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Habitat Associations and Behavior of Adult and Juvenile Splittail *(Cyprinidae: Pogonichthys macrolepidotus)* in a Managed Seasonal Floodplain Wetland

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ABSTRACT

Although there is substantial information about the benefits of managed seasonal wetlands to wildlife, little is known about whether this habitat can help support "at risk" native fishes. The Sacramento splittail *Pogonichthys macrolepidotus*, a California Species of Special Concern, does not produce strong year classes unless it has access to floodplain wetlands of the San Francisco Estuary and its tributaries. Our study examined the potential use of managed inundation to support spawning and rearing of splittail in years when the availability of seasonal habitat is limited. Wild adult splittail were captured during their spawning migration and transferred to a 3.8-ha engineered wetland, where they successfully spawned shortly after introduction. Radio telemetry studies suggested that post-spawning adults were relatively sedentary over the study period. Adult splittail were primarily located in habitats with open water or light vegetation, and in the deepest portions of the wetland. Snorkel sur-veys showed that early stages (mean 21-mm fork length [FL]) of young splittail produced in the wetland were strongly associated with shallow areas with shoreline emergent terrestrial vegetation and submerged aquatic vegetation, but moved offshore to deeper areas with tules and submerged terrestrial vegetation at night. Larger juveniles (mean 41-mm FL) primarily used deeper, offshore habitats during day and night. At night, schools of both younger and older juveniles dispersed, and individuals were associated with the bottom of the water column. These observations have important implications for the construction of managed and restored wetlands for the benefit of native fishes.

KEYWORDS

Seasonal wetlands, habitat use, fishes, splittail *Cyprinidae: Pogonichthys macrolepidotus*, cyprinids, behavior, San Francisco estuary, radio telemetry

SUGGESTED CITATION

INTRODUCTION

The importance of seasonal wetlands to fish spawning and rearing is well-recognized (Junk et al. 1989; Welcomme 1979; Mitsch and Gosselink 2000). In many regions, floodplain wetlands suffer from poor connectivity to adjacent rivers and streams, resulting in decreased suitability for fish that rely on seasonal habitat for spawning and rearing (Ward and Stanford 1995; Wiens 2002). Large areas of historical seasonal wetlands have been converted to artificially-managed systems to support waterfowl production. For example, in California, over 90 percent of historical wetlands have been lost, with most of the remaining areas managed as overwintering habitat for waterfowl and shorebirds (De Szalay et al. 1999). This pattern holds true in the San Francisco Estuary, where the largest remaining wetland areas are managed by government and private organizations. Characteristics of managed seasonal wetlands include pumps or siphons to artificially flood the habitat, along with weirs, dykes, and other control structures (Cowardin 1979; De Szalay et al. 1999). Additional actions to promote plants as wildlife food include burning, mowing or disking. Although there has been substantial progress in wetlands restoration, such projects typically focus on the needs of wildlife rather than fishes (Henning et al. 2006). Earlier studies have provided information about factors that structure fish communities in seasonal wetlands (Snodgrass et al. 1996), and the potential benefits of restoring tidal wetlands (Shreffler et al. 1992; Rozas and Minello 2001). New research has also provided insights into the features of floodplain wetlands that promote native fishes (Moyle et al. 2007). However, there is relatively little information about the value of managed seasonal wetlands for fish production, particularly for "at risk"

(e.g. threatened and endangered) fish species. Much of the reason for this gap is that basic life-history and habitat use is poorly understood for many native fishes (Moyle 2002). As evidence that managed wetlands have some potential for the enhancement of fisheries, Juardja et al. (2004) and Richards et al. (1992) found that artificially-constructed ponds provided some habitat value in areas where oxbows and off-channel perennial wetlands had been lost. Nonetheless, critical evaluations are needed on the effects of different management practices on fisheries; several studies have found that many structural techniques to encourage the growth of macrophytes in degraded coastal marshes have negative effects on fisheries production (Cowan et al. 1988; Herke et al. 1992; Rozas and Minello 1999). In response, alternative restoration strategies such as coastal marsh terracing have been developed that target fishery species (Rozas and Minello 2001).

Here, we examine the use of a managed seasonal wetland for the reproduction and rearing of Sacramento splittail *Pogonichthys macrolepidotus*, a native cyprinid. Sacramento splittail (herein referred to as "splittail") is the last surviving member of its genus; the only other species, Clear Lake splittail *P. ciscoides*, went extinct sometime during the late 1900s (Moyle 2003). Following substantial declines in juvenile production during an extended drought, splittail received protection under the Federal Endangered Species Act in 1999 (U.S. Fish and Wildlife Service [USFWS] 1999); however, its "threatened" status was remanded in 2003, based on recent evidence that abundance levels have improved, and efforts to restore the species (USFWS 2003; Sommer et al. 2007). California Department of Fish and Game (CDFG) also designated the fish as a Species of Special Concern in 1989, a status which it still retains.

Splittail has been the subject of intense research since it was initially proposed for listing in the 1990s. Recent studies have revealed that splittail is probably the most floodplain-dependent fish in the San Francisco Estuary (Figure 1) (Sommer et al. 2001a; Moyle et al. 2004; Sommer et al. 2007). The typical life-history pattern is for adult splittail to migrate
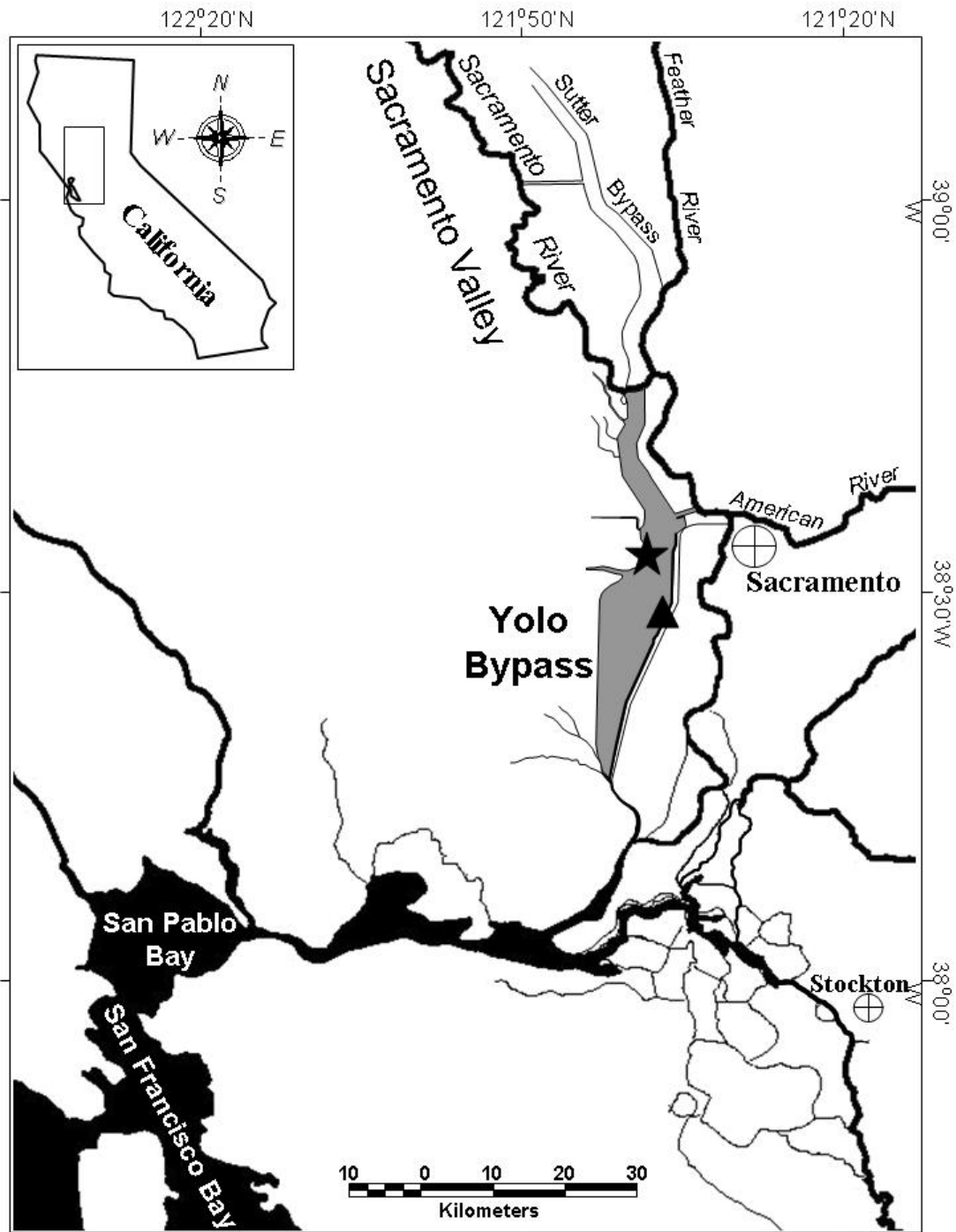
Figure 1. Location of Yolo Bypass (central dark shaded area). The San Francisco Estuary represents the region from San Francisco Bay upstream to Sacramento. The fyke trap location is shown with a dark triangle, and the study wetland is indicated with a dark star. The Yolo Bypass Wildlife Area occupies most of Yolo Bypass between the study area and the fyke trap.

upstream during high-flow periods into channels of the Sacramento-San Joaquin Delta and its tributaries in winter and spring (Daniels and Moyle 1983). Spawning activity is apparently concentrated on seasonal floodplain, which inundates during high flow events (Sommer et al. 1997; Moyle et al. 2004; Feyrer et al. 2006; Sommer et al. 2007). Spawning success is substantially lower in dry years, when the splittail population has limited access to floodplain spawning and rearing habitat. The relatively long life-span of splittail (up to 5–7 years) is therefore a valuable adaptation to the hydrologic variability of the Estuary. However, extended low flow conditions such as the drought during the 1980s and early 1990s can produce a major decline in abundance of young splittail (Meng and Moyle 1995; Sommer et al. 1997). This decline in abundance was a primary basis for concern among federal and state agencies during the 1990s (USFWS 1999; Sommer et al. 2007).

Several restoration programs are underway to increase fish populations of the estuary and its tributaries (Yoshiyama et al. 2000; Sommer et al. 2007). Floodplain restoration has been identified as a potential approach to support splittail and other native fishes. One major restoration goal for the San Francisco Estuary is to increase the amount of wetlands habitat, particularly in the Sacramento River's Yolo Bypass, the largest remaining floodplain (Figure 1). Historically, agriculture was the primary land use in the 24,000-ha Yolo Bypass. As a result of recent land acquisition by government and private organizations, the majority of the floodplain is managed as wildlife habitat. The largest managed area is the 6,500-ha Yolo Bypass Wildlife Area, which includes a mosaic of permanent wetlands, seasonal wetlands, grasslands, and riparian habitat. An additional regional restoration goal is to improve connectivity between the river and floodplain habitat. This has been achieved in nearby locations such as the Cosumnes River by actively breaching levees between rivers and floodplains (Florsheim and Mount 2002 and 2003). Although Yolo Bypass is one of the major spawning and rearing areas for splittail, the floodplain is only inundated from the Sacramento River in above-normal water years as a result of the system of levees and weirs constructed around its perimeter

(Sommer et al. 1997; Sommer et al. 2001a and b). In dry years when the floodplain is isolated from the river channels, managed inundation of wetlands has been suggested as an approach to improve production of splittail (Sommer et al. 2002).

To examine whether managed inundation of wetlands could be used to support splittail production in dry years, Sommer et al. (2002) stocked adult splittail into a model floodplain wetland. The effort resulted in successful spawning and preliminary observations on splittail early life-history. However, the study was conducted on a very small wetland (0.1 hectare) located outside of the Yolo Bypass, with no other fish species (i.e. competitors) and few predators. In the present study, we conduct a more "realistic" assessment of the potential use of managed habitat for splittail by using a large-scale seasonal wetland located in the Yolo Bypass Wildlife Area. The study wetland had a variety of other fish species, as well as avian and mammalian predators. An additional objective was to better describe the habitat use of adult and juveniles. Habitat associations for adults and early juveniles are poorly understood because they occur during high flow events, when high turbidity and extreme environmental fluctuations create major sampling problems. Moreover, the behavior of juvenile cyprinids has not been well-studied, particularly with respect to diel and ontogenetic changes (Garner 1996). We hoped that this information would be useful for the design and evaluation of habitat-restoration projects for splittail and other native fishes.

METHODS AND MATERIALS
Study Site

Our study was conducted in the Yolo Bypass, the largest floodplain of the San Francisco Estuary (Figure 1). As is typical of many estuaries on the Pacific Coast, it has been heavily modified by many factors including levee construction, river channelization, draining of wetlands, diversions, and introduced species (Bennett and Moyle 1996). The largest contiguous area of non-agricultural floodplain habitat is the Yolo Basin Wildlife Area, constructed in 1997 and managed by CDFG. During winter and spring, the floodplain is inundated from the Sacramento River

in about 70 percent of years (Sommer et al. 2004). However, extended droughts such as 1987–1992 can leave the floodplain dry for years. By summer, the floodplain is dewatered, except for perennial ponds and a single tidal channel.

Observational studies were conducted in a 3.8-ha floodplain wetland constructed in the Yolo Bypass Wildlife Area. To increase densities of fish during observations, we placed a 4.75-mm mesh barrier net near the northern tip of the wetland, creating a 0.6-ha triangular study site (Figure 2). Adding a barrier net was necessary because we were not able to capture enough adults (see below) to provide reasonable fish densities for the entire wetland. There were four basic habitat types in this study site:

1. emergent terrestrial vegetation (mud substrate with bermuda grass *Cynodon dactylon*; 2.9% of total study area)

2. submerged aquatic vegetation (dense beds of water primrose *Ludwigia peploides*; 4.9% of total study area)

3. submerged terrestrial vegetation (mud substrate with inundated bermuda grass; 55.6% of total study area)

4. beds of emergent tules (*Scirpus acutus*; 36.8% of total study area).

The first two habitats were primarily associated with the perimeter of the wetland. We obtained the surface area estimates by delineating the wetland with a global positioning system (Trimble Geo XT), then calculating surface area using a geographic information system (ESRI ArcGIS). Unlike the pilot 2001 study (Sommer et al. 2002), low densities (<10 individuals/ha) of at least three other fish species were present in the wetland during the study: mosquitofish *Gambusia affinis*, smallmouth bass *Micropterus dolomieu,* and catfish (*Ictaluridae*). Large-vertebrate predators were also present including a pair of river otters *Lontra canadensis* that resided adjacent to the wetland, and egrets *Casmerodius albus* that made intermittent visits (approximately one observation/week).

As is typical for managed seasonal wetlands in northern California, the wetland was initially flooded in October 2004. The depth profile sloped gradually (0.7 cm/m) from the edge to approximately 10 meters offshore. Water surface elevations were maintained by inundating the wetland with water from adjacent perennial channels, supplemented by surface runoff from precipitation events. Wetland depth was recorded daily, and had a mean depth of 0.41 m during the study period. Based on the mean depth, area, and recirculation rate, the fastest hydraulic residence time (i.e. flushing rate) was approximately 0.4/day, about three times as fast as estimates for peak natural flood events in Yolo Bypass (Sommer et al. 2004). Water-level fluctuations in our model floodplain wetland had a standard deviation of 0.03 m during the March–April fish observation period, compared to standard deviation levels of 0.20 m or more during recent long-duration (e.g. > 30 d) Yolo Bypass flood events (Sommer et al. 2004). Mean daily water temperatures (as measured by an Onset logger) were observed to increase gradually over the course of the study, from 12–18°C during March to 16–22°C during May. Water clarity was much higher in our floodplain wetland than in Yolo Bypass. Visibility for divers (see below) was 2–5 meters, while visibility during Yolo Bypass flood events is typically less than 0.5 m.

Spawning Stock

Methods for fish collection were similar to the 2001 pilot study (Sommer et al. 2002). During February 2 through March 7, 2005 we collected 68 adult splittail (295 mm ± 45 mm SD FL) on their upstream migration using a 3-meter-diameter fyke trap in a perennial tidal channel of the Yolo Bypass (Figure 1). Most of the catch occurred during the last 2 weeks of the period, when fish were transported immediately to the wetland. During other periods of lower catch, splittail were held in aerated tanks up to 2 days before transport. We believe that these fish were the sole source of spawning stock; splittail could not have swum naturally into the study wetland during this very dry year, when only pumped water was available to this particular site. In addition, the Yolo Wildlife Area pumps are highly unlikely to have transferred these relatively large fish into their distribution network.

Figure 2. Floodplain wetland study area. Snorkeling was conducted along west-east transects based on paired circles located on "opposite" sides of the wetland. The telemetry stations were located approximately at the 1st, 5th, and 10th paired circles from the fish barrier net. The habitats were: (1) tule (grey areas); (2) submerged aquatic vegetation (horizontal line areas); (3) submerged terrestrial vegetation (white areas); and (4) emergent terrestrial vegetation (black areas).

Adult Splittail Behavior

We examined adult splittail habitat use by radio-tagging 15 of the adult splittail and tracking their position and movements in the wetland. Immediately after capture in the fyke trap, fish were anesthetized with clove oil (Woody et al. 2002) and ATS (Advanced Telemetry Systems Inc., Isanti MN) radio-tags were surgically implanted into the peritoneal cavity. Tagged fish were placed in the ice chest with source water for recovery, and immediately transported to the study pond. Once at the wetland, fish were inspected to make sure they were fully recovered from the anesthesia and surgery (i.e. similar to pre-surgery swimming behavior and gill ventilation rates), and then released from shore.

Tracking was conducted during a 3-week period in March. We used triangulation with two ATS receivers, each outfitted with directional antennas, to locate the position of each fish in the wetland. Readings were taken by two trackers, who identified fish locations at three paired stations located on opposite sides of the wetland (Figure 2). For data analysis, an idealized grid with 10 × 10 m "cells" was overlaid on the wetland. The triangulated positions of the fish were plotted on the wetland grid to identify the cell in which the fish was located. Measurement error associated with fish position was estimated based on two tags (without fish) cast into the wetland at random locations by an independent observer. The locations of these tags were recorded as part of the normal field sampling. Based on a minimum of 22 observations for each tag, the 95 percent confidence interval for the methods was approximately +/- 2 meters from each grid cell.

Radio tracking was conducted during day (1200–1400 hours) and night (2000–2130 hours) to determine whether there were differences in distribution and behavior. We hypothesized that adult fish behavior would vary substantially based on time of day. Fish behavior was analyzed in terms of the vegetation type and mean depth used. For the purposes of these analyses, we assumed that the error distributions of the fish locations were random for each observation. Hence, the analyses were based on the habitat characteristics of each cell in which the fish was located

by telemetry. Each cell in the grid was grouped into three vegetation categories: <33% vegetation in cell, 33–66% vegetation in cell, or >66% vegetation in cell. Each grid cell was also grouped into three categories based on the mean depth of the cell: < 0.30 m; 0.31–0.45 m; and > 0.46 m. Adult behavior was evaluated in terms of "activity level" and "schooling behavior." Activity level was classified as: a change in fish position between observations of at least 3 grid units; or a change in fish position of less than 3 grid units. The 3-grid-unit threshold was selected because we believed that it would clearly exceed the measurement error (0.2 units) of each of the observations. For each fish observation, we characterized schooling behavior as: the presence of another fish located within a 1-grid-unit radius ("neighbor"); or no other fish within a 1-grid-unit radius ("no neighbors").

We did not statistically analyze diel or daily changes in vegetation use, depth use, or swimming activity level because of the relatively small number of fish that moved at least 3 grid units, our measurement error threshold. Chi-square goodness of fit analyses were used to compare the observed number of fish in each of the three vegetation or depth categories to the expected distributions based on the availability of cells containing each of the three vegetation or depth categories as estimated by GIS. The day and night observation data were combined for these analyses. We did not attempt to statistically evaluate whether schooling behavior ("neighbors") was non-random because of the complexity in defining an expected distribution of fish for each sampling period.

Juvenile Splittail Behavior

We observed juvenile splittail via snorkeling, an effective method developed in the 2001 pilot study (Sommer et al. 2002). Observations were made at a distance of at least 1 meter away from the fish, to minimize behavioral effects. This was consistent with our earlier observations on the responses of young splittail to divers; the fish showed no obvious change in behavior unless the observers moved to within less than 1 meter of the splittail. In very shallow water (< 0.30 m), observations were made from shore or by

wading. A team of three divers conducted the observations throughout the study, with 1–2 working each day. Dive lights were used for the night observations.

Snorkel surveys were conducted by divers during two sampling periods: 1) April 5–14, 2005; and 2) May 3–14, 2005. For each sampling period, observations were made during the day (1400–1600 hours) and at night (1–2 hours after sunset) to assess diel changes in distribution and behavior. The pond was divided into 20 transects along an east-west gradient—transect locations were based on the shoreline markers developed during the radio-tracking portion of the study. Each transect was 2 meters wide, and varied in length from 11 to 89 meters. On each sampling day, 4–12 transects were randomly chosen during daylight hours, and a similar number was selected at night. One diver was assigned to each transect, and recorded all of the fish observed. A single observation was defined as a single fish or "school" (2–1,000 individuals) within a 1-m^2 area (Sommer et al. 2002). 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, dominant habitat type within the nearest 0.5 m (emergent terrestrial vegetation, tule, submerged aquatic vegetation, submerged terrestrial vegetation), water column position (top third, middle third, or bottom third of water column), and depth (actual location for individuals, center of the school for groups). A sample of 9–13 fish was netted during each sampling period to measure mean fork length (FL). The growth rate of these fish was calculated by dividing the fork length by the estimated fish age (see below).

We summarized the juvenile data in three-way contingency tables using the following grouping variables: 1) sampling period (1 or 2); 2) time of day (day or night); and 3) 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 analysis was also used to compare habitat and depth use to the expected distributions based on the availability of each habitat type as calculated by GIS analysis.

Timing of Spawning

To provide information about the exact timing of fish spawning, we analyzed the age of the juveniles netted for FL measurements (see above) using otolith methods (Stevenson and Campana 1992). Lapilli otoliths were extracted from 11 randomly-selected fish and rinsed briefly with 10% sodium hypochlorate to remove any attached organic tissue. The otoliths were then rinsed in deionized water and allowed to air dry. Dry otoliths were individually mounted on glass microscope slides in CrystalBond mounting media (Lakebluff, Illinois) and polished to the core with 0.3-mm lapping film. Ages of individual fish were obtained by examining otoliths under $100 \times$ -300x magnification with the aid of an image-analysis system (Image Pro Plus 4.5.1, Silver Spring, Maryland). Ages were estimated by counting the number of increments from the core to the perimeter of the otolith. Daily increment formation for age-0 splittail has been validated by Feyrer et al. (2007). These analyses allowed us to calculate the date at which splittail hatched from eggs. Based on earlier studies of egg development (Feyrer et al. 2007; Moyle et al. 2004), we assumed that spawning occurred 4 days before hatching.

RESULTS

Adult Splittail Behavior

Overall, adult splittail exhibited relatively little movement during the telemetry study. Of 109 paired diel observations, only four moved at least 3 grid units between their day and night positions. Moreover, only nine of 104 total observations moved at least 3 grid units over any 24-hour sampling interval. Adult splittail were observed in all three vegetation categories (<33%, 33–66% and >66% vegetation coverage), but were most abundant in the lightest vegetation category (Figure 3a). Habitat use was significantly different than the expected distributions based on the availability of each of the three vegetation categories (Chi-square = 129, df = 2, p << 0.001). Fish were most abundant in deeper areas of the wetland (Figure 3b), which was significantly different than the expected levels for each depth range (Chi-square = 194, df = 2, p << 0.001). The majority of adult obser-

vations were within at least 1 cell unit of another neighbor (Figure 3c).

Juvenile Splittail Behavior

Larval splittail were first observed on March 28, 2005, about 2 months after adults were first introduced into the wetland. The young fish that we subsequently observed in our pond were unlikely to have been from any source other than the stocked spawners; no splittail were seen in limited observations of adjacent wetlands or canals, the source of water to this wetland.

The total number of observations varied somewhat between each sampling period: Period 1 day (n = 63); Period 1 night (n = 102); Period 2 day (n = 70); Period 2 night (n = 74). The mean size of young splittail collected with nets was 21 mm $\pm$ 3 mm SD during the first sampling period, and 41 mm $\pm$ 2 mm SD during the second. Based on otolith estimates of fish age in a random subset of 11 fish, mean growth rate was 0.35 mm/d $\pm$ 0.05 mm SD. The study was completed in June 2005 when the wetland was drained and the fish were allowed to emigrate to the Delta.

Young splittail were observed in all four habitat types (Figure 4a). However, habitat use was significantly different than the expected distributions based on habitat availability during Period 1 day (Chi-square = 223.6, df = 2, p << 0.001), Period 2 day (Chi-square = 23.3, df = 2, p << 0.001) and Period 2 night (Chi-square = 25.1, df = 2, p << 0.001), but not during Period 1 night (Chi-square = 3.3, df = 2, p = 0.20). The log-linear analysis showed that there were statistically significant interactions between sampling period and habitat use, and between time of day and habitat use (Table 1). For Period 1 during the daytime, there was a strong association with habitats located relatively close to the edge of the wetland, emergent terrestrial vegetation, and submerged aquatic vegetation (Figure 4a). At night during Period 1, there was a substantial shift into submerged terrestrial vegetation and tule stands.

Some fish were observed in the upper part of the water column during both periods, with a shift away
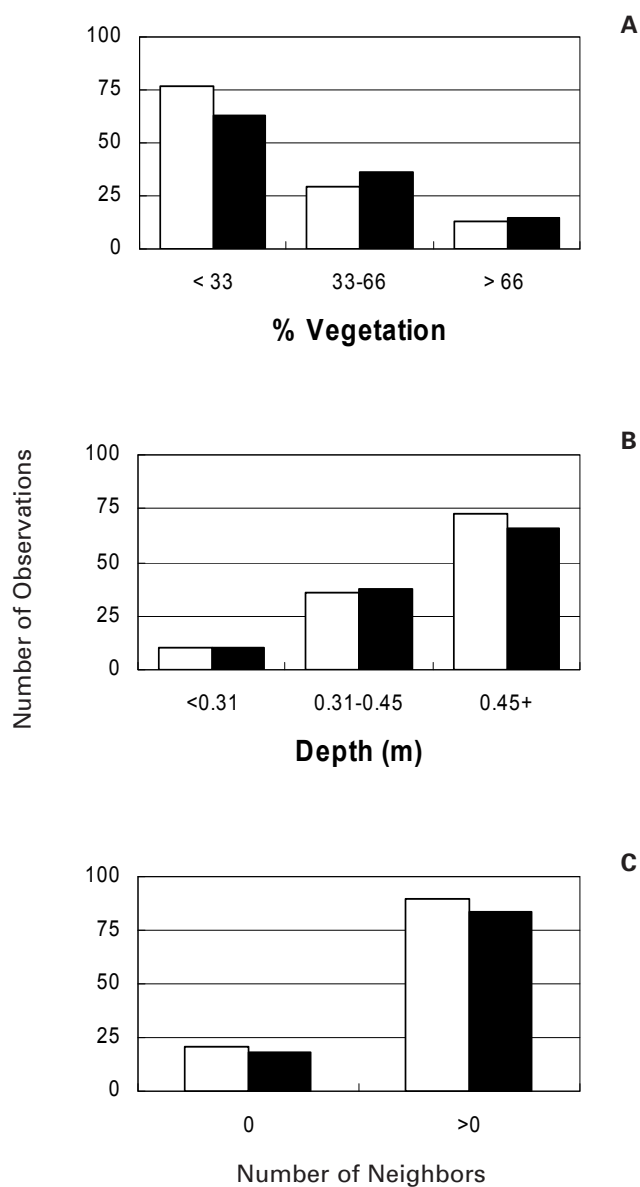

Figure 3. Adult splittail habitat use during day (open bars) and night (dark bars) during the study period. The y-axis for each variable is the total number of observations of adult splittail. (A) vegetation coverage within the sampling grid cell where fish were observed (%); (B) mean depth of water column (m); and (C) the number of neighbors as measured by the presence of other individuals within a radius of one study grid unit.
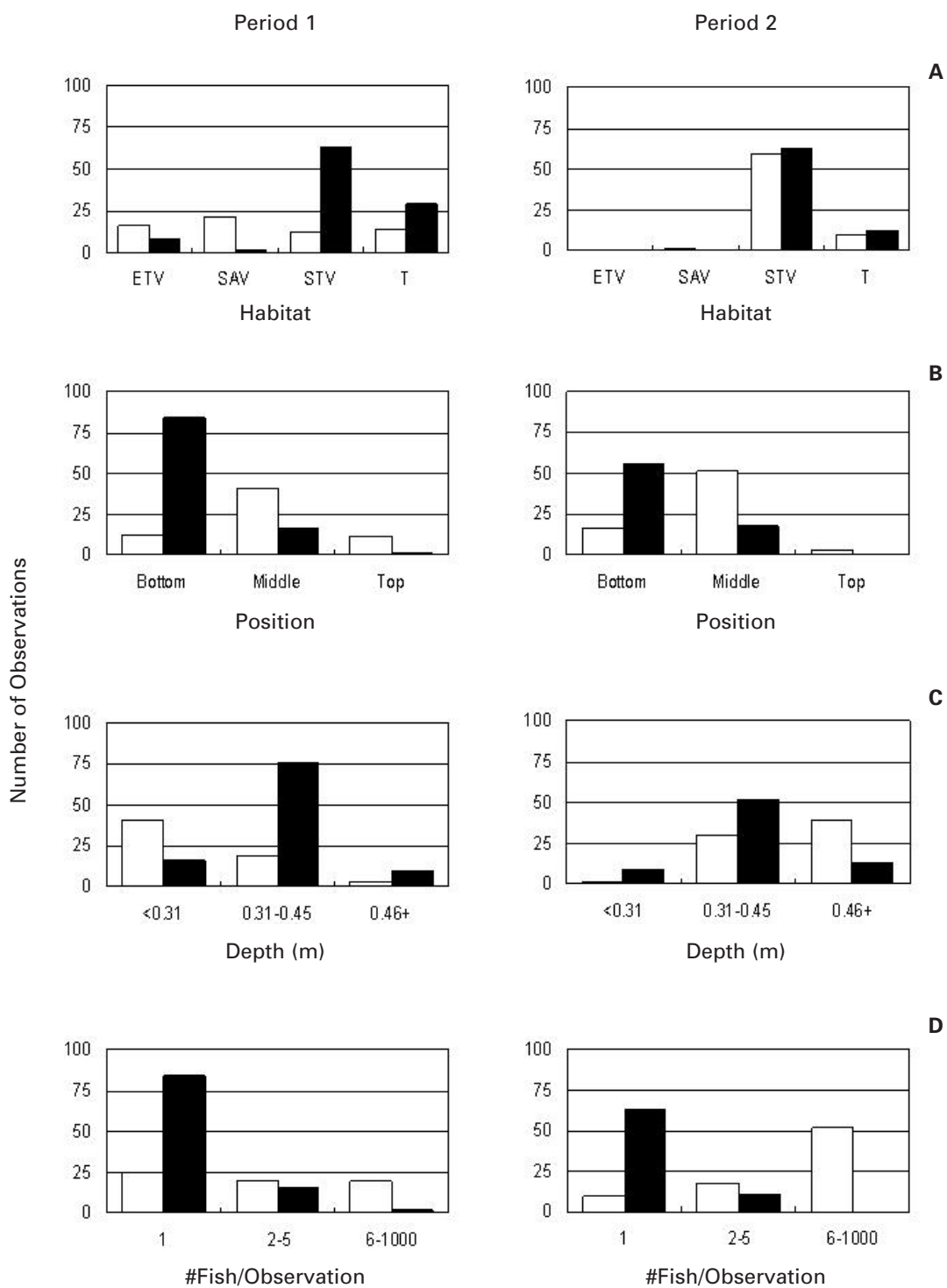
Figure 4. Juvenile splittail habitat use during day (open bars) and night (dark bars) for two sampling periods: "Period 1" and "Period 2." The y-axis for each variable is the total number of observations of one or more fish. (A) habitat type (ETV = emergent vegetation; SAV = submerged aquatic vegetation; STV = submerged terrestrial vegetation; and T = tule beds); (B) water column distribution ("top," "middle," "bottom"); (C) depth of water column (m); and (D) school size as measured by the number of fish in each observation.

from the surface during Period 2 (Figure 4b). At night, there was a marked shift toward the bottom of the water column; the majority of the fish were benthic, or within a few centimeters of the bottom. These changes in distribution were supported by log-linear analysis, which showed significant interactions between sampling period and water column position, and time of day and water column position (Table 1).

The depth distribution of fish changed substantially on a diel basis, and between periods 1 and 2 (Figure 4c). The majority of splittail were associated with very shallow (< 0.31 m) edge areas of the wetland during Period 1, but during night and Period 2 (day and night), the distribution shifted to deeper offshore areas. The data showed statistically-significant interactions between time of day and depth distribution, and between sampling period and depth distribution (Table 1). Depth use was significantly different than the expected distributions based on the availability of different depth ranges during Period 1 day (Chi-square = 57, df = 2, p << 0.001), Period 1 night (Chi-square = 26.5, df = 2, p << 0.001), Period 2 day (Chi-square = 39.9, df = 2, p << 0.001), and Period 2 night (Chi-square = 13.2, df = 2, p < 0.001).

There were marked changes in schooling behavior between day and night hours for both sampling periods (Figure 4d). During day hours, the majority of observations were schools of at least two fish, but school sizes were typically larger during Period 2. At night, the schools dispersed and most observations were of individual fish. These results were reflected in the log-linear analysis, which demonstrated significant interaction between sampling period and school size, and time of day and school size (Table 1).

Timing of Spawning

The estimated spawning date from otolith analyses and length observations revealed that the fish were spawned over a relatively broad time period, suggesting multiple cohorts (Figure 5). The earliest estimated spawning date coincided with the week that the first adults were stocked into the wetland, indicating that some spawning occurred as soon as adults were introduced.
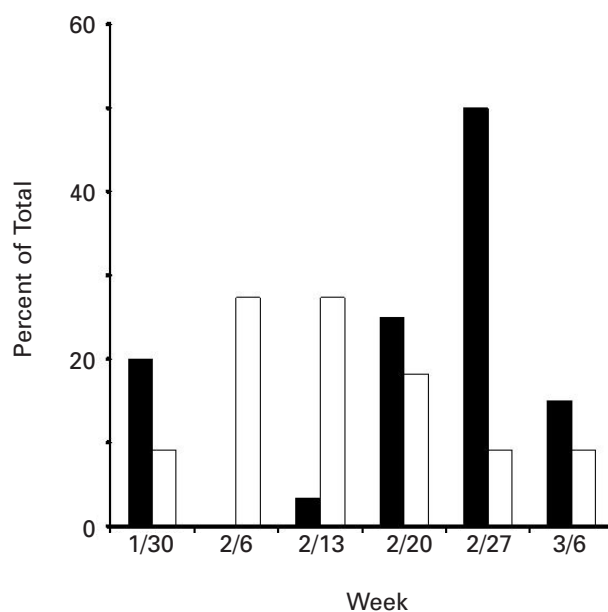

Figure 5. Estimated spawning dates for 11 randomly-selected juvenile splittail (light bars) in relation to when the 68 adults were stocked into the wetland (dark bars).

Table 1. Results of three-way log-linear analyses for observations of juvenile splittail distribution and school size. We tested for interactions amongst the following three effects: (1) sampling period; (2) time of day; and (3) distribution variable (habitat, water column position, or depth) or school size variable. The marginal Chi-square results are shown with the degrees of freedom in parentheses.

Effect	Habitat	Water Column Position	Depth	School Size
1 x 3	65.6 (3) **	8.1 (2)*	57.8 (2)**	20.5 (2)**
2 x 3	33.4 (3)**	111.1 (2)**	39.1.0(2)**	150.1 (2)**

*Statistical significance levels are indicated by asterisks: *p < 0.02, ** p << 0.001.*

DISCUSSION

The study results supported our hypothesis that managed wetlands could potentially be used to benefit splittail spawning and rearing in years when floodplain inundation is limited. Our findings are consistent with previous evidence that floodplain wetlands support fish production in tropical (Junk et al. 1989; Welcomme 1979) and temperate ecosystems (Bayley 1995; Gutreuter et al. 2000). We acknowledge that these findings may not be applicable to other regions, cyprinid species with different life-histories, or wetland types. Nonetheless, we believe that our study has applications to the management and biology of cyprinids.

Relevance to the Biology of Splittail and other Cyprinids

The idea that seasonal floodplain is critical for splittail reproduction is now well-established (Sommer et al. 1997; Sommer et al. 2002; Moyle et al. 2004; Feyrer et al. 2006). This pattern is consistent with other "at risk" North American cyprinids including humpback chub *Gila cypha* (Kaeding et al. 1990) and Colorado pikeminnow *Ptychocheilus lucius* (Tyus 1991), which use floodplain for rearing. The present study provides insight into why this is the case for splittail. Adult splittail were relatively sedentary in our study wetland, suggesting that post-spawning "resting" habitat may be important for the species. Similarly, our snorkel surveys showed that early stages (mean 21 mm FL) of young splittail produced in the wetland were strongly associated with shallow areas, a common response of freshwater fish (Glova and Jellyman 2000; Jakober et al. 2000). Hence, inundation of floodplain provides access to large areas of shallow, vegetated habitat for post-spawning recovery of adults, and rearing of juveniles. High levels of invertebrate prey provide an additional benefit of seasonally-inundated habitat (Sommer et al. 2001b; Sommer et al. 2004). As a consequence, young splittail grow better in floodplains (Feyrer et al. 2007)

The observed diel and ontogenetic changes in juvenile splittail distribution are consistent with observations from a pilot study of splittail in a wetland (Sommer et al. 2002); such changes are also apparently a common behavior in many freshwater fish (Matthews 1998). The degree to which our observations fully represent "wild" splittail is unknown— relatively low turbidity and flow conditions in the wetland could have altered their behavior. We did not specifically address the cues or mechanisms for these complex behaviors, which could be a result of physical factors (Young and Cech 1996), biological factors (Power 1984), or both. However, other studies on young cyprinids suggest that food availability and predation are the primary factors controlling habitat use (Rheinberger et al. 1987; Garner 1996). Predation was potentially a major issue in our study area, as we observed several potential predators including catfish, centrarchids, wading birds, and river otters. Diel variation in juvenile splittail schooling behavior may also be related to predation pressure, a pattern observed in other young cyprinids (Cerri 1983). This might explain why there were schools in the light of the day, but much less schooling activity in the dark.

Our study also builds on a growing body of knowledge about highly-mobile adult cyprinids, whose behavior can be complex during the spawning season (Huber and Kirchhofer 1998; Koed et al. 2002; Winter and Fredrich 2003). It is unclear whether the relatively sedentary behavior of adults in this study represents a typical pattern for post-spawning splittail in local floodplains, or whether the observed behavior was a consequence of the unique conditions in the study. As evidence that the observations may be realistic, many cyprinids migrate long distances for spawning and perhaps other purposes, and then become relatively sedentary for extended periods of time before returning to river and downstream habitat (Clough and Beaumont 1998; Huber and Kirchhofer 1998; Lucas and Baras 2001; Crook 2004). This sedentary behavior may represent a post-spawning recovery period. However, we acknowledge that the behavior of the adult splittail could have been influenced by several factors. Tagging may have been stressful, reducing the activity of the adults. Nonetheless, visual observations of adult splittail during our juvenile snorkel survey suggested that even untagged individuals were relatively inactive and cryptic. Water velocity has a substantial effect on

adult cyprinid behavior (Fore and Keckeis 1998), so it is possible that the inactivity resulted from the unnaturally low flow conditions in the wetland. Similarly, the confined, low flow and low turbidity conditions in the wetland may have created atypical predation pressure that substantially modified behavior. River otters preyed on at least several of the adult splittail in the study including one radio-tagged fish, whose tag was found near their den.

Potential Management Applications

Given the importance of floodplain for splittail reproduction, it is clear that seasonal habitat must be considered as part of the management strategy for this species (Moyle et al. 2004). First, floodplain restoration provides a way to increase total habitat availability for splittail and other species such as Chinook salmon (Sommer et al. 2001b). A complementary approach is to improve hydrologic connectivity between floodplain and the channels that splittail use for migration during spawning season (Moyle et al. 2004). The shifting diel and ontogenetic behavior of juvenile splittail provides evidence that wetland restoration projects should incorporate multiple habitat types. In other words, providing a mosaic of floodplain habitat types in the design restoration projects may help to ensure that the needs of different life stages are met. Note, however, that this does not mean that all types of wetlands are suitable for splittail or other cyprinids. For example, observations in permanent wetlands of the Yolo Bypass and the nearby Cosumnes River suggest that perennial wetlands may not support good production of native fishes because, in part, these habitats become dominated by alien competitors and predators (Feyrer et al. 2004; Moyle et al. 2006).

Our single-year study supports the idea that splittail reproduction also could be supported by managed wetlands. In the present study, splittail spawned after being transferred to a floodplain wetland, without targeted manipulations of physical conditions such as depth, flow, or turbidity. We acknowledge that our approach was not necessarily a practical way to improve populations of splittail and other native fishes. Capturing fish on their spawning migration and moving them to suitable wetlands requires substantial effort and introduces stress. A better approach might be to allow fish to migrate directly into the managed wetlands. Such a system probably could be developed in Yolo Bypass because of the extensive water distribution network for waterfowl; however, we chose to actively stock fish into the wetland because it allowed us to tag fish and conduct the study with known population levels. The suitability of "passive" movements of splittail and other native fishes on and off of managed seasonal wetlands needs to be critically evaluated because even continuously-open water-control structures can have negative effects (e.g., reduced passage, decreased production) on fisheries in coastal wetlands (Rozas and Minello 1999). One encouraging sign is that young Chinook salmon *Oncorhynchus tshawytscha* exhibited low stranding rates in the Yolo Bypass Wildlife Area's managed wetlands after flood events (Sommer et al. 2005). Relatively high rates of stranding were observed only next to the two major weirs of the floodplain, located far from our splittail wetland. Follow-up work is needed under low flow conditions to determine if adult and juvenile splittail can easily pass typical water-control structures in managed wetlands such as gates, pipes, and canals. Nonetheless, the merits of managed wetlands should be considered as part of an integrated strategy for the conservation, restoration, and enhancement of "at risk" fishes.

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