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Spawning and Rearing of Splittail in a Model Floodplain Wetland

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Abstract.—The splittail *Pogonichthys macrolepidotus*, which has been listed as threatened by the U.S. government, does not produce strong year-classes unless it has access to the floodplain habitat of the San Francisco estuary and its tributaries. In this small-scale, single-year study, we tested the hypothesis that managed inundation of a floodplain can be used to support splittail reproduction in dry years, when this habitat type is not readily available. Adult splittails were captured on their 2001 upstream spawning migration and transferred to a 0.1-ha model floodplain wetland. Our results suggest that adults will successfully spawn if they are provided access to floodplain habitat in dry years. In snorkel surveys, progeny showed a significant association with the lower portion of the water column. Young splittails (15–20 mm fork length [FL]) concentrated in edge habitat near an inflow during the day but at night moved into deeper-water habitats, including open water and habitats with submerged vegetation. Larger splittails (28–34 mm FL) used a broad range of habitats both during the day and at night. Juveniles showed significant schooling behavior during the day, then dispersed at night. These observations have potential implications for the design of habitat restoration projects for the splittail, the last remaining representative of its genus.

The splittail *Pogonichthys macrolepidotus*, a native cyprinid, is perhaps the most floodplain-dependent fish in the San Francisco estuary (Figure 1; Sommer et al. 2001a). During high-flow periods in winter and spring, adult splittails migrate upstream into the Sacramento−San Joaquin delta and its tributaries (Daniels and Moyle 1983), where spawning activity is apparently concentrated on the seasonal floodplain (Sommer et al. 1997). Abundance is reduced in dry years, when splittails have little or no access to floodplain spawning and rearing habitat. Although the relatively long life span (frequently >5 years) and high fecundity of this species helps to buffer the population against low-outflow conditions, an extended drought during the 1980s and early 1990s led to a major decline in the production of young splittails (Meng and Moyle 1995; Sommer et al. 1997). This decline in abundance was the primary basis for the U.S. government's listing of the splittail as threatened in 1999 (USFWS 1999). Major declines have also been noted for several other native fish in the estuary, although the causes vary (Bennett and Moyle 1996). The splittail is the last surviving member of its genus; the only other species in the genus, the Clear Lake splittail *P. ciscoides*, became extinct sometime during the previous century (Moyle 2002).

Several restoration programs are underway to increase the fish populations of the estuary and its tributaries (Yoshiyama et al. 2000). Floodplain restoration has been identified as a potential way to support splittail and other species (CALFED 2000). One major restoration goal for the San Francisco estuary is to improve the connectivity between river and floodplain habitat, particularly in the Yolo Bypass, the largest remaining floodplain. As a result of the system of levees and weirs constructed around its perimeter, the Yolo Bypass typically floods only in above-normal water years (Sommer et al. 2001a). Here, we use a model floodplain wetland to test the hypothesis that managed inundation of floodplain habitat during lower-flow years can be used to support splittail spawning and rearing. An additional objective was to provide diel observations of juvenile splittails; the habitat

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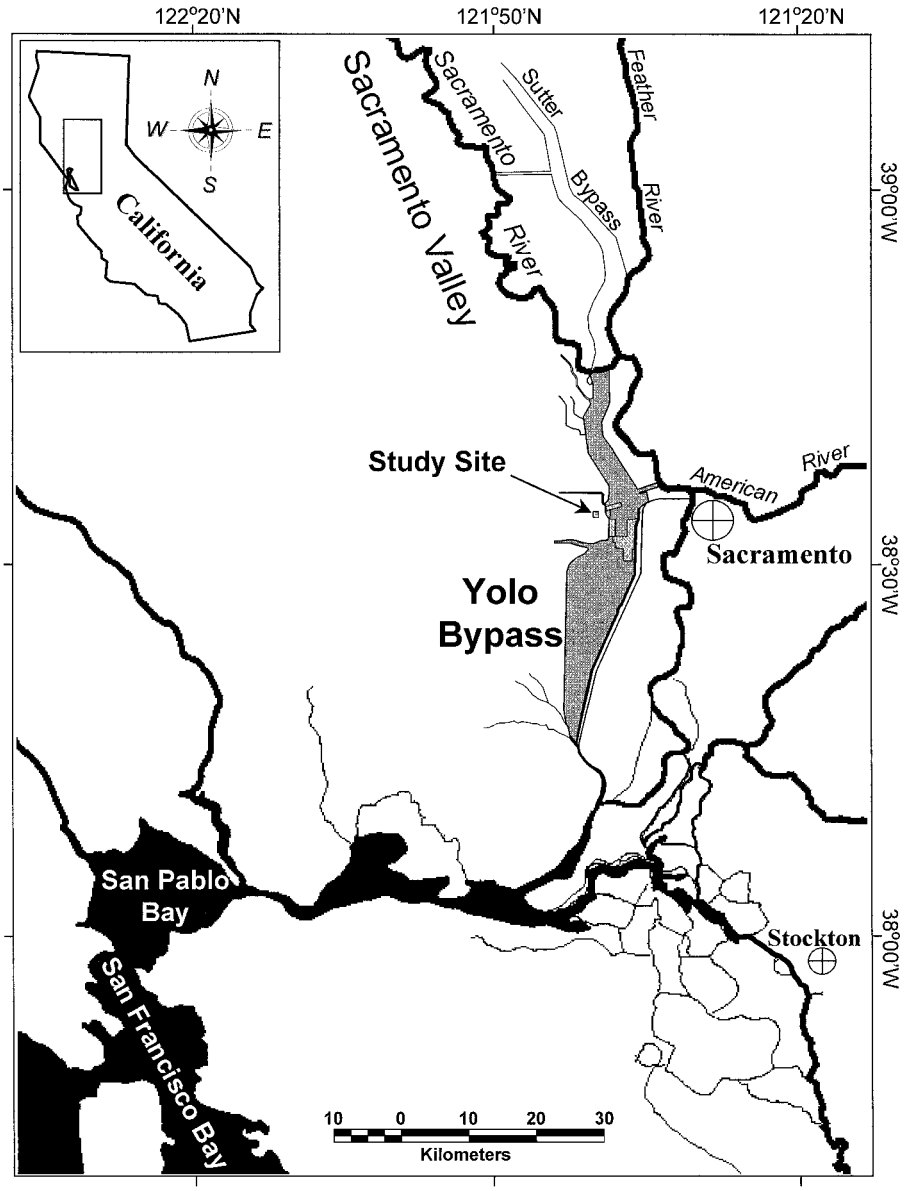

FIGURE 1.—Map showing the location of the Yolo Bypass (dark gray area). The San Francisco estuary includes the region from San Francisco Bay upstream to Sacramento. The Yolo Basin Wildlife Area is the light gray area within Yolo Bypass immediately southeast of the study site.

associations of this life stage are poorly understood because early juveniles typically occur during high-flow events, when high turbidity and extreme environmental fluctuations create major sampling problems. Young and Cech (1996) have described the physiological tolerances and requirements of young splittails in laboratory studies. However, little is known about the habitat preferences and distribution of early life history stages under natural conditions. Moreover, diel behavior has not been well studied for juvenile cyprinids (Garner 1996). This information is essential for the successful design and evaluation of splittail restoration projects.

Our basic approach was to capture adult splittails on their seasonal spawning migration during a dry year and relocate them to a model floodplain wetland. After successful spawning and hatching,

we conducted intensive observations of the diel distribution of juveniles in relation to different habitat types. Use of a single model floodplain wetland is somewhat artificial and limited in scope; however, similar studies using captive fish in seminatural habitats have yielded useful biological data for other threatened North American cyprinids (Blinn et al. 1998). Our objective was to collect basic information on the spawning and rearing of splittails that could be used to generate hypotheses for more comprehensive field studies and habitat restoration projects.

Study Site

Our study was conducted with adult splittails collected from the Yolo Bypass, the largest floodplain of the San Francisco estuary (Figure 1). The estuary has been heavily modified by many factors, including levee construction, river channelization, draining of wetlands, diversions, and introduced species (Bennett and Moyle 1996). The 24,000-ha Yolo Bypass floodplain is dominated by agricultural uses, but there are also substantial ''natural'' habitats such as seasonal wetlands and riparian and upland habitats (Sommer et al. 2001a). The largest contiguous area of nonagricultural floodplain habitat is the Yolo Basin Wildlife Area, which is managed by the California Department of Fish and Game. The Yolo Bypass typically floods in about 60% of years, when high winter and spring floodwaters enter from the Sacramento River and several small streams. The floodplain is seasonally dewatered in summer and fall, except for perennial ponds and a single tidal channel. During extended droughts, such as that of 1987–1992, the floodplain is not inundated from its tributaries. Observational studies were conducted in a 0.1-ha floodplain wetland constructed at the Yolo Basin Wildlife Area headquarters, which is immediately adjacent to the Yolo Basin Wildlife Area.

The model floodplain was constructed in 1997, then planted with wetland vegetation and seasonally flooded during September–May over the next three years. At the time of the study (2001), approximately 10% of the wetland area was bordered by partially submerged terrestrial vegetation, primarily willows *Salix* spp., mule-fat *Baccharis salicifolia*, boxelder *Acer negundo*, and willow herb *Epilobium* spp. About 15% of the wetland was covered by dense beds of bermuda grass *Cynodon dactylon*, and the remaining 75% was lightly vegetated with cattails *Typha* spp. Swamp timothy *Crypsis schoenoides* was another major vegetation type in the wetland, but it was dormant during the study. The wetland was flooded in September 2000 before the initiation of the splittail study. Water surface elevations were maintained by inundating the wetland with well water for 4–6 h/d, which was supplemented by surface runoff from precipitation events. In addition to fresh flow from external water sources, a screened submersible pump was used to recirculate water from the outlet to the inlet at a rate of 100 L/min. The wetland was approximately oval-shaped and had a mean depth of 0.47 m during the study period. The depth profile from edge to center was gradual (8:1 slope) except for one side, which had a 2:1 slope.

There were several notable differences between the model floodplain wetland and the Yolo Bypass. Based on the mean depth, area, and recirculation rate, the mean hydraulic residence time (i.e., turnover rate) in the model wetland was approximately 1 d, about twice as fast as that estimated for peak natural flood events in the Yolo Bypass (California Department of Water Resources, unpublished data). The water levels in our model floodplain wetland had a standard deviation of 0.09 m during the observation period, compared with 0.20 m or more during recent long-duration (e.g., >30 d) Yolo Bypass flood events. Finally, water clarity was much higher in our model floodplain wetland. Visibility for divers (see below) was 2–5 m, while visibility during typical Yolo Bypass flood events (not actually measured) is typically on the order of less than 0.5 m.

Methods

During February 2001, we collected 14 adult splittails (320 ± 31 mm [mean ± SD] fork length [FL]) on their upstream migration using a 3-m-diameter fyke trap in the Yolo Bypass Toe Drain, a perennial tidal channel of the floodplain. As none of the fish were ''ripe,'' we were unable to determine the sex of the fish at the time of collection. The fish were transported immediately to the model floodplain wetland. No other fish species were present in the wetland before introduction of the splittail.

We considered a variety of shallow-water habitat sampling approaches, including seining, dipnetting, and electrofishing (Rozas and Minello 1997), to sample the distribution and habitat use of juveniles produced within the model wetland. We determined that these methods were not appropriate because they would have substantially disturbed the fish and their habitat and because their relatively poor resolution would have made it difficult to evaluate fine-scale distributions (e.g.,

water column position). As an alternative, we relied on snorkel observations, a ''passive'' approach. Although snorkel surveys have been used in many other studies to collect fine-scale data on habitat use (Helfman 1983), they may have somewhat altered the behavior of young fish. As recommended by Helfman (1983), we conducted our observations on habitat use and distribution from a distance of several meters to minimize behavioral effects. This was consistent with our initial observations on the responses of splittails to divers; the fish showed no obvious change in behavior (e.g., an increase in swimming speed or change in water column position) unless the observers moved to within 1 m of the fish.

Snorkel surveys were conducted by divers during two sampling periods, April 6–17, 2001 (period 1), and April 27−May 30, 2001 (period 2). For each sampling period, observations were made during the day (1–2 h after sunrise and at midday) and at night (1–2 h after sunset) to assess diel changes in distribution and behavior. A team of two divers surveyed the entire wetland, which was stratified into four habitat types: (1) open water (mud substrate with light vegetation; 74% of total wetland area); (2) submerged vegetation (dense beds of bermuda grass; 14% of total wetland area); (3) emergent vegetation (partially submerged terrestrial vegetation bordering the wetland; 10% of total wetland area); and (4) inflow (inflow area with vegetation similar to that of habitats 1 and 3; 2% of total wetland area). On two of the sampling days, only one of the two divers was used. Small dive lights were used for the night observations. A single observation was defined as a single fish or small aggregation or ''school'' (<25 individuals) within a 1-m^2 area. When larger schools were present, the observation represented the entire area covered by the school. For each observation, divers recorded the approximate number of fish, water column position (top, middle, or bottom third), and depth (actual depth for individuals, center of the school for groups). During the second sampling period, the water column position category for the bottom third of the water column was further subdivided into benthic (at or within 2 cm of the substrate) and pelagic observations. A sample of 27–50 fish was netted during each sampling period to measure mean fork length. Wetland depth was recorded 3–5 times each week, and water temperature was measured continuously using an Onset Optic Stowaway logger (Onset Computer Corporation, Bourne, Massachusetts) located at the outlet.

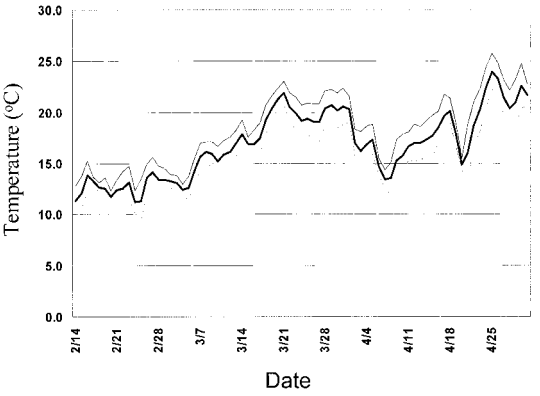

FIGURE 2.—Mean (thick line) and standard deviation (thin lines) of daily water temperature in the model floodplain wetland.

The observation data were summarized in three-way contingency tables using the following grouping variables: sampling period (1 or 2), time (day or night), and distribution (habitat type, depth, or water column position) or abundance (fish school size). We used three-way log-linear models to test the hypothesis that there were interactions between the categories of each of the contingency tables). Chi-square goodness-of-fit analyses were used to compare actual habitat use with the expected distributions based on the availability of each habitat type.

Results

Mean daily water temperatures ranged from 11°C to 24°C, with a gradual increase over the course of the study (Figure 2). The mean daily water temperature was 15–19°C during the first observation period and 21–23°C during the second. Larval splittails were first observed swimming at the edge of the wetland on April 3, 2001. The total number of observations varied somewhat among sampling periods: 63 and 74 for the day and night portions of period 1, respectively, and 52 and 78 for the day and night portions of period 2. However, the total number of fish observed was similar between periods for both day (286 ± 64 for period 1 and 241 ± 64 for period 2) and night (58 ± 1 for period 1 and 61 ± 2 for period 2). Fish densities were comparable to those in natural floodplain wetlands during previous high-flow years (California Department of Water Resources, unpublished data). The size range of young splittails collected with nets increased from 15–20 mm during the first sampling period to 28–34 mm during the second. The study was completed on May

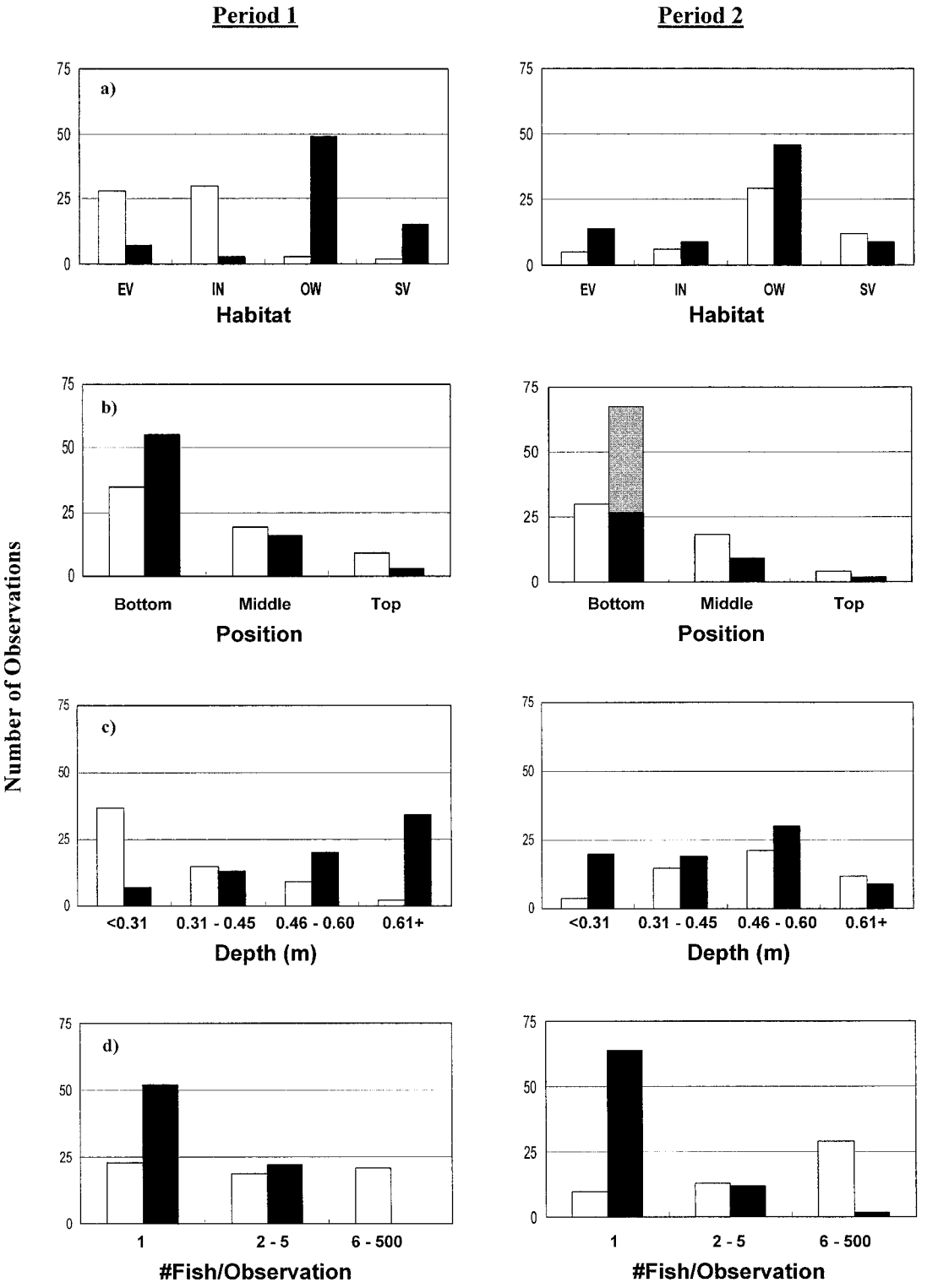

FIGURE 3.—Juvenile splittail habitat use during the day (open bars) and at night (solid bars) for two sampling periods. The *y*-axis for each variable indicates the total number of observations of one or more fish. Panels **(a)**

1–3, 2001, when the pond was drained and the fish removed. All of the original 14 adults were collected, along with 860 juveniles.

The snorkel surveys found young splittails in all habitat types (Figure 3a). Habitat use was significantly different from the expected distribution based on habitat availability during the day portions of periods 1 ($\chi^2 = 1{,}277$; df = 3; $P < 0.001$) and 2 ($\chi^2 = 29$; df = 3; $P < 0.001$) and the night portion of period 2 ($\chi^2 = 41$; df = 3; $P < 0.001$), but not during the night portion of period 1 ($\chi^2 = 4.3$; df = 3; $P > 0.05$). The log-linear analysis showed that there were statistically significant interactions between sampling period and habitat use ($P < 0.01$) and between time of day and habitat use ($P < 0.001$; Table 1). For period 1, there was a strong association with emergent-vegetation and inlet habitats during daytime (Figure 3a). At night and during period 2, there was increased use of open water and submerged-vegetation habitats.

Fish were most frequently observed in the bottom portion of the water column during all periods but showed an apparent shift towards the bottom at night (Figure 3b). During period 2, when we included ''benthic'' as an additional water column position, we found that 51% of all observations were made in benthic areas at night but that fish were entirely pelagic during the day. The diel shift in distribution was supported by log-linear analysis, which showed a significant ($P < 0.001$) interaction between time of day and water column position (Table 1).

The depth distribution of fish changed substantially between periods 1 and 2 (Figure 3c). During period 1, the majority of splittails were associated with very shallow (<0.40 m) edge areas of the wetland during the day but shifted to deeper water at night and at both times during period 2. Statistical analysis of the data indicated significant ($P < 0.001$) interactions between time of day and depth distribution and between sampling period and depth distribution (Table 1).

For both sampling periods, there were major changes in schooling behavior between day and night hours (Figure 3d). During the day, the majority of observations were of schools of 2–500 fish. At night the schools dispersed, and the majority of observations were of individual fish. These observations were reflected in the log-linear analysis, which demonstrated a significant ($P < 0.001$) interaction between time of day and school size (Table 1).

TABLE 1.—Results of three-way log-linear analyses of juvenile splittail distribution. Tests were performed for interactions between sampling period (1) or time of day (2) and distribution variables (3; habitat, water column position, and depth) and school size. The marginal χ^2 results are shown, with the degrees of freedom in parentheses; $P < 0.01$*, $P < 0.001$**.

Effect	Habitat	Water column position	Depth	School size
1 × 3	15.6 (3)*	2.9 (2)	16.0 (3)**	5.5 (2)
2 × 3	43.7 (3)**	18.0 (2)**	17.7 (3)**	95.0 (2)**

Discussion

Our results are most valid for a single year and location; they do not necessarily apply to all splittails in all restored and natural floodplain wetlands or to cyprinids elsewhere. However, we believe that the results have several implications for the biology and management of splittails. Our findings are consistent with previous evidence that floodplain habitat supports fish production in many locations, including tropical (Welcomme 1979; Junk et al. 1989) and temperate rivers (Bayley 1995; Gutreuter et al. 2000). At the regional level, the present study supports the conclusion of Sommer et al. (1997) that floodplain provides valuable spawning habitat for splittails. Flood events are known to be important for the spawning of several other federally listed cyprinids, including humpback chub *Gila cypha* (Kaeding et al. 1990) and Colorado pikeminnow *Ptychocheilus lucius* (Tyus 1991). Our data on juvenile distribution suggest that floodplains and perhaps other shallow-water habitats are also important for the early life stages of splittails. We found that the youngest splittails we studied (15–20 mm FL) were most abundant in the shallowest areas of the wetland with emergent vegetation, were associated with the lowest portion of the water column, and were largely benthic at night. As discussed in Sommer et al.

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show habitat type (EV = emergent vegetation, IN = inlet, OW = open water, and SV = submerged vegetation), panels **(b)** water column distribution (during the second observation period, the ''bottom'' category was subdivided into ''pelagic'' [solid bar] and ''benthic'' [shaded bar]), panels **(c)** the depth of the water column, and panels **(d)** school size as measured by the number of fish in each observation.

(2001b), in dry years native fish are confined to the Sacramento River and similar channels that are deep (>5 m) and steep sided and have minimal shallow-water habitat or vegetation. This distribution contrasts with that of high-flow years, when the Yolo Bypass and other floodplains in the region are inundated, providing tens of thousands of hectares of shallow, vegetated habitat for rearing. The availability of shallow (Childs et al. 1998) and benthic (Glova and Jellyman 2000; Jakober et al. 2000) habitats is important for the rearing of many other freshwater fishes. Additional benefits of floodplain rearing include the enhanced availability of invertebrate prey relative to that in adjacent river channels (Junk et al. 1989; Sommer et al. 2001b).

We observed both diel and ontogenetic changes in splittail distribution, a common behavior in many freshwater fish (Matthews 1998). The diel behavior is consistent with preliminary laboratory studies showing that young splittails exhibit decreased swimming activity and rheotaxis at night (T. Swanson, University of California–Davis, unpublished results). Other studies on young cyprinids suggest that predation and food availability are the primary factors controlling habitat use (Rheinberger et al. 1987; Garner 1996). We did not collect data on food availability, so we do not know whether this factor was important for splittail distribution. The mean number of fish observed during the first and second sampling periods was similar, suggesting that predation mortality was not substantial. However, the presence of piscivores could have triggered changes in habitat use even if predation rates were relatively low (Carpenter et al. 1987). We were aware of only two potential predators in the demonstration wetland, adult splittails and great egrets *Casmerodius albus*. During our study, we observed feeding behavior by great egrets at edge areas in the floodplain wetland during daylight hours. Response to avian predators provides a poor explanation for the behavior of young splittails during period 1, when they showed a strong association with shallow, edge habitat during daylight hours. In other words, during the daytime the young splittails were in the same habitat as the avian predators; they did not move into deeper water until night, when the great egrets were not present. Adult splittails, the other potential predators in the pond, may occasionally be piscivores (Daniels and Moyle 1983). During period 1, the attraction of young splittails to shallow, edge habitat during daylight may have been a way to avoid the larger adults, which tended to aggregate in the deepest areas of the wetland. The observed shift into deeper water at night would be reasonable if the risk of predation by visual predators were substantially reduced. Diel shifts in habitat use are apparently used by other cyprinids as an antipredator behavior (Cerri 1983). The increased use of deeper water during period 2 may have reflected improved swimming ability and predator avoidance as the splittails grew larger.

The diel change in schooling provides additional support for the hypothesis that response to potential or actual predators was a major part of the behavior of young splittails. We observed that these fish showed the strongest schooling behavior during the daytime, a diel pattern that is consistent with the responses of other juvenile cyprinids to the presence of predators (Cerri 1983). Schooling is a common phenomenon in teleosts and may function to increase feeding success and reduce predation risk (Pitcher 1986). Cerri (1983) suggested that schools probably disperse at night because they lose visual cues to aggregate.

Our study data are insufficient to adequately address the causes of shifting habitat use and behavior in young splittails. Responses to predators are often highly complex, involving a balancing of the risks from terrestrial and aquatic piscivores (Power 1984) and resulting in species- or size-specific responses on the part of the prey (Brown and Moyle 1991). Alternatively, some of the temporal changes in splittail habitat use could be explained by environmental factors. For example, it is possible that juvenile splittails were attracted to shallow, edge habitat during period 1 because water temperatures were slightly higher there, providing a bioenergetic advantage given adequate food availability. Mean water temperatures were higher throughout the pond in period 2, so a broader range of habitats may have been within the preferred temperature range of splittails during that period. We did not specifically measure the spatial variability in water temperature during the study, but temperature effects are consistent with laboratory studies on young splittails. Young and Cech (1996) found that the final preferred temperatures and growth optima for splittails in a size range similar to that in our study were 22–24°C, depending on acclimation temperature. The mean daily water temperatures in period 2 (21–23°C) overlapped with this range, whereas those in period 1, when the fish showed a stronger association with shallow, edge habitat (Figure 2) were markedly cooler (15–20°C).

Although this investigation was limited to a single location and year, we believe that our results have potential management implications that warrant a more comprehensive series of studies. This small-scale study supports the idea that splittail reproduction could be improved through floodplain restoration (CALFED 2000), particularly if river–floodplain connectivity is improved in dry years. In the present study, splittails spawned after being transferred to a floodplain wetland, a largely inaccessible habitat type in dry years such as 2001. The flow fluctuations and turbidity levels in our model system were modest compared with those under natural conditions in Yolo Bypass, indicating that major flow variation and high turbidity events may not be critical requirements for restoration projects to support splittail spawning. We also observed ontogenetic and diel changes in habitat use by juvenile splittails, suggesting that restoration projects should incorporate multiple habitat types. The early life stages were associated with shallow habitat near sources of flow and emergent vegetation, while larger fish used deeper water in open and vegetated areas. It is unclear whether these distribution changes were primarily related to behavioral preferences, responses to predators, bioenergetics, or environmental variables. In any case, it seems prudent to provide a mosaic of floodplain habitat types in the design of initial restoration projects to ensure that the needs of different life stages are met. Subsequent monitoring of larger restoration projects will help to show whether our results are valid under ''real-world'' conditions, such as increased habitat variability and the presence of other fish species. We wish to emphasize, however, that our study does not provide sufficient evidence that floodplain restoration alone is adequate to restore the splittail to its historical abundance. The species resides in the San Francisco estuary, perhaps the most invaded estuary on the planet (Cohen and Carlton 1998). Splittails produced on seasonal floodplain habitat still face substantial obstacles from introduced competitors and predators and a radically altered food web.

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