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Status of Splittail in the Sacramento-San Joaquin Estuary

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Status of Splittail in the Sacramento–San Joaquin Estuary

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Abstract.—Analysis of data from four extensive fish surveys in the Sacramento–San Joaquin estuary indicated that splittail *Pogonichthys macrolepidotus*, endemic to the Central Valley of California, declined by 62% over a 13-year period. Splittails are now found mostly in the estuary, a fraction of their former range. In a gill-net survey in August 1994, 50% of the splittails taken in the estuary were from the Suisun Bay area, and 50% were just upstream in shallow, well-vegetated areas. Splittails migrate into freshwater to spawn, and river outflow carries juveniles into productive, shallow, low-salinity areas downstream. The high correlation of abundance of young with river outflow (average r^2, 0.60) and a weak stock–recruitment relationship (r^2 = 0.22) indicate that spawning success depends on favorable environmental conditions created by high outflows, such as the number of days that lowland areas remain flooded in the spring. A repeated-measures analysis of variance indicated that splittails prefer shallow, low-salinity habitats. The reductions in splittail abundance and range and the movements and habitat preferences of splittail young and adults correspond to trends and habits of two other species characteristic of the estuary, delta smelt *Hypomesus transpacificus* and longfin smelt *Spirinchus thaleichthys*. The largest threats to these three species are changes in water management and increases in water diversions that reduce spawning and rearing areas and other low-salinity habitats in Suisun Bay.

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The splittail *Pogonichthys macrolepidotus* is a large cyprinid endemic to the Central Valley of California, where it was once widely distributed (Rutter 1908; Moyle 1976). It is the only surviving member of its genus following extinction (around 1970) of the Clear Lake splittail *P. ciscoides* in California (Miller et al. 1989). The species is now largely confined to the Sacramento–San Joaquin estuary, less than one-third of its former range (Meng and Kanim 1994). Within the estuary, splittail numbers have declined in recent years and the species has been recommended for threatened status by the U.S. Fish and Wildlife Service (Meng and Kanim 1994). A 6-year drought coupled with changes in the timing and amount of water diverted from the estuary may affect the ability of the species to return to its former abundance.

The Sacramento–San Joaquin estuary, the largest estuary on the Pacific coast, is highly modified by human activities (Conomos 1979; Nichols et al. 1986). Diking, dredging, filling of wetlands, and reduction of freshwater flows through the estuary by more than half for irrigated agriculture and urban use have altered fish habitat and resulted in fish losses (Nichols et al. 1986; Moyle et al. 1992). Reduced freshwater flow through the estuary is correlated with poor year-class success of many species found in the estuary, including striped bass *Morone saxatilis*, American shad *Alosa sapidissima*, chinook salmon *Oncorhynchus tshawytscha*, longfin smelt *Spirinchus thaleichthys* and splittail (Turner and Chadwick 1972; Stevens 1977; Kjelson et al. 1982; Daniels and Moyle 1983; Stevens and Miller 1983; Stevens et al. 1985). Four native estuarine-dependent species have declined to the point that they have some degree of consideration or protection under the U.S. Endangered Species Act of 1973; these are winter-run chinook salmon (endangered), delta smelt *Hypomesus transpacificus* (threatened), longfin smelt (category-2 species), and splittail (proposed as threatened).

Splittails grow to 40 cm standard length (SL) and can be readily distinguished from other cyprinids in the Central Valley of California by the enlarged dorsal lobe of the caudal fin. They mature at age 2 and most spawn from March to May (Caywood 1974; Daniels and Moyle 1983). Splittails may migrate upstream to spawn, as suggested by reports of spawning migrations in the Sacramento River from the 1950s (Caywood 1974), catches of splittail in fyke nets set to capture migrating striped bass (California Fish and Game, unpublished data), and capture of young in seines upstream in the Sacramento River (U.S. Fish and Wildlife Service, unpublished data). Splittails are

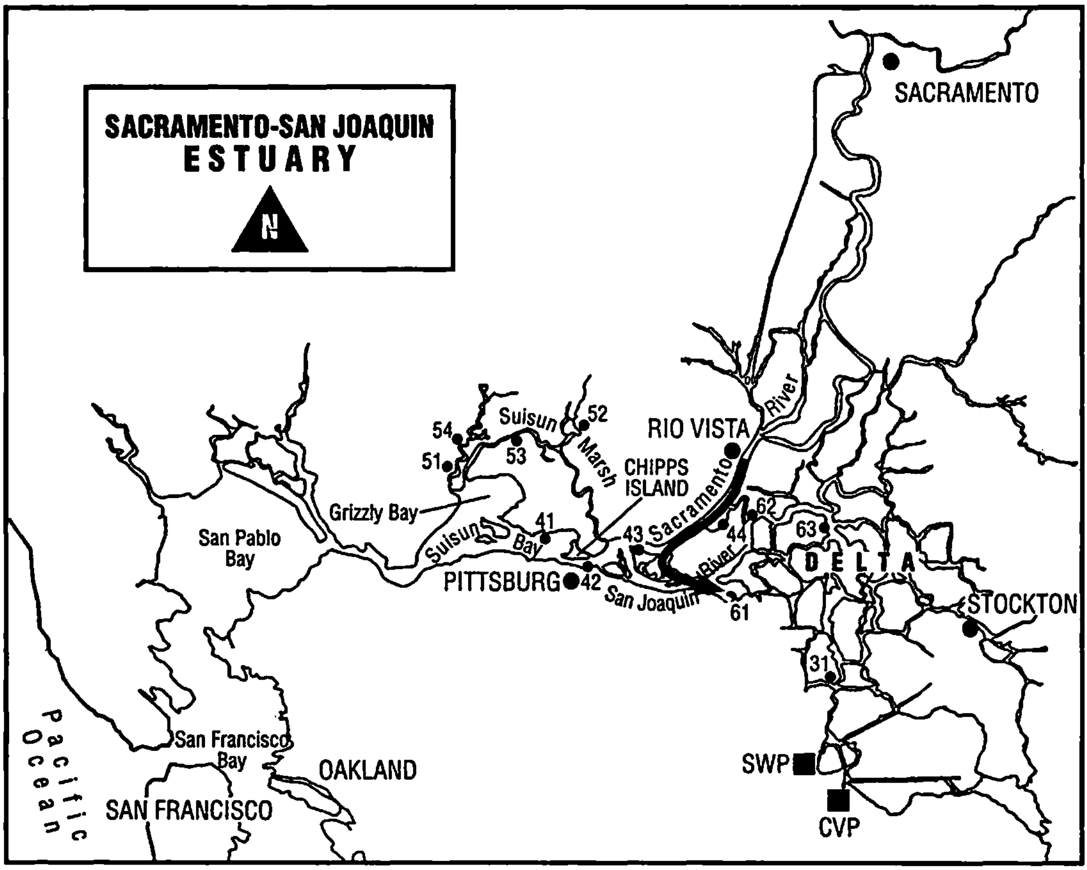

FIGURE 1.—Sacramento–San Joaquin estuary, California. Arrow denotes direction of across-delta flows drawn by the State Water Project pumping facility (SWP) and the federal Central Valley Project pumping facility (CVP). Numbers denote locations where splittails were caught during a 1994 gill-net survey. Location names are in Table 2.

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common in brackish backwaters of Suisun Bay, Suisun Marsh, and the inland delta near the juncture of the Sacramento and San Joaquin rivers (Rutter 1908; Moyle 1976). They feed heavily on *Neomysis mercedis*, a brackish-water mysid shrimp (Daniels and Moyle 1983). Detritus makes up most of their stomach contents, and other prey types (oligocheate worms, amphipods, copepods, insects, and clams) indicate that they are benthic foragers (Caywood 1974; Daniels and Moyle 1983). For cyprinids, splittails have an unusual tolerance to salinity; they have been captured in salinities as high as 18 ‰. Here we present additional information on splittails including abundance trends, distribution patterns, migration, habitat preference, and factors affecting recruitment.

Study Area

The Sacramento–San Joaquin estuary includes San Francisco, San Pablo and Suisun bays, and the inland delta (Figure 1). The delta is a maze of over 1,600 km of waterways and islands upstream of the confluence of the Sacramento and San Joaquin rivers. Federal and state water projects in the south delta (Figure 1) have a combined pumping capacity of over 300 m^3/s. During periods of low river outflow, these projects pull Sacramento River water across the delta and into the channel of the San Joaquin River downstream of the pumps. This results in net upstream (reverse) flow in the lower San Joaquin River (Figure 1; Moyle et al. 1992). Across-delta flows (rather than seaward flows) move and divert fish towards the pumps. A large part of the flow from the San Joaquin River above the delta is made up of agricultural drainage; pesticides and salts from this drainage are concentrated by reverse flows and result in poor water quality in the south delta. The position of the mixing zone, where incoming salt water mixes with outflowing fresh water, varies seasonally and with

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the amount of water diverted. In the mixing zone, salinities are about 2-3 ‰, and circulating currents trap planktonic organisms valuable to fish as food. Historically, the mixing zone was in Suisun Bay during most of the winter and spring.

The estuary is a highly altered system. Before 1850, freshwater marsh covered 1,400 km^2 of the delta (Nichols et al. 1986), but today less than 10% remains (Conomos 1979). Levee construction, farmland reclamation, and dam construction reduced winter and spring flows and confined the Sacramento and San Joaquin rivers to set channels. Flood control projects established the Yolo and Sutter bypasses (96 and 128 km upstream of the confluence of the Sacramento and San Joaquin rivers) to bypass flows of flood water. Federal and state water projects rely on large reservoirs upstream of the delta for storage. Because most precipitation occurs in California in winter and spring, large amounts of spring runoff are stored upstream to be delivered for agricultural and other uses during dry months.

Methods

Sampling.—Splittails were collected by six independent means: (1) a fall midwater trawl survey in the upper estuary by the California Department of Fish and Game (CFG), (2) a monthly bottom-trawl survey in the lower estuary by CFG (bay survey), (3) a monthly bottom-trawl survey of Suisun Marsh sloughs by the University of California–Davis (UCD), (4) a midwater trawl survey at Chipps Island in Suisun Bay by the U.S. Fish and Wildlife Service (USFWS), (5) fish salvage at state and federal pumping facilities in the south delta by the California Department of Water Resources and the U.S. Bureau of Reclamation, and (6) a summer gill-net survey in the Sacramento and San Joaquin rivers, delta, Suisun Bay, and Suisun Marsh by an interagency group (see Acknowledgments). Fish were identified, measured (SL in the UCD study, fork length in all other studies) and returned to the water.

The fall midwater trawl survey is conducted with a 17.6-m-long trawl with a mouth opening of 3.7 m^2, towed at about 70 cm/s (Stevens and Miller 1983). Fixed sites were sampled 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 (Figure 1). Surveys were conducted monthly from September to December at 87 sites in most years from 1967 to present. Splittail sizes were not available from this data set.

The bay survey is a monthly trawling program that began in 1980 (Armor and Herrgesell 1985). Its 35 sites are distributed throughout the lower estuary from South San Francisco Bay upstream to the confluence of the Sacramento and San Joaquin rivers (Figure 1). We restricted our analysis of bay survey data to 17 sites sampled in all years within the range of the splittail. Since 1981, the survey has recorded salinity and depth at each sampling site.

The Suisun Marsh fish survey (Figure 1) has been conducted monthly with a bottom trawl by UCD since 1979 (Moyle et al. 1986; Meng et al. 1994). The trawl is towed at about 4 km/h for 5 min in small sloughs and 10 min in larger sloughs. Longer tows are necessary in larger sloughs because of small catches. Salinities are measured at 10 locations (Moyle et al. 1986). Because the marsh sloughs are shallow (2–3 m), the bottom trawl samples most of the water column.

The Chipps Island survey is conducted with a 27.1-m-long trawl with a mouth opening of 20.4 m^2. Ten 20-min tows are made in Suisun Bay in the channel between Chipps Island and Pittsburg (Figure 1). Sampling effort has varied in the Chipps Island survey, but a core data set for April, May, and June was used in this analysis. Sampling began in 1976 and is conducted two to three times per week.

State and federal water project pumps in the south delta (Figure 1) are fitted with louvers that direct fish into salvage wells. Fish are removed from the wells (data hereafter referred to as salvage data) and transported upstream by truck to sites in the Sacramento River near Rio Vista. Fish are sampled at the fish facilities year-round at 2-h intervals; records for splittails date back to 1980. The amount of effort varies seasonally and depends upon the amount of water pumped.

An extensive night gill-net survey was conducted in the first 2 weeks of August 1994. Twenty-four sampling locations were selected throughout the known range of the splittail, including Suisun Marsh, Suisun Bay, the delta, and the Sacramento and San Joaquin rivers (Figure 1). Stations in the Sacramento River extended 317 river kilometers (rkm) upstream of the confluence of the Sacramento and San Joaquin rivers. Stations in the San Joaquin River extended 127 rkm above the confluence. Each location was sampled one night per week for 2 weeks. Crews fished three 30.8 × 2.5-m, variable-mesh gill nets at each location from 1830 to 0600 hours. Nets were set in water less than 6.2 m deep, and each net was oriented

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differently to assess differences in habitat use and maximize catch. Nets set inshore were perpendicular to shore near vegetation; offshore, they were perpendicular to shore; near shore, they were parallel to vegetated shallows.

Abundance trends and distribution.—For the Suisun Marsh and Chipps Island trawl surveys, data were summarized as the number of splittails per trawl tow for each month. We calculated abundance indices from fall midwater trawl and bay survey data by dividing the survey area into regions, multiplying mean catch at the stations within each region by estimated volume of water in each region, and summing those products (Stevens and Miller 1983). Numbers of fish salvaged monthly were divided by the amount of water pumped. Splittail age-groups were based on CFG bay survey length-frequency analyses (CFG unpublished data).

We determined percent declines in splittails for the fall midwater trawl, bay survey, Suisun Marsh, and Chipps Island studies by comparing point estimates with the Mann–Whitney *U*-test. We used a common core data set of 1980–1992 yearly abundances from each survey and divided them into pre- and postdecline periods. We chose 1985 as the beginning of decline because of evidence from plots of splittail abundance against years and because environmental and water management changes occurred in the estuary at about that time. The years preceding 1985 had highly variable water regimes that included drought and flooding. After 1984, winter and spring flows were diverted at higher rates, resulting in reverse flows in the San Joaquin River for about 50% of the spring spawning season (Moyle et al. 1992). Pre- and postdecline periods are approximate because the splittail probably declined over a multiyear period and the surveys used in this study took place in different habitats in different parts of the estuary, where different rates and timing of the decline would be expected. A repeated-measures analysis of variance (ANOVA; SAS Institute 1988) also provided a statistical test of decline for the bay survey data.

The 1994 summer distribution of splittails was assessed by a split-plot ANOVA with nets as treatments and locations as plots. Catch per unit effort (CPUE) for the gill-net study was calculated in two ways: (1) average catch per hour by net for each night ($\log_{10}$-transformed for ANOVA), and (2) average of six nightly CPUEs for each location (i.e., three nets/night for two nights) to show relative abundance by location.

Migration.—To answer questions about splittail migration, we used chi-square contingency tables. We used salvage data from 1980–1992 for this analysis because they were collected year-round near a possible migration corridor and included large numbers of fish. Contingency tables tested the hypothesis that salvage frequencies of age-0, age-1, and age-2 and older fish at the facilities were independent of time periods in winter (January–April), summer (May–August), and fall (September–December). These time periods corresponded to splittail migration and spawning (winter), juvenile rearing (summer), and growth (fall). These time periods also marked changes in river outflow in the estuary. Winter is a period of high river outflows. Outflow decreases during summer, and lowest outflows and highest salinities occur in fall. Since 1990, gillnetting of large predatory fish has been conducted in the forebay of the state pumping facility. The gillnetting also captures splittails, so we used numbers from this effort to corroborate trends in seasonal abundance of adults at the pumping facilities.

Habitat preference.—We used a repeated-measures ANOVA on bay survey bottom trawl data to determine habitat preference for splittails. We used bay survey data because they were collected year-round and covered a large geographical area. In this analysis we used stations where splittails had been captured. Stations were grouped by depth and salinity. We assigned each of the 17 stations as deep (>6.7 m) or shallow (≤6.7 m) and high salinity (>7 ‰) or low salinity (≤7 ‰). We used average depths at mean low water, and we used average January salinities because they were closest to mean annual salinities. Repeated measurements taken at each station were adult and juvenile catch per unit effort in three seasons from 1980 to 1984 and from 1985 to 1992. The seasons corresponded to time periods used for the fish facility data.

Recruitment.—We used regression analysis to examine the influence of river outflow on splittails. Abundance of age-0 splittails (age was estimated from length data) was regressed on February–May outflow for bay survey, Suisun Marsh, and Chipps Island trawl data. Abundance and outflow data were log-transformed. Outflow data were obtained from the DAYFLOW database of the California Department of Water Resources.

We used flooding of the Yolo bypass as a surrogate for flooded terrestrial habitat to examine the relationship between flooding and splittail recruitment. Flooded areas believed to be important to

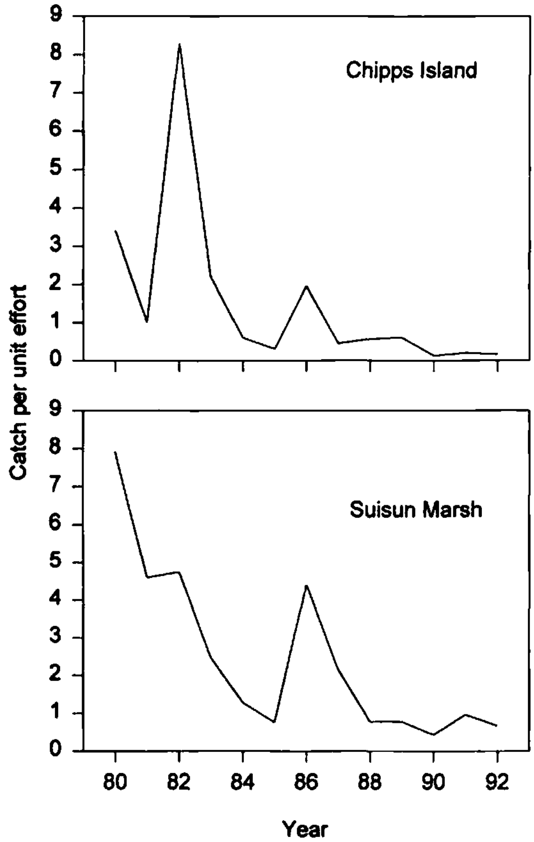

FIGURE 2.—Trends in splittail catch per unit effort from the Suisun Marsh sampling program and Chipps Island midwater trawl survey, 1980–1992. These surveys sampled a limited but central portion of splittail range. The Suisun Marsh program sampled year-round. Chipps Island trawl data from April through June were used for this analysis.

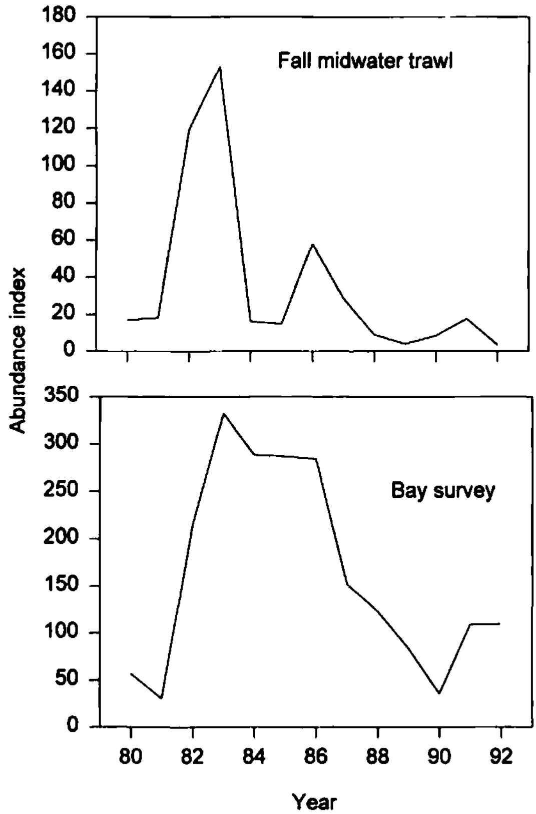

FIGURE 3.—Trends in splittail abundance indices from two California Department of Fish and Game programs that sampled a large portion of splittail range, 1980–1992. The bay survey sampled year-round and the fall midwater trawl sampled from September to December. Abundance indices are products of total catch and water volume, summed over standard suites of sampling areas.

splittail spawning and recruitment include bars and edges with willows and weeds adjacent to river channels and sloughs. A relationship between number of days that upstream areas (bypasses) were flooded from February to May and subsequent fall midwater trawl abundance was calculated from California Department of Water Resources data.

We calculated a linear stock–recruitment relationship for the splittail using log-transformed Suisun Marsh data. We used Suisun Marsh data because this survey had high catches of all age-groups of splittails. Ages were determined by back-calculated lengths (Daniels and Moyle 1983). Splittails age 0 and age 1 were considered recruits; splittails age 2 and older were designated spawners.

Results

Abundance Trends and Distribution

Splittail abundance declined an average of 62% over the 13 years from 1980 through 1992, as measured by four sampling programs. Declines varied among studies; statistically significant declines (two-tailed $P < 0.05$) occurred in the Suisun Bay area (Suisun Marsh, 73% decline; Chipps Island, 81% decline; Figure 2). Declines in the fall midwater trawl (70%) and bay survey (23%) were not statistically significant ($P > 0.05$) according to the Mann–Whitney *U*-test (Figure 3), but repeated-measures ANOVA indicated that the decline in bay survey splittail abundance was significant ($P < 0.02$; Table 1).

Suisun Marsh had the highest proportion of trawl tows with splittails. Overall, about 50% of the tows captured splittails in Suisun Marsh com-

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TABLE 1.—Results of repeated-measures analysis of variance of bay survey bottom trawl data to determine habitat preference for splittails. Stations (17) were grouped by depth (≤6.7 m or >6.7 m) and salinity (≤7‰ or >7‰). Repeated measurements taken at each station were adult and juvenile abundances from 1980 to 1984 and from 1985 to 1992 in three seasons (winter, January–April; summer, May–August; fall, September–December).

Source	df	P^a
Grouping factors		
Depth	1	0.007
Salinity	1	0.0001
Depth × salinity	1	0.0005
Repeated measurements		
Years	1	0.02
Season	2	0.03
Season × depth	2	0.005
Season × salinity	2	0.03
Season × depth × salinity	2	0.04
Age-group	1	0.002
Age-group × depth	1	0.0002
Age-group × salinity	1	0.007
Age-group × depth × salinity	1	0.0002

[a] Probability of a greater F-value.

pared with 6–10% for the fall midwater trawl and bay surveys. Before 1985, splittails were captured in 60% of the tows; after 1984, 34% of the tows in Suisun Marsh captured splittails. January salinities in Suisun Marsh increased from an average of 2.4 ‰ in 1980–1984 to 12.6 ‰ in 1985–1992.

In the fall midwater trawl (1967–1992) and bay (1980–1992) surveys, splittail catches were highest in shallow areas of Suisun and Grizzly bays, although upstream distribution shifted after 1984. Fall midwater trawl and bay survey data indicated that 72 and 56% of the splittail catch was in the Suisun Bay area (Figure 4). Before 1985, splittails were more abundant in lower Suisun and upper San Pablo bays (73 and 95% of the splittails captured in these areas were taken before 1985). After 1984, more splittails were captured in the lower river channels. In the bay survey and fall midwater trawl, 88 and 63% of the splittails taken in the lower Sacramento and San Joaquin rivers were taken after 1984.

No splittails were captured in the Sacramento or San Joaquin rivers upstream of the delta by the gill-net survey in August 1994. Of the 274 splittails taken that month, 36% were captured in Suisun Marsh, 13% were taken in Suisun Bay, and remaining catches were just upstream (Figure 1; Table 2). No age-0 splittails were captured, and only 10% were age 1. There were significant differences among locations (ANOVA; $P < 0.0001$) and Tukey multiple comparisons indicated that Nurse Slough in Suisun Marsh had a significantly higher average CPUE than other locations except Sherman Lake and Big Break (Table 2). Sherman Lake and Big Break were significantly different

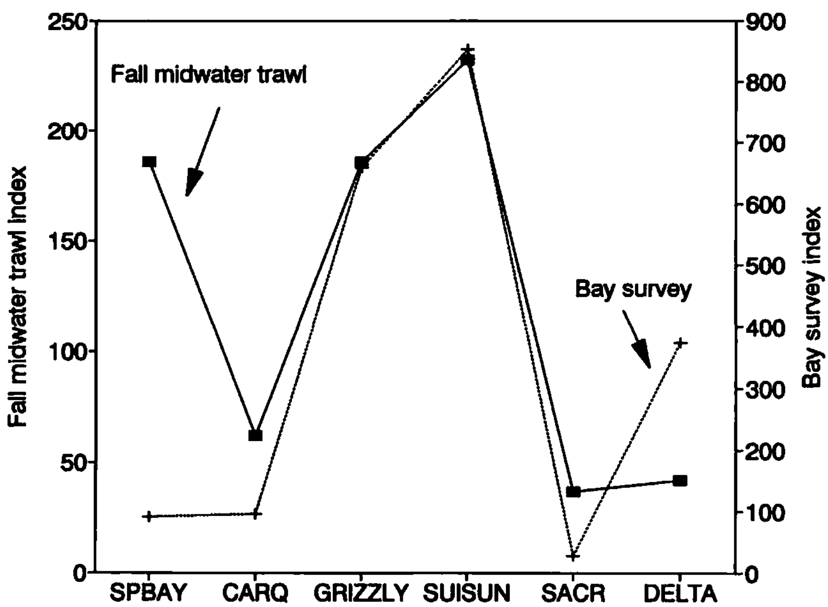

FIGURE 4.—Splittail abundance indices by area for the fall midwater trawl (1967–1992) and bay (1980–1992) surveys. Abbreviations are SPBAY, San Pablo Bay; CARQ, Carquinez Strait area; GRIZZLY, Grizzly Bay; SUIS, Suisun Bay; SACR, Sacramento River; and DELTA, central delta.

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TABLE 2.—Significant differences ($P < 0.05$) in 1994 gill-net catches of splittail among survey locations, based on Tukey multiple comparisons following a significant analysis of variance (ANOVA). Data for the ANOVA were average splittail catches per hour by net for each sampling night. Locations are arranged in descending order of average catch per unit effort (CPUE). Average CPUE (SD) was calculated from six nightly catches per hour for each location (three nets set on two nights at each location). Stations not listed had no splittail catches. Means followed by the same letter are not significantly different ($P > 0.05$).

Location	Location number (Figure 1)	Average CPUE (SD)
Nurse Slough	52	1.46 (1.04) z
Sherman Lake	43	1.04 (1.05) zy
Big Break	61	0.92 (0.61) zyx
Suisun Slough 1	54	0.41 (0.41) yxw
Montezuma Slough	53	0.36 (0.27) yxw
San Joaquin River 1	62	0.32 (0.56) yxw
Mallard Slough	42	0.29 (0.21) yxw
Suisun Slough 2	51	0.26 (0.46) w
Honker Bay	41	0.22 (0.31) w
Old River	63	0.18 (0.17) w
Horseshoe Bend	44	0.15 (0.14) w
Indian Slough	31	0.02 (0.04) w

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from locations with CPUEs less than 0.29 (Table 2). Other locations were not significantly different from locations where no splittails were caught (Table 2). There was no effect associated with different net orientations ($P = 0.30$), but there was an interaction between net orientation and location ($P < 0.017$).

Migration

Different age-groups of splittails appeared in the fish salvage wells at pumping facilities during different time periods (df = 4, $P < 0.0001$ for both facilities; Figure 5). Adults (age-2 or older) were salvaged more often between January and April, than in later months. Likewise, 67% of adult splittails captured in gill nets in the forebay of the state pumping facility were taken between January and April. Salvage of age-0 fish peaked between May and August.

Habitat Preference

Results of repeated-measures ANOVA for bay survey data indicated that splittails prefer low-salinity, shallow-water habitat (Table 1). More fish were captured in shallow ($P < 0.007$), low-salinity water ($P < 0.0001$), and there was an interaction between depth and salinity ($P < 0.0005$). Contrasts among means indicated that more fish were captured at low-salinity ($P < 0.03$), shallow ($P < 0.005$) stations in summer (May–August) than at other times of the year. The interaction among season, depth, and salinity indicated that more fish were taken in shallow, fresher water in drier months (May–December) than in wetter months (January–April; $P < 0.04$).

Age-groups differed in abundance and habitat preference. More fish were captured in summer than in other seasons ($P < 0.03$), and more adults than juveniles were taken ($P < 0.002$) by bottom trawl in the bay survey. Contrasts among means indicated that a higher proportion of adults were captured at shallow ($P < 0.0002$) and low-salinity stations ($P < 0.007$) than at other stations. The interaction between shallow depth and low salinity was particularly important to adults ($P < 0.0002$).

Recruitment

There was a strong relationship between abundance of splittail young and outflow. Changes in February–May outflow explained between 55 and 69% of the variability in abundance of splittail young, depending on abundance measure. Coefficients of determination and significance levels were 0.55 ($P < 0.0025$) for Suisun Marsh, 0.56 ($P < 0.0006$) for Chipps Island, and 0.69 ($P < 0.0002$) for the bay survey. Chipps Island age-0 catches indicated that young were most abundant in wet years, when a smaller percentage of the flow was diverted; according to the California Department of Water Resources, wet years were 1978, 1980, 1982, 1983, and 1986 (Figure 6). From 1987 through 1992, water diversions exceeded 30%, and catches of age-0 splittails were nil to low (Figure 6). Age-0 abundance in 1993 (155) was 3% of age-0 abundance in 1978 (5,493).

Fall abundance of splittails was correlated with the number of days that bypass areas remained flooded in spring. Flooding of the Yolo bypass explained 60% ($P < 0.01$) of the variability in subsequent fall midwater trawl catches. When these areas remained flooded for 50 d or more, the strongest year-classes were produced.

A linear stock-recruitment relationship based on Suisun Marsh data explained less than one-fourth of the year-to-year variability in splittail abundance and was not significant ($r^2 = 0.22$, $P < 0.09$, $N = 14$).

Discussion

The greatest declines in splittail abundance occurred in Suisun Bay and Marsh (Figure 2), the area where most fish were caught (Figure 4). Large catches of splittails taken in Suisun Marsh by the

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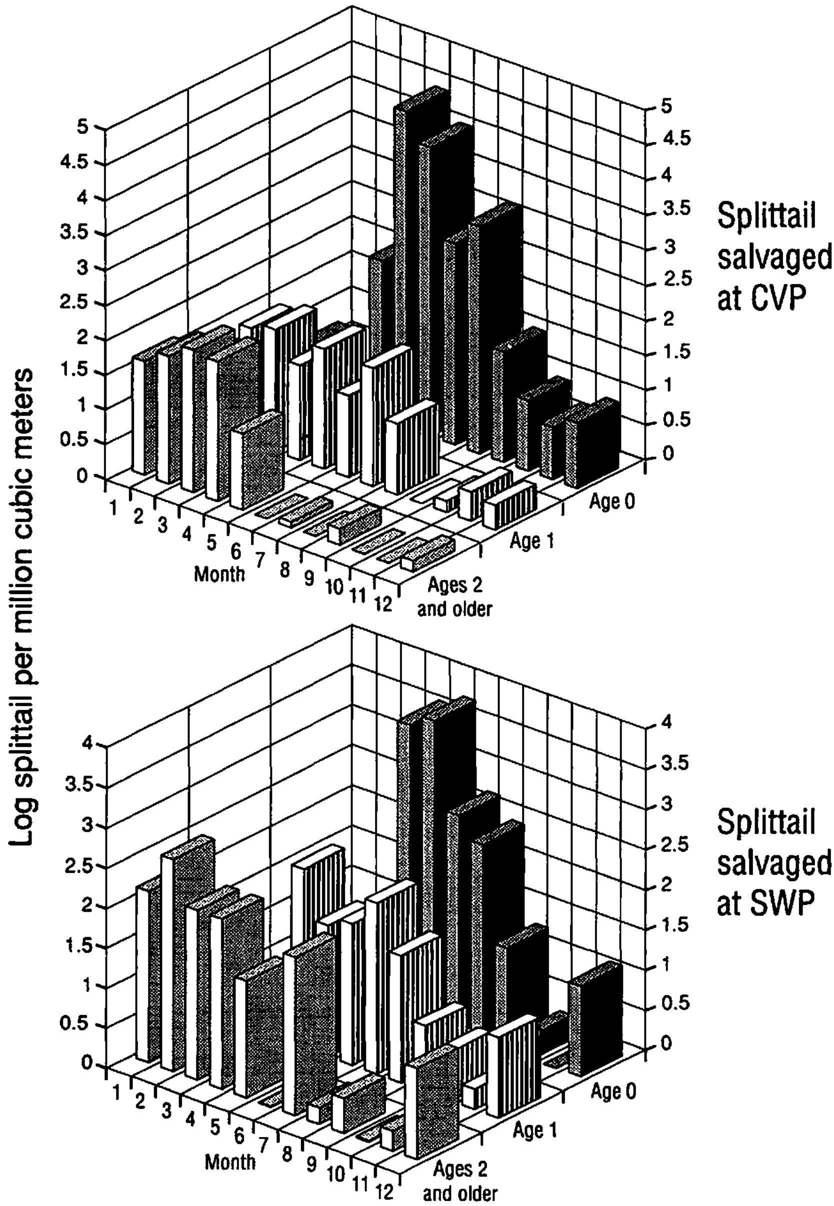

FIGURE 5.—Number of splittails (adjusted by amount of water pumped) by age-class salvaged at federal (Central Valley Project, CVP) and state (State Water Project, SWP) water facilities by month (month 1 is January), 1980–1992. Age-2 and older fish are sexually mature.

summer gill-net (Table 2) and Suisun Marsh surveys support earlier findings that the marsh is important habitat for this species (Daniels and Moyle 1983; Meng et al. 1994). Presumably, the shallow, dead-end sloughs of the marsh, lined with tules *Scirpus* spp. and reeds *Phragmites communis*, provide rich feeding grounds and refuge from predators. Grizzly Bay, adjacent to the marsh, offers similar shallow-water habitat with emergent vegetation. The highest concentrations of *Neomysis mercedis*, a primary splittail food, are also found in the Suisun Bay area (Orsi and Knutson 1979). The major declines in splittail abundance coincide with a loss of these preferred habitats because of increasing salinities in Suisun Bay and Suisun Marsh. Higher salinities resulted in loss of shal-

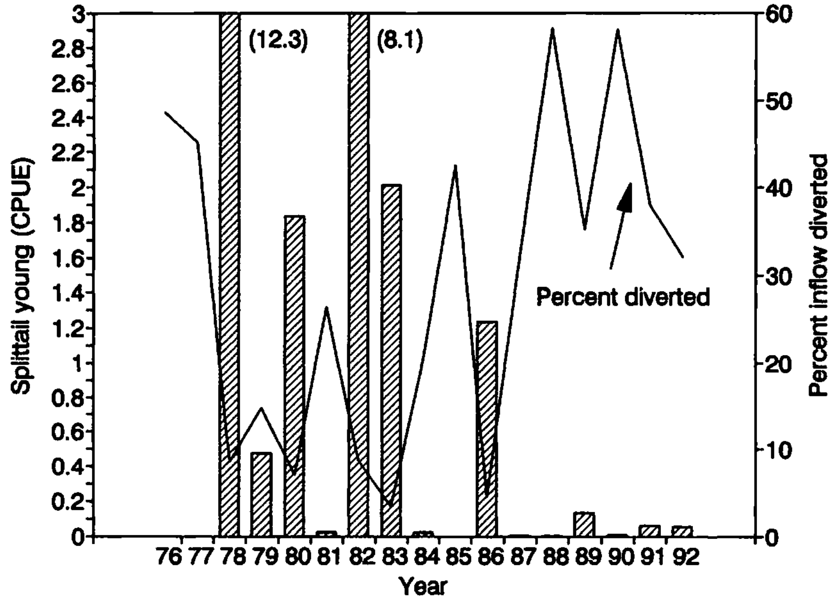

FIGURE 6.—Catches of age-0 splittails per unit trawling effort (CPUE) at Chipps Island and percentages of water inflow diverted. The CPUE was 12.3 in 1978 and 8.1 in 1982. Wet years were 1978, 1980, 1982, 1983, and 1986; all others were dry (California Department of Water Resources).

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low, low-salinity habitat (Meng et al. 1994) in an important part of the splittail's range. After 1984, splittail young were relatively abundant in the marsh only in 1986, presumably because of high outflows that improved habitat and spawning conditions (Daniels and Moyle 1983).

The loss of shallow, low-salinity habitat in Suisun Bay and Marsh coincided with an upstream shift in splittail distribution into the river channels. The river channels are poor habitat for splittails because of smaller populations of prey and increased risk of diversion into the south delta, where state and federal pumping plants are located and water quality is poorer. Pesticides (e.g., chlorpyrifos, carbfuran, and diazinon) and salts (e.g., sulfates, selenium, and total dissolved solids) from agricultural drainage are concentrated in the south delta by reverse flows resulting from high pumping rates and low flows (D. Westcot, Central Valley Regional Water Quality Control Board, personal communication). Workers at the federal pumping plant in the south delta, where water quality is poorer, have reported a high incidence of splittails with lesions associated with parasites (U.S. Bureau of Reclamation, unpublished data). Fish in the south delta, including striped bass, delta smelt, longfin smelt, and splittails are also vulnerable to losses in the pumping plants because of altered hydrological conditions resulting from high pumping rates and reverse flows (Moyle et al. 1992).

The appearance of large numbers of splittail adults at state and federal pumping facilities from January through April supports earlier observations that splittail undergo spawning migrations. More than two-thirds of the adults taken at the fish facilities (in predator gillnetting and salvage operations) were taken in the winter. Caywood (1974) noted movement of adults through the delta and up the Sacramento River during winter and spring and suggested that they migrated to spawn on flooded vegetation. Seasonal catches of adults in fyke nets (CFG, unpublished data), upstream catches of young in seines (USFWS, unpublished data), and information reported here indicate that splittails migrate upriver to spawn in freshwater from January through April. Tolerance of relatively high salinities and migrations from brackish to freshwater are unusual for cyprinids (Moyle and Cech 1988).

The large number of splittail young taken at the fish salvage facilities between May and July probably reflects downstream movement of juveniles. Splittails spawn in March and April (Caywood 1974). After hatching, larvae remain in shallow, weedy areas until the water recedes, and then they move into deeper water and migrate downstream

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with river flow (Caywood 1974; Wang 1986). Presumably, young move through river channels to downstream rearing grounds in Suisun Bay. The repeated-measures ANOVA indicated that lower proportions of juveniles were taken in shallow water. This is somewhat surprising for this species, which is benthic in the adult stage. However, relatively large catches of young from deep, open channels by the surface-oriented (midwater) Chipps Island trawl support these findings and suggest that young are migrating and perhaps feeding on plankton.

Migration of adults into freshwater to spawn and subsequent downstream migration of young into shallow, productive waters of Suisun Bay is characteristic of other native species in the Sacramento–San Joaquin estuary. Splittail, delta smelt, and longfin smelt form a suite of species characteristic of the estuary. Populations of all three species shifted upstream after 1984 (Moyle et al. 1992; Meng, Moyle, and CFG unpublished data). Abundant year-classes in these species and striped bass depend on sufficient riverine flow to move young downstream to productive rearing areas in Suisun Bay. Moreover, sufficient riverine flows are important to position the freshwater–saltwater mixing zone in Suisun Bay. Circulating currents created by the mixing zone trap fish larvae and zooplankton (Orsi and Knutson 1979). When the mixing zone is located in shallow Suisun Bay, productivity and production of important food species (e.g., *N. mercedis* and *Eurytemora affinis*) increase (Orsi and Knutson 1979). Between 1981 and 1984, the mixing zone was located in Suisun Bay from October through March, except during months with exceptionally high outflows (Moyle et al. 1992). After 1984, the mixing zone moved upstream to deeper river channels in all months until 1993, except during a brief period of record outflow in 1986 (Moyle et al. 1992). Splittails, delta smelt, and longfin smelt declined dramatically between 1984 and 1992, when the mixing zone was upstream (Moyle et al. 1992; CFG and USFWS, unpublished data; this study).

Splittails prefer shallow, low-salinity habitat, and results of the summer gill-net study underscore their preference for well-vegetated areas. The largest catches of splittails were in Suisun Marsh, Sherman Lake, and Big Break. Sherman Lake and Big Break, just upstream of the confluence of the Sacramento and San Joaquin rivers, were sites of levee breaches and now contain many marsh islets and large areas of emergent vegetation. The shallow areas of Sherman Lake, Big Break, and Suisun Marsh contain most of the wetlands in the estuary that resemble those that existed before large-scale reclamation activities occurred. We were unable to discern a finer level of habitat preference with our different net orientations, primarily because differences in locations caused the nets to fish differently.

The strong relationship between abundance of splittail young and river outflow may be partially explained by the use of flooded vegetation for spawning. The correlation between number of days the bypass remained flooded and abundance suggests that flooding may be one of the mechanisms underlying the strong relationship between abundance of splittail young and outflow. Other factors explaining the relationship are common to other delta fishes and include increasing quality and quantity of nursery habitat and wider dispersal of young (Stevens and Miller 1983). The stock–recruitment relationship we calculated is similar to that calculated for delta smelt (Moyle et al. 1992). This relatively weak relationship (less than one-quarter of variability explained) suggests that environmental factors limit abundance even in years of large populations (Moyle et al. 1992). The steady decline in splittail young in wet years coincided with changes in water project operations. The proportion of river flow diverted by state and federal water projects has increased irregularly since 1978 (Figure 6). Moreover, since 1983, pumping by the water projects has increased during winter, particularly during the spawning period of splittails and delta smelt (Moyle et al. 1992).

Another component of water project operations that affects splittails is diversion of water to storage. The strong relationship between number of days that areas remain flooded in spring and splittail abundance suggests that flooded areas are important for successful year-classes. Caywood (1974) observed presumed splittail spawning activity in flooded terrestrial habitats, such as bars with willows and weeds and small flood plains adjacent to river channels. Diversion of water to storage in upstream reservoirs during high spring runoff decreases river flow upstream of the delta and reduces floodable areas. Snow melt in March and April historically produced the highest river flows. Increased pumping in winter since 1983 (Moyle et al. 1992) depletes reservoirs and increases spring-time diversion of water to storage. In recent years, springtime diversions to storage have frequently exceeded the amount of water exported at pumps in the south delta (California Department of Water Resources 1993). Less water

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flows down the rivers, reducing floodable areas and splittail spawning habitat.

Like other native California minnows, particularly those found in larger rivers or lakes (Moyle et al. 1982), splittails are well adapted to wet and dry cycles typical of the Mediterranean climate of California. Its long life (5–7 years) and high fecundity allow the splittail to delay spawning during droughts or at other times when conditions are unsuitable (Moyle et al. 1982). The recent 6-year drought in California and changes in water management have reduced splittail recruitment. Before the drought of 1976–1977, the average proportion of inflow diverted was 30%; current diversions average 50% (Moyle et al. 1992). In 1988, the amount of river flow diverted exceeded the amount flowing out to sea (Moyle et al. 1992). High rates of water diversions during extended droughts that approach the length of the life span of the splittail limit the ability of this species to return to former levels of abundance.

Historically, splittails ranged from Redding on the Sacramento River to Millerton on the San Joaquin River (about 900 rkm; Rutter 1908). Spawning runs that ascended tributaries of the Sacramento and San Joaquin rivers largely disappeared after dams were constructed on those streams (Caywood 1974). Data sets analyzed here covered primarily the estuary and delta. However, the large catches of splittails made during the extensive summer gillnetting in the Suisun Bay area and just upstream indicate that these areas represent primary habitat for the adult population. Other data indicate that splittail migration and early juvenile rearing are mostly confined to about 250 km of the main-stem Sacramento and San Joaquin rivers, although a few records exist from as far as 300 km upstream on the Sacramento (CFG and USFWS, unpublished data). Reclamation activities, drought, increasing water demand, and changes in water management have reduced the range of the species and have also reduced its spawning and rearing success throughout its remaining range. The ability of splittails to return to former levels of abundance depends on careful management of flows and shallow-water habitats in order to provide flooded areas and maintain low-salinity habitat in Suisun Bay during winter and spring.

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