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Resilience of Splittail in the Sacramento–San Joaquin Estuary

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Abstract.—Splittail *Pogonichthys macrolepidotus*, an endemic cyprinid of the Sacramento–San Joaquin estuary, has been proposed for listing as threatened under the U.S. Endangered Species Act. Almost continuous low outflow conditions in the estuary from 1987 to 1994 led to reduced abundance of young splittails, but adult abundance did not decline consistently except in the downstream portion of the species' range. This range had decreased primarily as a result of historical levee and dam construction but did not appear to have changed substantially in the past 20 years. The distribution of young splittails appears to be relatively plastic on an interannual basis. Evidence of the resilience of the species was seen when high freshwater outflows in extremely wet years (such as 1982, 1983, 1986, and 1995) resulted in high numbers of young splittails. Splittail year-class strength was positively related to freshwater outflow during the spawning season. High outflow inundates the floodplain, which provides spawning, rearing, and foraging habitat. The relatively long life span, high reproductive capacity, and broad environmental tolerances of splittails are contrasted with delta smelt *Hypomesus transpacificus* and longfin smelt *Spirinchus thaleichthys*, other native species of special concern in the system.

Many aspects of the biology of the splittail *Pogonichthys macrolepidotus*, a cyprinid endemic to the Sacramento–San Joaquin estuary, seem to reflect the highly variable nature of aquatic environments in California. Splittails are found in the fresh and brackish waters of Suisun Bay, Suisun Marsh, and the Sacramento–San Joaquin Delta (Figure 1; Moyle 1976; Lee et al. 1980; Moyle et al. 1994). They have been captured in salinities as high as 18‰ (Meng and Moyle 1995) and have tolerated higher levels in laboratory experiments (Young and Cech 1996). Adult splittails undertake an annual upstream spawning migration from the estuary in late autumn and winter, when delta inflow increases from seasonal rains (Caywood 1974; Meng and Moyle 1995). Spawning is believed to occur primarily in winter and spring on flooded vegetation. Young splittails rear in upstream areas for a period lasting from a few weeks to a year or more before moving to tidal fresh and brackish waters. Year-class strength of splittails is significantly correlated with total annual flow of the Sacramento River (Daniels and Moyle 1983). Splittails mature at about 2 years and commonly live to 5 years (Daniels and Moyle 1983), presumably spawning annually. However, existing evidence suggests some individuals live longer (California Department of Water Resources [CDWR], unpublished data).

In 1994 the splittail was proposed as threatened under the U.S. Endangered Species Act of 1973. The species remains under consideration for listing by the U.S. Fish and Wildlife Service (FWS). Meng and Moyle (1995) reviewed the status of the splittail and concluded that abundance had declined 62% during a 13-year period and that spawning runs that formerly ascended tributaries of the Sacramento and San Joaquin rivers had largely disappeared. Meng and Moyle (1995) attributed recent declines in splittail abundance and distribution to several factors, including a 6-year drought; water diversions from the estuary and an associated reduction in low-salinity, shallow-water habitat; and a weak stock–recruitment relationship for the species. Meng and Moyle (1995) expressed concern that these factors may prevent the species from returning to its former abundance. Similar factors were identified in Meng and Kanim (1994), the FWS proposal that the splittail be listed as threatened.

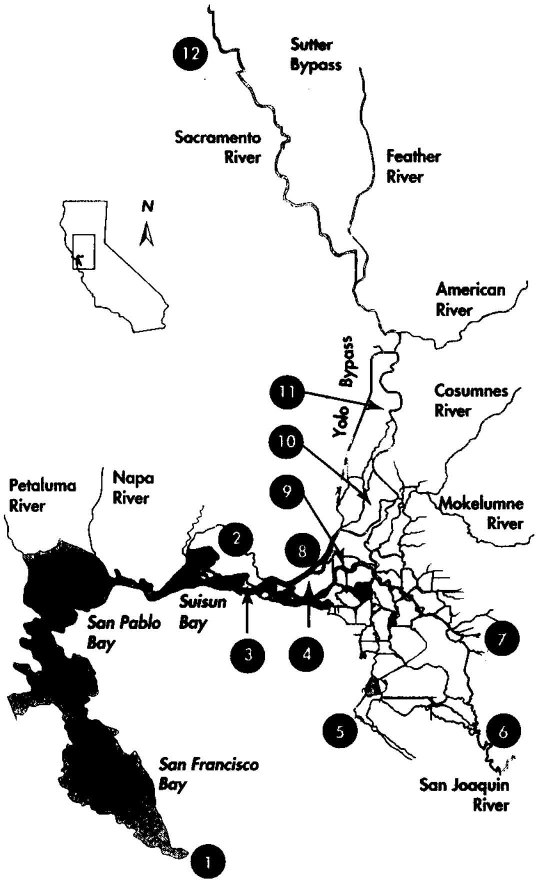

FIGURE 1.—Sacramento–San Joaquin estuary and tributaries in California. The major landmarks or sampling locations include (1) Coyote Creek; (2) Suisun Marsh; (3) Chipps Island; (4) Sherman Island; (5) Central Valley and State Water projects; (6) Mossdale; (7) Stockton; (8) Rio Vista; (9) Twitchell Island; (10) Grand Island; (11) Clarksburg; and (12) Colusa.

A 6-year drought in California ended in 1993, a moderately wet year, and 1995 was one of the wettest years in California's history. Thus, conditions were suitable for determining whether the reduced abundance and range reported by Meng and Moyle (1995) would prevent the species from responding reproductively to high river flows as normally expected from the results of Daniels and Moyle (1983). Recently, historical data have been found and new studies have been conducted that provide additional insights into the life history and distribution of the splittail. Data sets used by both Daniels and Moyle (1983) and Meng and Moyle (1995) were refined to separate the abundance and distribution of adults from those of juveniles. These data allow some determination of the relative importance of the factors affecting splittails as described by Meng and Moyle (1995).

Methods

Study Area

The Sacramento–San Joaquin estuary comprises San Francisco, San Pablo, and Suisun bays and an upstream delta (Figure 1). The delta is an extensive network of channels fed by inflow from the Sacramento and San Joaquin rivers and their tributaries. Flow patterns have been substantially altered by levees and dams, land reclamation activities, operation of upstream reservoirs, and diversions from the delta. Between 1940 and 1975, completion of several large dams further reduced spring flows and the frequency of floodplain inundation during the splittail spawning season. Exports from the delta include about 2,000 agricultural diversions and two large diversions in the south delta: the Central Valley and State Water projects. Diversions and associated entrainment result in losses of fish (Brown et al. 1996). During times of low inflow, high pumping rates in the south delta result in a net upstream (reverse) flow in the channels of the lower San Joaquin River. As a result of direct and indirect effects to the estuary, present bay–delta standards limit Central Valley and State Water Project diversions to 35% of delta inflow during February–June and 65% of inflow from July–January (Water Resources Control Board 1995). Additional major features of the upper reach of the system are the Sutter and Yolo bypasses, two extensive floodplain areas used for flood control, agriculture, and wildlife habitat (Figure 1). The bypasses serve as a controlled outlet for the Sacramento River, which historically flooded large areas of the adjacent valley during high water events in winter and spring. The bypasses frequently flood when Sacramento River flows surpass approximately 2,000 m^3/s. Much of the water diverted onto the bypasses drains back into the north delta near Rio Vista.

Abundance

We used length frequency analyses to separate age-0, age-1, and age-2+ (adult) in the catch obtained from eight long-term fish databases (Table 1) of the Interagency Ecological Program, a cooperative estuary study program involving nine public agencies. Details about each survey are described below. Catch-at-age data from each database were then used to calculate abundance indices for age-0 fish. Abundance indices for adults were calculated for all surveys except the fall midwater

TABLE 1.—Summary of eight Interagency Ecological Program databases. Adult abundance was not calculated for surveys with low catch or insufficient size data (NA).

Database	Period of record	Months for age-0 abundance[a]	Months for adult abundance[a]	Possible limitations[b]
Chipps Island survey	1977–1995	May–Jun	May–Jun	1, 5, 8
Suisun Marsh survey	1979–1995	Jun–Aug	Jan–Dec	1, 5, 7, 8
Fall midwater trawl	1967–1973, 1975–1978, 1980–1995	Sep–Dec	NA	2–5, 7, 8
Bay study otter trawl	1980–1995	May–Oct	Feb–Oct	2, 4, 5, 8
Bay study midwater trawl	1980–1993, 1995	May–Oct	Feb–Oct	2, 4, 5, 8
State water project salvage	1979–1995	May–Jul	Jan–Apr	1, 5, 6, 8
Central Valley project salvage	1979–1995	May–Jul	Jan–Apr	1, 5, 6, 8
Beach seine survey	1976–1984, 1992–1995	May–Jun	NA	4, 7

[a] Months were selected based on periods of peak catch for the survey.
[b] (1) Geographically localized.
(2) Relatively low catch of splittail.
(3) Data are insufficient to separate age-classes in years before 1975.
(4) Collects few adults.
(5) May not adequately sample shallow water habitat (<2 m) where splittails frequently occur.
(6) Abundance data may be affected by project operations and predation.
(7) Sampling was not performed in all of the specified months for each year.
(8) May not be representative of trends upstream of the estuary.

trawl and the beach seine survey, neither of which caught many adult fish. Each survey has strengths and weaknesses, therefore trends depicted by the majority of, or by all, indices most likely reflect estuarywide abundance trends.

Fall midwater trawl survey.—The California Department of Fish and Game (CDFG) fall midwater trawl survey (Stevens and Miller 1983) samples at 87 sites from San Pablo Bay to Rio Vista on the Sacramento River and to Stockton on the San Joaquin River (Figure 1). Each site is sampled monthly from September through December by using a 17-m-long midwater trawl with a 3.7-m^2 mouth. An annual abundance index is calculated as the sum of monthly indices for subareas of the system. To calculate monthly indices, catch per trawl is averaged for sites within each subarea, multiplied by a volumetric estimate for the subarea, then summed across all subareas.

Bay otter and midwater trawl surveys.—The CDFG Bay Study samples 35 sites from south San Francisco Bay to the western delta (Figure 1) by using both midwater and otter trawls (Armor and Herrgesell 1985). The midwater trawl is the same as the one used by the CDFG fall midwater trawl survey; the otter trawl is a 4.9-m-headrope bottom trawl. Annual abundance indices are calculated for each net as the average of monthly indices (Table 1). Monthly indices are calculated similarly to the fall midwater trawl, except that average catch per 10,000 m^3 and average catch per 10,000 m^2 were calculated for the midwater and otter trawls, respectively, rather than average catch per trawl. Although the bay study samples 52 sites at present, only the 35 sites sampled continuously since 1980 are used in calculating the index.

Suisun Marsh survey.—The University of California at Davis (UCD) Suisun Marsh (Figure 1) survey samples seven sloughs with an otter trawl similar to that of the CDFG bay survey (Moyle et al. 1986). A monthly abundance index is calculated as the sum of the mean catch per trawl for each of the seven sloughs in the marsh. Annual abundance indices are then calculated as the mean of the monthly values (Table 1).

Chipps Island survey.—The FWS Chipps Island survey samples a single location in the channel at Chipps Island (Figure 1) by using a midwater trawl towed at the surface. Ten 20-min tows are made each day, but the number of days sampled per week has varied. We used a core data set for May and June, the most consistently sampled months when splittails are present, to calculate mean catch per hour of trawling.

Central Valley and State Water Project salvages.—The Central Valley and State Water projects (Figure 1) operate louver facilities to direct fish away from the export pumps (Brown et al. 1996). Salvaged fish are counted year-round at 2-h intervals when the pumps are operating. Fish salvage data from these facilities are considered a valuable source of abundance data for the system (Stevens and Miller 1983). Splittail salvage is highest during adult spawning migrations and periods of peak juvenile abundance in the delta (Meng and Moyle 1995). We developed abundance indices based on the total salvage divided by the volume of water exported during the time periods when each life stage was most abundant at the facilities (Table 1).

Beach seine survey.—Data from the FWS beach seine survey were used to develop both abundance and distribution indices. A 15.5-m-long seine is used to sample the shoreline weekly at 21 core stations spread across five regions: (1) south delta (two sites south of Stockton), (2) west delta (four sites from Twitchell Island to Sherman Island), (3) central delta (five sites in lower Sacramento, Mokelumne, and San Joaquin rivers), (4) north delta (six sites from Clarksburg to the base of Grand Island), and (5) upper north delta (four sites from the American River to Clarksburg) (Figure 1). Some annual variability occurred in the number of hauls and sites for each region. The annual abundance indices were calculated as the mean catch per haul across all stations for May and June, respectively.

Trends in abundance were evaluated graphically and by comparing predrought (pre-1987) and postdrought abundance indices using a Mann–Whitney U-test. This predrought period was slightly different than the pre- and postdecline period used by Meng and Moyle (1995).

Distribution

We reviewed the available literature for the Sacramento and San Joaquin rivers, and selected tributaries to evaluate the distribution of splittail. Possible changes in range were evaluated by comparing occurrences within the past 5 years to earlier observations by Caywood (1974) and Rutter (1908). A confounding factor was that the collection season and life stage for most of the early observations were unknown, so the relative importance of each location to different age classes of splittail could not be established. For the purposes of comparing present and historical distributions, we assumed that collection of any life stage of splittail at a given location constituted evidence that the location was part of the range of the species. Note that this approach does not identify the relative importance of different areas for splittails and that historic and recent data should be considered as delimiting *minimum* ranges because sufficient sampling was not performed in either case to demonstrate that splittails were not present. With these limitations in mind, we evaluated the recent range of the splittail as the percent of available river used: river kilometer of farthest upstream capture divided by the river kilometer of the first impassable barrier.

Possible annual changes in splittail distribution were examined by using beach seine data from the five previously described regions and a sixth region upstream of the delta. The sixth subarea was based on five Sacramento River sampling sites located between Colusa and the confluence with the American River (Figure 1). This region was not used for the previously described beach seine abundance estimates because there were insufficient data from before 1981. Average catch per haul (May–June) for each of the six regions was calculated for three wet years (1982, 1993, and 1995) and three dry years (1981, 1992, and 1994). These years were selected because they included all of the six regions, had the fewest data gaps, and represented diverse hydrology.

Factors Affecting Abundance

To test for stock–recruitment relationships, we regressed $\log_{10}$- or $\log_{10}(x + 1)$-transformed age-0 abundance indices against similarly transformed adult indices. Only data from surveys which effectively captured adults (Table 1) were used in this analysis. The effect of water year type on age-0 and adult abundance was evaluated by comparing wet and dry year indices for each age-class by using a Mann–Whitney U-test. For the purposes of this analysis, years were considered dry or wet if the annual Sacramento Valley runoff index calculated by the CDWR was below or above 7.8, respectively (Water Resources Control Board 1995). The 7.8 threshold was approximately the median level of historical inflow from the four major tributaries of the Sacramento–San Joaquin Delta since 1906.

The effects of hydrology on abundance were also analyzed by using linear regression methods. The CDFG fall midwater trawl age-0 indices were independently regressed on delta outflow and floodplain inundation that occurred during the spawning season—these factors might have affected spawning success. Monthly outflow data were obtained from CDWR, and means were calculated for the February–May period. The total number of days the Yolo Bypass was flooded from the Sacramento River system (also from CDWR) was used as a surrogate for the inundation of all terrestrial habitat. Although inundation of this region does not necessarily represent flooding in the San Joaquin system, Yolo Bypass inundation was considered a reasonable surrogate because high flows typically occur simultaneously in the Sacramento and San Joaquin rivers. All data were log or $\log(x + 1)$ transformed.

We further examined the relative importance of the floodplain habitat to splittail spawning by sampling for larval and adult splittails in the bypasses and main channels of rivers. Adult sampling was conducted March–May 1995 in floodplain sites (Sutter Bypass) and the main channels of the Sacramento, Feather, Cosumnes, and Mokelumne rivers (Figure 1). A 5.8-m electrofishing boat (Smith Root, Inc., Washington) was used to produce a direct current of 100–5,000 V at 60 cycles/s. Effort was quantified as the number of seconds of current flow expended during each 20-min sample. Stunned fish were netted, identified, counted, and then measured to the nearest mm in fork length, FL.

Larval splittail sampling was conducted April 19–21, 1995, by using a 500-μm-mesh plankton net (Miller 1977) at seven sites: one each in the outflows of the Sutter and Yolo bypasses; three in the Sacramento River (1 km upstream of the confluence with Sutter Bypass, immediately upstream of the confluence with the American River, and 1 km upstream of the southwestern tip of Grand Island); one in the American River at river km 1; and one in the Feather River at river km 1 (Figure 1). At each location, sampling consisted of four 10-min oblique tows: two near shore and two towards the center of the channel. Tows alternated between nearshore and offshore paths located with landmarks and loran coordinates. All samples were rinsed into jars, preserved in 10% buffered formalin, and returned to the laboratory for identification. Catch per unit effort (CPUE) was calculated based on larval catch per thousand cubic meters filtered. Differences between stations were examined by using ANOVA (analysis of variance) techniques.

We examined splittail abundance across a salinity gradient by using UCD Suisun Marsh survey data. The analysis focused on the period of 1983–1992, which includes the "postdecline" period identified by Meng and Kanim (1994). Sampling effort was not equal at all salinities; therefore, data were grouped to provide equal confidence across salinity classes (Kimmerer 1992; Obrebski et al. 1992). The data were pooled for all months and stations for which salinity data were available, sorted according to increasing salinity (‰), then divided into intervals of nearly equal sample size (Table 2). Splittails were separated into age-classes by using size frequency analyses, then abundance data (catch/trawl) were log transformed before the

TABLE 2.—Salinity classes for analysis of Suisun Marsh data (1983–1992).

Salinity		Salinity	
Class	Range (‰)	Class	Range (‰)
1	0–0	10	4.21–4.8
2	0.01–0.4	11	4.81–5.2
3	0.41–0.9	12	5.21–5.9
4	0.91–1.6	13	5.91–6.5
5	1.61–2.1	14	6.51–7.5
6	2.11–2.6	15	7.51–8.5
7	2.61–3.2	16	8.51–9.8
8	3.21–3.8	17	9.81–11.0
9	3.81–4.2	18	11.01–21.5

means and 95% confidence intervals were calculated for each salinity class.

Fish entrained at the State Water Project diversion (Figure 1) were presumed to experience higher mortality as a result of screening, trucking, handling, and predation losses. We examined the issue of entrainment at the State Water Project by using three approaches. First, we regressed abundance indices of age-0 splittails from 1980–1995 fall midwater trawls against the total salvage for May–July for the same years. Most juveniles were collected at the State Water Project fish facilities during these months (Meng and Moyle 1995). All data were $\log(x + 1)$ transformed. Our rationale was that a significant inverse relationship would suggest that entrainment reduces abundance. The second approach was to regress log-transformed salvage against the residuals of the Yolo Bypass flooding–fall midwater trawl index relationship, discussed above. As we demonstrate later, inundation of the Yolo Bypass was a good surrogate for factors controlling abundance. The second salvage analysis was performed to determine whether State Water Project entrainment accounted for an additional significant portion of the variability in splittail abundance. Our third approach was based on a concern of Meng and Kanim (1994) that splittail mortality may be higher in drier years, during which a greater proportion of delta inflow is diverted by the state and federal water projects. Total May–July salvage for 1979–1995 (see above) was compared for wet and dry years by using a Mann–Whitney *U*-test. For comparison, similar analyses were performed for two other native species from the estuary, delta smelt *Hypomesus transpacificus,* a state- and federally listed species, and longfin smelt *Spirinchus thaleichthys.* The only difference in the analysis was that the salvage data were for March–August and April–June, which represent

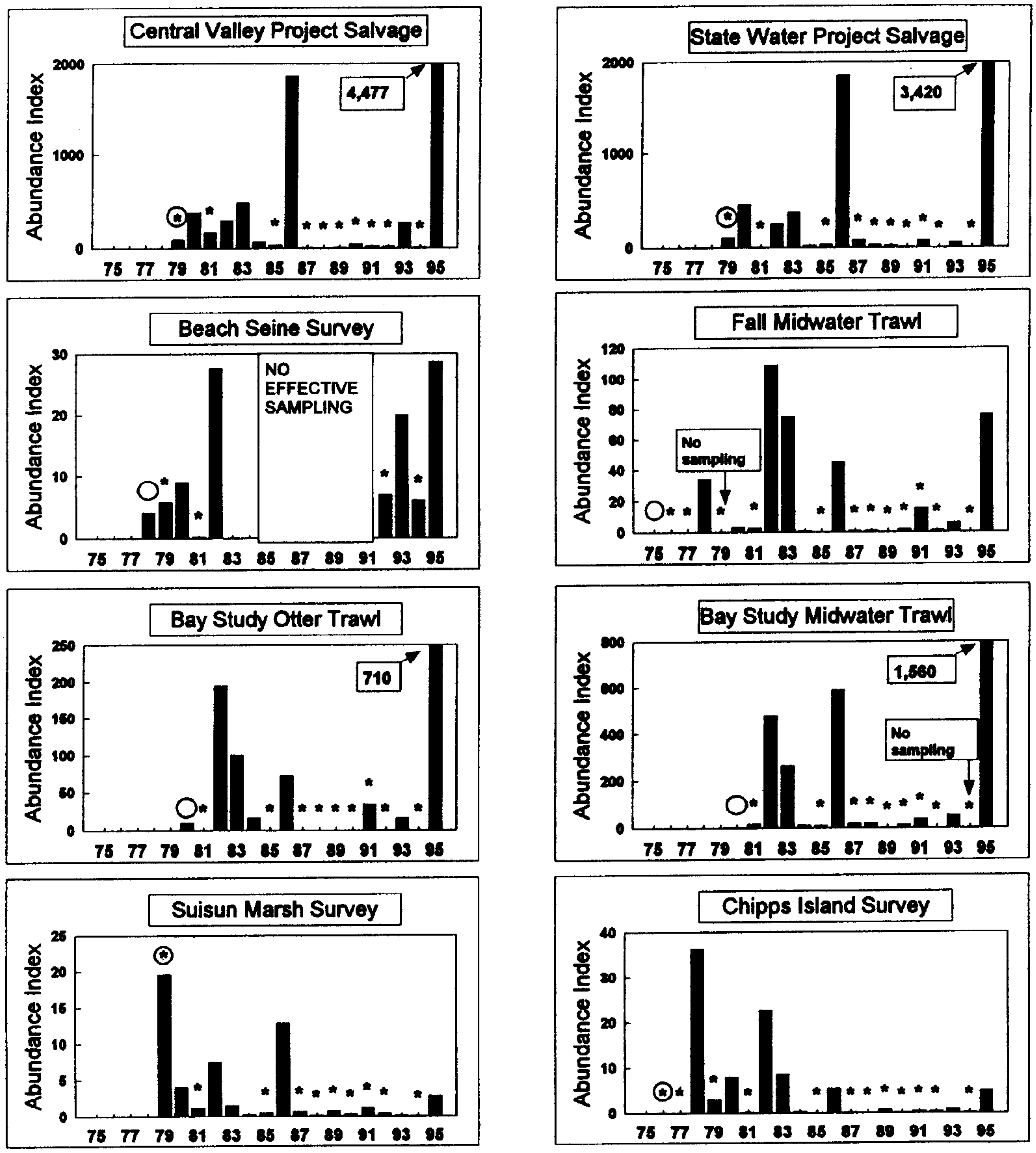

FIGURE 2.—Trends in age-0 splittail abundance for 1975–1995 as indexed by eight independent surveys. The first data point in each series is marked with a circle. Dry years are identified with asterisks above the data points—all other years were wet.

peak entrainment periods for delta smelt and longfin smelt, respectively.

Results

Abundance Trends

Age-0 abundance declined in the estuary during most dry years, particularly during the 6-year drought that began in 1987 (Figure 2). Recent low abundance levels are comparable to levels during 1976–1977, when the only other multiple-year drought in the series occurred. Although age-0 abundance appeared to have declined during the drought by at least 90% of the relatively high levels observed in 1986, the reduction was not permanent. The beach seine survey—the only survey that sampled potential rearing area upstream of the

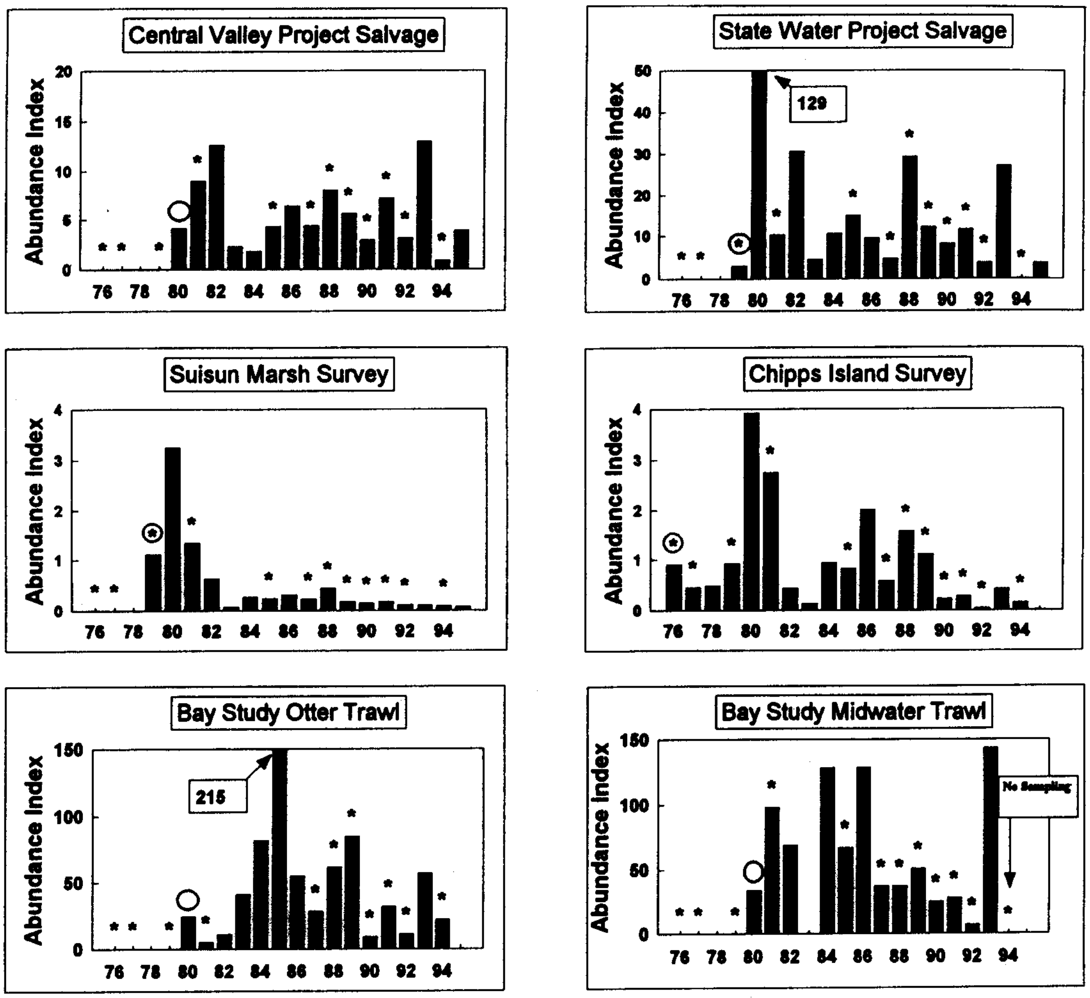

FIGURE 3.—Trends in adult splittail abundance for 1976–1995 as indexed by six independent surveys. The first data point in each series is marked with a circle. Dry years are identified with asterisks above the data points—all other years were wet.

estuary—showed two of the highest indices ever in 1993 and 1995, both wet years (Figure 2). In 1995, an increase in age-0 abundance occurred in all surveys. The 1995 abundance indices were the highest on record for the State Water Project and Central Valley Project salvages, the Bay study otter trawl, and the Bay study midwater trawl. The fall midwater trawl index in 1995 was the second highest on record. Although the 1995 response was not as large for Suisun Marsh and Chipps Island, a clear increase in abundance occurred for each, relative to the 1987–1992 drought. Similar strong year-classes are apparent for most of the surveys in the three other extreme wet years: 1982, 1983, and 1986.

Trends in adult splittail abundance are less clear (Figure 3). Unlike the age-0 results, no consistent decline in adult abundance occurred after the onset of the drought in 1987. Significant differences were detected in pre-1987 adult abundance relative to 1987 and later in the Suisun Marsh and Chipps Island surveys ($P < 0.05$, Mann–Whitney U-test) but not for the State Water Project and Central Valley Project salvages or either Bay study index ($P > 0.05$, Mann–Whitney U-test). An adult decline seems to have occurred between 1988 or 1989 and 1992 in most surveys, but there were several exceptions (e.g., Central Valley Project salvage, Bay study otter trawl). Four of the six adult indices exhibited large increases in 1993. The Sui-

TABLE 3.—Locations of historical and recent collections of splittails. River kilometer is the distance from the mouth of the river; "present" indicates specific location not given; NA is not applicable.

River system	Location (river km) of splittail collection: Rutter (1908)	Caywood (1974)	Recent	Distance (river km) to first dam[a]
Sacramento	483	387	331[b]	387
Feather	109	Present	94[c]	109
American	49	37	19[d]	37
San Joaquin	Present[e]	Present	201[f]	295
Mokelumne	NA	25	63[g]	63
Napa	NA	21	10[f]	NA
Petaluma	NA	25	8[f]	16

[a] First dams are Red Bluff (Sacramento), Oroville (Feather), Nimbus (American), Sack (San Joaquin), and Woodbridge (Mokelumne); Napa River is not dammed; first dam was removed from the Petaluma River in 1994.

[b] California Department of Fish and Game (unpublished data, 1995).

[c] ENTRIX, Inc. (unpublished data, 1993).

[d] Snider and McEwan (1993).

[e] Rutter (1908) was cited by Meng and Kanim (1994) as the source of an observation of splittail at Fort Miller (river km 435) near the current site of Friant Dam on the San Joaquin River. However, Rutter's (1908) distribution was based on Girard (1854), who reported two *Pogonichthys* species, "*P. symmetricus*" and "*P. inaequilobus*" in the San Joaquin system. "*Pogonichthys symmetricus*," collected from Fort Miler, was not likely to have been a splittail *P. macrolepidotus* because Girard (1854) reported the "lobes of the caudal fin are symmetrical." Girard's (1854) description of "*P. inaequilobus*" had an asymmetrical tail and other features similar to those of the splittail, but the collection location is listed as "San Joaquin River" without reference to a specific site.

[f] Interagency Ecological Program (unpublished data, 1995).

[g] D. A. Vogel (Natural Resource Scientists, Inc., unpublished data, 1995).

sun Marsh survey did not show an increase, and the Chipps Island survey increase was slight.

Splittail Distribution

The historical range of the splittail included the low-gradient portions of all major tributaries to the Sacramento and San Joaquin rivers as well as the Napa and Petaluma rivers and Coyote Creek (Figure 1), which are tributaries to San Francisco Bay (Rutter 1908; Leidy 1984; Saiki 1984; Moyle et al. 1994). Comparisons of historic and more recent data show that splittails still occur in most drainages within their historic range (Table 3), but data are insufficient to determine if they use all the habitat available below the first dam on each river. Splittails were also present in the Petaluma River in 1992 and at the end of the drought (CDFG, unpublished data; FWS, unpublished data) and in the Napa River in 1989 and 1995 (CDFG, unpublished data), but they have not been collected from Coyote Creek since the early 1900s (Aceituno et al. 1976; Leidy 1984).

Given the locations of recent collections (Table 3), the present splittail range includes at least 78% of the river kilometers available below the first dams on the Sacramento and San Joaquin rivers. Similarly, they were found in 77% of the available habitat in the Feather and American rivers.

Results from the FWS beach seine survey indicated substantial annual variability in age-0 splittail distribution, yet no trend was apparent between or within wet and dry years (Figure 4). No single subarea dominated the distribution of the species; however, except for 1982, catches were highest in the north delta and upstream into the Sacramento River.

Factors Affecting Abundance

No significant stock–recruitment relationships were apparent with data from the Chipps Island survey, the State Water Project and Central Valley Project salvages, the Bay study midwater trawl, and the Bay study otter trawl ($P > 0.05$). There was a weak statistical relationship (Figure 5) for the Suisun Marsh survey ($P < 0.05$).

Dry years had significantly lower age-0 abundance than wet years for four of eight Interagency Ecological Program surveys (Figure 2): Central Valley Project salvage, Bay study otter trawl, fall midwater trawl, and Chipps Island survey ($P < 0.05$, Mann–Whitney U-test). These results are consistent with regression analyses, which showed significant correlations ($P < 0.01$) between age-0 splittail abundance from the fall midwater trawl and flooding of Yolo Bypass (Figure 6) and between age-0 abundance and delta outflow (Figure 7).

Boat electrofishing surveys collected 22 adult splittails from Sutter Bypass, but none were found in the Cosumnes, Mokelumne, or Feather rivers. Of the seven larval sampling stations, splittail larvae were collected in Sutter and Yolo bypasses and at two sites in the Sacramento River channels. Based on larval sampling, location had a significant effect on CPUE ($F = 6.325$, df = 6, $P < 0.001$). Larval densities at locations where the bypasses drained back into the rivers were higher than at all or most other locations: CPUE below Yolo Bypass was significantly higher than all other locations ($P < 0.05$) except Sutter Bypass. There were no other significant differences.

Age-0 and adult splittails were caught within a wide range of salinity-classes, from freshwater to higher than 11‰ (Figure 8). Both age-classes were

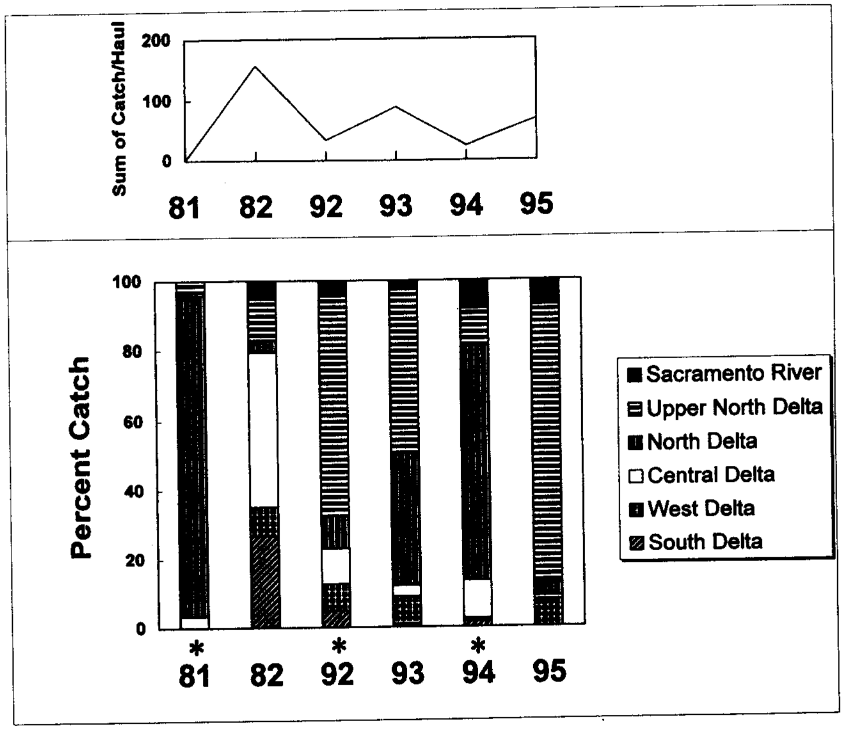

FIGURE 4.—Sum of average number of age-0 splittails caught per haul in beach seine surveys from six regions of the Sacramento–San Joaquin River system (upper graph) and percent of catch located in each region (lower graph) by year (1981, 1982, and 1992–1995). Dry years are identified with an asterisk (*) above the year—all other years were wet.

relatively abundant from 0.01‰ to 11.0‰ with no single distinct peak.

We found a significant positive relationship ($P < 0.01$) between salvage of age-0 splittails and the fall midwater trawl index (Figure 9), but no significant relationship ($r^2 = 0.005$, $P > 0.05$) occurred between salvage and the residuals from the previously described Yolo Bypass flooding–fall midwater trawl index relationship (i.e., Figure 6).

Splittail salvage was generally highest in wet years, whereas longfin smelt salvage was highest in dry years (Figure 10). Delta smelt salvage was more variable but was frequently higher in dry years. Differences were significant between wet and dry years for splittails and longfin smelt ($P < 0.005$, Mann–Whitney U-test) and close to significant for delta smelt ($P < 0.10$, Mann–Whitney U-test).

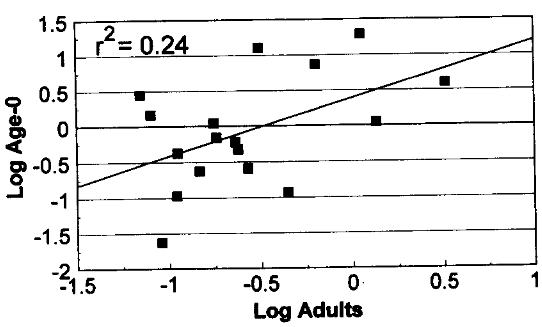

FIGURE 5.—Suisun Marsh survey stock–recruitment relationship ($\log_{10}$) for adult versus age-0 splittails.

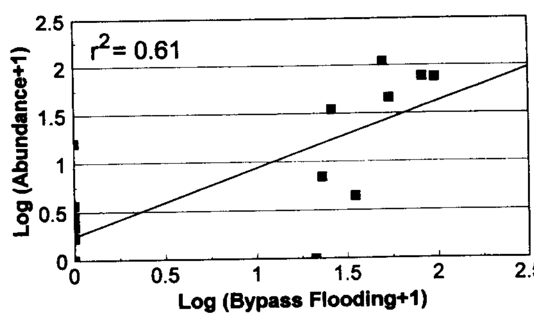

FIGURE 6.—Relationship ($\log_{10}$) between age-0 fall midwater trawl abundance and the number of days that Yolo Bypass was flooded during February–May.

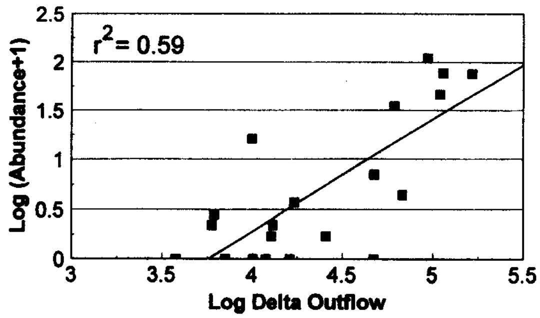

FIGURE 7.—Relationship ($\log_{10}$) between age-0 fall midwater trawl abundance and average delta outflow during February–May.

Discussion

In 1995, an extreme wet year, splittail recruitment indices were comparable or exceeded previous wet years in the 1980s despite drought conditions in 1987–1992 and 1994, representing 7 out of 8 preceding years. Any reduction in adult abundance from successive years of low age-0 abundance was not sufficient to impair the ability to rapidly respond to favorable environmental conditions. Seasonal distribution of the species appeared wider and more plastic than assumed. Although splittails have relatively broad environmental tolerances, high salinity and temperature may limit their distribution.

Floodplain inundation appears to be a primary factor required for strong year-classes. A strong

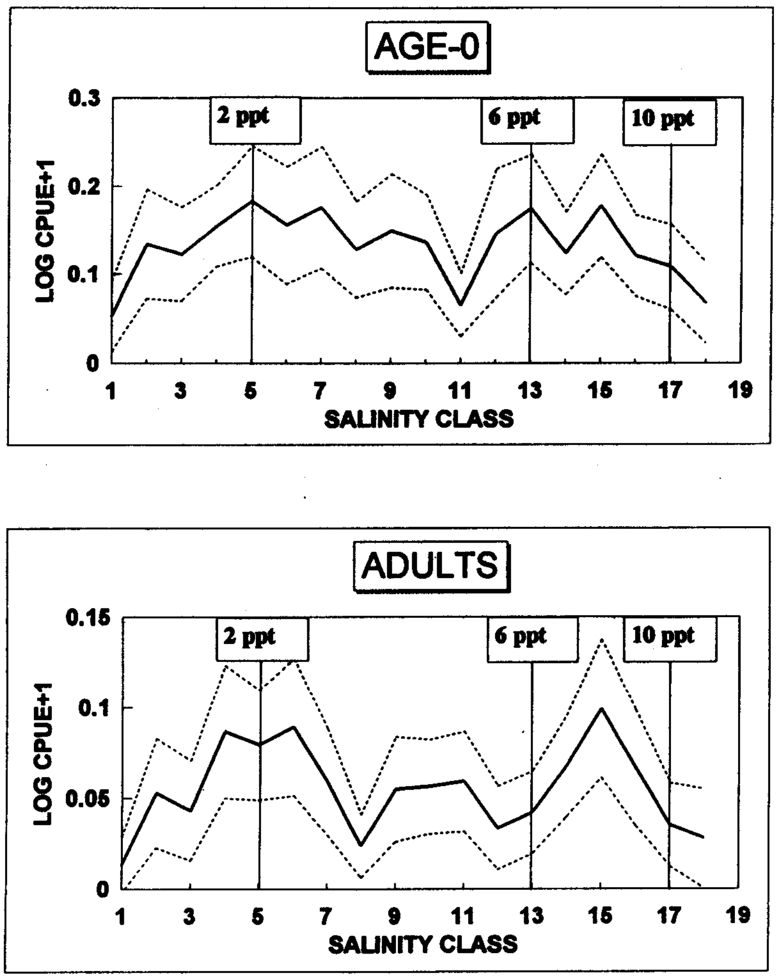

FIGURE 8.—Mean (solid line) and 95% confidence intervals (dashed lines) for age-0 (top) and adult (bottom) splittail abundance by salinity class (Table 2) based on 1983–1992 Suisun Marsh data. The approximate positions of different salinity levels (ppt = ‰) are shown. Log is $\log_{10}$.

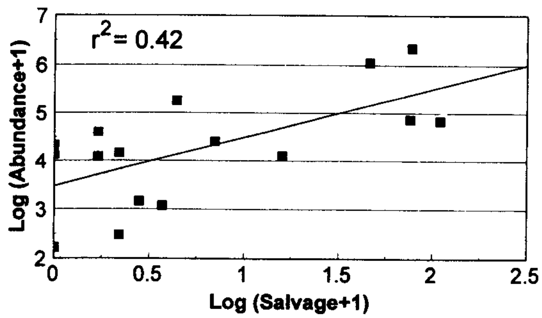

FIGURE 9.—Relationship ($\log_{10}$) between State Water Project salvage of splittails and age-0 fall midwater trawl abundance index for 1979–1995.

association exists between age-0 abundance and the duration of inundation of the Yolo Bypass. Statistical relationships between flow and splittail abundance have previously been reported by Daniels and Moyle (1983) and by Meng and Moyle (1995), but we believe that floodplain inundation is more closely linked to factors that improve spawning success in wet years. Flooded terrestrial habitat can provide abundant food for prespawning adults, and flooded vegetation provides spawning substrates and larval rearing habitat (Caywood 1974). Use of ephemeral flooded areas may reduce loss of eggs and larvae to aquatic predators. Access to terrestrial invertebrate food sources may be nutritionally important for prespawning fish (Caywood 1974) because other key foods are at annual lows (Herbold 1987). Our 1995 adult and larval data provide further support for the importance of floodplain habitat, specifically the Yolo and Sutter bypasses. Densities of larvae collected from the bypass plumes were exceptionally high when compared with 1988–1995 plankton surveys conducted in the main river channels (CDFG, unpublished data).

Splittails use inundated floodplain as spawning habitat. Given the present levee and bypass system, a critical threshold level of flooding is probably required to produce strong year-classes. The major year-classes occurred in extreme wet years, such as 1982, 1983, 1986, and 1995, when flooding was most extensive and fairly continuous. Moderately wet years such as 1978, 1980, and 1993 had shorter flood events of about 1 month or less and did not produce high indices for most surveys. Consistent with this trend, preliminary indices for 1996, another moderate outflow year, are much lower than 1995 indices (CDWR, unpublished data). Although we used a linear fit on log-transformed data to describe the relationship between bypass flooding and abundance, the pattern of data suggests a step function (Figure 6). Bypass inundation for a month or more appears to be needed for the development of a strong year-class. This period must incorporate adult immigration and spawning, egg incubation, and larval development of an air bladder for successful outmigration. Initial laboratory studies suggested that at least 10–14 d are required for fertilized splittail eggs to develop into free swimming larvae (H. Bailey, University of California at Davis, unpublished data).

The abundance of young splittails in the estuary was significantly lower in low outflow years, yet adult abundance did not show an immediate effect from recent drought conditions. Instead, adult indices suggested at least a modest decline in 1989–1992, particularly for Chipps Island and Suisun Marsh, which represent the more saline downstream portion of the range of the splittail. Although somewhat-reduced adult abundance from 1989 onward is attributable to reduced age-0 abundance with the initiation of the drought 2 years earlier, the decline was slight compared with age-0 abundance. The most apparent anomaly was the abrupt increase in adult abundance indices in 1993, following little or no apparent age-0 production during the previous 6 years. Several possible explanations exist for the lack of a distinct adult decline. First, the adult age-group was composed of three or more year-classes (age-2 to age-5+), providing a buffer against a few years of poor recruitment. Second, most of the adult indices during this period were based on the capture of relatively small numbers of fish and, therefore, might have lacked the sensitivity to describe a downward trend. Finally, age-0 production may not be as detectable during dry years as wet years because (1) larvae and juveniles in the rivers may not be swept to the delta, where most sampling occurs, and (2) most juveniles in the delta remain close to shore, whereas most trawling was conducted midchannel. In any case, the high 1993 adult indices following a period of drought longer than the typical splittail life span suggests that at least limited recruitment occurs in all types of water years.

Even if there was a substantial decline in the number of adults as a result of the drought, the exceptionally strong year-class in 1995 demonstrated that the population retained its high reproductive capacity. Splittails have a relatively high fecundity (Caywood 1974; Daniels and Moyle 1983), which helps the species respond rapidly to improvements in environmental conditions and to

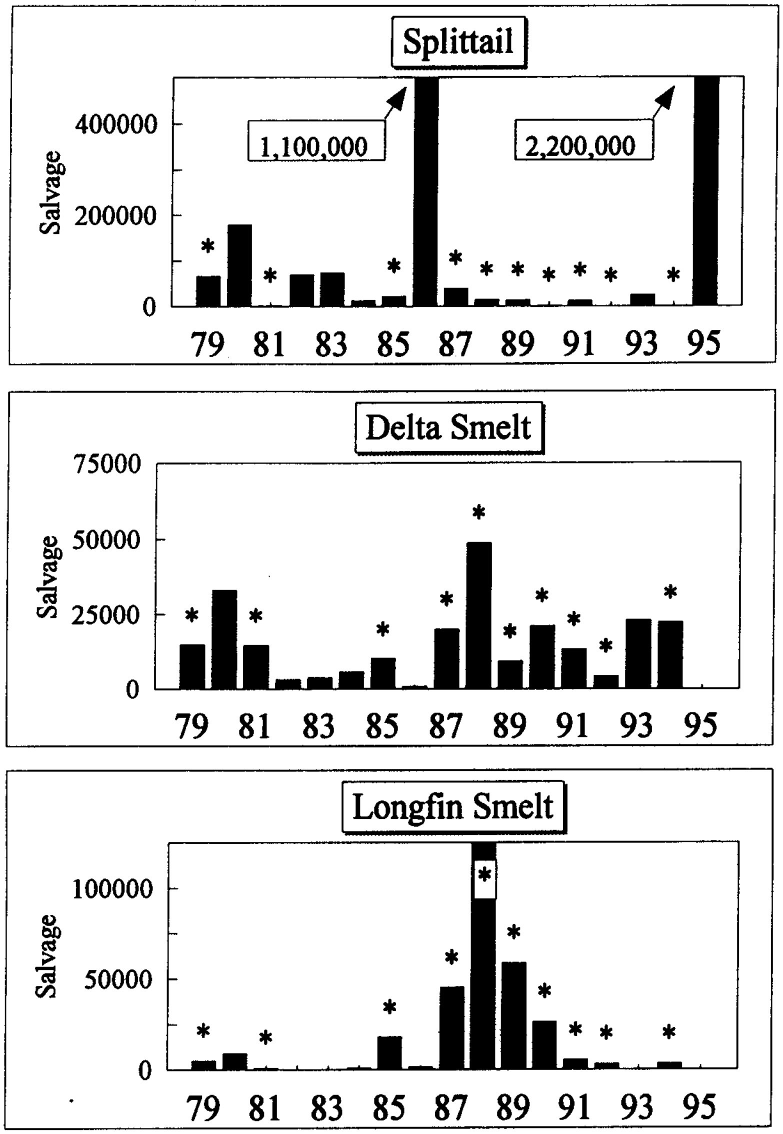

FIGURE 10.—State Water Project salvage for age-0 splittails, delta smelt, and longfin smelt during the months when most individuals of each species were entrained for 1979–1995. Dry years are identified by an asterisk above the bar.

survive with a low-to-modest adult stock. The absence of a significant stock–recruitment relationship reflects the overriding effect of year-to-year habitat conditions on production of young. A possible anomaly is the Suisun Marsh region, where weak stock–recruitment relationships were identified by the present study and by Meng and Moyle (1995).

The geographic range reported in this paper is wider than that described by Meng and Moyle (1995), Lee et al. (1980), or Moyle et al. (1994). Recent sampling (1993–1995) clearly showed that the distribution was not restricted to the lower Sacramento and San Joaquin rivers and estuary, as described by the above authors, but that it extended to several upstream tributaries including the Mokelumne, Feather, and American rivers, as well as downstream areas, such as the Napa and Petaluma rivers. Part of the discrepancy might have resulted from the migratory patterns of splittails. The broadest range occurs from late fall to spring when adults ascend the rivers to spawn and before age-

0 fish have emigrated to the estuary. Some do not emigrate from the rivers until they reach about 1 year of age (CDFG, unpublished data). Gill-net surveys in 1994 suggested that adult splittails appeared to be confined to the intertidal fresh and brackish water in summer (Meng and Moyle 1995). Thus, season of sampling influenced the observed distribution. There was some indication that the distribution of splittails historically shifted back to the estuary after spawning. Walford's (1931) discussion of commercial and game fishes of California reported that catches of splittail occurred in the Sacramento and San Joaquin rivers "during late fall, winter, and spring months," suggesting that the adults might have moved downstream to the estuary in summer. Similarly, 1928 commercial catch statistics for California identify the following monthly catch (kg) in Sacramento and San Joaquin counties for January–December, respectively: 1,112, 1,369, 795, 20, 0, 0, 0, 0, 0, 0, 844, 517 (Bureau of Commercial Fisheries 1930). Again, the lack of reported catch in May–October suggests that splittail distribution shifted after the spawning season.

Additional differences between the range reported by the present study and that described by other recent authors might have resulted from interannual differences in spawner distribution or age-0 splittail production (Figure 5). For example, poor success in capturing splittails from the San Joaquin River during the 1980s led researchers to conclude that these fish were rare and no longer resident in the system (Saiki 1984; Brown and Moyle 1993). This was consistent with FWS beach seine sampling, which caught only one young splittail in San Joaquin River stations during 1988–1992. Yet the total catch of more than 118,000 age-0 splittails for daily Kodiak trawling in the San Joaquin River from May 9–June 30, 1995 (Interagency Ecological Program, unpublished data), indicates that the river provided suitable habitat under some conditions. Similarly, beach seine sampling in the San Joaquin River collected substantial numbers of splittails in 1986, a wet year, but few during 1987–1989 drought year sampling (T. Ford, Turlock Irrigation District, unpublished data).

Although there is little question that a historical reduction has occurred in the range of the splittail, we concur with Caywood (1974) that "the present distribution of splittail appears only moderately reduced." The overall distribution of splittails in the system might have been reduced somewhat during the drought, particularly in the San Joaquin River and Suisun Marsh, but this reduction was not permanent. The recent upstream limit of the splittail range was fairly close to the first major obstruction on a number of tributaries, indicating that migration barriers limit distribution. An additional factor influencing splittail range was the presence of levees below the dams, which limited access to much of the historical foraging and spawning habitat on the floodplain. These changes occurred before the 1970s and could not be responsible for any recent changes in range limits. Historical and recent water development in the system might have affected splittail range and abundance by storing water behind upstream dams, reducing the frequency and amplitude of spring flow events (Williams 1989; Meng and Moyle 1995). These flows might otherwise have provided splittail foraging and spawning habitat on the remaining floodplain. This was particularly true during the recent drought.

Our analyses suggested that entrainment at south delta water export pumps did not have an important effect on the splittail population. Contrary to the hypothesis that entrainment in the south delta pumps could result in negative population level effects, there was a significant *positive* relationship between salvage and the fall midwater trawl abundance (Figure 9). Salvage also did not explain a significant additional portion of the variability in the Yolo Bypass–fall midwater trawl relationship (Figure 6), which we believe is a good surrogate for factors controlling year-class strength. The incidence of age-0 splittail entrainment in the export pumps increased during wet years (Figure 10) when abundance was also high (Figures 6, 7). Thus, entrainment effects were greatest when the splittail population was better able to accept losses. This does not mean, however, that entrainment never affects the species. In 1982, a wet year, the distribution of age-0 splittail appeared to shift toward the south delta export pumps (Figure 4). If such a shift occurred in a dry year, there could be substantial entrainment effects to a year-class. But because the species is long-lived, risks to the population would be reduced.

Splittails are apparently adapted to a broad range of environmental conditions. Distribution data indicated that age-0 fish and adults occurred within a wide range of salinities, with no single distinct peak (Figure 8). In Suisun Marsh, both age-classes of splittail were abundant in all salinities up to at least 10‰. A broad salinity tolerance is supported by physiological studies: Young and Cech (1996) found that age-0, age-1, and immature age-2 split-

TABLE 4.—Comparison of the attributes and factors affecting abundance of three native fishes of the Sacramento–San Joaquin estuary.

Factor	Splittail	Delta smelt	Longfin smelt
Typical maximum life span	5 years[a]	1 year[b]	2 years[c]
Fecundity	High[d]	Low[e]	Moderate–high[f]
Stock–recruitment relationship	Little or none[g]	None[h]	Weak at best[i]
Typical diet	Terrestrial and aquatic invertebrates[a]	Zooplankton[b]	Mysids and crustaceans[c]
Salinity distribution	Broad (0–10‰)[g]	Distinct peak (0.2–1.0‰)[h]	Broad (0–35‰)[c]
Response to wet years	Higher age-0 abundance[a,g]	Variable[b]	Higher age-0 abundance[j]
Peak entrainment at diversions	Wet years[g]	Dry years[g]	Dry years[g]

[a] Daniels and Moyle (1983); Caywood (1974).
[b] Moyle et al. (1992).
[c] Dryfoos (1965).
[d] 20,000–200,000+ eggs/female (Daniels and Moyle 1983).
[e] 1,200–2,600 eggs/female (Moyle et al. 1992).
[f] Greater than 5,000–25,000 eggs/female (Moyle 1976).
[g] Present study.
[h] CDWR and USBR (1994).
[i] California Department of Fish and Game, unpublished data.
[j] Stevens and Miller (1983).

tails had 6-h mean critical salinity maxima of 20, 24, and 24‰ at 17°C for the age-classes listed. Additional tests showed that splittails are eurythermal, tolerant of low levels of dissolved oxygen and strong water currents. Nonetheless, these physical factors probably have an important effect on distribution. During the 6-year drought, water temperatures in the San Joaquin River were some of the highest recorded (CDWR 1994), perhaps explaining why few splittails were caught there during that period. For example, for one third of the days in May 1992, maximum water temperatures at Mossdale (Figure 1) were greater than 24°C, the calculated upper limit of safe temperatures for adults acclimated at 17°C (Young and Cech 1996). Suboptimal salinities might have shifted the distribution of splittails upstream during the drought, leading to low abundance in Suisun Marsh (Figure 2; Meng and Moyle 1995). During 1985–1992, the average January salinities measured in Suisun Marsh channels were 12.6‰ (Meng and Moyle 1995), a level at which we saw evidence of reduced abundance (Figure 8). However, it was unclear why adult abundance did not increase in this region after high outflow in 1993 and 1995. An alternative explanation is that the distribution of young splittails showed major annual changes (Figure 4), so perhaps high Suisun Marsh age-0 abundance in the late 1970s and subsequent high adult abundance in the early 1980s was related to a local spawning event or exceptional immigration into the region.

The life history strategy and population status of splittails have been compared with two other native species in the system, delta smelt and longfin smelt (Meng and Moyle 1995). These authors concluded that all three species (1) experienced recent reductions in abundance and range, (2) have similar habitat preferences, and (3) had a similar response to increases in water diversions. Although the three species share some similarities, major differences exist which have direct implications for the resilience of each population (Table 4).

Compared with the two osmerids, splittails have a longer life span (i.e., more spawning opportunities) and a higher fecundity, and they are more opportunistic feeders (Table 4). None of the species show a strong stock–recruitment relationship. The salinity tolerance of splittails is between that of delta smelt and longfin smelt. The spawning migrations and spawning areas of splittails extend further upstream than either smelt species; neither osmerid migrates much beyond tidal influence to spawn. Moreover, splittails may remain in freshwater longer than either osmerid, using upstream habitat for foraging during winter (Caywood 1974). Longfin smelt inhabit the entire San Francisco Bay (Figure 1) and nearshore coastal areas during different portions of their life history. Although delta smelt disperse upstream during their spawning period, during much of the year the species shows a distinct narrow abundance peak at approximately 0.2–1.0‰ (CDWR and USBR 1994). Both splittails and longfin smelt show statistically significant increases in abundance with outflow, whereas delta smelt have a highly variable response that is not statistically significant (Moyle et al. 1992).

Our results indicate that the main factor affecting splittail entrainment at the State Water Project is year-class strength, typically greatest in wet years when the population is in a better position to accept some losses. By contrast, the osmerids show higher entrainment in dry years (Figure 10), when their abundance levels are already low as a result of less suitable environmental conditions. The probable cause is that in dry years the distributions of the smelts shift upstream, closer to the diversions, where entrainment risks are higher.

The net result of these differences is that splittails appear to be the most resilient of the three species. Since splittails are iteroparous and can live to age-5 or more, their spawning stock is less variable than the semelparous, short-lived longfin smelt and delta smelt. The production of young for all three species is controlled more by environmental conditions than stock size, and each appears to produce some young in every year. However, splittails are able to use a wider variety of food sources and are less sensitive to water project diversion.

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