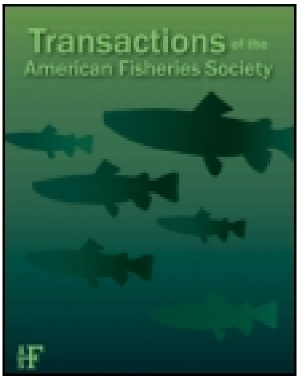

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Life History and Status of Delta Smelt in the Sacramento-San Joaquin Estuary, California

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Abstract.—The delta smelt *Hypomesus transpacificus* is endemic to the upper Sacramento–San Joaquin estuary. It is closely associated with the freshwater–saltwater mixing zone except when it spawns in fresh water, primarily during March, April, and May. The delta smelt feeds on zooplankton, principally copepods. Its dominant prey was the native copepod *Eurytemora affinis* in 1972–1974 but the exotic copepod *Pseudodiaptomus forbesi* in 1988. Because the delta smelt has a 1-year life cycle and low fecundity (mean, 1,907 eggs/female), it is particularly sensitive to changes in estuarine conditions. Tow-net and midwater trawl samples taken from 1959 through 1981 throughout the delta smelt's range showed wide year-to-year fluctuations in population densities. Surveys encompassing different areas showed declines in different years between 1980 and 1983. After 1983, however, all studies have shown that the populations remained at very low densities throughout most of the range. The recent decline of delta smelt coincides with an increase in the diversion of inflowing water during a period of extended drought. These conditions have restricted the mixing zone to a relatively small area of deep river channels and, presumably, have increased the entrainment of delta smelt into water diversions. Restoration of the delta smelt to a sustainable population size is likely to require maintenance of the mixing zone in Suisun Bay and maintenance of net seaward flows in the lower San Joaquin River during the period when larvae are present.

The delta smelt *Hypomesus transpacificus* is a small fish endemic to the upper Sacramento–San Joaquin estuary, California (McAllister 1963; Moyle 1976; Wang 1986). It has declined in abundance in recent years, and its ability to persist in the estuary is in doubt because of major environmental changes that include increased diversion of freshwater inflow for irrigated agriculture and urban use (Nichols et al. 1986; Moyle et al. 1989; Williams et al. 1989). Reduced freshwater outflow is correlated with poor year-classes of striped bass *Morone saxatilis*, chinook salmon *Oncorhynchus tshawytscha*, American shad *Alosa sapidissima*, longfin smelt *Spirinchus thaleichthys*, and splittail *Pogonichthys macrolepidotus*, presumably because of decreased survival of larvae and juveniles (Turner and Chadwick 1972; Stevens 1977a; Kjelson et al. 1982; Daniels and Moyle 1983; Stevens and Miller 1983; Stevens et al. 1985). Since the late 1970s, most fishes with pelagic larvae have declined in the upper estuary, including delta smelt (Moyle et al. 1985; Herbold and Moyle, unpublished data). Stevens and Miller (1983), however, did not find any relationship between delta smelt abundance and outflow.

We here present information on delta smelt (1) life history, (2) diet, especially in relation to the recent invasion by several exotic species of zooplankton (Orsi et al. 1983; Ferrari and Orsi 1984), (3) fecundity, (4) population trends since 1959, (5) distribution patterns since 1980, and (6) factors affecting abundance. This information supports the proposed federal listing of delta smelt as a threatened or an endangered species.

Life History

Delta smelt are confined to the Sacramento–San Joaquin estuary, mainly in Suisun Bay and the Sacramento–San Joaquin Delta (Figure 1). Historically, the upstream limits of their range have been the upper limits of the delta (Sacramento on the Sacramento River and Mossdale on the San Joaquin River); the lower limit is western Suisun Bay (Radtke 1966; Moyle 1976). During times of exceptionally high outflow from the rivers, they may be washed into San Pablo Bay, but they do not establish permanent populations there (Ganssle 1966). Delta smelt inhabit surface and shoal waters of the main river channels and Suisun Bay, where they feed on zooplankton, as documented

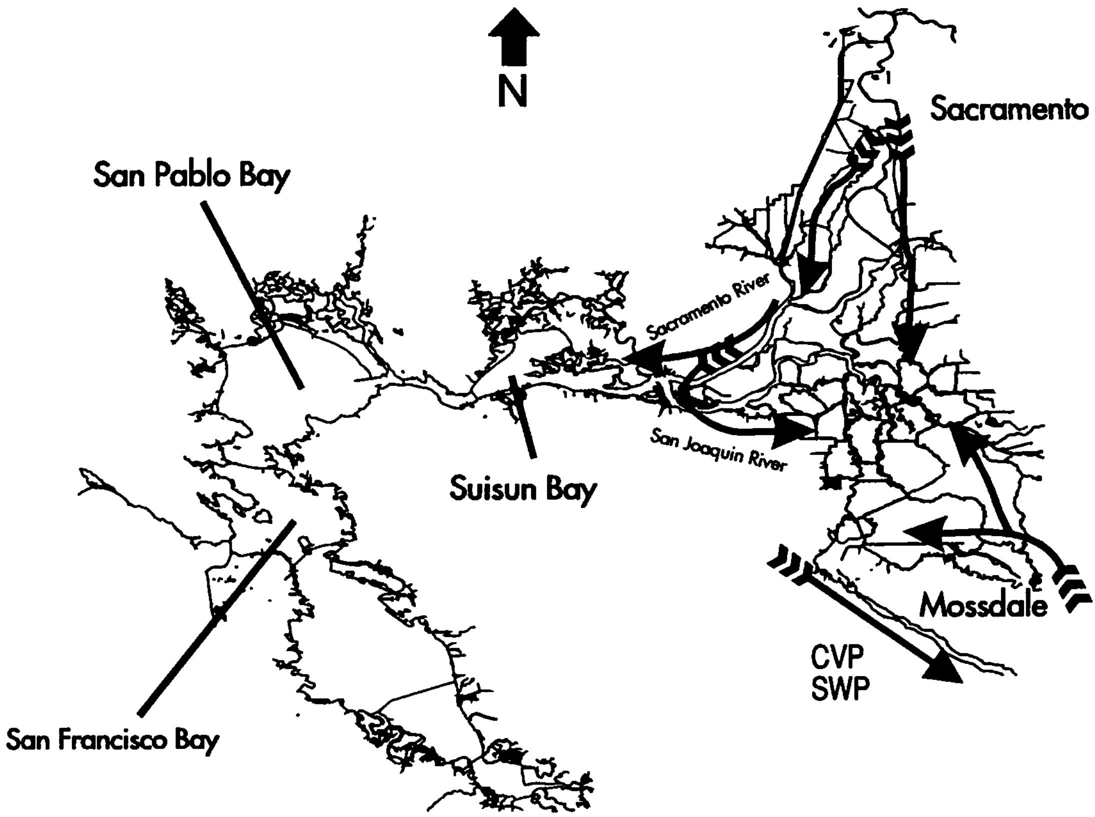

FIGURE 1.—Historical range of delta smelt in the Sacramento–San Joaquin estuary. Delta smelt have been found regularly in Suisun Bay. Years of high outflow have distributed them as far downstream as San Pablo Bay. Upstream limits, occurring usually during the spawning migration in spring, are at Mossdale on the San Joaquin River and Sacramento on the Sacramento River. The arrows show the directions of water flow during periods of high diversions and low outflow. Note the flow of Sacramento River water across the delta and the net reverse flow of the lower San Joaquin River. CVP = Central Valley Project, SWP = State Water Project.

in this paper. Their distribution within the estuary shifts from year to year depending on outflow.

Captures of larvae indicate that spawning takes place in fresh water at any time from late February through May, when water temperatures range from 7 to 15°C (Wang 1986). During this period, adults move from Suisun Bay or river channels in the lower delta to spawning areas upstream. Spawning apparently occurs along the edges of the rivers and adjoining sloughs in the western delta (Radtke 1966; Wang 1986), but spawning behavior has not been observed. Embryos are demersal and adhesive, sticking to substrates such as rocks, gravel, tree roots, and emergent vegetation (Moyle 1976; Wang 1986). Hatching occurs in 12–14 d if development rates of embryos are similar to those of the closely related wakasagi *Hypomesus nipponensis* (Wales 1962).

After hatching, the buoyant larvae are carried by currents downstream into the upper end of the mixing zone of the estuary, where incoming salt water mixes with outflowing fresh water (Peterson et al. 1975; other synonyms or related terms for this region include null zone, entrapment zone, and zone of maximum turbidity). The mixing currents keep the larvae circulating with the abundant zooplankton also found here (Orsi and Knutson 1979; Siegfried et al. 1979; Stevens et al. 1985). Growth is rapid, and the juvenile fish are 40–50 mm fork length (FL) by early August (Erkkila et al. 1950; Ganssle 1966; Radtke 1966). Delta smelt become mature at 55–70 mm FL and rarely grow larger than 80 mm FL. The largest delta smelt on record was 126 mm FL (Stevens et al. 1990). Delta smelt larger than 50 mm FL become increasingly rare in March–June samples, indicating that most adults die after spawning, having completed their life cycle in 1 year (Erkkila et al. 1950; Radtke

1966; California Department of Fish and Game, unpublished data).

Methods

Sampling.—Only two smelt species commonly occur in the Sacramento–San Joaquin estuary—delta smelt and longfin smelt; once past the larval stages, they are easily distinguished on the basis of color, smell, and gross anatomy (Moyle 1976; Wang 1986). Delta smelt were collected in four independent surveys: (1) a summer tow-net survey by CFG, (2) an autumn midwater trawl survey in the upper estuary by CFG, (3) a monthly midwater trawl survey in the lower estuary by CFG (bay survey), and (4) a monthly otter trawl survey of Suisun Marsh, a tidal marsh next to Suisun Bay, by the University of California, Davis (UCD). In all surveys, fish captured were identified, measured (FL in CFG studies, standard length [SL] in the UCD study), and either returned to the water or preserved for dietary analysis.

The summer tow-net survey samples the delta and Suisun Bay during June and July to determine the abundance of young striped bass (Turner and Chadwick 1972). The sampling gear and methods were described in detail by Turner and Chadwick (1972) and Stevens (1977b). This sampling program began in 1959 and has been conducted in all subsequent summers except 1966, although no records were kept of delta smelt numbers in 1967 and 1968. On each survey, three tows are made at each of 30 fixed sites; two to five surveys are made each year at 2-week intervals. To standardize effort among years, we used only the data from the first two surveys of each year. Annual abundance indices for delta smelt were calculated by summing, over all sample sites, the products of total catch in all tows at a site and the water volume at the site in acre-feet (Chadwick 1964). The index for each year is the mean of the indices for the two surveys. Except during wet years (when fish are washed into San Pablo Bay), the summer tow-net survey encompasses the nursery areas of delta smelt, so it should provide a good indication of abundance in early summer.

The autumn midwater trawl survey is conducted with a 17.6 m-long trawl with a mouth opening of 3.7 m^2 (described by Von Geldern 1972). The trawl is dragged at about 70 cm/s and is most effective in catching fish less than 10 cm long. Collecting sites were established at standardized locations scattered from San Pablo Bay through Suisun Bay and the delta upstream to Rio Vista on the Sacramento River and to Stockton on the San Joaquin River. Each month, unless severe weather or malfunctioning equipment interfered, 87 sites were each sampled with one 12-min, depth-integrated tow. Surveys were conducted in September, October, November, and December from 1967 through 1988 (except for 1974 and 1979), in November 1969, and in September and December 1976. Monthly abundance indices for delta smelt were calculated by summing, over 17 subareas of the estuary, the product of the mean catch per trawl and the water volume for each subarea. The annual abundance index equals the sum of the four monthly indices; abundance indices for months not surveyed in 1969 and 1976 were extrapolated from the months actually sampled.

The bay survey is a monthly trawling program that began in 1980 (Armor and Herrgesell 1985). Its 42 sites are distributed throughout the lower estuary from South San Francisco Bay upstream to the confluence of the Sacramento and San Joaquin rivers. To permit comparison of catches across years, we restricted our analysis of the bay survey data to the 19 sites sampled in all years within the range of delta smelt. The bay study uses midwater trawls and otter trawls; since 1981, it has recorded salinity and temperature profiles at each sampling site.

The Suisun Marsh fish survey has been conducted monthly by UCD since 1979 with an otter trawl that has a 2 × 5.3-m opening (Moyle et al. 1985). Two 5- or 10-min tows are made at 10 consistent locations. Because the sloughs of the marsh are relatively shallow (2–3 m), the otter trawl samples most of the water column and is most effective in catching fish smaller than 10 cm SL.

In summary, the summer tow-net survey and the autumn midwater trawl survey provide long-term abundance data and encompass most of the historical range of delta smelt, but their data are available for only part of each year. The bay survey encompasses all months of the year, but it began in 1980 and is limited to the western half of the delta smelt's historical range. The Suisun Marsh study, begun in 1979, samples year-round in habitat types not sampled by other studies but in a limited geographic area.

Feeding habits.—Diet was determined by examining the stomachs of (1) adults captured between September 1972 and July 1974 in the midwater trawl and tow-net surveys, (2) postlarvae collected in May 1977, and (3) adults captured in surveys during November and December 1988. Each fish was measured (SL), and its stomach con-

TABLE 1.—Diet (percent volume) of delta smelt in 1972–1974 and 1988.

Food category or statistic	1972				1973								1974	
	Sep	Oct	Nov	Dec	Jan	Mar	Jun	Jul	Sep	Oct	Nov	Dec	Jan	Feb
Prey (% of volume)														
Copepoda[a]	39	5	98	84	37	23	100	88	81	81	87	28	17	85
Neomysis mercedis	58	95	1	16	43	12		3	14	14	1	8	6	14
Corophium spp.								6	5	5	10	13	4	1
Gammaridae					13	1								
Daphnia sp.	3		<1		1	34						12	4	
Bosmina longirostris											2	33	68	
Chironomidae					4	30					<1	4	<1	
Others					2			3				2	1	
Delta smelt samples														
Mean standard length (mm)	61	67	63	60	64	62	58	41	51	56	58	60	61	65
Number of stomachs	23	20	23	30	50	64	5	15	129	84	60	60	44	72
Percent empty	43	10	50	27	40	16	0	20	16	23	0	23	20	0

[a] Copepods were mainly *Eurytemora affinis* in 1972–1974 and *Pseudodiaptomus forbesi* in 1988.

tents were examined. All food organisms were identified and counted, and their relative volume was determined with the points system of Hynes (1950). When the 1972–1974 stomachs were examined (in 1974), copepods were not identified to species. However, examination in 1989 of the stomachs of 45 additional delta smelt from the same samples indicated that the only copepod present was *Eurytemora affinis.*

Fecundity.—Fecundity was determined from ovaries removed from 24 females collected in mid-January and early March 1973. Ovaries from each female were air-dried until eggs were hard and could be easily separated from other tissue. Once the ovarian tissue was removed, eggs were weighed to 0.01 mg. Subsamples of eggs were then removed, weighed, and counted until at least 20% (by weight) of the eggs had been counted. Total number of eggs was calculated with the number-per-weight proportion determined from the subsamples. All eggs were counted from four ovaries, and the fecundity was compared with that determined from subsamples; the comparison indicated the subsample method overestimated fecundity by about 15%. Consequently, we calculated two means—the uncorrected mean based on the actual estimates and the corrected mean based on the estimates minus 15%.

Abundance trends.—Abundance data for the four surveys were summarized in several ways to permit comparison of various data sets. For the bay and UCD studies, which had year-round sampling at fixed sites, summaries comprised (1) number of delta smelt per trawl for each month, expressed as an abundance index, (2) presence or absence of delta smelt in trawls for each month, (3) mean number of delta smelt caught per trawl in those trawls containing delta smelt for each month, and (4) total delta smelt caught per trawl for each year. The results of the various analyses were similar, so those that showed trends most clearly were used.

Environmental factors.—Four major factors were examined in relation to distribution and abundance of delta smelt: salinity (measured as conductivity in CFG studies), temperature, depth, and freshwater outflow. At each sampling station in the bay and UCD studies, and at many of the sampling stations of the summer and autumn surveys, temperature and conductivity or salinity were measured at the surface by various means. Some conductivity measurements were also made with a conductivity bridge in the laboratory from water samples collected in the field. To determine the location of the mixing zone, we used conductivity data collected monthly since January 1981 by the bay study, which measured both surface and bottom conditions by mounting the probe on a weighted support, dropping it to the bottom, and retrieving it to the surface. Values of salinity were calculated from the measured conductivities and temperatures. Large differences in salinity between the surface and bottom indicated the presence of stratification. A small salinity difference indicated the water column was well mixed or consisted entirely of fresh water.

A single depth measurement (m) at mean low water was used to characterize each study site for the duration of the study, although factors such as tide and outflow resulted in depths at each site varying as much as 1 m among sampling times.

TABLE 1.—Extended.

Food category or statistic	1974 Apr	1974 Jul	1988 Nov	1988 Dec
Prey (% of volume)				
Copepoda[a]	22	69	100	82
Neomysis mercedis		23		
Corophium spp.	2	1		1
Gammaridae				<1
Daphnia sp.	13			2
Bosmina longirostris	59			13
Chironomidae				2
Others				
Delta smelt samples				
Mean standard length (mm)	65	44	58	61
Number of stomachs	25	161	23	16
Percent empty	0	42	19	0

Data used to examine monthly amounts and patterns of freshwater outflow were obtained from the DAYFLOW data base of the California Department of Water Resources (DWR). DAYFLOW contains estimates of a number of variables related to the amount of fresh water flowing through the estuary, including net delta outflow, the proportion of water diverted, and the amount and direction of flow in the lower San Joaquin River (DWR 1986).

Results

Feeding Habits

Postlarval delta smelt (mean SL, 15 mm; N = 24) collected in 1977 fed exclusively on copepods; their stomachs contained 68% *Eurytemora affinis*, 31% *Cyclops* sp., and 1% harpacticoid copepods. Adults fed primarily on copepods at all times of the year, although cladocerans were seasonally important; opossum shrimp *Neomysis mercedis* usually were of secondary importance (Table 1). In the 1972–1974 samples, the principal copepod eaten was *Eurytemora affinis*, but in the 1988 samples the dominant copepod was *Pseudodiaptomus forbesi*, an exotic species first noted in the estuary in 1987. A few *Sinocalanus doerrii*, an exotic species first collected in 1978 (Orsi et al. 1983), were also eaten in 1988.

Fecundity

Mean corrected fecundity for delta smelt (N = 24) was 1,907 eggs, with a range of 1,247–2,590 (uncorrected mean was 2,191, with a range of 1,433–2,975). Lengths of fish examined were from 59 to 70 mm SL. There was no relationship between length and fecundity. All eggs were about the same size, so each fish probably spawned over a fairly short time.

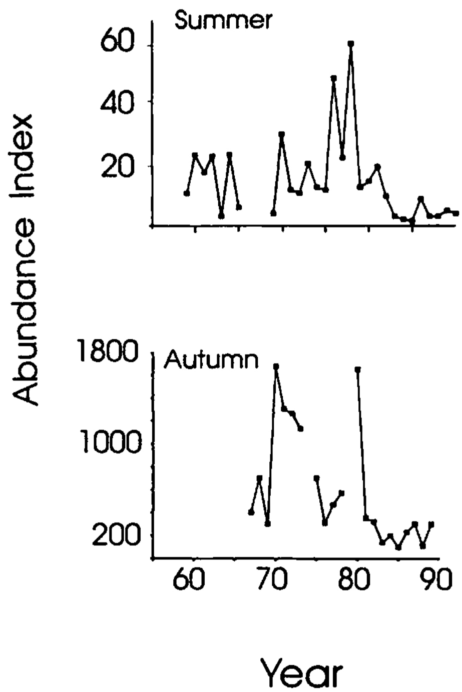

FIGURE 2.—Trends in total catches of delta smelt from two sampling programs encompassing more than 20 years each throughout the historical range of delta smelt but undertaken during a limited part of each year. The autumn midwater trawl samples have been taken in deep-water habitats from September to December of most years since 1967. Summer tow-net surveys, which sample midwater populations of smaller fishes during June and July, began in 1959 and have provided data on delta smelt abundance for all years except 1966–1967. Abundance indices are products of total catch and water volume, summed over standard suites of sampling areas.

Abundance Trends

In the two long-term studies, catches of delta smelt varied widely across years (Figure 2). In the summer tow-net survey, the peak index of 62.5 in 1978 was 78 times greater than the lowest index of 0.8 in 1985. Before 1981, the index fluctuated between 3 and 62.5. After 1981, the index declined, and it has remained below 10 since 1982. Although similar low indices occurred in 1963, 1965, and 1969, they did not occur in consecutive years as in the 1980s. In the autumn midwater trawl survey, the highest index was 1,675 (in 1970), which was 15 times greater than the lowest index of 109 (in 1985). Until 1980, the annual index fluctuated between 470 and 1,675 (mean catch of

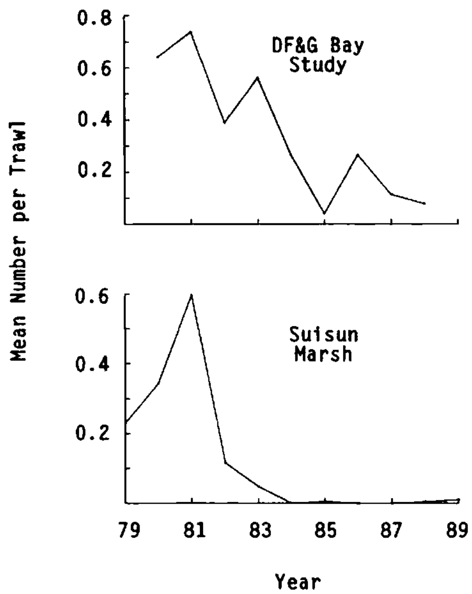

FIGURE 3.—Trends in delta smelt catches from two monthly sampling programs in the lower Sacramento–San Joaquin estuary. Sampling began in 1979 in Suisun Marsh, a shallow-water habitat in the middle of the delta smelt's historical range. The DFG Bay Study has sampled the western half of the delta smelt's historical range since 1980.

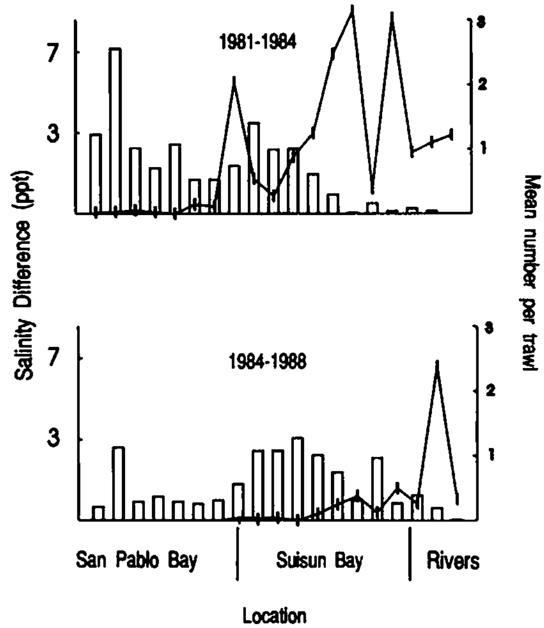

FIGURE 4.—Mean delta smelt catches per trawl (lines) in three regions in the Sacramento–San Joaquin estuary during the periods before (January 1981–September 1984) and after (October 1984–December 1988) the collapse of delta smelt populations. The location of the mixing zone is indicated by large differences (bars, parts per thousand) between salinities of surface and bottom waters in upstream areas. Upstream stations are to the right.

1–5 delta smelt per trawl) except in 1976, when it was 310. After 1980, the index was consistently less than 350 (mean catch of less than one delta smelt per trawl). The frequency of occurrence of delta smelt in the autumn trawls also declined. Until 1981, delta smelt were in 30–75% of the trawl catches. After 1981, they were never caught in more than 25% of the trawls.

The trend of decreasing numbers of delta smelt is reflected as well in annual catch data from the CFG bay survey and the UCD Suisun Marsh survey, for which effort was more or less constant (Figure 3). In both surveys delta smelt catch declined dramatically after 1981 and numbers have remained low. In the bay survey, delta smelt were caught in all months from 1981 through 1984 but only in 9 months in 1985, 10 in 1986, 6 in 1987, and 5 in 1988. During the 11-year Suisun Marsh survey, 468 delta smelt were collected, all but four before 1984; the peak catch was 229 fish in 1981.

Because of the delta smelt's 1-year life cycle, its abundance is potentially limited by egg production of the previous year-class. However, the wide year-to-year variability in abundance of this species prior to its decline in 1981 offers little evidence to support the effect of parent population size on subsequent recruitment. A spawner–recruit relationship based on the autumn midwater trawl data from successive years explained only about one-quarter of the year-to-year variability ($r^2 = 0.24$, $N = 19$). The weak stock–recruitment relationship suggests that environmental factors severely limit delta smelt abundance even in years of large population size.

Environmental Factors

Delta smelt are most abundant in low-salinity water associated with the mixing zone in the estuary, except when they are spawning. When the mixing zone is in Suisun Bay, where both shallow and deep water exist, the fish are caught most frequently in shallow water. In the bay survey, 62% of the delta smelt catch in Suisun Bay occurred at three stations less than 4 m deep. The remaining 38% were captured at six deeper stations. The salinity profiles from the bay study show that most of the delta smelt catches occurred either in Suisun Bay upstream of areas where there was a large difference between surface and bottom salinities or in the channels of the lower Sacramento and

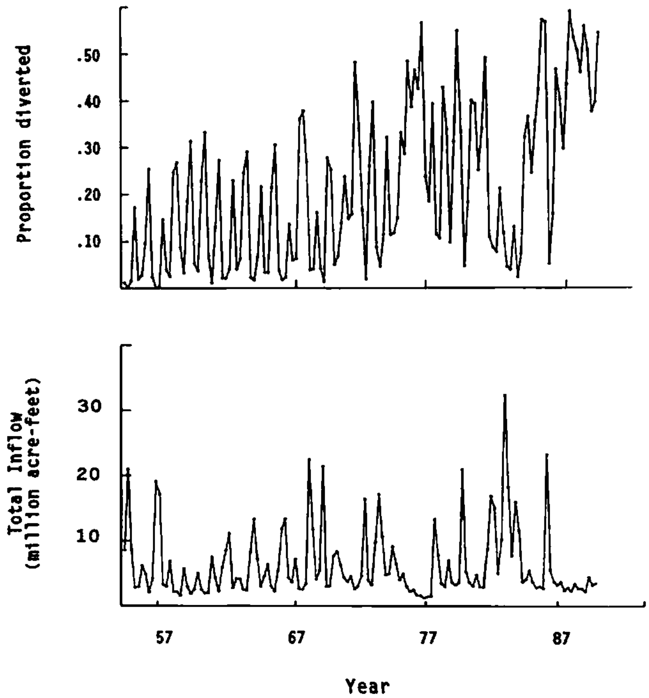

FIGURE 5.—Proportions of water flowing into the Sacramento–San Joaquin Delta that were exported from state and federal pumping plants in southern delta (top), and total freshwater inflows into the delta (bottom), 1957–1987. Points represent quarterly values.

San Joaquin rivers (Figure 4). A small peak in abundance regularly occurred downstream of the mixing zone at a shallow station adjacent to a tidal marsh. Delta smelt were captured in salinities of 0–14‰ (mean, 2 ‰; $N = 281$) and at temperatures of 6–23°C (mean, 15°C; $N = 281$). No relationship was found between surface temperature and delta smelt distribution at each station, because temperature varied more among months than among stations.

Between 1981 and 1984, the mixing zone was in Suisun Bay during October through March, except during months with exceptionally high outflows. During April through September, the mixing zone was usually upstream in the channels of the rivers. Since 1984, the mixing zone has been mainly in the channels of the rivers during all months of the year except during one period of record outflow in 1986. This shift in the zone's location during winter has coincided with an upstream shift and confinement of the delta smelt population to the deeper water of the main river channels (Figure 4).

Relationship of Abundance to Outflow

Movement of the mixing zone into river channels in the delta is related to the sporadic decrease in inflowing water during years of low precipitation and to the steady increase in the proportion of fresh water diverted each year and month by the pumps and canals of the State Water Project and federal Central Valley Project. Since 1983, the proportion of water diverted during October through March (the first half of the official water year) has remained at high levels (Figure 5). Because high levels of diversion pull Sacramento River water across the delta and into the channel of the San Joaquin River downstream of the pumps, the net movement of water in the lower San Joaquin River is frequently upstream during these periods (Figure 1). The number of days of net reverse flow of the lower San Joaquin River has increased during periods of low outflow in response to steadily increasing rates of diversion. Until 1984, years with more than 100 d of reverse flow were sporadic, and reverse flows rarely occurred during the delta smelt spawning season. From 1985 on, reverse flows have characterized the lower San Joaquin for more than 150 d of the year, and in every year except 1986 reverse flows have occurred for 15–85 d of the spawning season (Figure 6). Consequently, the restriction of the mixing zone to an area around the mouths of the rivers has greatly increased the likelihood of dis-

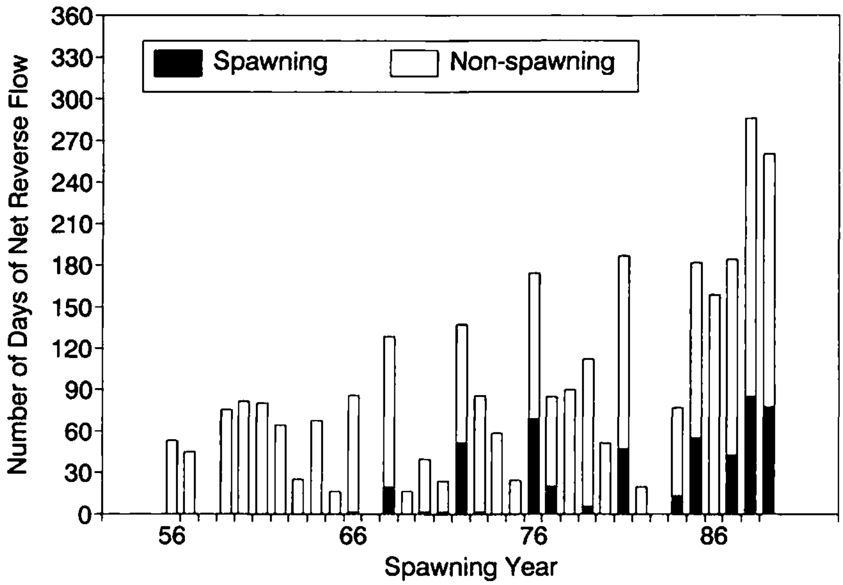

FIGURE 6.—Number of days of net reverse flow in the San Joaquin River during water years (October–September) 1956–1989. The black portion of each bar shows the number of the days of reverse flow that occurred during the spawning season of delta smelt (February–May).

placement of delta smelt. Reverse net flows in the lower San Joaquin have been a constant feature of the delta in recent years during the months when delta smelt are spawning except for 1986, when a record tropical storm in February produced enough water to maintain adequate flows through the spring of what was otherwise a dry year.

The recent decline in delta smelt has coincided with the increase in proportion of water diverted and the confinement of the mixing zone to a small area in the river channels. Low catches during the 1976–1977 drought also coincided with record high proportions of water diverted. Increasing rates of diversion since the earlier drought resulted in greater proportionate diversion during the more recent drought, so for 1988 the amount of water diverted exceeded the amount flowing out to sea.

Despite the correspondence of increased diversion and delta smelt decline, the relationship between outflows and delta smelt abundance is not a simple one, as it seems to be for other species (Stevens and Miller 1983). To see if delta smelt might be favored by moderate outflows, which would keep them in Suisun Bay, we regressed the autumn midwater trawl abundance index on delta outflow and delta outflow squared. Outflow squared would allow the regression values to decline if delta smelt abundance peaked at moderate flows and declined at high or low flows. No relationship was found; all values of r^2 were less than 0.23, after all possible subsets of data for two consecutive months from February to June were examined. These results may have been confounded by extreme conditions since 1982: most years have been unusually wet (1983) or unusually dry (1987–1991). Under such extremes, the responses of delta smelt to outflow may not have been consistent with patterns shown within the normal range of outflows.

Discussion

The delta smelt is adapted to living in association with the mixing zone of the Sacramento–San Joaquin estuary, where it feeds on copepods and other zooplankton concentrated there. Because it has a limited range, essentially a 1-year life cycle, low fecundity, and planktonic larvae, the species is unusually sensitive to changes in estuarine conditions. This sensitivity has caused its population to remain extremely low since 1980. As Pimm et al. (1988) showed, small species with variable populations, such as delta smelt, become increasingly vulnerable to extinction as their populations decrease. Thus, the delta smelt fits the definition of an endangered species under the U.S. Endangered Species Act, because it is in danger of extinction throughout its limited range. Given its persistence through 7 years of severe conditions, however, "threatened" status may be more appropriate.

A species may be threatened or endangered according to the Endangered Species Act because of: "(A) the present, or threatened, destruction, modification, or curtailment of its habitat or range, (B) over-utilization for commercial, recreational, or educational purposes, (C) disease or predation, (D) inadequacy of existing regulatory mechanisms, or (E) other natural or manmade factors affecting its continued existence." There is no evidence that reasons B or C have reduced delta smelt numbers, but A and D have both played a role. Other factors (E) possibly affecting the existence of delta smelt include toxic compounds in the water, reduction in abundance of key food organisms, and competition from recently introduced species of fish and invertebrates. However, evidence that other factors have reduced delta smelt abundance is weak or lacking, so only habitat destruction and inadequacy of regulatory mechanisms will be discussed.

Destruction of Habitat

The principal habitat of the delta smelt is the mixing zone and the freshwater area immediately upstream of it. Habitat for delta smelt increases when the mixing zone is in Suisun Bay, because the zone extends over a much wider area than when it is confined to the deep narrow channels of the delta. When the mixing zone is in Suisun Bay, the system is also more productive (Arthur and Ball 1979), so presumably more zooplankton is available as food, especially for larvae. Because the delta smelt is essentially an annual fish with relatively low fecundity, a food-rich area immediately downstream from its spawning areas must have been a consistent feature that promoted high survival of larvae during most of its evolutionary history.

Increased diversion of fresh water from the estuary has altered both the location of the mixing zone and the flow patterns through the delta during much of the year. The shift of the mixing zone to river channels not only decreases the amount of suitable habitat for delta smelt but results in decreased phytoplankton and zooplankton abundance (Arthur and Ball 1979; Herbold and Moyle 1989). During the months when delta smelt are spawning, the changed flow patterns presumably lead to greater entrainment of spawning adults and newly hatched larvae into water diversions. The combined effects of habitat constriction and fish entrainment provide the most likely explanation of the declines in abundance.

This problem has no doubt been exacerbated by drought conditions that have existed in the drainage since 1987, coupled with the record-high outflows in February 1986 (which flushed fish out of the estuary). However, since 1984 the percentage of inflow diverted has been higher, and has stayed higher longer, than in any previous period including the severe 1976–1977 drought.

Inadequacy of Existing Regulatory Mechanisms

The regulation of delta outflows, delta water quality, and flow patterns through the delta is complex and under the jurisdiction of several agencies (Herbold and Moyle 1989). The present regulatory system primarily benefits water exporters at the expense of fish and other estuarine-dependent organisms; even valuable sport and commercial fishes such as striped bass and chinook salmon have suffered major declines in recent years despite efforts to sustain them (Nichols et al. 1986). Large numbers of pelagic fishes, especially larvae, are entrained in water diversions of the federal Central Valley Project, the State Water Project, agriculture on delta islands, power plants of Pacific Gas and Electric Company, and other industries. Present rescue and mitigation efforts do not seem to compensate for the losses. This is particularly true of delta smelt, which (1) are frequently exposed to entrainment (Stevens et al. 1990), (2) are unlikely to survive any rescue attempts that involve handling of fish because of the high resultant mortality (personal observation), and (3) have received little attention from management agencies until recently. In short, the present mechanisms that regulate freshwater flows through the estuary have not adequately protected delta smelt.

Regardless of cause, the consistently low numbers of delta smelt in recent years indicate that immediate action is needed to reduce the probability of the species becoming extinct. In the past the delta smelt population has shown extreme fluctuations from year to year, as might be expected of an annual species with narrow habitat requirements in a highly disturbed system. Presumably, the population is continuing to fluctuate but at such low numbers that the fluctuations cannot be reliably detected with present methods. With such low numbers, the delta smelt population could fluctuate into extinction in a single year (Pimm et al. 1988).

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References

Armor, C., and P. L. Herrgesell. 1985. Distribution and abundance of fishes in the San Francisco Bay estuary between 1980 and 1982. Hydrobiologia 129: 211–227.

Arthur, J. F., and M. D. Ball. 1979. Factors influencing the entrapment of suspended material in the San Francisco Bay–Delta estuary. Pages 143–174 *in* T. J. Conomos, editor. San Francisco Bay, the urbanized estuary. American Association for Advancement of Science, Pacific Division, San Francisco.

Chadwick, H. K. 1964. Annual abundance of young striped bass (*Roccus saxatilis*) in the Sacramento–San Joaquin Delta, California. California Fish and Game 50:69–99.

Daniels, R. A., and P. B. Moyle. 1983. Life history of the splittail (Cyprinidae: *Pogonichthys macrolepidotus*) in the Sacramento–San Joaquin estuary. U.S. National Marine Fisheries Service Fishery Bulletin 81:647–654.

DWR (Department of Water Resources). 1986. DAYFLOW program documentation and DAYFLOW data summary user's guide. DWR, Sacramento, California.

Erkkila, L. F., J. W. Moffett, O. B. Cope, B. R. Smith, and R. S. Nielson. 1950. Sacramento–San Joaquin Delta fishery resources: effects of Tracy Pumping Plant and Delta crosschannel. U.S. Fish and Wildlife Service Special Scientific Report–Fisheries 56: 1–109.

Ferrari, F. D., and J. Orsi. 1984. *Oithona davisae*, new species, and *Limnnoithona sinensis* (Burckhardt, 1912) (Copepoda, Oithonidae) from the Sacramento–San Joaquin estuary, California. Journal of Crustacean Biology 4:106–126.

Ganssle, D. 1966. Fishes and decapods of San Pablo and Suisun bays. California Department of Fish and Game, Fish Bulletin 133:64–94.

Herbold, B., and P. B. Moyle. 1989. The ecology of the Sacramento–San Joaquin Delta: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.22).

Hynes, H. B. H. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of food of fishes. Journal of Animal Ecology 19:36–58.

Kjelson, M. A., P. F. Raquel, and F. W. Fisher. 1982. Life history of fall-run chinook salmon, *Oncorhynchus tshawytscha*, in the Sacramento–San Joaquin estuary, California. Pages 393–411 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

McAllister, D. E. 1963. A revision of the smelt family, Osmeridae. National Museum of Canada Bulletin 191.

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

Moyle, P. B., R. A. Daniels, B. Herbold, and D. M. Baltz. 1985. 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., J. E. Williams, and E. D. Wikramanayake. 1989. Fish species of special concern in California. California Department of Fish and Game, Sacramento.

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.

Orsi, J. J., T. E. Bowman, D. C. Marelli, and A. Hutchison. 1983. Recent introduction of the planktonic calanoid copepod *Sinocalanus doerrii* (Centropagidae) from mainland China to the Sacramento–San Joaquin estuary of California. Journal of Plankton Research 5:357–375.

Orsi, J. J., and A. C. Knutson. 1979. The role of mysid shrimp in the Sacramento–San Joaquin estuary and factors affecting their abundance and distribution. Pages 401–408 *in* T. J. Conomos, editor. San Francisco Bay: the urbanized estuary. American Association for the Advancement of Science, Pacific Division, San Francisco.

Peterson, D. H., T. J. Conomos, W. W. Brockow, and P. C. Doherty. 1975. Location of the non-tidal current null zone in northern San Francisco Bay. Estuarine, Coastal and Shelf Science 16:415–429.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132:757–785.

Radtke, L. D. 1966. Distribution of smelt, juvenile sturgeon, and starry flounder in the Sacramento–San Joaquin Delta. California Department of Fish and Game, Fish Bulletin 136.

Siegfried, C. A., M. E. Kopache, and A. W. Knight. 1979. The distribution and abundance of *Neomysis mercedis* in relation to the entrapment zone in the western Sacramento–San Joaquin Delta. Transactions of the American Fisheries Society 108:262–270.

Stevens, D. E. 1977a. Striped bass (*Morone saxatilis*) year class strength in relation to river flow in the Sacramento–San Joaquin estuary. Transactions of the American Fisheries Society 106:34–42.

Stevens, D. E. 1977b. Striped bass (*Morone saxatilis*) monitoring techniques in the Sacramento–San Joaquin estuary. Pages 91–109 *in* W. Van Winkle, editor. Proceedings of the conference on assessing the effects of power-plant mortality on fish populations. Pergamon Press, New York.

Stevens, D. E., D. W. Kohlhorst, L. W. Miller, and D. W. Kelley. 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.

Stevens, D. E., L. W. Miller, and B. C. Bolster. 1990. A status review of the delta smelt (*Hypomesus transpacificus*) in California. California Department of Fish and Game, Candidate Species Status Report 90-2, Sacramento.

Turner, J. L., and H. K. Chadwick. 1972. Distribution and abundance of young-of-year striped bass, *Morone saxatilis*, in relation to river flows in the Sacramento–San Joaquin estuary. Transactions of the American Fisheries Society 101:442–452.

Von Geldern, C. E. 1972. A midwater trawl for threadfin shad, *Dorosoma petenense*. California Fish and Game 58:268–276.

Wales, J. H. 1962. Introduction of the pond smelt from Japan into California. California Fish and Game 48: 141–142.

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

Williams, J. E., and seven coauthors. 1989. Fishes of North America endangered, threatened, of special concern: 1989. Fisheries (Bethesda) 14(6):2–20.

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