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Splittail "Delisting": A Review of Recent Population Trends and Restoration Activities

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ABSTRACT Splittail *Pogonichthys macrolepidotus*, a minnow native to the San Francisco Estuary, was originally listed by the U.S. Fish and Wildlife Service as threatened in 1999. The listing was remanded in 2003 based on recent evidence about its status and efforts to restore the species. Although young-of-year production declined during a 6-year drought prior to the listing, the return of wet conditions in the late 1990s resulted in record indices of abundance. Much of the minnow's historical off-channel habitat was lost by the early 1900s, but surveys suggest that the current range of splittail has stabilized. Year-class strength is directly related to the duration of inundation of remaining floodplain. Adults migrate upstream in winter or early spring to spawn on seasonally inundated vegetation. Their offspring rear in the food-rich floodplain habitat before emigrating with receding floodwaters. Based on the recognition that the species is perhaps one of the most floodplain-dependent fishes in the estuary, floodplain restoration became a central component of a major agency/stakeholder effort to fix long-standing problems in the region. Floodplain restoration is likely to substantially improve the long-term status of splittail, although extreme alterations in the food web from alien species may prevent the minnow from returning to historical levels.

In September 2003, the U.S. Fish and Wildlife Service (USFWS) removed splittail *Pogonichthys macrolepidotus* (Figure 1) from the list of threatened species under the Endangered Species Act (ESA; USFWS 2003a). This unprecedented step represented the first extant fish ever to be removed from the federal list of threatened and endangered species. Splittail had been the subject of intense scrutiny and research prior to and following its initial listing in February 1999 (USFWS 1999). The attention to splittail was not limited to the federal review, as the California Department of Fish and Game (CDFG) listed the fish as a species of special concern in 1989, a status that has continued to the present.

Following the extinction of Clear Lake splittail *P. ciscoides* by the 1970s, splittail presently represents the only surviving member of its genus (Moyle 2002; Moyle et al. 2004). The distinguishing feature of splittail compared to other minnows is the enlarged dorsal lobe of the caudal fin. Like most California cyprinids, the splittail is a relatively large member of its family, sometimes exceeding 40 cm standard length. Adults are characterized by an elongated body, a distinct nuchal hump (on the back of the head), and a small, blunt head. Splittail adults usually also have barbels at the corners of the slightly subterminal mouth, an unusual feature among North American cyprinids. Splittail are typically dull, silvery-gold on the sides and olive-gray dorsally, but during spawning season, the pectoral, pelvic, and caudal fins have an orange-red tinge. Males also develop small white nuptial tubercles on the head, with additional tubercles on the base of the fins.

This paper reviews some of the recent data and activities that contributed to the 2003 USFWS decision: (1) trends in abundance and distribution, (2) factors that affect the population, and (3) restoration efforts that could benefit splittail. Over-

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all, our understanding of splittail biology has increased dramatically over the past decade, leading to the development of promising restoration efforts to help enhance production.

Figure 1. Adult splittail *Pogonichthys macrolepidotus.*

Study Area

Splittail occur only in the San Francisco Estuary and its tributaries (Figure 2). The estuary includes extensive downstream bays (Suisun, San Pablo, and San Francisco) and a delta, a network of tidal channels that receive inflow from the Sacramento and San Joaquin rivers. San Pablo Bay, the lower limit of the present range of splittail, has small tributaries, including Petaluma and Napa rivers, each of which has substantial marsh habitat. The most extensive marshes of the region occur in the 34,000-ha Suisun Marsh, which includes a network of vegetation-lined tidal sloughs (Matern et al. 2002). Most of the major delta channels are deep (frequently > 5 m), tidally influenced waterways bordered by steep, rock-covered banks with a narrow riparian corridor and minimal emergent vegetation (Sommer et al. 2001a, 2001b). Two key features of the delta are the State Water Project (SWP) and the Central Valley Project (CVP), large water diversions that presently divert from 35% to 65% of delta inflow, depending on the time of year (Brown et al. 1996; Sommer et al. 1997). The primary floodplain of the delta is the Yolo Bypass, a 61-km long, partially leveed basin that floods in winter and spring in about 60% of years (Sommer et al. 2001a). Land use in the Yolo Bypass was predominantly agricultural during the past several decades, but recent restoration and land acquisition have reallocated the majority of the area to wildlife habitat. The only other substantial area of floodplain within the

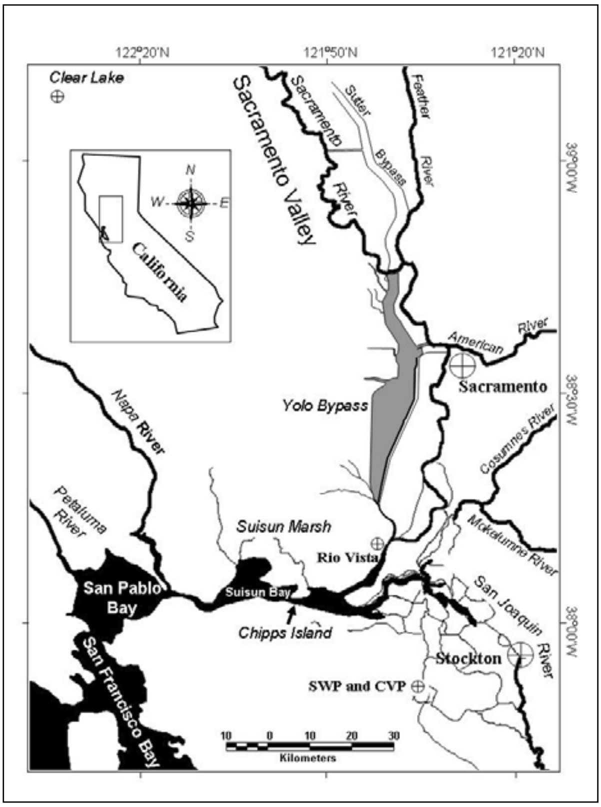

Figure 2. The range of splittail, including the San Francisco Estuary and its tributaries. The San Francisco Estuary includes the region from San Francisco Bay upstream to Sacramento and a location 56 km upstream of Stockton. The delta represents the portion of the estuary upstream of the confluence of the Sacramento and San Joaquin rivers. The confluence is located at Chipps Island, which represents river kilometer 0 for both rivers.

delta is the lower Cosumnes River, which has a suite of habitats, including freshwater wetlands, riparian forests, grasslands, and tidal sloughs (Crain et al. 2004). Other tributaries to the delta include the Sacramento, Feather, American, Mokelumne, and San Joaquin rivers. These rivers are extensively channelized, although several have setback levees on their lower reaches that provide some floodplain habitat (Mount 1995). For these upstream areas, the largest contiguous area of floodplain is the Sutter Bypass, a 7,300-ha seasonal flood basin immediately upstream of Yolo Bypass (Sommer et al. 2001a).

The entire range of splittail has been substantially altered by a variety of anthropogenic factors, including levees, dams, land reclamation activities, water diversions, and contaminants (Atwater et al. 1979). In addition to changes in physical habitat, the biota of the estuary has been altered by a large number of species introductions (Cohen and Carlton 1998). Native fishes have shown population decreases due to multiple factors (Bennett and Moyle 1996), resulting in the listing of Central Valley steelhead *Oncorhynchus mykiss*, two races of Chinook salmon *O. tshawytscha*, delta smelt *Hypomesus transpacificus*, and, formerly, splittail.

Life History of Splittail

Splittail may live for 8–10 years but do not typically live longer than 5 years (Moyle 2002; Moyle et al. 2004). The largest and oldest fish are females, which are highly fecund, laying up to 200,000 eggs per fish (Feyrer and Baxter 1998). Fish usually reach sexual maturity by the end of their second year (Daniels and Moyle 1983). Spawning success is highly variable among years but is correlated with freshwater outflow and the availability of shallow-water habitat with submerged vegetation (Daniels and Moyle 1983; Sommer et al. 1997). In typical years, adults begin a gradual upstream migration towards spawning areas sometime between late November and late January, but substantial migration can also occur in spring. Upstream movement appears to coincide with flow pulses that inundate floodplains and riparian areas in which splittail forage and spawn (Harrell and Sommer 2003; Moyle et al. 2004). Peak spawning occurs from the months of March through April, although records of spawning exist for late January to early July (Wang 1986; Moyle 2002). Splittail are thought to lay their adhesive eggs on submerged vegetation in flooded areas in the lower reaches of rivers and sloughs (Caywood 1974; Moyle 2002). Laboratory studies indicate that developing embryos hatch in 3–5 d at 18.5°C (Moyle et al. 2004). Splittail are 7–8 mm total length when the yolk is absorbed and feeding begins, typically on small rotifers, at 5–7 d posthatch. Pond studies indicate that the early life stages of splittail use a variety of different habitats but are strongly associated with shallow water areas (Sommer et al. 2002).

Distribution

Splittail are endemic to the sloughs, lakes and rivers of the Central Valley that connect to the estuary (Caywood 1974; Moyle 2002; Moyle et al. 2004). In the Sacramento Valley, they were found in early surveys as far up the Sacramento River as Redding, up the Feather River as high as Oroville, and in the American River to Folsom (Rutter 1908). Archaeological evidence from the San Joaquin basin indicates that splittail were abundant in two large lakes, where they were harvested by native people (Moyle 2002; Moyle et al. 2004).

Part of the rationale for the proposed listing of splittail in 1994 was that the USFWS believed that there had been a recent major restriction in the range of the species (USFWS 1994). Specifically, they concluded that the distribution of splittail had become confined to the Sacramento–San Joaquin Delta and Suisun Bay. The upstream extent of the distribution of splittail for most of the major rivers within its range is summarized in Table 1. For comparative purposes, we list data for (1) the historical range of splittail as described by Rutter (1908), (2) the known range in the 1970s (Caywood 1974), (3) results for the mid-1990s (Sommer et al. 1997), (4) our most recent observations (Feyrer et al. 2005), and other previously unpublished observations. These data suggest that splittail has retained much of its historical range in the major rivers, although the data do not reflect extensive losses of channel edge complexity and riparian habitat or off channel floodplain habitat due to levee construc-

Table 1.

Upstream-most locations of historical and recent splittail collections (1998–2002). River kilometer (rkm) is the distance from the mouth of the river.

River system	Historical (Rutter 1908)	1970s (Caywood 1974)	Mid-1990s (Sommer et al. 1997)	Recent (Feyrer et al. 05) unless noted otherwise	Distance to first dam[a]
	Location (rkm) of splittail collection				
Sacramento	483	387	331	391[b]	387
Feather	109	Present	94	94[c]	109
American	49	37	19	No new data	37
San Joaquin	Widespread	Present	201	218.5[d]	295
Mokelumne	NA	25	63	96[e]	63
Napa	NA	21	10	32	NA
Petaluma	NA	25	8	28	NA

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

[b] D. Killam, California Department of Fish and Game, personal communication.

[c] B. Oppenheim, NOAA Fisheries, personal communication.

[d] R. Baxter, California Department of Fish and Game, unpublished data.

[e] J. Merz, East Bay Municipal Utility District, personal communication, November 2000.

tion (Mount 1995). Further, Feyrer et al. (2005) demonstrated that upstream distribution of age-0 fish in the Sacramento River has remained persistent at 232–296 km upstream from the estuary, as measured by a monitoring program spanning 28 years (1976–2003). In any case, the geographic distribution of splittail is broader than previously believed and has not changed detectably over the past several decades.

One factor complicating comparisons with historical data is that the distribution of splittail changes seasonally and annually (Sommer et al. 1997; Feyrer et al. 2005). At present, the dominant life history pattern is for the majority of the splittail population to remain in the estuary during summer and early fall, with adults migrating upstream to spawn in the delta and its tributaries in late fall–early spring. Walford (1931) observed seasonal trends in catch of splittail in the delta, strongly suggesting that seasonal shifts in distribution also occurred historically. However, the historical data are insufficient to determine whether large numbers of splittail typically remained in upstream tributaries on a year-round basis. Annual variation in the present distribution is also evident from the juvenile splittail data. Sommer et al. (1997) used beach seine data to examine the annual distribution of age-0 splittail. The data continue to show that the distribution of young splittail varies substantially among years (Figure 3). There is some indication that the distribution of splittail tends to be furthest upstream in dry years, likely because the lack of inundated floodplain or vegetated channel boarders within low elevation areas forces splittail to migrate further upstream to find suitable spawning habitat (Feyrer et al. 2005). Again, it is unknown whether this trend occurred historically.

The fact that distribution of splittail remains relatively broad is likely a major factor that has helped it avoid extinction. A large potential range reduces the risk of a localized extinction and helps expand the potential area of habitat. By contrast, its extinct cogener, *P. ciscoides*, was only known to occur in Clear Lake (Figure 2) and its tributaries (Moyle 2002). The relatively isolated 17,670-ha lake has been substantially altered by habitat degradation and species introductions, both of which were likely primary causes of its extinction.

Splittail Abundance Trends

The historic abundance of splittail is not known, but they were abundant enough to be harvested by native peoples and commercial fisheries in the 19th and early 20th centuries (Walford 1931; Moyle 2002; Gobalet et al. 2004). There has never been an effort to estimate the population size of splittail.

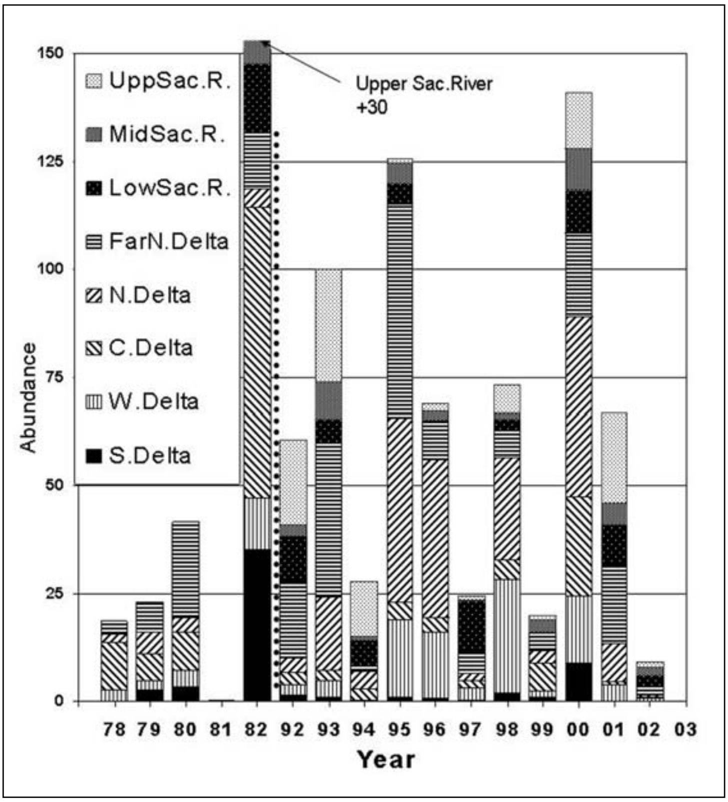

Figure 3. Age-0 splittail (>24 mm FL) abundance and distribution based on U.S. Fish and Wildlife Service beach seine survey, 1978–1982, 1992–2002. Data are mean catch per haul by region for May and June. Regions follow Sommer et al. (1997), except for those upstream of the delta: (1) lower Sacramento River ("LowSac.R"—Feather River [river kilometer 129] to American River [river kilometer 97]); (2) middle Sacramento River ("MidSac.R."—Butte Creek [river kilometer 222] to Knights Landing [river kilometer 145]); and (3) Upper Sacramento River ("UppSac.R."—Ord Bend [river kilometer 296] to Colusa State Park [river kilometer 239]). Sampling in the latter three regions began in 1981.

However, there are seven sampling efforts by the Interagency Ecological Program, a consortium of state and federal agencies that capture splittail frequently enough to allow the development of abundance indices (Sommer et al. 1997; Baxter 1999). Abundance data for age-0, age-1, and age-2+ splittail are summarized for several of the surveys in Figures 3–5. The CDFG fall midwater trawl is a monthly survey that samples 100+ sites from San Pablo Bay to Rio Vista during September through December (Sommer et al. 1997). The survey represents one of the best long-term data sets and covers a large portion of the range of splittail. Key limitations of the survey for splittail include a low catch of adults, insufficient coverage of the upstream range, and insufficient data to separate age classes before 1975. The University of California at Davis Suisun Marsh otter trawl is a monthly survey that samples seven sloughs in Suisun Marsh. The survey is geographically localized and therefore may not be representative of the range of splittail, but it is particularly valuable because it has relatively good catch of multiple age-classes. The SWP salvage is an abundance index based on collection of migrating splittail at the water diversion's fish screens. Like the Suisun Marsh survey, SWP salvage is geographically localized; however, it is also considered an important abundance index because it has the largest splittail catch of any of the surveys for all age-classes.

Based on these data, it is clear that splittail abundance varies widely between years, particularly for age 0 (Figure 4). A consistent trend is that abundance of age-0 splittail is relatively low during dry years (Meng and Moyle 1995; Sommer et al. 1997; Baxter 1999; Moyle et al. 2004). This effect was most pronounced during drought years in 1987–1992 and 1994. From 1995 to 2001, age-0 splittail abundance indices improved substantially, with 1998 showing the highest splittail abundance index ever recorded for most surveys. Age-1 year-classes tend to reflect age-0 abundance in the preceding year, with the highest abundance in years following a strong year-class (Figure 5). Overall, age-2+ trends are much less variable, likely because the multiyear age structure buffers the populations (Figure 6). There is also a discernable increase in adult abun-

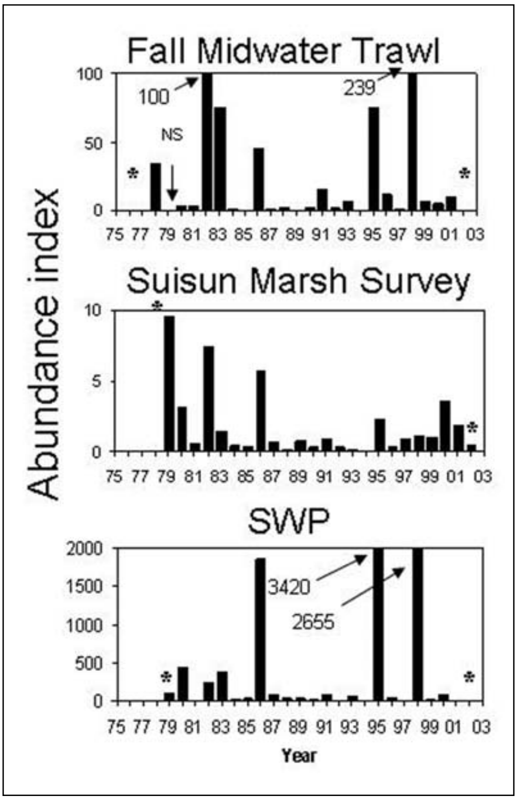

Figure 4. Medium-term trends (late 1970s through 2002) in age-0 splittail abundance, as indexed by three surveys. Asterisks indicate the start of the survey or of length records for age determination and the most recent index calculated (2002). No sampling (NS) and thus no index is indicated by downward arrows. Survey and index calculation methods were as described in Sommer et al. (1997) except for Suisun Marsh, which used a slightly different approach: (1) age-0 indices were calculated based on May–December catch, not just June–August catch (Sommer et al. 1997); and (2) indices were calculated based on mean catch/trawl for all stations combined, rather than the sum of the mean catch for each of seven sloughs (Sommer et al. 1997).

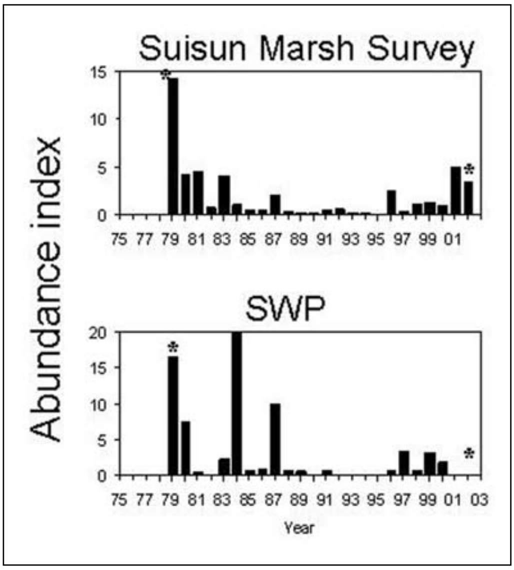

Figure 5. Medium-term trends (late 1970s through 2002) in age-1 splittail abundance, as indexed by two surveys. Asterisks indicate the start of the survey or of length records for age determination and the most recent index calculated (2002). Survey and index calculation methods were as described for age-0 with different months and size categories appropriate to age-1.

dance 2–3 years after high age-0 abundance years, indicating that good year-classes have at least a moderate influence on the adult population size.

Largely because of the variability in age-0 abundance, the population trends of splittail have been one of the major sources of debate about the species. Following the listing of splittail in 1999, the USFWS reopened the comment period for the final rule on four occasions to seek peer review and public comment on various issues, including abundance trends. The most recent analysis of population trends in a peer-reviewed journal was by Kimmerer (2002a), who used a regression approach to determine whether freshwater flow or trophic linkages influenced the abundance of age-0 splittail. He found that the abundance of age-0 splittail varied positively with freshwater outflow, but that there was no discernable change in abundance after 1987, the point at which a major drought began, and the food web in the estuary was substantially modified by the proliferation of the introduced clam brackish-water corbula *Corbula amurensis* (also known as *Potamocorbula amurensis*). These results are consistent with an earlier analysis by Sommer et al. (1997), who concluded that there had been no long-term change in the abundance indices of either adult or juvenile splittail. Using a conservative 20% level of statistical significance, the USFWS (2003a) found that almost half of the indices of abun-

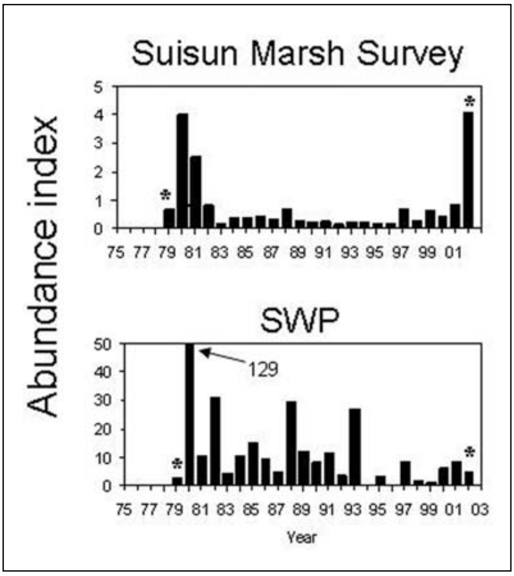

Figure 6. Medium-term trends (late 1970s through 2002) in age-2+ (adult) splittail abundance, as indexed by two surveys. Asterisks indicate the start of the survey or of length records for age determination and the most recent index calculated (2002). Survey and index calculation methods were as described for age-0 with different months and size categories appropriate to age-2+.

dance showed some evidence of decline; however, they ultimately concluded that this trend is unlikely to lead to extinction.

Factors that May Influence the Abundance and Distribution of Splittail

In its determination of threatened status for splittail, the USFWS (1999) identified altered hydraulics and reduced outflow caused by water exports as the principal causes of the population decline. Additional threats were listed as direct loss (mortality) at pumping plants and diversions, loss of spawning and nursery habitat as a consequence of draining and diking for agriculture, reduction in the availability of highly productive brackish-water habitat, urban and agricultural pollution, introduced species, and exacerbation of these factors as a result of 6 years of drought.

Our present understanding of the population dynamics of splittail is that year-class strength of the species is largely determined by the frequency and duration of floodplain inundation. Of the other factors identified by the USFWS (1999), urban and agricultural pollution and introduced species remain potentially major but poorly understood threats. There is, however, no evidence to support the conclusion that direct loss at pumping plants has had a significant effect on abundance, at least since the 1970s. Although diking and draining of floodplain areas for agriculture have resulted in loss of spawning and nursery habitat, most of this activity occurred well before recent observations of poor recruitment. These and other factors are reviewed briefly below.

Floodplain inundation

Although much of the historical floodplain in the valley has been lost to levee construction and river channelization, some substantial areas of floodplain remain in the region. The largest of these are the Yolo and Sutter bypasses, the primary floodplains of the Sacramento River. Studies by Sommer et al. (1997) have demonstrated that floodplain inundation represents the primary factor that determines spawning success. They found that the duration of flooding of the Yolo Bypass was strongly correlated with splittail year-class strength. Sommer et al. (1997) also showed that adults move onto the floodplain in winter and early spring to forage and spawn on flooded vegetation. After spawning, adults typically return to the delta, Suisun Bay, and Suisun Marsh to forage during the summer and fall. Juvenile splittail rear on the Yolo Bypass floodplain from April through June (Sommer et al. 2004a). Small-scale floodplain wetland studies suggest that young splittail are associated with shallow areas (<1 m depth) but that juvenile distribution varies on a diel basis (Sommer et al. 2002). Young splittail may become entirely benthic at night, another reason why the inundation of large areas of shallow water habitat (thereby creating more benthic resting areas) may help to support high splittail production. Sommer et al. (2004b) found higher abundances of phytoplankton, diptera, and terrestrial invertebrates in Yolo Bypass than the adjacent Sacramento River channel. A major portion of the diet of juvenile splittail is apparently larval chironomids (Kurth and Nobriga 2001), which are present in Yolo Bypass at much higher densities than in that main river channels (Sommer et al. 2001b, 2004b). Juvenile splittail subsequently emigrate to the river channels and estuary as floodwaters recede (Sommer et al. 1997). Observations from the Yolo Bypass are consistent with studies in the Cosumnes River, a nearby undammed watershed that was recently identified as a major spawning and rearing area for splittail (Moyle et al. 2003; Crain et al. 2004). Crain et al. (2004) observed larval splittail rearing in the floodplain during March–May, with peak occurrence during April and May. As in Yolo Bypass, young splittail in the Cosumnes River were most commonly associated with submerged terrestrial plants.

Based on these observations, it appears that splittail is perhaps the most floodplain-dependent species in the San Francisco Estuary (Sommer et al. 2001a). It is likely that the decline of splittail during the 1987–1992 drought was due to the lack of access to floodplain spawning habitat (Sommer et al. 1997). The relatively long life span of the fish (sometimes >5 years) is an important attribute that helps it survive periods without access to this habitat. Recent studies by Sommer et al. (2002) indicate that the species can be successfully induced to spawn in dry years if it is provided with access to inundated vegetation. Successful spawning also takes place on vegetated river margins during years with no floodplain inundation (Moyle et al. 2004; Feyrer et al. 2005).

SWP and CVP water export operations

The two major water projects, the SWP and CVP, seasonally entrain adult and juvenile splittail. Individuals greater than about 20 mm TL are salvaged by fish screening facilities and transported and released back to the estuary, although overall survival rates are unknown (Brown et al. 1996). Juveniles are entrained primarily during May–July, and adults are mostly collected during December– March (Meng and Moyle 1995; Sommer et al. 1997).

Most evidence suggests that entrainment losses do not have a major effect on year-class strength. The possible effects of SWP exports were evaluated by Sommer et al. (1997) using three different approaches, none of which provided evidence of population-level effects. Overall, splittail entrainment at the water diversion is correlated with abundance levels. In other words, losses are highest in wet years, when the population is most robust. These trends contrast with delta smelt, a threatened species under the ESA, and longfin smelt *Spirinchus thaleichthys*, a California species of special concern. Both smelt species were observed at the water diversion in higher numbers in dry years, when their populations were relatively low. As a consequence, Sommer et al. (1997) predicted that the effects of entrainment on the smelt populations would be more substantial than for splittail.

Although it is possible that there could be population level entrainment effects under some conditions (Sommer et al. 1997), there is no evidence that this has occurred since the 1970s. Nonetheless, entrainment of splittail remains an ongoing issue for project operations; for example, pumping was curtailed substantially in 1995 due to the salvage of millions of juvenile splittail during a relatively short period.

Changes to the food web

The number of alien species introductions to the San Francisco Estuary has made it perhaps the most invaded estuary in the world (Cohen and Carlton 1998). The food web was changed most dramatically after the introduction of the clam *C. amurensis* by the mid-1980s, causing declines in phytoplankton and invertebrates (Jassby et al. 2002; Kimmerer 2002a). For splittail, of greatest concern is a decline in the abundance of *Neomysis* shrimp, a major food source (Daniels and Moyle 1983; Feyrer et al. 2003). However, Kimmerer (2002a) found no evidence that a significant decrease in *Neomysis* in 1987 resulted in a significant decline in age-0 splittail abundance. Nonetheless, Feyrer et al. (2003) found that food web alterations have had a substantial effect on the diets of older (age-1 and older) splittail in Suisun Marsh, where splittail populations decreased during the postclam period. Mysids were formerly the dominant prey of splittail but are now are nearly absent from gut contents. During the postclam period, splittail diet increasingly focused on bivalves and amphipods. Feyrer and Baxter (1998) found evidence that the fecundity of splittail was lower in the

1990s than in the 1980s, lending credence to the hypothesis that *C. amurensis* had population-level effects on splittail by reducing its food supply.

Contaminants

Major pollutants in the San Francisco estuary include a wide variety of chemicals, including heavy metals, pesticides, herbicides, and polycyclic aromatic hydrocarbons (Nichols et al. 1986). The fact that these compounds vary substantially in time and space makes it very difficult to predict biological effects; however, many co-occur with vulnerable early life stages of fishes (Kuivila and Foe 1995; Kuivila and Moon 2004). Toxicity has been documented for a few fishes in the estuary, including striped bass *Morone saxatilis* and Chinook salmon (Saiki et al. 1992; Bailey et al. 1994; Bennett et al. 1995), but there is little data for splittail. Under laboratory conditions, Teh et al. (2004a) found that exposure to the widely used pesticide diazinon caused spinal deformities and decreased growth in young splittail. However, little is known about population-level effects in the field. Contaminants in the sediments are potentially the greatest threat to splittail because these fish are benthic foragers and consume a large amount of detritus (Daniels and Moyle 1983; Feyrer et al. 2003; Moyle et al. 2004). Perhaps of greatest concern are possible effects of selenium, which can occur in high concentrations in one of their primary food sources, the clam *C. amurensis* (Stewart et al. 2004). Because the fish are long-lived, splittail may accumulate selenium to levels that might affect development and survival of eggs and larvae. Feyrer et al. (2003) found that splittail diet was largely composed of detritus and bivalves (including *C. amurensis*) following the decline in mysid abundance. Feyrer and Baxter (1998) documented lowered fecundity of splittail during the late 1990s compared to the early 1980s, suggesting that this hypothesis merits further investigation. In another study, results from Teh et al. (2004b) indicate that splittail fed high concentrations of selenium grow significantly slower and have higher liver and muscle selenium concentrations.

Agricultural water diversions

In addition to the large SWP and CVP diversions, the San Francisco Estuary has 2,209 agricultural diversions in the delta and 366 diversions in Suisun Marsh used for enhancement of waterfowl (Herren and Kawasaki 2001). These small diversions continue to be a concern for fisheries management as the majority of the structures do not have fish screens. This issue has not been studied in detail; however, the limited evidence suggests that splittail may not be especially vulnerable to delta agricultural diversions. The most intensive study is by Nobriga et al. (2004), who examined entrainment at a diversion near the confluence of the Sacramento and San Joaquin rivers during July 2000 and 2001. They found that splittail entrainment was exceptionally low, just one fish over two intensive sampling periods (M. Nobriga, California Department of Water Resources, personal communication).

Stock recruitment effects

An additional concern for splittail is that a reduction in the number of spawning adults may lead to poor recruitment of young fish to the population. Sommer et al. (1997) used simple linear regression to test for stock–recruitment effects in several different indices of abundance. Data through 1995 indicated that there was no significant stock– recruitment effect for five abundance indices, but there was a weak statistical relationship for the University of California Davis Suisun Marsh survey. As part of the present review, we updated the analysis using abundance data (log + 1 transformed) through 2002 (Figures 4 and 6). For the recent data, there were no statistically significant relationships between age-2 and older abundance and age-0 abundance for any of the indices. The lack of strong stock–recruitment relationships suggests that environmental factors (i.e., floodplain inundation), not the number of adults, controls splittail recruitment.

Recreational harvest

Historically a commercial fishery (Walford 1931), splittail continue to be a popular target for a modest sport fishery (Moyle 2002; Moyle et al. 2004). The activity primarily occurs from November through May, when adult splittail migrate to and from spawning habitat. Creel surveys for striped bass and salmon suggest that up to several hundred adult splittail may be caught on a daily basis.

Although the USFWS (2003a) concluded that the fishery had little effect on the population, it is possible that sportfishing could affect egg supply because nearly all fish are retained, especially females and the largest individuals.

Restoration

During the mid-1990s, two major restoration efforts were initiated to help address declines in fisheries resources in the San Francisco Estuary and its watershed: (1) the Central Valley Project Improvement Act (CVPIA), and (2) the CALFED program. Current and planned restoration activities by these two programs were identified by USFWS (2003a) as key reasons for delisting splittail.

Central Valley Project Improvement Act

Enacted by Congress in 1992, the Central Valley Project Improvement Act (Public Law 102–575) represented the most far-reaching change in CVP operation since its construction. The most significant component of this legislation was that it placed fish and wildlife protection, restoration, and mitigation as project purposes with equal priority to water diversions for irrigation and domestic purposes. One major change was that CVPIA reallocated 800,000 acre-feet of project yield to be used for environmental purposes. A key part of this legislation was the Anadromous Fisheries Restoration Program (AFRP), which sought to double populations of Chinook salmon, steelhead, American shad, striped bass, and sturgeon as compared to 1967–1991 levels (USFWS 2003b). During 1995–2000, the AFRP spent approximately $26 million on projects to improve fisheries resources and monitoring (USFWS 2003b). Although this program does not specifically target splittail, we estimate that at least one-third of the funds spent during 1995–2000 on projects, including habitat protection, restoration, and fish passage, could have benefits to this species.

CALFED

While water conflicts in California represent an ongoing part of the state's history, the listing of winter-run Chinook salmon and delta smelt in the early 1990s created dramatic new pressures on water allocation (Koehler 1995). Specifically, losses of salmon and smelt became a major operational consideration at the SWP and CVP diversions, directly affecting water supply reliability. Several other species including splittail, longfin smelt, spring-run Chinook salmon, and steelhead were also being considered for federal listing, raising concerns that water diversions would be further curtailed. These issues helped bring together many of the key stakeholders to try to address long-standing resource conflicts in the San Francisco Estuary and its watershed. The result of these negotiations was the formation of CALFED, a cooperative effort of more than 20 state and federal agencies, including California Department of Water Resources, California Department of Fish and Game, State Water Resources Control Board, U.S. Bureau of Reclamation, U.S. Fish and Wildlife Service, U.S. Geological Survey, and Army Corps of Engineers. In 2003, CALFED was renamed the California Bay-Delta Authority (CBDA) after it was officially designated as a new state agency.

The CBDA program most relevant to the status of splittail is the Ecosystem Restoration Program. In the 7 years since this was initiated in 1995, the program has invested $335 million in more than 300 restoration projects (CBDA 2003). Recent data collected on splittail had a major effect on habitat restoration priorities, particularly the importance of floodplain, shallow water tidal, and riparian habitat. Projects that targeted these habitat types, or constructed fish screens or passage facilities within the range of splittail, are likely to have the greatest benefits to the species. Since 1995, the total expenditure on these categories of projects was $195 million. The total amount of habitat protected or restored was 45,700 ha, 6,500 ha of which was for floodplain, the habitat type most likely to limit splittail abundance. An additional $32 million was spent on improving water and sediment quality and invasive species control that could also benefit splittail.

Conclusions

Much of the initial rationale for the listing of splittail focused on an apparent decrease in range and abundance (USFWS 1994; Meng and Moyle 1995).

Over the past decade, it has become clear that the range of the species is much wider than previously realized, encompassing most of the available habitat below the major dams. Although there is general agreement that there were substantial losses of off-channel habitat and river reaches upstream of dams during the past century (Meng and Moyle 1995; Sommer et al. 1997; USFWS 2003a), data collected over the past three decades show no evidence of a recent range restriction. Moreover, the strong year-classes produced in the late 1990s demonstrate that the splittail population is much more resilient than previously understood. The inherent variability in splittail abundance and the lack of exact population estimates have sparked a lively debate about whether there has been at least a modest decline in population levels; however, we concur with USFWS (2003a) that the population has enough resilience to avoid extinction in the foreseeable future.

While abundance and distribution are often primary considerations in listing decisions, the ESA also requires the USFWS to evaluate whether there are present or future threats to the habitat or range of a species. In their recent review, the USFWS (2003a) identified many of the same potential threats reviewed in the present paper, including the negative effects of water diversions, contaminants, and invasive species. Despite some potential threats, we agree with the USFWS finding that the adverse effects are adequately offset by recent beneficial actions such as CALFED and CVPIA restoration and cooperative resource management. The scope of these efforts is extensive, representing one of the most ambitious restoration efforts in the United States (Koehler 1995).

From a fisheries perspective, the listing debate fueled new research on splittail and other native fishes and helped change habitat restoration priorities. Until the 1990s, there was little research or monitoring of native fishes in California other than salmonids. It is therefore not surprising that the initial proposal to list splittail assumed that the species was declining for reasons similar to other native fishes, including delta and longfin smelt (USFWS 1994). Since then, splittail has became a major focus of fisheries research in the San Francisco Estuary, helping to reveal that different native fishes are responding to different cues (Bennett and Moyle 1996; Kimmerer et al. 2002b). In particular, it appears that splittail are perhaps the most floodplain dependent species in the estuary (Sommer et al. 2001a), whereas delta and longfin smelt do not make extensive use of this type of habitat. Splittail-related research has also revealed that the floodplain is a major nursery habitat for Chinook salmon and stimulates lower trophic levels in the estuary. This recognition led to a new emphasis on floodplain restoration in programs such as CALFED that should benefit a suite of aquatic organisms. Although splittail populations should improve substantially as a consequence of floodplain restoration, we do not believe that the species will ever return to historic levels because of the extensive habitat alteration and large numbers of alien species in the estuary (Atwater et al. 1979; Mount et 1995; Cohen and Carlton 1998).

The fact that the splittail population has been able to survive a multitude of stressors over the past century provides a good example of resilience in western native fishes. A major reason that it has been able to cope with changes in the physical habitat is that splittail are physiologically hardy and able to tolerate a relatively wide range of temperature, salinity, and dissolved oxygen levels (Young and Cech 1996). This tolerance contrasts with several other native fishes of the San Francisco Estuary, including longfin and delta smelt (Sommer et al. 1997). However, physiological hardiness does not adequately explain the resilience of splittail in the face of the large number of species introductions. Unlike many other regions in the west, flood managers in California decided to retain substantial parts of the historical floodplain in the lower Sacramento Valley (Yolo and Sutter bypasses) to provide passive flood protection for valley communities (Sommer et al. 2001a). Our working hypothesis is that this large remaining area of floodplain habitat may be the major reason that the species has not gone extinct. Specifically, the ability to use floodplain habitat early in the year may provide competitive advantages to splittail. Splittail spawn and rear during winter and spring and are therefore able to use the highly productive seasonal floodplain inundated during that period (Sommer et al. 2001a, 2004). By contrast, nonnative fishes typically spawn in late spring or summer when the floodplain is dewatered and the fish are confined to less-productive perennial channels.

Note, however, that these life history characteristics will not necessarily protect splittail in the future. For example, it is unclear whether programs such as CALFED and CVPIA are adequate to protect splittail if there is a repeat of multidecade droughts that occurred in the past millennium (Ingram et al. 1996). We are also particularly concerned about the potential spread of northern pike *Esox lucius*, which has recently become abundant in a reservoir on the Feather River (Rischbieter 2000). Unlike most other alien fishes in the San Francisco Estuary, this highly predaceous species is able to spawn and maintain relatively high consumption rates in relatively cold conditions, particularly in shallow, vegetated areas like Yolo Bypass (Craig 1996). As a result, we believe that it is prudent to retain splittail as a species of special concern under the California Endangered Species Act, and for the USFWS to periodically evaluate the status of the population (USFWS 2003).

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