

Primary Research Paper

Managing floodplain inundation for native fish: production dynamics of age-0 splittail (*Pogonichthys macrolepidotus*) in California's Yolo Bypass

F. Feyrer*, T. Sommer & W. Harrell

Aquatic Ecology Section, California Department of Water Resources, 3251 S Street, Sacramento, CA 95816, U.S.A.
(* Author for correspondence: E-mail: ffeyrer@water.ca.gov)

Received 17 January 2006; in revised form 9 June 2006; accepted 16 June 2006; published online 31 August 2006

Key words: flood pulse concept, Cyprinidae, Sacramento River, California's Central Valley, Sacramento-San Joaquin Delta, flow regime

Abstract

We used data gathered across seven hydrologically diverse years (1998–2004) from Yolo Bypass, the primary floodplain of the Sacramento River, California (U.S.A.), to examine how physical and hydrological characteristics of floodplain habitat influence spawning and patterns of occurrence and production of age-0 splittail (*Pogonichthys macrolepidotus*). We estimated that spawning in Yolo Bypass occurred from January to May but typically peaked in March in close association with the vernal equinox. Production of age-0 splittail varied significantly among years. Using an information-theoretic approach to evaluate several factors, the amount of inundated floodplain habitat available during the primary spawning and rearing period of January–June was the most important factor we examined in explaining annual production (81% of variance explained in a linear regression model). Peak emigration of age-0 splittail from Yolo Bypass varied temporally among years but always occurred when fish were 30–40 mm in length, suggesting an ontogenetic influence on floodplain emigration. Annual system-wide production of age-0 splittail derived from a separate long-term monitoring program exhibited an apparent positive relationship with annual production in Yolo Bypass, suggesting that site-specific floodplain-derived production within Yolo Bypass may be important at a regional scale. Our results support the flood pulse concept for cyprinids in regulated temperate river–floodplain systems and demonstrate floodplain inundation in regulated systems can be managed to benefit native fish.

Introduction

River–floodplain systems are among the most dynamic and complex habitats on earth. Annual flood events have the ability to dramatically alter landscapes over relatively short time periods and directly affect local productivity and biotic interactions (Junk et al., 1989; Gladden & Smock, 1990; Bayley, 1991). Fishes and other organisms have developed life history adaptations, which enable them to exploit seasonal floodplain habitats for their benefit. For fishes, floodplain provides refugia from high flows and important spawning

and nursery habitat because of increased availability and diversity of habitat, enhanced food resources, and favorable physical conditions (e.g., Junk et al., 1989; Winemiller & Jepsen, 1998; Sommer et al., 2001a). Nonetheless, difficulty in separating the relative contribution of floodplain versus channel processes for fish production has made quantifying the importance of floodplain particularly challenging.

We examined the importance of seasonal floodplain habitat to splittail (*Pogonichthys macrolepidotus* Ayers), a cyprinid endemic to the upper San Francisco Estuary and its lower watershed.

Formerly a federally listed threatened species, splittail remains a species of special concern for the U.S. Fish and Wildlife Service and the California Department of Fish and Game. Splittail exhibits a unique life history among North American cyprinids in that it makes annual spawning migrations from the brackish estuary to upstream freshwater tributaries and floodplains (Daniels & Moyle, 1983; Sommer et al., 1997; Moyle et al., 2004). After spawning, larvae and juveniles remain upstream in inundated habitats until they begin to dry and then move downstream to tidal freshwater and brackish portions of the estuary during early summer (Feyrer et al., 2005). Juveniles will rear in the estuary 1–2 years until they become sexually mature and then initiate spawning migrations (Daniels & Moyle, 1983; Moyle et al., 2004). Studies indicate that overall production of age-0 splittail is generally greatest in wet years, presumably because of increased floodplain inundation (Meng & Moyle, 1995; Sommer et al., 1997). However, management options for flows and physical habitat restoration have been hindered because it is not known what characteristics of the flood pulse are best for spawning and rearing of splittail (Moyle et al., 2004).

While understanding the value of seasonal floodplain habitat is of broad interest for natural resource management, there is relatively little information available on the ecology of managed floodplains. In addition to splittail, many native and special status aquatic and terrestrial species use floodplains to complete their life cycles (Sommer et al., 2001a,b; Harrell & Sommer, 2003; Crain et al., 2004). Because of the numerous ecological benefits it affords, floodplain restoration has been identified as a potential approach to enhance native fish populations and contribute to ecosystem rehabilitation in the highly altered San Francisco Estuary and its watershed (CALFED, 2000; Sommer et al., 2001b). Thus, understanding how floodplain inundation can be managed to benefit splittail and other species will provide valuable information for resource managers to set relevant restoration and management strategies.

We used relatively long-term data from Yolo Bypass, the primary floodplain of the Sacramento River, California (U.S.A.), to examine how physical and hydrological characteristics of floodplain habitat influence spawning, patterns of occurrence,

and production of age-0 splittail. Yolo Bypass is an engineered floodplain and is separated from the Sacramento River by levees except when water overtops isolated weirs for flood control purposes. This unique configuration provides an ideal ‘natural laboratory’ because riverine and floodplain processes are isolated, making them easier to identify and study (Sommer et al., 2001a, b). Further, existing long-term monitoring data enabled a comparison of production in Yolo Bypass relative to overall system-wide production of age-0 splittail. The study period encompassed seven hydrologically diverse years (1998–2004) allowing direct evaluation of how local and regional production of splittail varied with seasonal floodplain inundation characteristics.

Methods

Study site

California’s Central Valley is drained primarily by the state’s two largest rivers, Sacramento River from the north and San Joaquin River from the south. The rivers drain a watershed encompassing 40% of California’s surface area (100,000 km²) and converge to form the Sacramento-San Joaquin Delta, a complex mosaic of tidal freshwater channels covering 3000 km². Water from the delta flows west through Suisun and San Pablo Bays before entering San Francisco Bay and ultimately the Pacific Ocean. The primary floodplain in the Sacramento River basin, which conveys 85% of total flow into the delta (Kimmerer, 2002a), is Yolo Bypass (Fig. 1; Sommer et al., 2001b). The 61 km-long, 24,000 ha engineered floodplain was created in the early 1930’s to protect the greater Sacramento region from flooding. Under typical flood events, water spills into Yolo Bypass at Fremont Weir when Sacramento River flows surpass approximately 2000 m³/s and also at Sacramento Weir at flows of approximately 5000 m³/s. Yolo Bypass can convey flows up to 14,000 m³/s, representing 75% of total Sacramento River basin flow. It typically floods in winter and spring in about 60% of years. During periods when flow does not enter Yolo Bypass from the Sacramento River weirs, substantial flooding can also occur in the bypass from smaller west side tributaries.

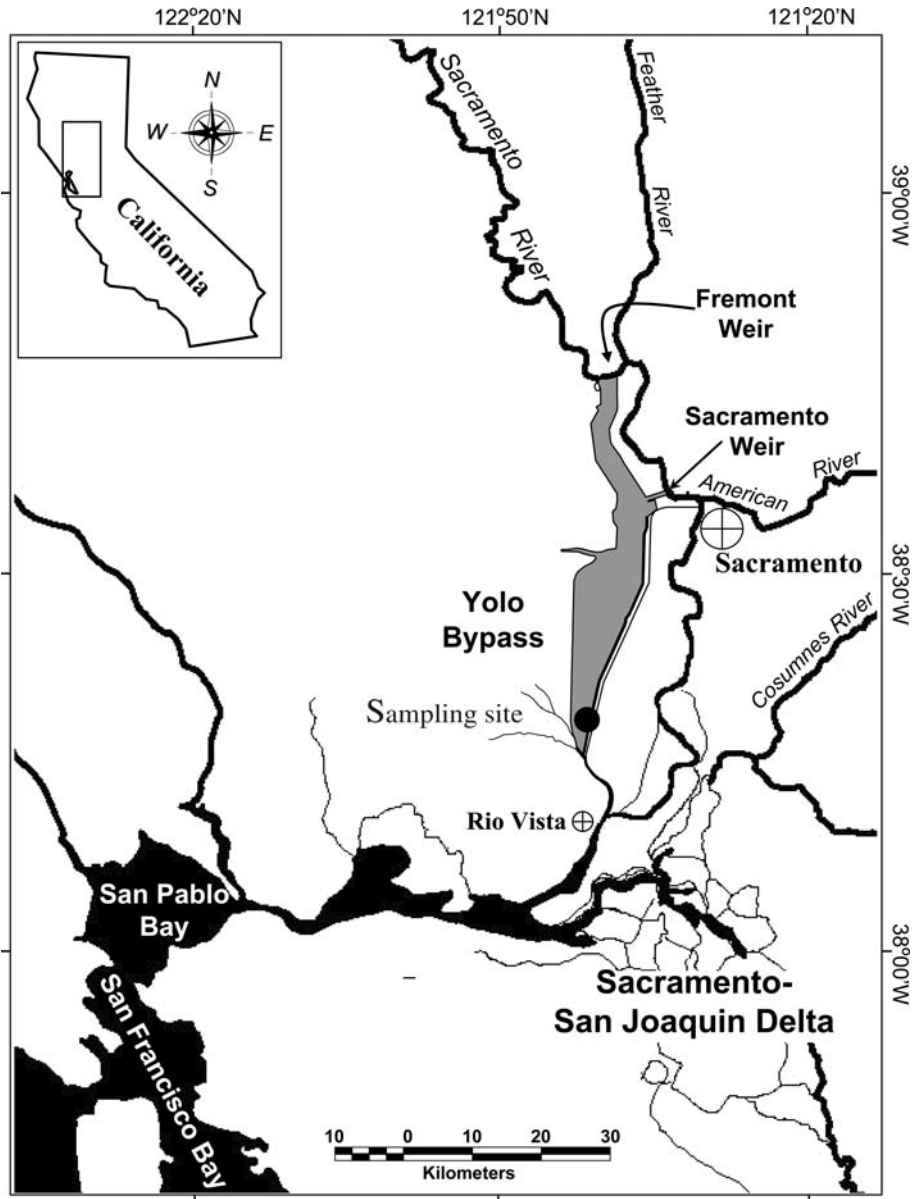


Figure 1. Map showing the location of Yolo Bypass and our sampling site.

Water entering Yolo Bypass initially flows through a perennial channel on the eastern edge of the basin before spilling onto the floodplain when discharge in this small channel exceeds $100 \text{ m}^3/\text{s}$. During dry seasons the channel remains inundated as a result of tidal action. Except during extreme high flow events, the mean depth of the floodplain is generally less than 2 m, creating broad expanses of shallow water habitat. Land use in Yolo Bypass is dominated by agriculture during the dry season,

but approximately one third of the area is a mosaic of 'natural' habitat types including riparian and upland habitat, emergent marsh, and permanent ponds (Feyrer et al., 2006).

Field sampling

Age-0 splittail were sampled in Yolo Bypass with a 2.4-m diameter rotary screw trap (EG Solutions, Corvallis, Oregon) (Sommer et al., 2004b). Sam-

pling was conducted January–June from 1998 to 2004. We operated the trap up to 7 days each week, with daily effort varying from 1 to 24 h, depending on debris load and safety considerations. The trap was located in the perennial channel at the base of Yolo Bypass (Fig. 1). This particular site was ideal for evaluating a migratory species that spawns in Yolo Bypass such as splittail because it drains the floodplain and therefore enabled an assessment of the production of young fish as well as the timing of their emigration. All age-0 splittail collected in the trap were counted and measured for fork length (mm), except that during instances of extremely large catches only a representative subsample was measured.

Apparent spawn dates

We estimated dates on which spawning occurred in Yolo Bypass by back-calculating from the date of capture of individual fish that were measured in the field, using the following formula: spawn date = date of capture – (((length at capture – mean length at hatch)/mean growth rate) – mean egg incubation period). All values except length at capture were consistent for all calculations based upon known mean values: mean length at hatch = 6.0 mm (Wang, 1986; Moyle et al., 2004), mean growth rate = 0.5 mm/day (Ribeiro et al., 2004; our unpublished otolith data), mean incubation period = 4.0 days (Feyrer et al., 2004a; Moyle et al., 2004). We acknowledge that the utility of non-empirically derived spawn dates may be less robust than those derived directly from hard structures such as otoliths. Nonetheless, depending upon the desired level of resolution, such data can provide information suitable to several types of analyses. Indeed, this method has been successfully used in the past to derive spawn date distributions for cyprinids (Nesler et al., 1988) and other life history characteristics for fishes (e.g., Rooker et al., 1998). Our goal was simply to frame the general spawning period and examine the role of large scale environmental variables during this period. Thus, the use of non-empirically derived spawn dates was a reasonable approach considering our interest in mean population-level response. Additional information to justify our approach included (1) mean incubation time and length at hatch of splittail varies little

over a wide temperature range (Wang, 1986; Feyrer et al., 2004a; Moyle et al., 2004), (2) a temperature shift of nine degrees was needed to produce detectable changes in growth of larval splittail reared in a laboratory setting (Deng et al., 2002), (3) mean temperatures in Yolo Bypass differed by less than two degrees among years during our study, (4) growth rate of age-0 splittail appears to be uniform until fish reach approximately 60 mm in length (J. Hobbs, personal communication), and (5) we employed a conservative approach to interpreting statistical tests performed on the data.

We used binary logistic regression to examine the role of environmental variables in determining when spawning occurred. Binary logistic regression was particularly appropriate for this analysis because our goal was to classify spawning occurrences into two categories, days on which spawning did or did not occur. Additionally, binary logistic regression does not assume linearity and normally distributed errors of independent variables as in the case of simple linear regression (Trexler & Travis, 1993). The response variable in the analysis was coded as either 1 or 0, based upon the incidence of spawning, and we structured the analysis such that only the days within the overall spawning period of each year were included in the model. Independent variables included in the model were mean daily values of flow (m³/s), stage (m), total inundated area of the floodplain < 2 m deep (ha), water temperature (°C), moon phase (percent of moon illuminated), and photoperiod (day length). Flow was the total amount of water entering Yolo Bypass from Sacramento River and adjacent tributaries measured at permanent gauging stations. Stage was obtained from a permanent gauging station located within Yolo Bypass near our sampling site. Total inundated area of the floodplain < 2 m deep is an index of the amount of shallow water spawning habitat available for splittail and was obtained from a three dimensional hydrologic model of Yolo Bypass based on basin geometry and stage and flow time series (Sommer et al., 2004a). Due to the physical structure of the floodplain basin, surface area < 2 m deep exhibits a unimodal relationship with stage that peaks when stage reaches approximately 5 m. Further information on the physical modeling procedure and the relations among stage, flow,

and surface area < 2 m deep are available in detail in Sommer et al. (2004b). Water temperature was obtained from a continuous recorder (Onset Computer Corp.) installed in Yolo Bypass at our sampling site. Percent of moon illuminated was defined as the ratio of the moon surface area illuminated by direct sunlight to its total area and ranges from 0.0 (new moon) to 1.0 (full moon); data were obtained from the U.S Naval Observatory, Astronomical Applications Department (<http://aa.usno.navy.mil/data/docs/MoonPhase.html>). We corrected the data for the logistic regression analysis by subtracting values that were < 0.5 from 1.0. This provided a single non-circular range of values from 0.5 to 1.0, establishing a neap tide-spring tide scale. Photoperiod was defined as the ratio of time from sunrise–sunset to sunset–sunrise. Again for the logistic regression analysis, the data were adjusted such that values > 0.5 were corrected by subtracting them from 1.0. This provided a single non-circular range of values with a maximum of 0.5 decreasing to a value corresponding to most distant in time at which spawning initiated or terminated, essentially establishing a scale at which values decrease from the vernal equinox.

Patterns of production and occurrence

Production of splittail in Yolo Bypass was estimated by calculating catch per unit effort (CPUE) indices for age-0 fish. Total catch of each sample collected from April to June was standardized for effort by dividing it by time sampled (hours the trap operated until it was serviced); effort focused on the April–June period because 100% of age-0 splittail were collected in these months. The CPUE value was then standardized for relative trap efficiency by dividing it by stage (m) measured at a permanent gauging station in Yolo Bypass near our sampling site. Given the large size of the floodplain and its broad width during flood events, it was not feasible to directly evaluate trap efficiency. However, this standardization reasonably assumes that it is directly related to the cross sectional area of the water column across the floodplain at our sampling site, which according to physical modeling studies is directly indexed by the stage measurement (Sommer et al., 2004a).

Variation in splittail production in Yolo Bypass was examined with a repeated measures analysis of variance (ANOVA). Data examined were log ($x + 1$)-transformed CPUE values from April to June in a model that had months nested within years. This model tested whether CPUE varied among years, months, and if there was an interaction. Significance was determined at $\alpha = 0.05$ and Tukey's *post hoc* multiple comparison tests were used to characterize differences. The analysis was modeled with a balanced design of nine samples for each month each year, resulting in a total of 27 samples per year. It was limited to nine samples per month because that was the fewest number collected in any given month; for months that had greater than nine samples, samples were randomly excluded to reduce the number to nine. The potential importance of fish size as a factor contributing to emigration from Yolo Bypass was examined by plotting fish length against the timing of peak abundance each year, summarized as the julian week in which it occurred.

An information-theoretic approach was used to examine the importance of physical habitat features on annual production of splittail in Yolo Bypass (Burnham & Anderson, 1998). This technique allows for a comparison of models with varying numbers of parameters and is based upon a strength-of-evidence context rather than traditional statistical tests of null hypotheses. Least squares regression was used to model linear relationships between several physical habitat variables and production, and the best fitting model was identified based upon Akaike's information criterion (described below). Annual production, the dependent variable, was calculated as April–June mean CPUE based upon the samples described above for the repeated measures ANOVA. The independent variables were stage, flow (m^3/s), and water temperature ($^{\circ}\text{C}$) summarized as mean values during the primary spawning and age-0 rearing period of January–June. Production was log ($x + 1$)-transformed and the independent variables were log-transformed. Regression models were developed for each independent variable by itself (simple regressions) and also for each possible combination of multiple variables (multiple regressions). It has been demonstrated that splittail production is greatest in wet years (Meng & Moyle, 1995; Sommer et al., 1997). We

evaluated the fit of each regression model because we wanted to determine which element of the flood pulse, stage or flow, was most important to splittail production. We also wanted to evaluate the role of temperature because Sommer et al. (2001a) found that higher temperatures in the Yolo Bypass floodplain improved growth of juvenile Chinook salmon. Each candidate model was evaluated with AIC_c , Δ_i , and w_i (Burnham & Anderson, 1998): AIC_c is Akaike's information criterion adjusted for small sample size; Δ_i (AIC_c differences) provides a level of empirical support for each model and is evaluated in relative rather than absolute terms, values of 0–2 provide substantial support for a given model (0 being best), 4–7 considerably less support, and >10 virtually no support; w_i provides a relative weight of evidence in support of a given model with the largest value being best.

The relationship between splittail production in Yolo Bypass relative to overall production in San Francisco estuary was examined by regressing $\log(x + 1)$ -transformed values of annual Yolo Bypass production against abundance calculated from the California Department of Fish and Game's Fall Midwater Trawl Survey (FMWT). The FMWT is a long-term monitoring program that started in 1967 and is used to estimate annual production of splittail by calculating abundance indices for age-0 fish (Sommer et al., 1997; Moyle et al., 2004). The FMWT and abundance indices derived from it are described in detail by Sommer et al. (1997) and Moyle et al. (2004). Essentially, an abundance index for age-0 splittail is calculated from samples collected at over 100 sites monthly from September to December throughout the low to mesohaline portions of the San Francisco

Estuary. Age-0 splittail leave upstream habitats and are distributed in this region of the system by summer (Feyrer et al., 2005), thus FMWT samples across the primary distribution of age-0 splittail and is a suitable survey from which to index overall production.

Results

Physical conditions in Yolo Bypass differed seasonally and among years (Table 1). Mean daily water temperatures ranged from approximately 9 °C in January to 23 °C in June with little variation among years. Mean daily flow varied substantially among years (20–909 m³/s). Flow also exhibited seasonal variation such that the timing, magnitude, and duration of floodplain inundation greatly differed among years. Such extreme flow variation caused the number of days of floodplain inundation in Yolo Bypass to vary by a factor of six among years.

A total of 11,342 age-0 splittail were collected, 2439 of which were measured for length in the field. Overall, we estimated that spawning in Yolo Bypass occurred from January to May but typically peaked in March (Fig. 2). The binary logistic regression results indicated that increasing values of photoperiod, stage, and water temperature were the best predictors of days on which spawning was likely to have occurred (Table 2; test that all slopes are zero: $G = 202.54$, $df = 6$, $p < 0.001$; goodness of fit: Pearson Chi-Square = 582.14, $df = 602$, $p = 0.71$). Photoperiod appeared to be by far the most influential variable. The regression results indicated that spawning was many orders of magnitude more likely to have occurred as photoperiod approached 0.5, indicating a strong tendency for the vernal equinox period. This overwhelming result over several hydrologically diverse years suggests our approach with non-empirically derived spawn dates was sufficient to capture the primary trend of the population.

The repeated measures ANOVA indicated that production of splittail in Yolo Bypass varied significantly among years, months, and their interaction term (Table 3). Tukey's multiple comparison tests indicated that production in 1998 was higher than all other years except 2004, and that 2004 was higher than 2001 and 2002. Mean

Table 1. Mean daily January–June flow, days of floodplain inundation, and mean daily water temperature in Yolo Bypass

Year	Flow (m ³ /s)	Floodplain inundation (days)	Water temp. (°C)
1998	909 ± 1432	131	14.7 ± 4.6
1999	168 ± 302	73	14.5 ± 5.3
2000	185 ± 388	43	16.2 ± 5.4
2001	20 ± 33	22	16.0 ± 6.0
2002	39 ± 117	23	15.9 ± 4.9
2003	73 ± 94	80	16.3 ± 4.7
2004	151 ± 344	67	16.5 ± 5.3

Error terms are one standard deviation.

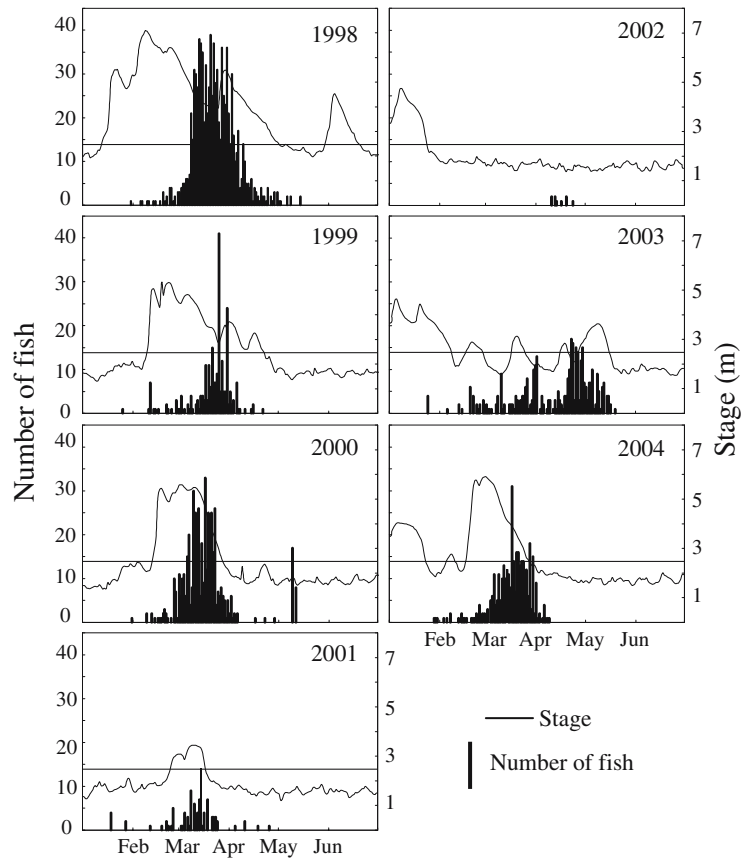


Figure 2. Mean daily stage in Yolo Bypass and estimated spawn dates of splittail collected and measured during rotary screw trap sampling. Straight horizontal lines represent the stage threshold for floodplain inundation in Yolo Bypass.

CPUE values \pm 95% confidence intervals ($\times 10$) for all years were as follows: 1998 = 3.29 ± 1.51 , 1999 = 0.23 ± 0.18 , 2000 = 0.90 ± 0.57 , 2001 = 0.14 ± 0.11 , 2002 = 0.02 ± 0.02 , 2003 = 1.46 ± 0.97 , and 2004 = 1.98 ± 1.08 . Tukey's multiple

comparison tests indicated that April consistently had lower abundances than May or June. May and June were not significantly different, but the significant interaction term indicated that peak within-year abundance varied between these

Table 2. Binary logistic regression results using habitat variables as predictors of days on which splittail spawning was estimated to have occurred in Yolo Bypass

Predictor	Coef.	SE Coef.	Z	p	Odds ratio
Constant	-17.66	2.13	-8.28	<0.01	
Stage*	0.63	0.26	2.42	0.02	1.88
Flow	<-0.01	<0.01	-1.56	0.12	1.00
Area <2m deep	<-0.01	<0.01	-1.42	0.16	1.00
Water temperature*	0.13	0.03	4.20	<0.01	1.14
Moon phase	-0.41	0.65	-0.63	0.53	0.66
Photoperiod*	31.51	4.45	7.09	<0.01	4.81E + 13

Asterisks denote meaningful variables based upon a significant *p*-value and odds ratio.

Table 3. Summary statistics for a repeated measures analysis of variance model that examined the influence of year and month nested within year on abundance of age-0 splittail in Yolo Bypass

Factor	df	MS	F	p
Year	6	0.38	12.19	2.29E-11
Month	2	0.38	12.08	1.25E-05
Year*month	12	0.21	6.78	6.64E-05

months across years. Although the timing of peak abundance varied among years, mean size of age-0 splittail consistently ranged between 30 and 40 mm during the peak, suggesting that fish size may be an important factor influencing emigration of age-0 splittail from Yolo Bypass (Fig. 3).

According to the information-theoretic approach, availability of floodplain habitat during January–June, as indexed by stage, was the most important factor influencing the annual production of splittail (Table 4; Fig. 4). Based upon a statistically significant linear regression ($p < 0.05$), stage explained 81% of the variation in annual production (Fig. 5). Two additional models, one incorporating flow and the other incorporating stage and temperature, provided considerably less support with Δ_i values between 5.0 and 7.0. There was virtually no support for any other model.

Annual system-wide production of age-0 splittail, as indexed by FMWT, was significantly positively related to production in Yolo Bypass ($y = 0.42 + 4.53x$, $p = 0.05$, $r^2 = 0.57$; Fig. 5). The linear model appeared to be strongly influenced by two individual extreme high and low values, suggesting other models such as a multiple step function would better fit the data; we made no attempt to fit other models to the data because of limitations with sample size.

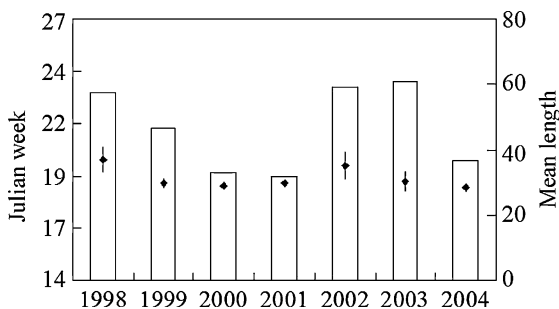


Figure 3. Julian week in which peak emigration occurred (open bars) and mean length (± 1 standard deviation) of age-0 splittail among years.

Discussion

Our results provide evidence in support of the flood pulse concept (Junk et al., 1989) for cyprinids in a regulated temperate river–floodplain system. Spawning and rearing of fish on seasonal floodplains is known from diverse locations ranging from small streams (Halyk & Balon, 1983; Ross & Baker, 1983) to large rivers (Copp & Penaz, 1988) in temperate (Gehrke, 1992; Turner et al., 1994) and tropical locations (Winemiller & Jepsen, 1998). However, relatively long-term studies examining the influence of seasonal floodplain on local and system-wide fish production are limited primarily to the tropics (De Graaf, 2003). Here, production of splittail exhibited a significant positive relationship with the amount of floodplain habitat available during the peak spawning and juvenile rearing period over seven hydrologically diverse years. This indicates that the increased availability of habitat and resources such as food in the floodplain (Sommer et al., 2001a, 2004a) provide important spawning and nursery habitat for splittail.

Floodplain associated behaviors of splittail, especially the strong tendency to spawn in association with the vernal equinox, appear to be direct adaptations to local environmental conditions. In many temperate regions, floodplain inundation is stochastic and unpredictable because of dynamic precipitation patterns (Winemiller, 1996). In California's Central Valley, however, timing of floodplain inundation is fairly predictable. Due to local climate and snow melt patterns, peak historical river flow entering the San Francisco Estuary from California's Central Valley (Kimmerer, 2002a) coincides approximately with the vernal equinox, so it seems reasonable to assume that the availability of seasonal floodplain habitat would have been highest during this time period. Although flow timing is relatively predictable, flow

Table 4. Least squares regression models relating annual production of splittail in Yolo Bypass to mean January–June stage (S), flow (F), and water temperature (T)

Model	Rank	AIC _c	Δ_i	w_i
S	1	-28.78	0.00	0.89
F	2	-23.77	5.00	0.07
$S*T$	3	-21.80	6.97	0.02
$S*F$	4	-17.75	11.03	0.00
T	5	-16.82	11.95	0.00
$F*T$	6	-11.87	16.90	0.00
$S*F*T$	7	13.45	42.24	0.00

Models were ranked by Akaike's information criterion for small samples size (AIC_c) differences (Δ_i) and relative weights (w_i).

magnitude can vary greatly among years with periodic drought conditions that can greatly limit the availability of prime floodplain habitat. The large body size, long life span, high fecundity, and broad environmental tolerances of splittail enable the species to be resilient under such conditions when floodplain habitat may be limiting (Young & Cech, 1996; Feyrer & Baxter, 1998; Moyle et al., 2004).

Gravid adult splittail typically migrate upstream and enter Yolo Bypass starting in January following pulse flow events (Harrell & Sommer, 2003; Moyle et al., 2004), suggesting that river flow and/or photoperiod probably cue splittail spawning migrations and activity. Flow pulses are also associated with the spawning activity of a number of relatively large-sized cyprinids and

catostomids in river systems of the western United States (Nessler et al., 1988; Tyus & Karp, 1989; Moyle, 2002), suggesting widespread behavioral adaptation of fishes to the dynamic Mediterranean climate and hydrograph. After spawning, the descending hydrograph facilitates movement of offspring from floodplains to main channels in order to efficiently move downstream to the upper San Francisco Estuary, where fish will rear until becoming sexually mature in 1–2 years. During this downstream movement, age-0 splittail favor offchannel habitats and will enter the estuary in summer (Feyrer et al., 2005).

It appears that the timing of splittail spawning has evolved to coincide when suitable physical habitat is maximized and environmental conditions are optimal for the growth and survival of offspring. The timing of the vernal equinox appears to be a temporally stable cue for such conditions. Any stable reoccurring phenomena within the sensory capabilities of a fish can act as a timing cue for reproduction (Bye, 1984). Further, it is well established in the literature that photoperiod can be an important factor controlling gonadal development in fishes, especially cyprinids (DeVlaming, 1972; Lam, 1983; Moyle, 2002). In general, it appears that spawning by cyprinids is related to specific external factors relevant to reproductive success (Stacey, 1984). For example, submerged vegetation is an important spawning cue for goldfish (*Carassius auratus* Linnaeus), even at suboptimal temperatures; in the absence of submerged vegetation goldfish only spawned under

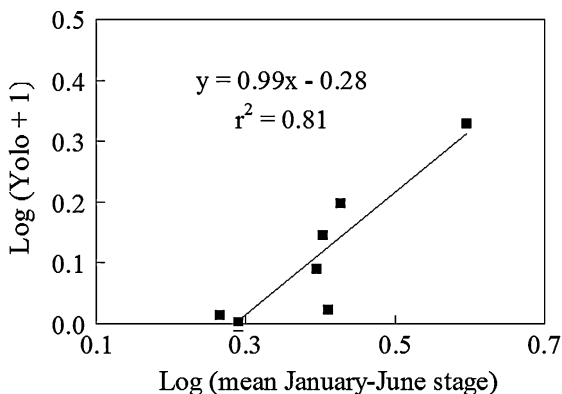


Figure 4. Linear regression model for the relationship between production of age-0 splittail versus mean January–June stage in Yolo Bypass.

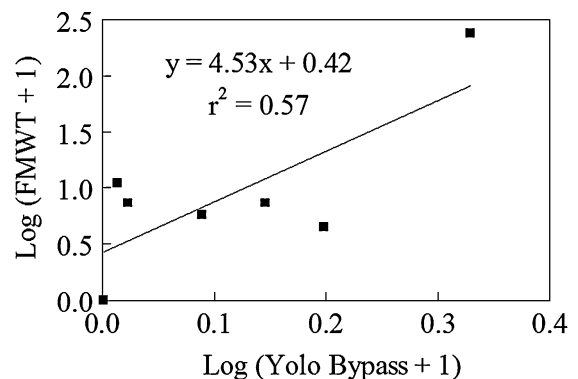


Figure 5. Relationship between production of age-0 splittail in Yolo Bypass compared to overall system-wide production as estimated from the California Department of Fish and Game's Fall Midwater Trawl Survey (FMWT).

optimal temperatures (Stacey et al., 1979). Similar factors may be important for splittail considering they produce large year classes (Sommer et al., 1997) and have apparently extended spawning periods (Fig. 2) in wet years with substantial inundated floodplain habitat.

These results and those of Harrell and Sommer (2003) suggest there are two key elements necessary to promote splittail production in floodplain habitats: pulse flows during winter are needed to initiate spawning migrations and attract fish into floodplains, and sustained floodplain inundation during late winter and spring is needed to maximize benefits for spawning and rearing. The apparent benefits of seasonal floodplain and off-channel habitat to splittail are probably similar to what has been observed for other species. Enhanced feeding, growth, and survival of fish have been observed in both large and small river–floodplain systems in many regions (e.g., Junk et al., 1989; Gutreuter et al., 1999; Sommer et al. 2001a). For splittail, floodplain provides both important spawning habitat for adults and nursery areas for offspring. Benefits to spawning on seasonal floodplain include large expansive areas of foraging habitat for ripening adults, submerged terrestrial vegetation on which splittail spawn adhesive eggs, and decreased risk of fish predation on both adults and deposited eggs (Caywood, 1974; Crain et al., 2004). For offspring, the floodplain is warmer with more abundant food resources than the adjacent Sacramento River channel (Sommer et al., 2001a) and is likely to have fewer fish predators. Similar conditions have been reported for other river–floodplain systems in the western United States (Modde et al., 2001). Such conditions appear to enhance the growth and body condition of young splittail (Ribeiro et al., 2004), as well as other fishes (Sommer et al., 2001b), and may ultimately improve survival and enhance year class strength.

The consistent 30–40 mm size of splittail during emigration peaks that varied temporally among years suggests that fish size may be an important factor controlling floodplain emigration. Trap bias does not appear to have overly influenced this observation. Overall, we collected age-0 splittail ranging in size from 16 to 87 mm and visual inspection of abundance plotted against mean length across all samples indicated

that abundance was uniformly distributed between 20 and 60 mm, indicating the trap was effective at collecting fish across this size range. In a model floodplain wetland, Sommer et al. (2002) found that young splittail used a broad range of habitats but shifted to a predominantly offshore distribution by approximately 30 mm. Further, Young & Cech (1996) found that age-0 splittail in this size range, collected from natural freshwater habitats along the Sacramento River, exhibited remarkable tolerance to salinity up to 22.4 ppt. Together, these behavioral and physiological observations provide evidence suggesting young splittail are able to actively emigrate freshwater habitats for the estuary during the first few months of life. These observations corroborate the findings of Feyrer et al. (2005) who found that young splittail were typically distributed in the Sacramento-San Joaquin Delta by summer, regardless of water year type or upstream spawning distribution.

Due to the dynamic nature of river–floodplain systems, there is the possibility that fish can become stranded in isolated pools during a descending hydrograph, which may cause significant mortality that could, to some extent, offset the perceived benefits obtained from utilizing the floodplain. This is particularly true for regulated systems where managed flows may decrease significantly faster than in natural systems and rapidly isolate floodplain habitats, standing fishes and exposing them to a number of mortality sources. Salmonids have been the primary focus of stranding issues because of their great commercial and recreational importance (Higgins & Bradford, 1996; Bradford, 1997; Sommer et al., 2005), however, all fishes utilizing floodplain habitats including cyprinids such as splittail are potentially vulnerable to stranding. Although stranding may pose a potentially serious threat to fishes that need to rapidly emigrate to other habitats to complete their life cycle (e.g., salmonids or other highly migratory taxa) it may not be a significant problem for other species. For instance, in Mediterranean climates, cyprinids often remain in isolated habitats for considerable periods of time before rejoining main channel habitats when flows increase (Lucas & Baras, 2001). Whether or not it poses a significant threat to the population requires substantial study, however, stranding of

splittail in isolated habitats does not appear to be common in Yolo Bypass. Feyrer et al. (2004b) did not collect any splittail in a study of fish communities in perennial aquatic habitats of Yolo Bypass. Further, because the species has evolved in a dynamic flood-prone environment, it is probably capable of utilizing floodplain habitats in a manner, which will provide net benefits to the population.

The apparent positive relationship between splittail production in Yolo Bypass and overall system-wide production suggests that Yolo Bypass produces a consistent proportion of total production annually and may significantly contribute to overall year class strength. Evidence that floodplain habitat significantly contributes to splittail year class strength comes from previous studies that have noted extremely large year classes are produced in the wettest years, a significant positive relationship between year class strength and flow entering the San Francisco Estuary, and marked abundance declines during drought periods (Daniels & Moyle, 1983; Meng & Moyle, 1995; Sommer et al., 1997). Given the indirect correlative nature of these previous studies, this study provides the first direct evidence that the availability of floodplain habitat directly influences local and possibly regional production of splittail. Although the analysis was limited by a small sample size and was influenced by two extreme points, it is nonetheless logical given the current understanding of splittail population dynamics. First, it is well established that splittail spawn and rear on floodplains and that flows affect year class strength (Meng & Moyle, 1995; Sommer et al., 1997). Second, the degree to which Yolo Bypass contributes to overall year class strength is probably significant because it provides the largest amount of floodplain habitat available for splittail in California's Central Valley (Sommer et al., 2001b; Feyrer et al., 2006). Further, even in relatively dry years when Sacramento River flows do not inundate Yolo Bypass or other floodplains, a substantial amount of floodplain in Yolo Bypass can still be inundated from other tributaries such as Cache and Putah Creeks (Sommer et al., 2001b).

In San Francisco Estuary, abundance or survival of many organisms is related to what has been locally termed X_2 , which is the horizontal

distance up the axis of the estuary to where tidally averaged near-bottom salinity is 2 psu (Jassby et al., 1995; Kimmerer, 2002b). Because of these strong relationships, manipulating the position of X_2 is a key tool used to manage salinity via flows entering the estuary. Although these relationships are well established, mechanisms supporting them are not well understood. For splittail, the relationship is characterized by increased abundance (measured by the FMWT) as mean February–May X_2 decreases, indicating a significant positive relationship between FMWT abundance and flow entering the estuary during February–May (Kimmerer, 2002b). Based upon our observations, several lines of evidence are proposed to suggest the mechanism supporting this relationship for splittail lies within the covarying relationship between X_2 and flow patterns upstream entering the estuary: (1) the vast majority of splittail spawning occurs upstream of the estuary in freshwater rivers and floodplains (Moyle et al., 2004), (2) the averaging time frame (February–May) for X_2 coincides with the primary spawning and upstream rearing period for splittail, (3) the availability of floodplain habitat, as indexed by Yolo Bypass stage, is directly related to X_2 during February–May ($y = 4.38 - 2.21x$; $p < 0.001$; $r^2 = 0.97$), (4) the center of age-0 splittail distribution does not reach the estuary until summer (Feyrer et al., 2005), and (5) the splittail– X_2 relationship has not been affected by dramatic food web changes (Kimmerer, 2002b) that have significantly altered the diet of young splittail in the estuary (Feyrer et al., 2003). Thus, it appears that upstream covariates of X_2 such as the availability of suitable floodplain and offchannel spawning and nursery habitat are the attributes supporting this relationship for splittail.

Our study supports the findings of Sommer et al. (2001b) that floodplain inundation in regulated systems such as Yolo Bypass can be managed to provide benefits for special status native fishes. In efforts to improve navigation, convey water supplies, and protect human lives and property, water reclamation activities throughout the developed portions of the world have significantly altered natural riverine habitats. This has included either isolating or eliminating the ability of high flows to inundate expansive floodplains (Power et al., 1995; Ward & Sanford, 1995; Vitousek et al., 1997). In cases where floodplain inundation

can be managed at isolated water entrance points such as weirs or by flow manipulations in regulated rivers, both of which are available tools for Yolo Bypass, management strategies could be developed to provide benefits to fish and other resources. Manipulating flows entering Yolo Bypass such that floodplain inundation is maximized during January–June will likely provide the greatest overall benefit for splittail, especially in relatively dry years when overall production is lowest. Additionally, other fishes of interest including Sacramento blackfish (*Orthodon microlepidotus* Ayers) and juvenile Chinook salmon (*Oncorhynchus tshawytscha* Walbaum), as well as other aquatic and terrestrial species would also benefit (Sommer et al., 2001a, b, 2004b). Further, the production and transport of phytoplankton and detrital material downstream resulting from floodplain inundation in Yolo Bypass enhances the food web of the San Francisco Estuary (Jassby & Cloern, 2000; Sommer et al., 2001b; Mueller-Solger et al., 2002). Thus, properly managed floodplains have potential to provide widespread benefits at multiple levels ranging from individual organisms to ecosystems.

Acknowledgements

This study was funded by the Interagency Ecological Program, California Bay-Delta Water Authority, and the California Department of Water Resources. Many seasonal technicians, including J. Heublein, S. Zeug, G. O'Leary, C. Hogle, G. Benigno, and L. Conrad, assisted with collecting field data.

References

- Burnham, K. P. & D. R. Anderson, 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag.
- Bayley, P. B., 1991. The flood pulse advantage and the restoration of river-floodplain systems. *Regulated Rivers* 6: 75–86.
- Bradford, M. J., 1997. An experimental study of stranding of juvenile salmonids on gravel bars and in side channels during rapid flow decreases. *Regulated Rivers* 13: 395–401.
- Bye, V. J., 1984. The role of environmental factors in the timing of reproductive cycles. In Potts, G. W. & J. Wootton (eds), *Fish Reproduction: Strategies and Tactics*. Academic, London, 87–205.
- CALFED, 2000. Programmatic record of decision, August 28, 2000. <http://calwater.ca.gov/archives/generalarchive/recordofdecision2000.shtml>.
- Caywood, M. L. 1974. Contributions to the Life History of the Splittail *Pogonichthys macrolepidotus* (Ayers). Masters Thesis, California State University, Sacramento, 77 pp.
- Copp, G. H. & M. Penaz, 1988. Ecology of fish spawning and nursery zones in the floodplain, using a new sampling approach. *Hydrobiologia* 169: 209–224.
- Crain, P. K., K. Whitener & P. B. Moyle, 2004. Use of a restored central California floodplain by larvae of native and alien fishes. In Feyrer F., L. Brown, R. Brown & J. Orsi (eds), *Early Life History of Fishes in the San Francisco Estuary and Watershed*. American Fisheries Society, Symposium 39, Bethesda, Maryland, 125–140.
- Daniels, R. A. & P. B. Moyle, 1983. Life history of the splittail (Cyprinidae: *Pogonichthys macrolepidotus*) in the Sacramento-San Joaquin Estuary. *Fishery Bulletin* 84: 105–117.
- De Graaf, G., 2003. Dynamics of floodplain fisheries in Bangladesh, results of 8 years fisheries monitoring in the Compartmentalization Pilot Project. *Fisheries Management and Ecology* 10: 191–199.
- Deng, D. F., S. J. Teh, F. C. Teh & S. S. O. Hung, 2002. Effects of diets and water temperatures on growth performance of splittail larvae. *North American Journal of Aquaculture* 64: 242–247.
- DeVlaming, V. L., 1972. Environmental control of teleost reproductive cycles: a brief review. *Journal of Fish Biology* 4: 131–140.
- Feyrer, F. & R. Baxter, 1998. Splittail fecundity and egg size. *California Fish and Game* 84: 119–126.
- Feyrer, F., B. Herbold, S. A. Matern & P. B. Moyle, 2003. Dietary shifts in a stressed fish assemblage: consequences of a bivalve invasion in the San Francisco Estuary. *Environmental Biology of Fishes* 67: 277–288.
- Feyrer, F., T. Sommer & R. Baxter, 2005. Spatial-temporal distribution and habitat associations of age-0 splittail in the lower San Francisco Estuary watershed. *Copeia* 2005: 159–168.
- Feyrer, F., T. Sommer & W. Harrell, 2006. Importance of flood dynamics versus intrinsic physical habitat in structuring fish communities: evidence from two adjacent engineered floodplains on the Sacramento River, California. *North American Journal of Fisheries Management* 26: 408–417.
- Feyrer, F., T. Sommer, J. Hobbs & B. Bridges, 2004a. Otolith aging of age-0 splittail: techniques, validations, and limitations. *Interagency Ecological Program for the San Francisco Estuary Newsletter* 17(1): 24–27.
- Feyrer, F., T. Sommer, S. Zeug, G. O'Leary & W. Harrell, 2004b. Fish assemblages of perennial floodplain ponds of the Sacramento River, California (USA), with implications for the conservation of native fishes. *Fisheries Management and Ecology* 11: 335–344.

- Gehrke, P. C., 1992. Diel abundance, migration and feeding of fish larvae (Eleotridae) on a floodplain billabong. *Journal of Fish Biology* 40: 695–707.
- Gladden, J. E. & L. A. Smock, 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. *Freshwater Biology* 24: 533–545.
- Gutreuter, S., A. D. Bartels, K. Irons & M. B. Sandheinrich, 1999. Evaluation of the flood-pulse-concept based on statistical models of growth of selected fishes of the upper Mississippi River system. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2282–2291.
- Halyk, L. C. & E. K. Balon, 1983. Structure and ecological production of the fish taxocene of a small floodplain system. *Canadian Journal of Zoology* 61: 2446–2464.
- Harrell, W. C. & T. Sommer, 2003. Patterns of adult fish use on California's Yolo Bypass floodplain. In Faber, P. H. (ed.), *California Riparian Systems: Processes and Floodplain Management, Ecology, and Restoration*. Riparian Habitat and Floodplains Conference Proceedings, Riparian Habitat Joint Venture, Sacramento, California 88–93.
- Higgins, P. S. & M. J. Bradford, 1996. Evaluation of a large-scale fish salvage to reduce the impacts of controlled flow reduction in a regulated river. *North American Journal of Fisheries Management* 16: 666–673.
- Jassby, A. D., W. Kimmerer, S. Monismith, C. Armor, J. Cloern, T. Powell, J. Schubel & T. Vendlinski, 1995. Isohaline position as a habitat indicator for estuarine populations. *Ecological Applications* 5: 272–289.
- Jassby, A. D. & J. E. Cloern, 2000. Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). *Aquatic Conservation: Marine and Freshwater Ecosystems* 10: 323–352.
- Junk, W. J., P. B. Bayley & R. E. Sparks, 1989. The flood pulse concept in river–floodplain systems. *Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences* 106: 110–127.
- Kimmerer, W. J., 2002a. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. *Estuaries* 25: 1275–1290.
- Kimmerer, W. J., 2002b. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages. *Marine Ecology Progress Series* 243: 39–55.
- Lam, T. J., 1983. Environmental influences on gonadal activity in fish. In Hoar, W. S., D. J. Randall & E. M. Donaldson (eds), *Fish Physiology*, Volume 9, Part B. Academic, New York, 65–116.
- Lucas, M. C. & E. Baras, 2001. *Migration of Freshwater Fishes*. Blackwell Science, Iowa State University Press, Ames, Iowa, 420 pp.
- Meng, L. & P. B. Moyle, 1995. Status of splittail in the Sacramento-San Joaquin Estuary. *Transactions of the American Fisheries Society* 124: 538–549.
- Modde, T., R. T. Muth & G. B. Haines, 2001. Floodplain wetland suitability, access, and potential use by juvenile razorback suckers in the Middle Green River, Utah. *Transactions of the American Fisheries Society* 130: 1095–1105.
- Moyle, P. B., 2002. *Inland Fishes of California*. Revised and Expanded. University of California Press, Berkeley, California, 502 pp.
- Moyle, P. B., R. D. Baxter, T. Sommer, T. C. Foin & S. A. Matern, 2004. Biology and population dynamics of Sacramento Splittail (*Pogonichthys macrolepidotus*) in the San Francisco Estuary: a review. *San Francisco Estuary and Watershed Science* 2, 2(May 2004), Article 3; <http://repositories.cdlib.org/jmie/sfew/vol2/iss2/art3>.
- Mueller-Solger, A. B., A. Jassby & D. C. Mueller-Navarra, 2002. Nutritional quality for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta, USA). *Limnology and Oceanography* 47: 1468–1476.
- Nesler, T. P., R. T. Muth & A. F. Wasowicz, 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. *American Fisheries Society Symposium* 5: 68–79.
- Power, M. E., G. Parker, W. E. Diedrich & A. Sun, 1995. How does floodplain width affect floodplain river ecology – a preliminary exploration using simulations. *Geomorphology* 13: 301–317.
- Ribeiro, F., P. K. Crain & P. B. Moyle, 2004. Variation in condition factor and growth in young-of-year fishes in floodplain and riverine habitats of the Cosumnes River, California. *Hydrobiologia* 527: 77–84.
- Rooker, J. R., S. A. Holt, G. J. Holt & L. E. Fuiman, 1998. Spatial and temporal variability in growth, mortality, and recruitment potential of postsettlement red drum, *Sciaenops ocellatus*, in a subtropical estuary. *Fishery Bulletin* 97: 581–590.
- Ross, S. T. & J. A. Baker, 1983. The response of fishes to periodic spring floods in a southeastern stream. *American Midland Naturalist* 109: 1–14.
- Sommer, T., R. Baxter & B. Herbold, 1997. Resilience of splittail in the Sacramento-San Joaquin Estuary. *Transactions of the American Fisheries Society* 126: 961–976.
- Sommer, T. R., L. Conrad, G. O'Leary, F. Feyrer & W. Harrell, 2002. Spawning and rearing of splittail in a model floodplain wetland. *Transactions of the American Fisheries Society* 131: 966–974.
- Sommer, T. R., W. Harrell, R. Kurth, F. Feyrer, S. Zeug & G. O'Leary, 2004b. Ecological patterns of early life stages of fishes in a river-floodplain of the San Francisco Estuary. In Feyrer, F., L. Brown, R. Brown & J. Orsi (eds), *Early Life History of Fishes in the San Francisco Estuary and Watershed*. American Fisheries Society, Symposium 39, Bethesda, Maryland: 111–123.
- Sommer, T. R., W. Harrell, A. Mueller-Solger, B. Tom & W. Kimmerer, 2004a. Effects of flow variation on channel and floodplain biota and habitats of the Sacramento River, California, USA. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14: 247–261.
- Sommer, T., W. Harrell & M. Nobriga, 2005. Habitat use and stranding risk of juvenile Chinook salmon on a seasonal floodplain. *North American Journal of Fisheries Management* 25: 1493–1504.
- Sommer, T., W. Harrell, M. Nobriga, R. Brown, P. B. Moyle, W. Kimmerer & L. Schemel, 2001b. California's Yolo Bypass: evidence that flood control can be compatible with fisheries, wetlands, wildlife, and agriculture. *Fisheries* 26: 6–16.
- Sommer, T. R., M. Nobriga, W. Harrell, W. Batham & W. Kimmerer, 2001a. Floodplain rearing of juvenile Chinook

- salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 325–333.
- Stacey, N. E., 1984. Control of the timing of ovulation by exogenous and endogenous factors. In Potts, G. W. & J. Wootton (eds), *Fish Reproduction: Strategies and Tactics*. Academic, London, 207–222.
- Stacey, N. E., A. F. Cook & R. E. Peter, 1979. Spontaneous and gonadotropin-induced ovulation in the goldfish, *Carassius auratus* L.: effects of external factors. *Journal of Fish Biology* 15: 349–361.
- Turner, T. F., J. C. Trexler, G. L. Miller & K. E. Toyer, 1994. Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. *Copeia* 1994: 174–183.
- Trexler, J. C. & J. Travis, 1993. Nontraditional regression analyses. *Ecology* 74: 1629–1637.
- Tyus, H. M. & C. A. Karp, 1989. Habitat and streamflow needs of rare and endangered fishes, Yampa River, Colorado. U.S. Fish and Wildlife Service Report 89(14): 26 pp.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco & J. M. Melillo, 1997. Human domination of the earth's ecosystems. *Science* 277: 494–499.
- Ward, J. V. & J. A. Sanford, 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regulated Rivers: Research and Management* 11: 105–119.
- Wang, J. C. S., 1986. Fishes of the Sacramento-San Joaquin Estuary and adjacent waters, California: a guide to their early life histories. Interagency Ecological Program. Technical Report 9. California Department of Water Resources, Sacramento, California.
- Winemiller, K. O., 1996. Factors driving temporal and spatial variation in aquatic floodplain food webs. In Polis, G. A. & K. O. Winemiller (eds), *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall, New York, 289–312.
- Winemiller, K. O. & D. B. Jepsen, 1998. Effects of seasonality and fish movement on tropical food webs. *Journal of Fish Biology* 53(Suppl. A): 267–296.
- Young, P. S. & J. J. Cech, 1996. Environmental tolerances and requirements of splittail. *Transactions of the American Fisheries Society* 125: 664–678.