduced invertebrates of San Francisco Bay. Pages 427–444 *in* T. J. Conomos, editor. San Francisco Bay, the urbanized estuary. American Association for the Advancement of Science, Pacific Division, San Francisco.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 121:789–817.

Conomos, J. T., editor. 1979. San Francisco Bay, the urbanized estuary. American Association for the Advancement of Science, Pacific Division, San Francisco.

Haaker, P. L. 1979. Two Asiatic gobiid fishes, *Tridentiger trigonocephalus* and *Acanthogobius flavimanus*, in Southern California. Bulletin of the Southern California Academy of Sciences 78:56–61.

Herbold, B. 1987. Patterns of co-occurrence and resource use in a non-coevolved assemblage of fishes. Doctoral dissertation. University of California, Davis.

Herbold, B. A., A. D. Jassby, and P. B. Moyle. 1992. Status and trends report on aquatic resources in the San Francisco estuary. U.S. Environmental Protection Agency, Public Report, San Francisco.

Herbold, B., and P. B. Moyle. 1986. Introduced species and vacant niches. American Naturalist 128:751–760.

Kahrl, W. J., editor. 1978. The California water atlas. California Department of Water Resources, Sacramento.

Meng, L., and J. J. Orsi. 1991. Selective predation by larval striped bass on native and introduced copepods. Transactions of the American Fisheries Society 120:187–192.

Moyle, P. B. 1976. Inland fishes of California. University of California Press, Berkeley.

Moyle, P. B. 1986. Fish introductions into North America: patterns and ecological impact. Pages 27–43 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Moyle, P. B., R. A. Daniels, B. Herbold, and D. M. Baltz. 1986. Patterns in the distribution and abundance of a non-coevolved assemblage of estuarine fishes. U.S. National Marine Fisheries Service Fishery Bulletin 84:105–117.

Moyle, P. B., B. Herbold, D. E. Stevens, and L. W. Miller. 1992. Life history and status of the delta smelt in the Sacramento–San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67–77.

Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. Science (Washington, D.C.) 231:567–573.

Nichols, F. H., J. K. Thompson, and L. R. Schemel. 1990. Remarkable invasion of San Francisco Bay (California, U.S.A.) by the Asian clam *Potamocorbula amurensis*. II. Displacement of a former community. Marine Ecology Progress Series 66:95–101.

SAS Institute. 1988. SAS user's guide, version 6.03. SAS Institute, Cary, North Carolina.

Stevens, D. E. 1977. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento–San Joaquin Estuary, California.

Transactions of the American Fisheries Society 106: 34–42.

Stevens, D. E., D. W. Kohlhorst, and L. W. Miller. 1985. The decline of striped bass in the Sacramento–San Joaquin Estuary, California. Transactions of the American Fisheries Society 114:12–30.

Stevens, D. E., and L. W. Miller. 1983. Effects of river flow on abundance of young chinook salmon, American shad, longfin smelt, and delta smelt in the Sacramento–San Joaquin River system. North American Journal of Fisheries Management 3:425–437.

Wang, J. C. S. 1986. Fishes of the Sacramento–San Joaquin Estuary and adjacent waters, California: a guide to early life histories. Interagency Ecological Study Program for the Sacramento–San Joaquin Estuary, Technical Report 9, Sacramento, California.

Received June 25, 1993
Accepted January 13, 1994