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[Article]

Living in a Dynamic Environment: Variability in Life History Traits of Age-0 Splittail in Tributaries of San Francisco Bay

FREDERICK FEYRER* AND TED SOMMER

Aquatic Ecology Section, California Department of Water Resources, 3251 S Street, Sacramento, California 95816, USA

JAMES HOBBS

Bodega Marine Laboratory, University of California–Davis, Post Office Box 247, Bodega Bay, California 94923, USA

Abstract.—Splittail *Pogonichthys macrolepidotus* is a relatively large cyprinid endemic to the San Francisco Estuary watershed. During late winter and early spring, splittails migrate from the estuary to upstream rivers and floodplains for spawning. During 2002 and 2003, we examined the diet composition, muscle stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$), and growth rates of age-0 splittails in the four primary rivers used for spawning. Overall, we found substantial variability in all three traits in spatial and temporal comparisons. Age-0 splittails consumed a variety of prey taxa, consisting almost exclusively of aquatic invertebrates, larval stages of chironomids or copepods generally being the most common. We found that the $\delta^{15}N$ and $\delta^{13}C$ signatures of age-0 splittails significantly varied spatially and temporally ($\delta^{15}N$ range = 6.1–19.6‰; $\delta^{13}C$ range = −36.3 to −17.5‰). Environmental conditions, namely flow and how it manipulates habitat connectivity, appeared to affect $\delta^{13}C$. Age-0 splittails exhibited substantial variability in growth rate both spatially and temporally. However, this variability was not associated with diet composition or stable isotope signatures, suggesting that food availability and physical habitat conditions were important factors affecting growth rates during our study.

A fundamental goal in aquatic ecology is to understand how populations persist in highly variable environments. Spatial and temporal variability in environmental conditions can exert strong influences on life history traits, which may ultimately affect population parameters (Baltz and Moyle 1982; Frazer et al. 1991; Bronikowski et al. 2002). For fish, the quantification of early life history traits is an important step in building population models that can evaluate the relative affects of environmental conditions and other factors on abundance (Houde 1987; Levin and Stunz 2005). This is particularly true for fishes that exhibit periodic life history strategies (Winemiller and Rose 1992). Periodic strategists exhibit variable non–density-dependent recruitment episodes that are typically driven by favorable environmental conditions for early life stages (Winemiller and Rose 1992; Winemiller 2005). Moreover, many species have alternative life histories that may be influenced by habitat use at early life stages (Secor 1999). Thus, information on how early life history traits vary along environmental gradients may provide valuable insights on mechanisms of recruitment for fish living in dynamic environments.

The splittail *Pogonichthys macrolepidotus* is a species of high management concern in California. It was formerly a federally listed threatened species because of presumed long-term declines in abundance and distribution, and remains a species of special concern for the U.S. Fish and Wildlife Service and the California Department of Fish and Game. It is also the last living member of its genus following the extinction of the Clear Lake splittail *P. ciscoides* during the previous century (Moyle 2002). Splittail exhibits periodic life history attributes that suggest environmental conditions early in life control recruitment. There is no stock–recruit relationship for splittail, and large fluctuations in annual recruitment coincide with wet (high recruitment) or dry (low recruitment) conditions (Daniels and Moyle 1983; Meng and Moyle 1995; Sommer et al. 1997). It is believed that the availability of expansive floodplains and inundated river margins during wet years provide optimal spawning and rearing habitat that leads to high recruitment (Sommer et al. 1997; Moyle et al. 2004; Feyrer et al. 2006a). The splittail's longevity, large size, high fecundity, and broad environmental tolerances presumably enable it to withstand extended dry periods, such as droughts, between wet years (Daniels and Moyle 1983; Young and Cech 1996; Feyrer and Baxter 1998; Moyle et al. 2004).

* Corresponding author: ffeyrer@water.ca.gov

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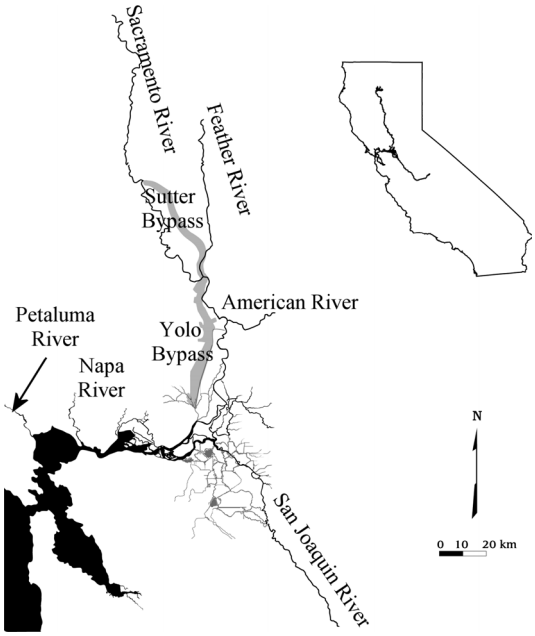

FIGURE 1.—Map of the San Francisco Estuary showing the sections of the Petaluma, Napa, San Joaquin, and Sacramento rivers where age-0 splittails were collected.

Given the splittail's periodic life history strategy, it is important to understand how environmental variation affects early life stages. The San Francisco Estuary is a very dynamic, river-dominated system (Kimmerer 2002). The combined effects of tides and intra- and interannual variability in river flows entering the estuary create substantial temporal and spatial variability in physical habitat conditions. Splittails are broadly distributed and have established two separate genetically distinct populations in the estuary (Feyrer et al. 2005; Baerwald et al. 2007). We conducted a study during the springs of 2002 and 2003 to examine the factors affecting the growth and feeding ecology of age-0 splittails across their distribution because these factors are often strong determinants of early life history success. We quantified growth rates, diet composition, and stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) of muscle tissue of individual age-0 splittail. We examined these traits across spatial (regional) and temporal (annual) scales and asked if growth rate, diet, and trophic position vary in different rearing environments, and what implications this has for management. Ultimately, we hope to use this information in population models (Moyle et al. 2004) in order to better examine the relative impact of environmental variability and management actions on splittail abundance.

Methods

Study area.—San Francisco Estuary (Figure 1) is the largest estuary on the Pacific coast of the United States. The estuary is well known for anthropogenic modifications that have highly altered most natural elements of the system (Nichols et al. 1986). Modifications include the loss of wetlands via draining and diking for agriculture, channel modifications for flood control and navigation, and a variety of water management activities including storage, conveyance, and large-scale water diversion from the southern delta. Similar to many other estuaries, freshwater flow is a principal cause of physical variability in the system. The local Mediterranean climate has a strong effect on flows entering the estuary (Kimmerer 2002). Seasonally, flows can vary by more than 10-fold with most flow entering the system late winter through spring. Interannually, flows can also vary by over 10-fold owing to regional climate patterns. Water enters the estuary primarily from California's two largest rivers—the Sacramento (from the north) and San Joaquin (from the south)—which drain a watershed encompassing 40% of California's surface area. The rivers converge in the upper estuary to form the Sacramento–San Joaquin Delta, a 3,000-km^2 network of tidal freshwater channels. Water in the estuary gradually increases in salinity as it moves west through Suisun Bay, San Pablo Bay, San Francisco Bay, and ultimately into the Pacific Ocean. Two additional rivers—the Napa River and the Petaluma River—enter the estuary near San Pablo Bay. The Napa River joins San Pablo Bay at its northeastern corner near Carquinez Strait, and the Petaluma River joins at the northwestern corner at Black Point.

We studied life history traits of age-0 splittails in the Sacramento, San Joaquin, Napa, and Petaluma rivers. These rivers encompass the full distribution of both genetically distinct populations of splittail: one population is represented in the Napa and Petaluma rivers, while the other population is represented in the Sacramento and San Joaquin rivers (Baerwald et al. 2007). These four rivers differ substantially in environmental characteristics including flow, water temperature, and salinity due to variation in watershed characteristics and proximity to marine habitats. Approximate watershed sizes are as follows: Petaluma River, 378 km^2; Napa River, 1,100 km^2; San Joaquin River, 35,000 km^2; and Sacramento River, 62,000 km^2. We obtained flow data for the Sacramento and San Joaquin rivers from the Interagency Ecological Program's DAYFLOW database (www.iep.water.ca.gov/dayflow/index.html) and for the Napa and Petaluma rivers from the California Data Exchange Center

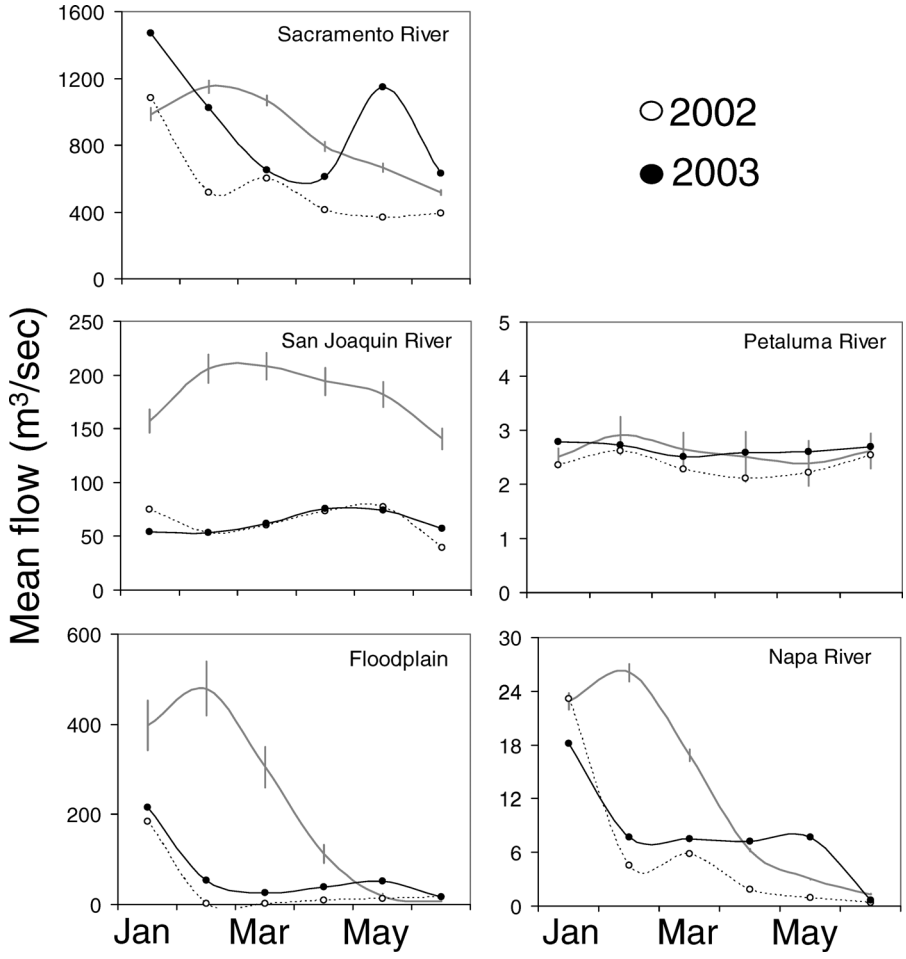

FIGURE 2.—Mean flow at locations where age-0 splittails were sampled. Note that the data for the Petaluma River are stage (meters above sea level). Floodplain data are from Yolo Bypass. The gray lines represent historical averages and 2 SEs and are based on available data. The historical time period for the Sacramento River, floodplain, and San Joaquin River is 1956–2004, that for the Petaluma River is 1998–2003, and that for the Napa River is 1984–2004.

(cdec4gov.water.ca.gov/); the Petaluma River is gauged only for stage. During our study in 2002 and 2003, flow patterns matched historical trends in that they were highest in the Sacramento River, intermediate in the San Joaquin River, and lowest in the Napa and Petaluma rivers (Figure 2). Flows during the springs of 2002 and 2003 were generally at or below long-term average conditions for each individual river (Figure 2). Temperature profiles of the rivers (obtained from continuous recorders that we deployed) all exhibited typical winter–spring (cool–warm) seasonality. Mean daily temperatures ranged from 12°C to 15°C in March up to 20–23°C in June, and on average were slightly warmer in 2002 (Figure 3). Salinities measured at the time of fish sampling (Feyrer et al. 2005) were relatively high for the Petaluma River (mean values = 13‰ in 2002 and 6‰ in 2003) and the Napa River (5‰ in 2002 and 0‰ in 2003), while the Sacramento and San Joaquin rivers are freshwater.

The four rivers also differ in physical habitat characteristics. The Napa and Petaluma rivers are essentially brackish intertidal sloughs except during spring, when periods of runoff produce freshwater flow. In a broad sense, the habitat in these rivers can be characterized as shallow channels with soft mud or detritus substrate. Small channels or mud flats can become fully exposed during low tides. Shoreline habitats are typically lined with either tules *Scirpus* spp. or by riprap (rock reinforcement). In contrast, the San Joaquin and Sacramento rivers are predominately not tidal where splittails spawn and age-0 fish were sampled. These rivers have been highly altered for

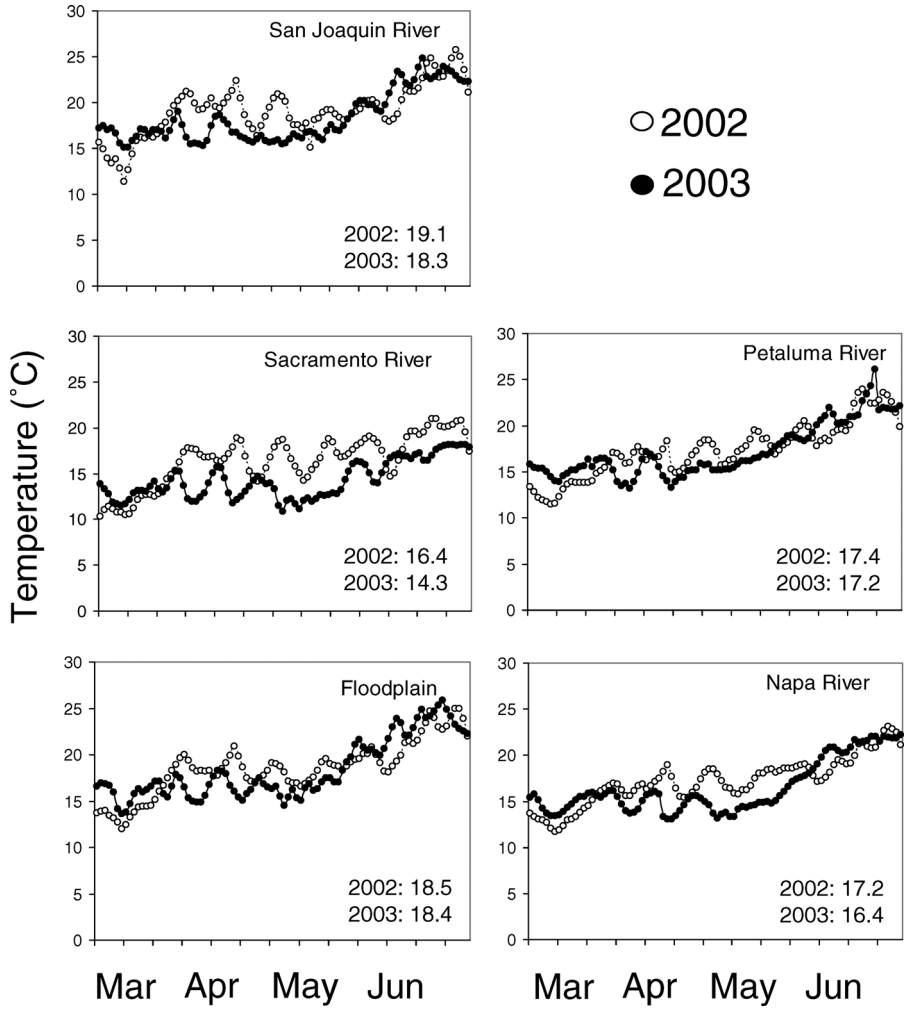

FIGURE 3.—Mean daily water temperature at locations where age-0 splittails were sampled. Floodplain data are from Yolo Bypass. The values given within the plots are annual averages.

water and flood management. Thus, flow regimes and natural floodplain and channel meander habitats have been greatly altered or diminished. A major difference in the two rivers is that most of the San Joaquin River flow is diverted to other locations at upstream dams, while the Sacramento River is used heavily to convey water into and through the delta. Thus, flows in the Sacramento River are not degraded to the extent of the San Joaquin River, allowing the persistence of a relatively healthy native fish population (May and Brown 2002; Nobriga et al. 2005). The rivers are lined on either side by levees, and shoreline habitats are dominated by mud or sand banks with extensive riprap. The Sacramento River also has regions where levees are set back from the river channel far enough to allow the formation of backwater habitats. Following Feyrer et al. (2005), we defined backwaters as bodies of water distinct from the main channel, which are connected to the main channel at a single point and have no current. Additionally, two large engineered floodplains, Yolo and Sutter bypasses (combined surface area $>$ 30,000 ha), are present on the Sacramento River. These floodplains historically inundate in about 60% of years and provide the most substantial spawning and rearing habitat for splittails and other native fishes (Sommer et al. 2001; Feyrer et al. 2006a, 2006b).

Sample collection.—The individual fish examined in this study were subsampled from collections made during a study of the distribution of age-0 splittails across the entire range of the species (Feyrer et al.

2005). Field sampling was conducted April–June in 2002 and 2003 with beach seines, and all age-0 splittails collected were retained and preserved in a 97% solution of ethanol. We supplemented this group with some fish collected by existing monitoring programs that sampled with rotary screw traps in Yolo and Sutter bypasses (Feyrer et al. 2006a, 2006b); upon collection, these fish were preserved and handled in the same manner as the others. For the present study, we subsampled from this large core group of samples in attempt to obtain an approximately equal number of individual fish of the same size range from each region and year. For all analyses outlined below, data were summarized by year and according to the following regions: the Petaluma, Napa, San Joaquin, and Sacramento rivers. We further subdivided the Sacramento River samples into main channel, backwater, and floodplain categories (Yolo and Sutter bypasses combined). We partitioned samples from the Sacramento River region into these habitat categories to test for differences that might provide insights into the relative importance of these habitats because (1) as stated above, it has been hypothesized that floodplains provide optimal rearing habitat for age-0 splittails (Meng and Moyle 1995; Sommer et al. 1997; Moyle et al. 2004), and (2) age-0 splittails are significantly more common in backwaters than in adjacent main river channel habitats (Feyrer et al. 2005), suggesting they may serve important functions. Samples from the other regions were not similarly categorized because habitat diversity was lower, or we could obtain samples only from main channel habitats. The same individuals were used across analyses to the extent possible. The one notable exception is that fish collected by rotary screw trap were excluded from diet composition analyses because of the possible bias resulting from trap residency affecting gut contents. Overall, the fish we examined ranged in size from 16 to 56 mm standard length, and length ranges were similar across regions (Petaluma River: mean standard length = 34 mm, SD = 6; Napa River: mean standard length = 33 mm, SD = 10; San Joaquin River: mean standard length = 28 mm, SD = 6; Sacramento River channel: mean standard length = 26 mm, SD = 5; Sacramento River backwater: mean standard length = 24 mm, SD = 5; floodplain: mean standard length = 29 mm, SD = 6).

Age and growth rate estimation.—We examined otolith microstructures to determine the ages of individual fish. We followed the aging procedures outlined by Feyrer et al. (2004), who validated that daily growth increments start at hatch in age-0 splittails. Lapilli otoliths were extracted, cleaned of any attached tissue, and individually mounted on glass microscope slides in thermoplastic resin (Crystalbond, Aremco Products, Ossining, New York). The otoliths were polished on one side with 0.3-μm lapping film to expose a sagittal plane. Digital images of the polished otoliths were taken with a CoolSNAP-Pro *cf* monochrome camera coupled with a Nikon E400 microscope. Age was estimated from the total number of daily growth increments, which was determined from the digital images with the aid of image analysis software (Image Pro Plus 4.5, Media Cybernetics, Inc.).

We evaluated the precision of our age estimates by the coefficient of variation method (CV = 100 × SD/mean; Campana and Jones 1992; Campana 2001). We aged 18% of the fish twice and calculated a mean CV of 3.5%, which is better than most otolith aging studies (Campana 2001). Using linear models, we regressed $\log_{10}$(length) against age to estimate instantaneous growth coefficients for fish in each of our locations and sampling periods. We tested for significant differences in growth rates across space and time by analysis of covariance (ANCOVA). The ANCOVA model included $\log_{10}$(length) as the dependent variable, region and year (and their interaction) as the independent variables, and age as the covariate. Statistical significance was determined at $\alpha \leq 0.05$, and Tukey's post hoc multiple comparison tests were used to characterize differences. We evaluated the fit of the ANCOVA model by visually examining residual plots for homogeneity of variance and tested the hypothesis that the residuals were normally distributed with the Anderson–Darling test.

Diet composition.—We examined the gut contents of individual fish to obtain data on diet composition. Entire gut segments were extracted from fish and individually dissected under a dissecting microscope to determine their contents. Splittails do not possess a true stomach but rather a gut with two 180° bends forming three distinct segments. We identified all contents in each gut segment and summarized the data together as percent frequency of occurrence within the following categories: chironomid larvae, other Diptera, Odonata, other Insecta, Copepoda, Cladocera, Annelida, Ostracoda, Amphipoda, unidentified, and other. Each of the individual fish guts we examined had at least one of these categories present. The category "other" consisted of rare prey items that occurred in 1% or less of splittail guts and included bryozoan statoblasts, plant material, unidentified eggs, mysids, and isopods.

We examined the variation in diet composition with nonmetric multidimensional scaling (NMDS). Nonmetric multidimensional scaling is an effective multivariate indirect gradient analysis because it reduces dimensionality while accurately maintaining sample dissimilarities. We used the Bray–Curtis coefficient to construct the similarity matrix used in the NMDS

ordination because we did not want joint absences to influence similarity. The goodness of fit of an NMDS ordination is characterized by the value termed "stress," which is a unitless measure of how well the ordination preserves sample dissimilarities. Stress values less than 0.1 correspond to strong ordinations that result in little chance of misleading interpretations (Clarke and Gorley 2001). The presence or absence of all prey categories except "unidentified" and "other" for each individual fish was included in the NMDS. We constructed biplots of NMDS scores (axis 1 versus axis 2) to examine variation in diet composition among locations and years. To facilitate interpretation, we plotted average scores and 95% confidence intervals for each of our comparisons.

Energy sources and trophic position.—We examined the stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic composition of muscle tissue in individual fish to obtain information on the energy sources and trophic position of age-0 splittails (Vander Zanden and Rasmussen 1999). Consumers typically become enriched in $\delta^{15}N$ by 2–5‰ per trophic level (Peterson and Fry 1987). Thus, $\delta^{15}N$ can provide a time- and space-integrated measure of trophic position in a food web. Whereas $\delta^{15}N$ is enriched, $\delta^{13}C$ is conserved by consumers at increasingly higher trophic levels but can vary at the base of the food chain (Vander Zanden and Rasmussen 1999). As a consequence, $\delta^{13}C$ can provide information on the sources of energy to higher trophic levels.

Muscle tissue located above the lateral line was extracted from each fish and placed into individually labeled sterile containers and allowed to air dry; the ethanol preservation method essentially dehydrated the muscle tissue so it was not dried in an oven. One milligram of dried muscle tissue was placed into tin capsules for mass combustion. The N and C isotope ratios of samples were determined at the Stable Isotope Facility, University of California at Davis, using a Europa Scientific Hydra 20–20 continuous flow mass spectrometer and Europa ANCA-SL elemental analyzer. The ratio of heavy and light isotopes is expressed as δ values as follows:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3,$$

where $X = {}^{13}C$ or ${}^{15}N$, and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

The standards are Peedee Belemnite for C and atmospheric diatomic nitrogen for N (Lajtha and Michener 1994). We constructed biplots of $\delta^{13}C$ versus $\delta^{15}N$ to examine variation among locations and years, and formally tested differences by ANCOVA with region and year as factors and fish length as the covariate. As above, significance was determined at $\alpha \leq 0.05$ and differences among pairs of locations were identified with Tukey's post hoc multiple comparison tests.

Results

Growth Rates

Age-0 splittails exhibited considerable variability in length at age for different locations and years (Figure 4). Age–length regressions for Sacramento River channels in 2002 and 2003, and Sacramento River backwaters and the Petaluma River in 2002 were not statistically significant. The statistically significant regressions for the other locations had coefficients of determination that ranged from 0.14 to 0.65 (Figure 4). Despite this variability, the ANCOVA demonstrated that length was significantly affected by age ($F_{1, 366} = 118.9$; $P < 0.001$), region ($F_{5, 366} = 7.7$; $P < 0.001$), and year ($F_{1, 366} = 4.4$; $P = 0.04$). There was no significant interaction between region and year ($F_{5, 366} = 1.54$; $P = 0.18$). The residuals from the ANCOVA model were normally distributed (Anderson–Darling P-value = 0.95) and exhibited no apparent trend with the fitted values, suggesting the model adequately fit the data. Tukey's multiple comparison tests indicated that fish from the Sacramento River channel and backwater habitats were smaller at age than fish from all other locations, and that, overall, fish were larger at age during 2002 compared with 2003.

Diet Composition

Age-0 splittails ate a variety of prey taxa consisting almost exclusively of aquatic invertebrates (Table 1). Overall, larval stages of chironomids were the most common prey for fish in all regions except the Petaluma River, where copepods were the most common. Petaluma River fish also consumed annelids and amphipods more frequently compared with the other regions. Odonates were the second most common prey for fish collected in Sacramento River channel and backwater habitats and the San Joaquin River. Cladocerans were common prey items for fish collected from floodplain habitats. Copepods and ostracods were relatively common prey items for Napa River fish.

The two-dimensional NMDS stress value was 0.07, indicating that the ordination provided a reliable representation of diet variation that was significantly different from random. In each year, there was substantial variability in diet composition across regions (Figure 5). In 2002, NMDS axis 1 exhibited the primary mode of separation among regions. The Napa and Petaluma rivers clustered together and were

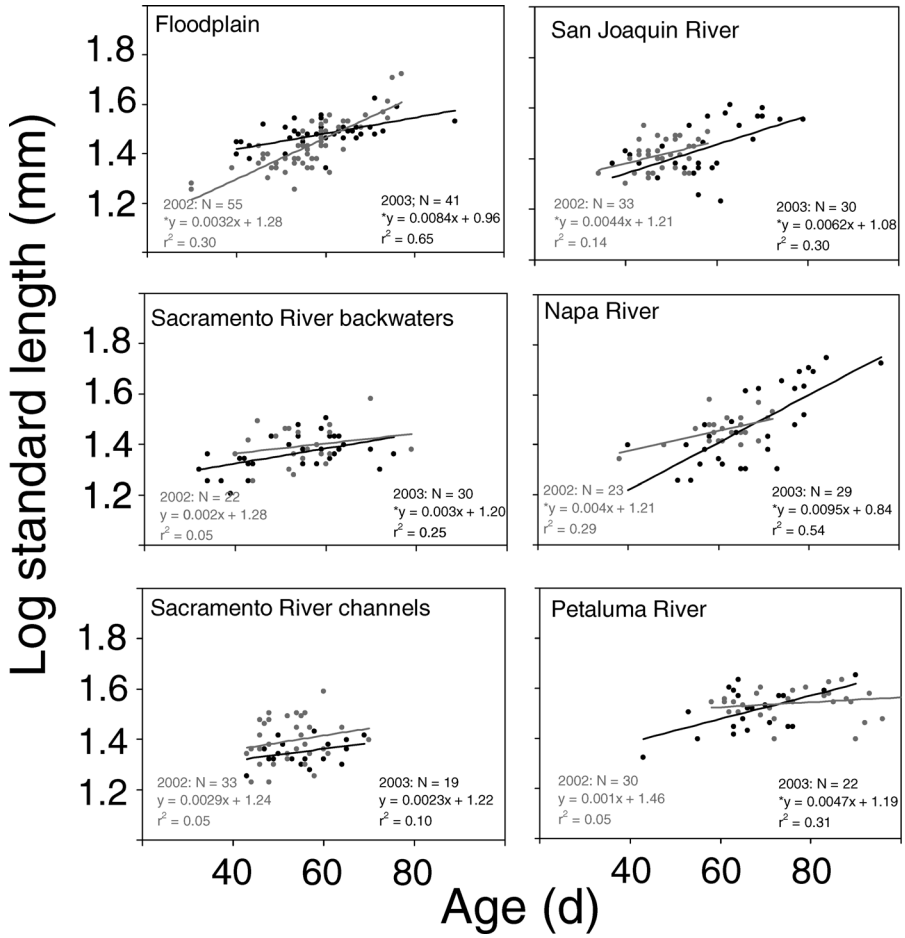

FIGURE 4.—Linear growth models for age-0 splittails in 2002 and 2003.

TABLE 1.—Percent frequency of occurrence of prey items found in the guts of age-0 splittails by decreasing overall frequency.

Variable and category	Napa River		Petaluma River		San Joaquin River		Sacramento River channel		Sacramento River backwater		Floodplain Yolo and Sutter bypasses	
	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003	2002	2003
N	37	40	40	40	40	40	43	22	21	35	19	58
Standard length (mean ± SD)	32 ± 8	33 ± 12	35 ± 5	33 ± 6	28 ± 5	29 ± 7	26 ± 5	26 ± 4	26 ± 5	24 ± 5	30 ± 5	29 ± 8
Chironomid larvae	30	73	10	10	65	50	56	73	48	74	58	38
Unidentified	49	23	38	40	0	53	16	23	5	0	26	10
Odonata	3	40	0	3	30	10	26	59	86	46	5	14
Copepoda	68	23	28	63	3	0	7	0	0	0	11	2
Cladocera	5	3	3	0	8	5	12	41	0	0	21	52
Other Insecta	3	0	5	8	8	0	23	9	29	6	11	0
Annelida	3	18	18	23	3	8	0	0	5	0	0	0
Amphipoda	19	0	26	8	0	3	0	0	0	6	11	2
Other Diptera	3	0	5	3	13	0	14	5	0	20	16	3
Ostracoda	22	33	5	3	0	5	2	9	0	0	5	0
Other	0	0	3	0	3	3	5	0	10	3	11	5

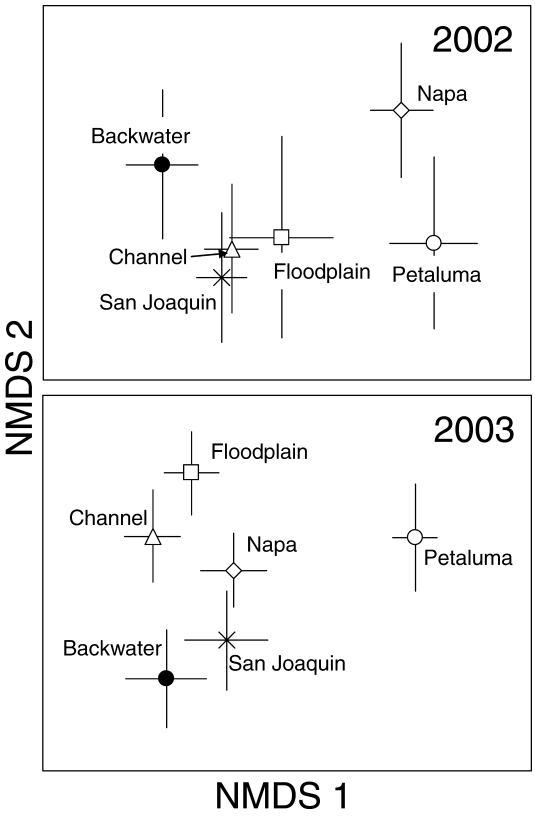

FIGURE 5.—Scores from the two axes of a nonmetric multidimensional scaling (NMDS) ordination (mean ± 95% confidence intervals) based on the presence or absence of prey items (stress value = 0.07).

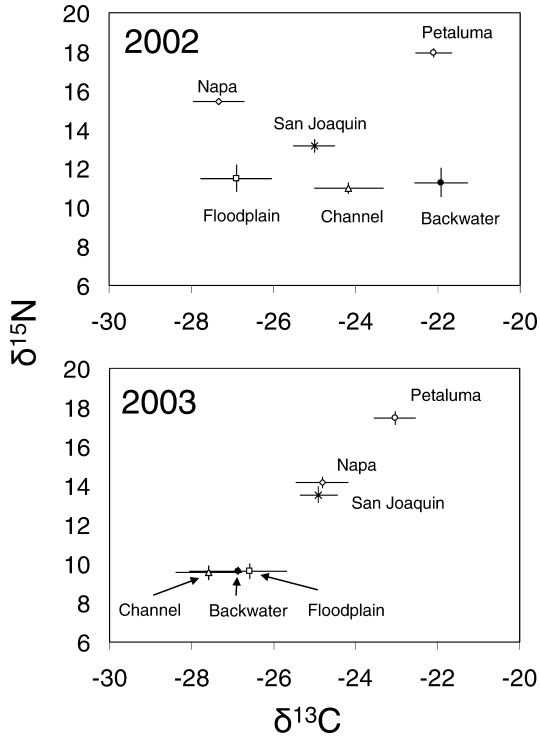

FIGURE 6.—Mean $\delta^{15}N$ versus $\delta^{13}C$ values for age-0 splittails in 2002 and 2003. The vertical and horizontal lines through each point represent 95% confidence intervals.

clearly distinct from the other regions, which were also grouped together. In 2003, NMDS axis 1 distinguished the Petaluma River from the other regions. The other regions then could be distinguished by NMDS axis 2. Sacramento River channels and floodplains formed a cluster that separated from another cluster comprised of Sacramento River backwaters and the San Joaquin River. The Napa River was intermediate and overlapped these two groups.

Energy Sources and Trophic Position

There was substantial variability in the isotopic composition of muscle tissue across the fish we examined; $\delta^{15}N$ ranged from 6.1‰ to 19.6‰, and $\delta^{13}C$ ranged from −36.3‰ to −17.5‰ (Table 2; Figure 6). The $\delta^{13}C$ signatures were significantly affected by length ($F_{1, 456} = 55.3$; $P < 0.001$), region ($F_{5, 456} = 32.4$; $P < 0.001$), year ($F_{1, 456} = 22.9$; $P < 0.001$), and the region × year interaction ($F_{5, 456} = 24.5$; $P < 0.001$). Tukey's multiple comparison tests indicated that $\delta^{13}C$ signatures were not significantly different between years for the Petaluma River ($P = 0.95$), the San Joaquin River ($P = 1.0$), and floodplains ($P =$

TABLE 2.—Values of $\delta^{15}N$ and $\delta^{13}C$ for age-0 splittails; min = minimum, max = maximum.

Location	*N*	Standard length (mean ± SD)	$\delta^{15}N$			$\delta^{13}C$		
			Mean ± SD	Min	Max	Mean ± SD	Min	Max
Napa River	81	33 ± 10	14.8 ± 0.9	12.5	17.2	−26.1 ± 2.4	−30.9	−19.9
Petaluma River	80	34 ± 6	17.7 ± 0.9	13.2	19.6	−22.6 ± 1.6	−26.0	−17.5
San Joaquin River	80	28 ± 6	13.3 ± 1.2	11.2	17.0	−25.0 ± 1.5	−29.2	−21.2
Sacramento River channel	64	26 ± 5	10.6 ± 1.1	7.6	14.6	−25.3 ± 2.9	−31.0	−19.6
Sacramento River backwater	60	25 ± 5	10.2 ± 1.4	8.5	16.9	−25.1 ± 3.9	−36.3	−19.1
Floodplain	104	24 ± 7	10.1 ± 1.9	6.1	15.3	−26.7 ± 2.7	−32.7	−20.7

0.98). For the other regions, the Napa River was significantly lower ($P = 0.0001$) in 2002 compared with 2003, while both Sacramento River backwaters and channels were significantly higher ($P < 0.0001$).

The $\delta^{15}N$ signatures were significantly affected by length ($F_{1, 451} = 8.8$; $P = 0.003$), region ($F_{5, 451} = 421.2$; $P < 0.001$), year ($F_{1, 451} = 83.1$; $P < 0.001$), and the region × year interaction ($F_{5, 451} = 9.9$; $P < 0.001$). Tukey's multiple comparison tests indicated that $\delta^{15}N$ signatures were not significantly different between years for the Petaluma River ($P = 0.76$) and the San Joaquin River ($P = 0.95$). However, there was significant enrichment in 2002 compared with 2003 for the Napa River ($P = 0.0002$), Sacramento River backwaters ($P < 0.0001$), Sacramento River channels ($P = 0.0006$), and floodplains ($P < 0.0001$).

Post hoc pairwise site comparisons for 2002 exhibited separate groups based on $\delta^{13}C$ and $\delta^{15}N$. There were three statistically significant groups based on $\delta^{13}C$: Petaluma River and Sacramento River backwaters formed a group with the highest values, Sacramento River channels and the San Joaquin River formed a group with intermediate values, while the Napa River and floodplains formed a group with the lowest values. There were three statistically significant groups based on $\delta^{15}N$: the Petaluma and Napa rivers were distinguishable and had the highest values, the San Joaquin River had intermediate values, and Sacramento River channels, Sacramento River backwaters, and floodplains formed a group with the lowest values.

Post hoc pairwise site comparisons for 2003 exhibited three statistically significant groups that could be distinguished by both $\delta^{13}C$ and $\delta^{15}N$. The Petaluma River had the highest $\delta^{13}C$ and $\delta^{15}N$, the Napa and San Joaquin rivers formed a group with intermediate values, and Sacramento River channels, Sacramento River backwaters, and floodplains formed a group with the lowest $\delta^{13}C$ and $\delta^{15}N$.

Discussion

For migratory fish species such as splittail, life histories can be strongly influenced by events during early life stages (Secor 1999). Hence, our study was designed to evaluate patterns in growth, diet, and trophic interactions and had the goal of understanding the mechanisms of recruitment in dynamic environments such as the San Francisco Estuary. We found that for age-0 splittails in 2002 and 2003, diet composition and stable isotope signatures were not effective indicators of growth rate. Other factors, such as food quantity and physical habitat conditions, were likely important during our study.

Growth Rate

It has been demonstrated that temperature and food supply are major factors affecting the growth rate of fish (Mills 1988). Further, in a laboratory setting, Deng et al. (2002) found a significant interaction between water temperature and food quality on the growth of young splittails. For fish living in estuarine habitats, salinity may also affect growth rate by affecting metabolism (Moyle and Cech 2004). It appears that combinations of these three factors apparently produced different growth environments and affected length at age within and among locations in our study. Age-0 splittails migrate considerable distances from spawning habitats to estuarine nursery areas (Feyrer et al. 2005). Habitat heterogeneity (i.e., spatial and temporal variability in habitat conditions during this migration period) is a likely mechanism for the variability in length at age within our comparisons. For instance, water temperature can vary by up to 9.0°C between main channel and immediately adjacent backwater habitats on the Sacramento River (Feyrer et al. 2005), which is sufficient to affect growth rate of young splittails (Deng et al. 2002). Salinity can also vary substantially across small geographic areas, especially in the Napa and Petaluma rivers (Feyrer et al. 2005). Data from the field sampling (Feyrer et al. 2005) indicate that age-0 splittails use a broad range of salinities (from 0‰ to more than 13‰) in the Petaluma and Napa rivers. Another factor leading to high within-comparison variability in growth rates could be the relatively long time span over which fish were sampled and collected each year. Growth rate has been shown to vary intra-annually among cohorts (Rilling and Houde 1999; Jordan et al. 2000); thus, it is possible that the 3-month time period over which we compiled samples could have included multiple cohorts with different growth histories. However, high variability in length at age for age-0 splittails is consistent the results of Ribeiro et al. (2004), who found that it could vary by a factor of nearly 4 on the Cosumnes River floodplain (California). Finally, our study took place over two relatively dry years; we suspect that variability and habitat responses may be different during wetter years when floodplains are inundated for extended periods of time.

Diet Composition

Our results on the diet composition of age-0 splittails filled a key data gap between larvae (Moyle 2002) and age-1 and older fish (Feyrer et al. 2003). The diet composition of splittail larvae up to 15 mm in length is dominated by zooplankton (primarily cladocerans), chironomid larvae becoming important once splittails

reach 15 mm in length (Moyle 2002). For age-1 and older splittails, detritus is the dominant item found in fish collected from the estuary (Feyrer et al. 2003). Various macro-invertebrates (including amphipods, clams, and mysid shrimp) are the most common nondetrital items in the diet of age-1 and older splittails (Feyrer et al. 2003). Our results, combined with those of these two previous studies, provide strong evidence that splittails are opportunistic feeders whose diets reflect patterns in habitat use through ontogeny.

We found evidence that geography and environmental conditions affected the diet composition of age-0 splittails. With respect to geography, the largest amount of variation in diet composition was between the Petaluma River and the other regions. The primary difference was that annelids, amphipods, and copepods were common prey items at the Petaluma River, while chironomid larvae and other insects were common prey items at the other sites. Fish diets in the Napa River exhibited an interesting shift between years. In 2002 diet composition was very similar to that in the Petaluma River. However, in 2003 diet composition shifted and more closely resembled that in the other sites. This diet shift was coincident with higher flow, lower salinity, and lower water temperature in the Napa River during 2003.

Stable Isotopes

We found that the $\delta^{15}N$ and $\delta^{13}C$ signatures of age-0 splittails significantly varied spatially and temporally, a typical pattern for fish across riverine and estuarine habitats (Wainright et al. 1996; Fry 2002; Gido et al. 2006). However, large-scale spatial comparisons of $\delta^{15}N$ are often complicated by variation in the ^{15}N signal of the primary producers at the base of the food chain (Vander Zanden et al. 1997). Regionally, Cloern et al. (2002) demonstrated substantial variation in $\delta^{15}N$ and $\delta^{13}C$ in all organic matter sources across the San Francisco Estuary. As a consequence, our challenge was to elucidate the mechanisms behind the observed variability in the $\delta^{15}N$ and $\delta^{13}C$ signatures. Although we did not measure source signatures, our interpretation of $\delta^{15}N$ and $\delta^{13}C$ for age-0 splittails was aided by concomitant data on diet composition and environmental conditions. A combination of stable isotope and diet data can be a powerful technique to elucidate carbon sources and trophic position for fish (Vander Zanden et al. 1997). There is also some recent information available on the $\delta^{15}N$ and $\delta^{13}C$ signatures of other organisms collected within our general study area from which we could make inferences for splittail (Sommer et al. 2001b; Cloern et al. 2002; Stewart et al. 2004).

The $\delta^{13}C$ signals for fish in the Petaluma River, San Joaquin River, and floodplain habitats were similar each year, suggesting stable homogenous carbon sources. For the other sites, large-scale environmental conditions and food availability may be important in explaining these differences as they were all coincident with major changes in flow and diet. For example, Sacramento River channel and backwater habitats both exhibited depletion in $\delta^{13}C$ in 2003, a higher flow year than 2002. This response is consistent with the findings of Finlay et al. (1999), who reported a negative relationship between the $\delta^{13}C$ signals and flows. We do not have sufficient data to fully explain the $\delta^{13}C$ response; however, one possibility is that lower flow conditions in 2002 may have kept these habitats relatively isolated and caused differences in the availability of prey items. This hypothesis is supported by the shift in diet composition described above.

The Petaluma River was a curious location in terms of stable isotope ratios because fish from this region consistently exhibited the highest values of both $\delta^{15}N$ and $\delta^{13}C$. The $\delta^{15}N$ were particularly high compared with values of fish from other the regions but also with previous $\delta^{15}N$ values obtained for adult splittails (Stewart et al. 2004). This does not necessarily mean that fish from the Petaluma River were feeding at the highest trophic level. In fact, the data on diet composition suggests that splittails across all regions were feeding at approximately the same trophic level since prey items consisted almost exclusively of primary and secondary consumers. In terms of $\delta^{13}C$ signals for the Petaluma River fish, high salinity due to its close proximity to marine water probably also had an important effect. In estuaries, $\delta^{13}C$ is typically enriched coincident with location along the salinity gradient (Spiker and Schemel 1979).

Ecological and Management Implications

Effective management of aquatic resources, such as special-status fish species like splittail, requires an understanding of the factors controlling their production. Growth rate is a key determinant of production for young fish because body size is an important predictor of fitness. We found few large-scale geographic differences in growth rate of age-0 splittails. This was despite apparent differences in physical habitat, diet composition, and stable isotope indicators of carbon sources and trophic position. The only significant difference we found was that age-0 splittails collected in Sacramento River channel and backwater habitats grew more slowly than fish from the other groups. These results suggest that large-scale habitat restoration projects, such as rehabilitating floodplains and restoring river–floodplain connectivity, may provide the best opportunity for local resource managers to provide

measurable benefits for splittail. This is further supported in that the availability of floodplain habitat has been demonstrated to have a significant positive effect on the production of splittail (Feyrer et al. 2006a). Results from similar studies suggest that other native fishes also benefit from floodplains (Sommer et al. 2001a; Crain et al. 2004; Ribeiro et al. 2004; Sommer et al. 2004) and that the production and transport of phytoplankton and detrital material downstream resulting from floodplain inundation enhances the food web of the San Francisco Estuary (Jassby and Cloern 2000; Mueller-Solger et al. 2002; Sommer et al. 2004). Thus, properly managed floodplains have the potential to provide widespread benefits at multiple levels, ranging from individual organisms to ecosystems.

Our results also provide new insights into the generality of existing ecosystem models, especially for large river–floodplain systems. The flood pulse concept (FPC; Junk et al. 1989) states that fish yield and production is a function of accessible floodplain habitat. Enhanced growth and production (Feyrer et al. 2006a) of age-0 splittails in floodplain habitats clearly provides support for this element of the FPC for temperate river floodplains. We found evidence that the coupling of food web pathways supporting age-0 splittails in riverine and floodplain habitats was affected by flows connecting the two habitats. This suggests that flow and connectivity have an important effect on trophic relationships in river–floodplain systems. Energy sources for aquatic animals in floodplains have been extensively studied (e.g., Hamilton et al. 1992; Forsberg et al. 1993; Thorp et al. 1998). However, further research is clearly needed to understand the temporal variability in carbon sources supporting river–floodplain food webs (e.g., Fisher et al. 2001) and its effect on the production or abundance of high-level consumers of interest, especially in highly managed river–floodplain systems.

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