

Floodplain rearing of juvenile chinook salmon: evidence of enhanced growth and survival

T.R. Sommer, M.L. Nobriga, W.C. Harrell, W. Batham, and W.J. Kimmerer

Abstract: In this study, we provide evidence that the Yolo Bypass, the primary floodplain of the lower Sacramento River (California, U.S.A.), provides better rearing and migration habitat for juvenile chinook salmon (*Oncorhynchus tshawytscha*) than adjacent river channels. During 1998 and 1999, salmon increased in size substantially faster in the seasonally inundated agricultural floodplain than in the river, suggesting better growth rates. Similarly, coded-wire-tagged juveniles released in the floodplain were significantly larger at recapture and had higher apparent growth rates than those concurrently released in the river. Improved growth rates in the floodplain were in part a result of significantly higher prey consumption, reflecting greater availability of drift invertebrates. Bioenergetic modeling suggested that feeding success was greater in the floodplain than in the river, despite increased metabolic costs of rearing in the significantly warmer floodplain. Survival indices for coded-wire-tagged groups were somewhat higher for those released in the floodplain than for those released in the river, but the differences were not statistically significant. Growth, survival, feeding success, and prey availability were higher in 1998 than in 1999, a year in which flow was more moderate, indicating that hydrology affects the quality of floodplain rearing habitat. These findings support the predictions of the flood pulse concept and provide new insight into the importance of the floodplain for salmon.

Résumé : Notre étude démontre que le canal de dérivation Yolo, la principale plaine d'inondation de la région aval de la rivière Sacramento (Californie, É.-U.), offre de meilleurs habitats pour l'alevinage et la migration des jeunes Saumons Quinnet (*Oncorhynchus tshawytscha*) que les bras adjacents de la rivière. En 1998 et 1999, la taille des saumons a augmenté plus rapidement dans la plaine d'inondation agricole, sujette aux débordements saisonniers de crue, que dans la rivière, ce qui laisse croire à de meilleurs taux de croissance. De plus, des jeunes saumons marqués à l'aide de fils de métal codés et relâchés dans la plaine d'inondation étaient plus gros au moment de leur recapture et avaient des taux de croissance apparente plus élevés que des poissons relâchés dans la rivière en même temps. L'amélioration des taux de croissance dans la plaine de débordement résultait en partie d'une consommation significativement plus importante de proies, le reflet d'une plus grande disponibilité des invertébrés de la dérive. Un modèle bioénergétique laisse croire que le succès de l'alimentation a été meilleur dans la plaine d'inondation que dans la rivière, en dépit du coût métabolique d'alevinage significativement plus grand dans les eaux plus chaudes de la plaine d'inondation. Les indices de survie des poissons marqués et relâchés dans la plaine d'inondation étaient quelque peu plus élevés que ceux des poissons de la rivière, mais les différences n'étaient pas statistiquement significatives. La croissance, la survie, le succès de l'alimentation et la disponibilité des proies étaient tous supérieurs en 1998 par comparaison avec 1999, une année à débit plus modéré, ce qui indique que l'hydrologie affecte la qualité des habitats d'alevinage dans la plaine d'inondation. Nos résultats appuient les prédictions du concept de pulsion de crue (flood pulse concept) et mettent en lumière l'importance de la plaine d'inondation pour le saumon.

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Introduction

Although the trophic structure of large rivers is frequently dominated by upstream processes (Vannote et al. 1980), there is increasing recognition that floodplains play a major role in the productivity and diversity of riverine communities (Bayley 1995). Based largely on observations from relatively undisturbed river-floodplain systems, Junk et al. (1989) pro-

posed the flood pulse concept, which predicts that annual inundation is the principal force determining productivity and biotic interactions in river-floodplain systems. Floodplains can provide higher biotic diversity (Junk et al. 1989) and increased production of fish (Bayley 1991; Halyk and Balon 1983) and invertebrates (Gladden and Smock 1990). Potential mechanisms for floodplain effects include increased habitat diversity and area (Junk et al. 1989), large inputs of

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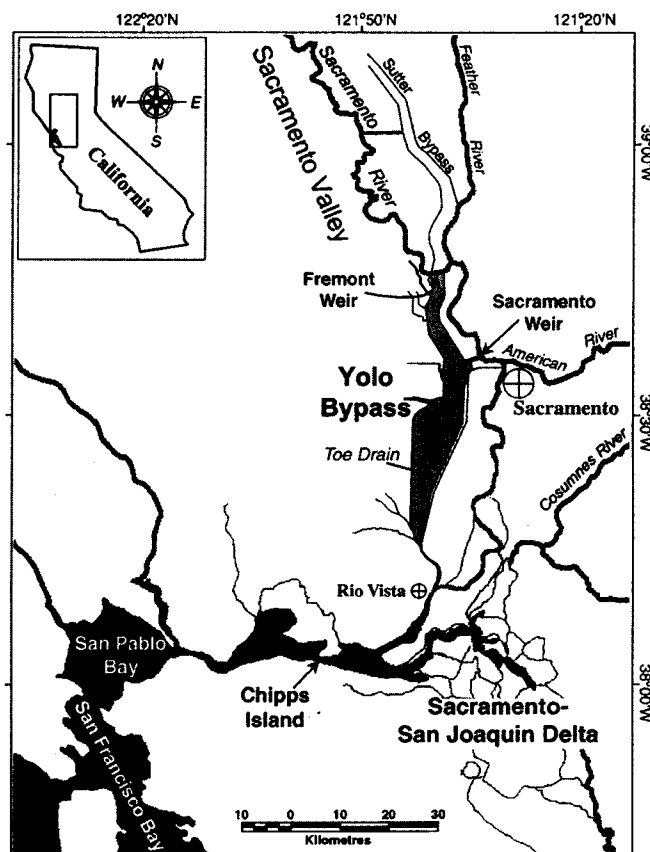
terrestrial material into the aquatic food web (Winemiller and Jepsen 1998), and decreased predation or competition due to intermediate levels of disturbance (Corti et al. 1997). Nonetheless, the degree to which floodplains support riverine ecosystems remains poorly understood, particularly in regulated and temperate rivers. Uncertainties about river-floodplain relationships are due, in large part, to the difficulty in separating the relative contribution of floodplain versus channel processes and sampling problems in seasonal habitats, which are frequently subject to extreme environmental variation.

In this study, we examined the relative importance of floodplain and riverine habitat to juvenile chinook salmon (*Oncorhynchus tshawytscha*) in the Sacramento River (California, U.S.A.), a large regulated river (Fig. 1). The system is particularly well suited to a comparative study, because young salmon migrating down the lower Sacramento River to the San Francisco Estuary in wet years have two alternative paths: they may continue down the heavily channelized main river or they may pass through the Yolo Bypass, an agricultural floodplain bordered by levees. We had two reasons to believe that the floodplain might be important habitat for young salmon. First, years of high flow are known to enhance populations of a variety of species in the San Francisco Estuary (Jassby et al. 1995) and the survival of chinook salmon (Kjelson et al. 1982). However, the specific mechanisms for these benefits have not been established. Possible reasons for the positive effects of flow on fish include increased habitat availability, migration cues, food supply, larval transport, and reduced predation rates (Bennett and Moyle 1996). Floodplain inundation is one of the unique characteristics of wet years, during which the Yolo Bypass is likely to be a significant migration corridor for young chinook salmon in the Sacramento Valley. During high-flow events, the Yolo Bypass can convey >75% of the total flow from the Sacramento River basin, the major producer of salmon among tributaries of the San Francisco Estuary. Second, floodplains are known to be among the most important fish-rearing areas in a variety of river systems, yet in developed regions, the availability of this habitat has been greatly reduced by channelization and levee and dam construction (Rasmussen 1996). A high degree of habitat loss may greatly enhance the biological significance of remnant floodplains in heavily modified systems, such as the San Francisco Estuary and its tributaries.

This study tests the hypothesis that the agricultural floodplain provides better habitat quality than the adjacent river channel. For the purpose of this analysis, we focus on salmon growth, feeding success, and survival as indicators of habitat quality. Obviously, there are many other possible measures of habitat quality, such as reproductive output of adults or physiological indicators. However, we believe that the chosen suite of parameters is reasonably representative of habitat quality. For example, Gutreuter et al. (2000) successfully used growth as a factor to test the hypothesis that floodplain inundation had a major effect on fish production.

The San Francisco Estuary is one of the largest estuaries on the Pacific Coast (Fig. 1). The system includes downstream bays (San Pablo and San Francisco) and a delta, a broad network of tidally influenced channels that receive inflow from the Sacramento and San Joaquin rivers. The estu-

Fig. 1. The location of Yolo Bypass in relation to the San Francisco Estuary and its tributaries. The San Francisco Estuary encompasses the region from San Francisco Bay upstream to Sacramento. Feather River Fish Hatchery is located on the Feather River approximately 112 km upstream of Yolo Bypass.



ary and its tributaries have been heavily altered by levees, dams, land reclamation activities, and water diversions. The primary floodplain of the Sacramento River portion of the delta is the Yolo Bypass, a 24 000-ha leveed basin that conveys excess flow from the Sacramento Valley, including the Sacramento River, Feather River, American River, Sutter Bypass, and westside streams. The 61 km long floodplain floods seasonally in winter and spring in about 60% of years, and is designed to convey up to $14\,000\text{ m}^3\cdot\text{s}^{-1}$. During a typical flooding event, water spills into the Yolo Bypass via the Fremont Weir when Sacramento Basin flows surpass approximately $2000\text{ m}^3\cdot\text{s}^{-1}$. Except during extremely high flow events, the mean depth of the floodplain is generally less than 2 m, creating broad shoal areas. During dry seasons, the Toe Drain channel, a permanent riparian corridor, remains inundated as a result of tidal action. At higher levels of Sacramento Basin flow (e.g., $>5000\text{ m}^3\cdot\text{s}^{-1}$), the Sacramento Weir is also frequently operated. Agricultural fields are the dominant habitat type in Yolo Bypass, but approximately one-third of the floodplain area is natural vegetation, including riparian habitat, upland habitat, emergent marsh, and permanent ponds.

There are four races of chinook salmon in the Sacramento Valley: winter, spring, late fall, and fall run (Yoshiyama et al. 2000). Historical data indicate that all races have de-

creased in abundance since the 1950s, but the spring, winter, and late-fall runs have shown the most pronounced declines. There are multiple causes for these long-term reductions, including habitat loss, habitat degradation, water diversions, and oceanic conditions. In the present study, we focused on the fall run, the numerically dominant race in the Sacramento Valley. The typical life-history pattern for these salmon is for young to migrate from the tributaries to the bay-delta area at the "fry" stage (Brandes and McLain 2001), when most individuals are approximately 35- to 70-mm fork length (FL). In low flow years, there may be substantial upstream rearing in the Sacramento River. Peak juvenile emigration from the tributaries occurs during winter and spring (Kjelson et al. 1982).

Materials and methods

Physical conditions

During 1998–1999, flow measurements in Yolo Bypass and the adjacent stretch of the Sacramento River were obtained from gauges operated by the U.S. Geological Survey (USGS). Daily water temperatures for each site were calculated as the mean of maximum and minimum daily measurements for single stations in the Sacramento River (USGS) and a temperature recorder (Onset Corp.) installed in the Yolo Bypass Toe Drain channel (Fig. 1). However, from 1 February to 26 March 1998, these data were not available for Yolo Bypass. During this period, before the recorder was installed, discrete measurements were taken at the same location, typically during mid or late morning.

Fish sampling

Salmon FL (mm) was measured during January–April in 1998 and 1999 on samples collected with 15-m beach seines (4.75-mm mesh). Samples were collected weekly at five core locations located around the perimeter of the Yolo Bypass, during periods when the basin was flooded. After the bypass drained, additional samples were collected at random locations around the perimeter of ponds near the core locations. Comparative data on salmon size in the adjacent reach of the Sacramento River were collected by the U.S. Fish and Wildlife Service (USFWS) at five beach-seine sites, using techniques similar to those used when the the bypass was flooded.

FLs of salmon obtained from beach-seine sampling were compared to determine whether there was evidence of major differences in salmon size between the Yolo Bypass and the Sacramento River. However, these data were not considered unambiguous evidence of growth differences, because the two systems were open to immigration and emigration during much of the study, and migrating salmon include multiple races of salmon that cannot be readily separated. We addressed this issue by using paired releases of coded-wire-tagged (CWT) juvenile salmon in Yolo Bypass and the Sacramento River. This approach allowed comparisons of growth among fish of similar origin and provided a relative estimate of migration time and survival. The salmon were produced and tagged at the Feather River Fish Hatchery and released on 2 March 1998 and 11 February 1999. The release sites were in Yolo Bypass below Fremont Weir (52 000 in 1998; 105 000 in 1999) and in the adjacent reach of the Sacramento River (53 000 in 1998; 105 000 in 1999). The fish had a mean FL of 57.5 ± 0.5 mm (SE) in 1998 and of 56.8 ± 0.4 mm (SE) in 1999. A small portion of each group was subsequently collected by trawling at the seaward margin of the delta at Chipps Island, which is located downstream of the confluence of the Yolo Bypass and the Sacramento River (Fig. 1). The USFWS Chipps Island survey samples a single channel location with a midwater trawl towed at the surface (Baker et al. 1995;

Brandes and McLain 2001). Ten 20-min tows were made each day, except during March in 1998 and 1999, when sampling was conducted every other day. Data on migration time (days) and FL (mm) were recorded for fish recaptured from each release group. Apparent growth rate was also calculated for each fish, as: $(\text{FL of individual at Chipps Island} - \text{mean FL of CWT release group}) \times (\text{migration time})^{-1}$. Survival indices of the paired CWT releases were calculated by USFWS by dividing the number of fish recovered for each release group at Chipps Island by the number released, corrected for the fraction of time and channel width sampled (Brandes and McLain 2001).

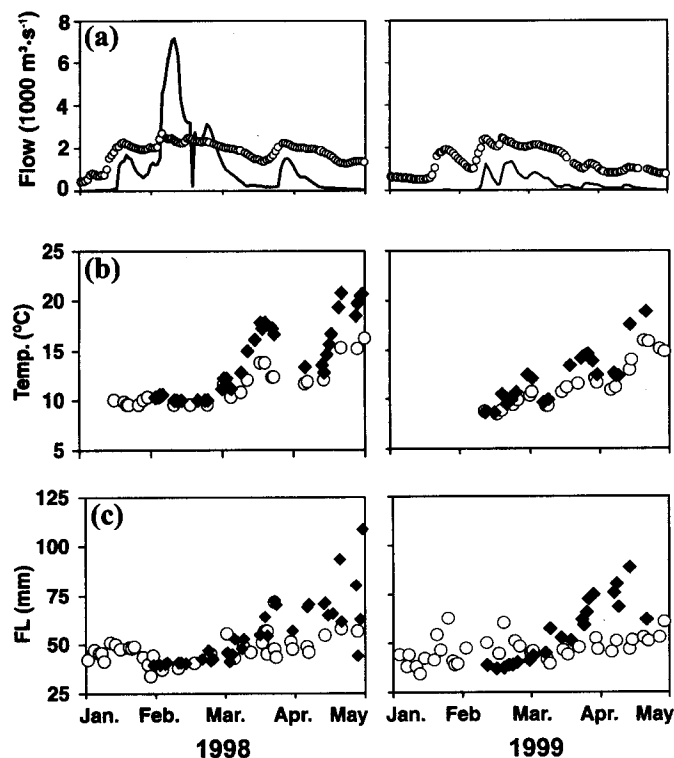
Diet

We performed diet comparisons on fall-run juvenile salmon (33–81 mm) collected in beach-seine samples during February–March of 1998 and 1999 from the Yolo Bypass (103 individuals) and the Sacramento River (109 individuals). Fish samples were tagged and stored individually in a deep freeze. After thawing, stomachs were removed from the fish and the contents were identified (using a dissecting microscope) to order (insects and arachnids), genus (crustaceans), or phylum (rarely eaten taxa such as oligochaetes). To develop average invertebrate length estimates, up to 10 individuals of each prey type encountered were measured. Prey dry weight estimates were calculated from average lengths, using regression equations for delta crustaceans obtained from J. Orsi (California Department of Fish and Game, Stockton, CA 95205, unpublished data) and from literature sources. Diet results were compared as an index of relative importance (IRI) (Shreffler et al. 1992) for each month. The index was calculated as: $\text{IRI} = (\% \text{ numeric composition} + \% \text{ weight composition}) \times \% \text{ frequency of occurrence}$.

Prey availability

Invertebrates were sampled in February–March of 1998 and 1999, to examine prey availability in the Yolo Bypass and the Sacramento River. Sampling was not designed as a comprehensive evaluation of spatial and temporal variation of prey. Rather, it was intended to provide information on whether variation in salmon diets between the two locations was consistent with gross differences in prey type or relative abundance. We focused on Diptera (adults, pupae, and larvae) and crustacean zooplankton, which comprised over 90% of the diets of Yolo Bypass and Sacramento River juvenile salmon. Weekly drift samples were collected at fixed stations on the Yolo Bypass and the Sacramento River during periods when the floodplain was inundated. The sampling points were located away from overhanging vegetation and bank eddies, in water velocities of approximately $15\text{--}60 \text{ cm}\cdot\text{s}^{-1}$, depending on flow. Net (500- μm mesh) dimensions were $0.46 \times 0.3 \text{ m}$ mouth and 0.91 m length. The nets were fished for approximately 30 min during mid-morning, to coincide with the time period when most fish-stomach samples were taken. Sample volume was calculated using a flow-meter (General Oceanics Model 2030R) and net dimensions. Drift samples were stored in ethanol or formaldehyde, then identified to family or order using a dissecting microscope. In 1998, zooplankton were collected in the Yolo Bypass at two fixed stations with battery-operated rotary-vane pumps with a mean flow rate of $17 \text{ L}\cdot\text{min}^{-1}$. Samples were taken via pipes with outlets at multiple locations beneath the water surface. Discharge was directed into a $150 \mu\text{m}$ mesh net held in a basin on the bank. Flow rate was recorded at the beginning and end of the sample period, which varied from 1 to 6 h. No samples were taken in the Sacramento River during a comparable period in 1998. In 1999, zooplankton samples were taken with a Clarke–Bumpus net (160- μm mesh, diameter 0.13 m, length 0.76 m) placed in surface flow in the Yolo Bypass and Sacramento River. Sample volume was recorded as for the drift net. Zooplankton samples were concentrated and stored in 5%

Fig. 2. Chinook salmon size versus physical conditions in Yolo Bypass and the Sacramento River during winter and spring in 1998 and 1999. (a) Mean daily flow ($\text{m}^3\cdot\text{s}^{-1}$) in Yolo Bypass (solid line) and the Sacramento River (circles). (b) Mean water temperature ($^{\circ}\text{C}$) in Yolo Bypass (solid symbols) and the Sacramento River (open symbols). (c) Mean daily chinook salmon FL for Yolo Bypass (solid symbols) and Sacramento River (open symbols) beach-seine stations. For presentation purposes, only the daily mean FLs are shown; however, individual observations for February–March were used for statistical analyses.



formaldehyde, for later identification to genus using a dissecting microscope.

Bioenergetics

Feeding success was examined in two ways: (1) prey biomass estimated from stomach contents and (2) prey biomass estimated as a function of maximum theoretical consumption. For the first measure, we used the previously described stomach-content data to calculate total-prey biomass for individual fish.

A limitation of using prey biomass as a measure of feeding success between locations is that thermal history affects how consumption alters growth rate (Hewett and Kraft 1993). As will be discussed in further detail, water temperatures were significantly higher in the Yolo Bypass floodplain than in the Sacramento River. To correct for this problem, our second approach used bioenergetic modeling to incorporate the metabolic effects of water temperature. We used methods similar to those of Rand and Stewart (1998) to calculate a wet weight ration index, which uses prey biomass for each sampled individual as a proportion of the theoretical maximum daily consumption. The stomach-content data were used as our estimate of prey biomass for individual fish. The theoretical maximum daily consumption rate (C_{\max}) was modeled using Fish Bioenergetics 3.0 (Hanson et al. 1997), using observed body size and water temperature at the time each beach-seine sample was collected. The model input also required fish mass, which we estimated from FL data, using length–weight relationships from Sacra-

Table 1. Robust regression statistics for Yolo Bypass and Sacramento River salmon FLs for 1998 and 1999.

	1998		1999	
	Parameter \pm SEM	<i>t</i>	Parameter \pm SEM	<i>t</i>
Intercept	29.4 \pm 0.6	46.8	23.5 \pm 0.5	43.7
Location	6.4 \pm 0.6	10.2	11.1 \pm 0.5	20.6
Day	0.3 \pm 0.01	34.5	0.3 \pm 0.01	48.5
Location:day	-0.14 \pm 0.01	-18.4	-0.21 \pm 0.01	-33.6

Note: The *t* values are all highly significant ($p < 0.0001$).

mento River juvenile salmon (Petrusso 1998). The caloric value of the prey was taken from weight conversion factors provided by Hanson et al. (1997). Model parameters were derived from those of Stewart and Ibarra (1991) for chinook salmon. The model was run for individual fish collected at each sampling location in 1998 and 1999.

We emphasize that the second approach provides an *index*, rather than an *absolute* measure of feeding success. The wet weight ration index is conceptually analogous to “*P*” in Hanson et al. (1997), a model parameter that indicates what fraction of C_{\max} is obtained over the course of the day. The major difference is that *P* is based on prey consumption over a 24-hour period, whereas our wet weight ration index is based on instantaneous measurements of stomach contents, which may not represent mean trends over the entire day. An additional limitation is that the Stewart and Ibarra (1991) model parameters were developed for adult salmon and we applied the model to juveniles. We did not have sufficient field or laboratory data to develop bioenergetic-model parameters specific to the earliest life stages. Nonetheless, other studies (Rand and Stewart 1998) have demonstrated that similar wet weight ration indices can provide an effective technique for comparing relative salmonid feeding success between seasons and years.

Statistical analysis

Overlapping temperature measurements from continuous recorders and the discrete measurements during 26 March – May 1998 were analyzed with Wilcoxon’s matched-pairs test, to determine whether the two methods yielded different results. Mean water temperature for Yolo Bypass and the Sacramento River during the primary period of floodplain inundation (February–March) was analyzed with a generalized linear model with a variance function that increased with the mean squared, since variances were not homogeneous (Venables and Ripley 1997). Salmon FL measurements for Yolo Bypass and the Sacramento River during February–March of 1998 and 1999 were compared with a robust iteratively reweighted least squares regression procedure (“rlm”; Venables and Ripley 1997), because we detected substantial numbers of outliers in preliminary graphical evaluations of the data. Initial analyses revealed a substantial difference in the effects of location between years, so years were analyzed separately. Results from the CWT and bioenergetic studies were analyzed using a factorial-design analysis of variance, to evaluate the effects of location (Yolo Bypass, Sacramento River) and year (1998, 1999). Residuals from each model were examined graphically, to confirm that they met the assumption of normality and homogeneity of variance. Cochran and Levene’s tests were also used, to test the assumption of homogeneity of variance. Logarithmic transformation was performed where necessary.

Results

Physical conditions

Yolo Bypass was inundated in 1998 and 1999 but the hydrology was substantially different in the two years (Fig. 2).

Table 2. Results of salmon collections at Chipps Island for 1998 and 1999 coded-wire-tagged groups released concurrently in Yolo Bypass and the Sacramento River.

	1998		1999	
	Yolo Bypass	Sacramento River	Yolo Bypass	Sacramento River
Fork length (mm)	93.7±2.0	85.7±1.4	89.0±2.6	82.1±1.7
Migration time (days)	46.2±2.3	55.4±3.5	58.2±2.8	58.6±4.1
Apparent growth rate (mm·day ⁻¹)	0.80±0.06	0.52±0.02	0.55±0.06	0.43±0.03
Survival index	0.16	0.09	0.09	0.07
Sample size	9	10	9	8

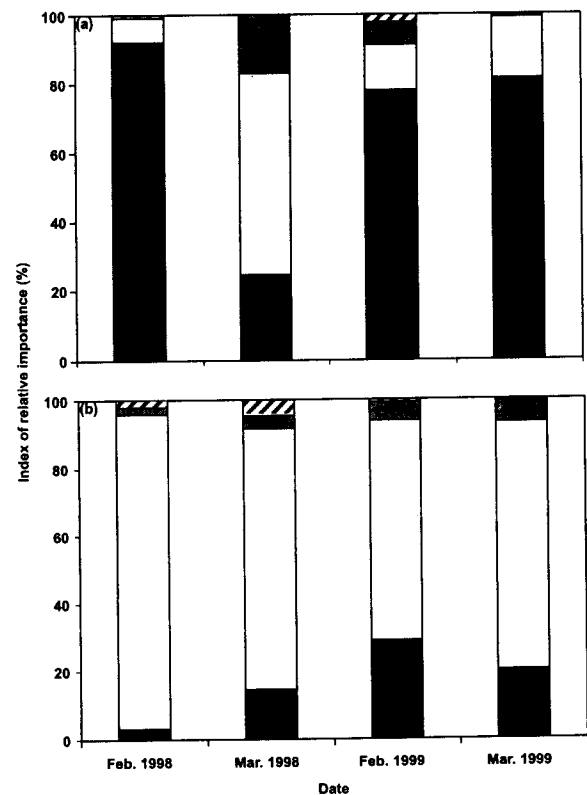
Note: Values for FL, migration time, and apparent growth rate are mean ± standard error (SEM).

The first year was extremely wet, with multiple flow pulses and a peak flow of 7200 m³·s⁻¹. In 1999, floodplain hydrology was more moderate, with a peak of 1300 m³·s⁻¹. Flows in the Sacramento River were much less variable than in the floodplain and generally remained at or below 2000 m³·s⁻¹, a level within the design capacity (3100 m³·s⁻¹) of the channel. Overlapping sampling between the continuous-temperature recorders and the discrete measurements during March–May 1998 showed a mean difference of 0.9°C between the two approaches, but this disparity was not statistically significant (Wilcoxon's matched-pairs test, $p > 0.25$). In 1998 and 1999, temperatures increased fairly steadily throughout the study period; however, in both years, temperature levels in Yolo Bypass were up to 5°C higher than those in the adjacent Sacramento River during the primary period of inundation, February–March. Temperature in the Yolo Bypass was described in 1998 by $T_y = -7.7 \pm 2.1 + (1.9 \pm 0.2)T_s$ and in 1999 by $T_y = -3.5 \pm 1.2 + (1.5 \pm 0.1)T_s$, where T_y is the temperature of the Yolo Bypass, T_s is the temperature of the Sacramento River, and the range for each value is the 95% confidence limit.

Fish growth, migration time, apparent growth rate, and survival

Salmon increased in size substantially faster in the Yolo Bypass than in the Sacramento River during each of the study years (Fig. 2). Robust regression results showed that the effect of location was highly significant ($p < 0.00001$) in each year (Table 1). This result is consistent with the CWT data (Table 2), which showed that the 1998 and 1999 Yolo Bypass CWT release groups had significantly larger mean length ($F = 14.34$, $p = 0.0006$) and higher apparent growth rates ($F = 20.67$, $p = 0.0007$) than the Sacramento River release groups. There was also a statistically significant effect of year: both release groups had larger mean sizes ($F = 4.42$, $p = 0.04$) and higher apparent growth rates ($F = 16.47$, $p = 0.0002$) in 1998 than in 1999. The 1998 Yolo Bypass CWT group showed the fastest migration time, arriving an average of at least 9 days ahead of any other release group. However, there was no statistically significant ($F = 2.22$, $p = 0.15$) effect of release location on migration time in the analysis of variance (ANOVA). As for fish size and apparent growth rate, mean migration time was slower in 1999 than in 1998 ($F = 5.60$, $p = 0.02$). There was no statistically significant interaction between location and year for salmon size ($F = 0.07$, $p = 0.78$), apparent growth rate ($F = 1.62$, $p = 0.21$), or migration time ($F = 1.8$, $p = 0.18$). The survival indices were somewhat higher for CWT groups released in the Yolo By-

Fig. 3. Chinook salmon diet during February and March of 1998 and 1999 in Yolo Bypass (a) and the Sacramento River (b). The index of relative importance (y-axis) is defined in the text. Diptera (solid bars), zooplankton (open bars), other aquatic prey (shaded bars), and other terrestrial prey (striped bars) are shown for each month.

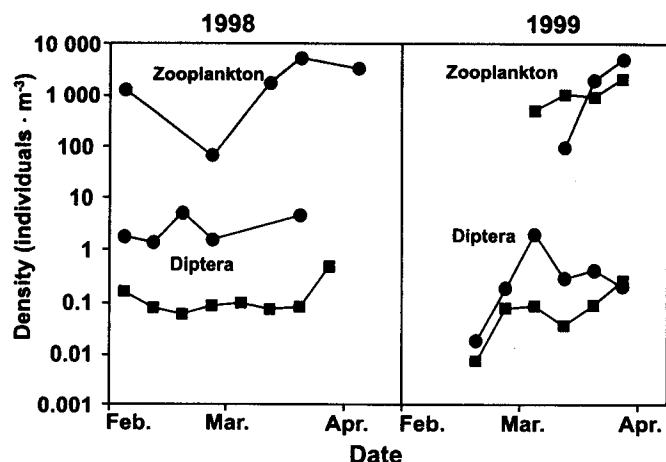


pass than for those released in the Sacramento River for both 1998 and 1999. However, the lowest coefficient of variation based on a Poisson distribution of the CWT recaptures is 32%, and the actual (unknown) distribution of counts is likely to have higher variance than a Poisson distribution. Clearly the confidence limits of the paired survival indices would overlap, so the differences are not statistically significant.

Diet

The diet of young salmon in the Yolo Bypass was dominated by dipterans, principally chironomid pupae and adults (Fig. 3). The second most common prey item was zooplank-

Fig. 4. Log₁₀-scaled weekly abundance (individuals·m⁻³) of zooplankton and Diptera in Yolo Bypass (circles) and the Sacramento River (squares) during 1998 and 1999. Note that 1998 zooplankton data were not available for the Sacramento River.



ton, mostly cladocerans and copepods. Except for March 1998, zooplankton comprised less than 15% of the Yolo Bypass diets. Other aquatic (mainly amphipods and collembola) and terrestrial (mainly ants and arachnids) prey were relatively minor diet items. As for the floodplain samples, dipterans and zooplankton comprised over 90% of the diets of Sacramento River salmon; however, zooplankton were the dominant prey item in all months. Other aquatic (mostly amphipods, oligochaetes, and collembola) and terrestrial (mostly ants and other terrestrial insects) prey were consumed infrequently.

Prey availability

The drift samples contained many of the same taxa observed in the salmon diets, with Diptera (principally chironomids) as the major type at both sampling locations. However, the density of Diptera was much higher in the Yolo Bypass than in the Sacramento River (Fig. 4), particularly in 1998, when densities were consistently an order of magnitude higher. In general, dipteran drift densities were higher at each location in 1998 than in 1999. There was little difference in zooplankton density in the Yolo Bypass between 1998 and 1999 or between Yolo Bypass and the Sacramento River in 1999.

Bioenergetics

Young salmon from the Yolo Bypass had higher total-prey weights ($F = 39.2$, $df = 1$, $p < 0.0001$) than those from the Sacramento River (Fig. 5). The bioenergetic-modeling results showed that Yolo Bypass salmon also had higher wet weight ration indices than those from the Sacramento River ($F = 19.3$, $df = 1$, $p < 0.0001$). The interaction between location and year was significant for both the wet weight ration indices ($F = 10.0$, $df = 1$, $p = 0.02$) and the prey weights ($F = 4.7$, $df = 1$, $p = 0.03$).

Discussion

Chinook salmon that rear in the Yolo Bypass floodplain have higher apparent growth rates than those that remain in

the adjacent Sacramento River channels. Mean length increased faster in the Yolo Bypass during each study year, and CWT fish released in the Yolo Bypass were larger and had higher apparent growth rates than those released in the Sacramento River. It is possible that these observations are due to higher mortality rates of smaller individuals in the Yolo Bypass or of larger individuals in the Sacramento River; however we have no data or reasonable mechanism to support this argument.

Apparent growth differences between the two areas are consistent with water temperature and stomach-content results. We found that the Yolo Bypass floodplain had significantly higher water temperatures and that young salmon from the floodplain ate significantly more prey than those from the Sacramento River. The wet weight ration indices calculated from bioenergetic modeling suggest that the increased prey availability in Yolo Bypass was sufficient to offset increased metabolic requirements from higher water temperatures. Higher water temperatures in the Yolo Bypass are expected as a result of the shallow depths on the broad floodplain. Increased feeding success in the Yolo Bypass is consistent with trends in prey availability. While Yolo Bypass and the Sacramento River had similar levels of zooplankton, Yolo Bypass had more dipteran prey in the drift, particularly in 1998. Studies of juvenile chinook salmon diets by Rondorf et al. (1990) showed that zooplankton were the least-favored prey items. Therefore, the dominance of zooplankton in the diets of Sacramento River salmon probably reflects a relatively low availability of other more energetically valuable prey items.

Recoveries of paired releases were too few to determine whether the higher survival indices for the Yolo Bypass release groups represent actual survival differences or random variation. Additional validation is needed from new release studies and from CWT recoveries in the adult ocean fishery and escapement. Nonetheless, the hypothesis that floodplain rearing could improve survival is substantiated by the growth data and bioenergetic modeling. Faster growth rates reflect improved habitat conditions, which would be expected to lead to improved survival, both during migration and later in the ocean. Elevated Yolo Bypass survival rates are also consistent with significantly faster migration rates in 1998, the likely result of which would be reduced exposure time to mortality risks in the delta, including predation and water diversions.

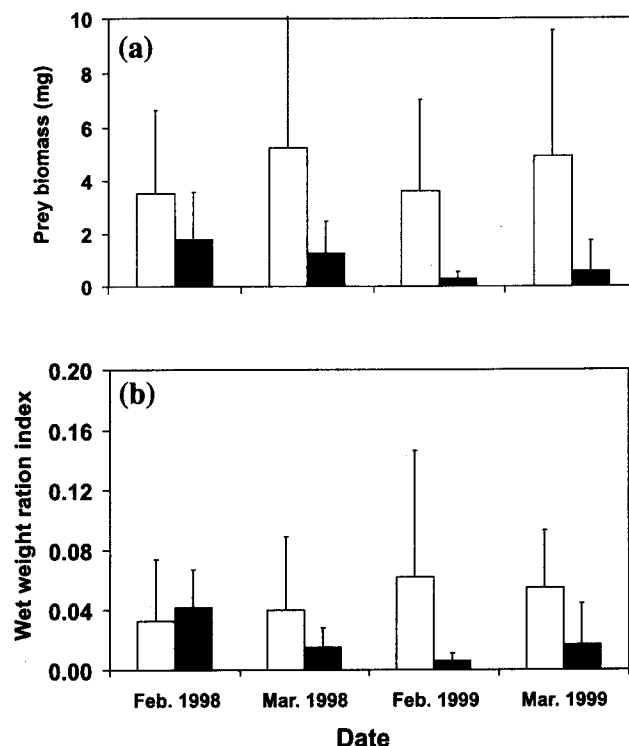
Improved survival is consistent with other habitat differences between the Yolo Bypass floodplain and the Sacramento River channel. We estimate that complete inundation of the Yolo Bypass creates a wetted area approximately 10 times larger than the reach of the Sacramento River we studied. This level of inundation is equivalent to a doubling of the wetted area of the entire delta portion of the San Francisco Estuary. Much of the floodplain habitat consists of broad shoals composed of soil and vegetation that are typical of the low-velocity conditions selected by young salmon (Everest and Chapman 1972). An increase in rearing area should reduce competition for food and space and perhaps reduce the probability of encountering a predator. In contrast, the Sacramento River channel is relatively narrow, with steep rock-reinforced banks and little shallow habitat. Migration through the Yolo Bypass corridor would also prevent

fish from entering the channels of the central delta, in which there are various risks, including major water diversions (Brandes and McLain 2001). However, the Yolo Bypass is a less-stable environment, with stranding risks when flood waters recede. The relatively well-drained topography of the Yolo Bypass floodplain may help to reduce the magnitude of this problem. This is not to say, however, that access to floodplain rearing habitat represents the only mechanism to account for possible improvements in juvenile salmon survival in wetter years. Other covariates, such as reduced water temperature (Baker et al. 1995), reduced predation losses from higher turbidity (Gregory and Levings 1998), and reduced water diversion effects (Kjelson et al. 1982), also contribute to improved wet-year survival of salmon that migrate through the San Francisco Estuary.

The results from this study suggest that hydrology may affect salmon feeding success, migration, and survival in both floodplain and river habitat. The CWT results indicate that salmon grew faster, migrated faster, and may have had better survival rates in 1998 than in 1999. One clear difference between the years is that the flow pulses were higher and of longer duration in 1998 than in 1999. Higher flow could directly increase migration rates through higher water velocities and have multiple indirect effects on growth through factors such as food supply or water temperature. The abundance of Diptera in drift samples was substantially higher in 1998 than in 1999 in both locations. The significant interaction between location and year for both prey weights and the wet weight ration index indicates that the combined effects of diet and water temperature under 1998 hydrology should have resulted in higher growth rates. Higher growth rates and faster migration times in 1998 may, in turn, have improved survival by reducing predation risk. Higher-flow conditions in 1998 increased the quantity and duration of floodplain rearing area, perhaps reducing resource competition and predator encounter rates. Increased flow duration and magnitude in 1998 could also have improved survival on the floodplain by reducing stranding risks.

These results provide new insight into the significance of seasonal floodplain habitat for salmon rearing, which has been studied primarily in perennial waterways such as estuaries and rivers (Healey 1991; Kjelson et al. 1982). Indeed, this is the first study we are aware of demonstrating that off-channel floodplain provides major habitat for chinook salmon. We do not believe that the benefits of the floodplain to chinook salmon are unique to Yolo Bypass. Initial results from the Cosumnes River, an undammed watershed in the delta, show similar growth enhancements for juvenile chinook salmon that rear on the floodplain rather than in adjacent river channels (Peter Moyle, University of California, Davis, CA 95616, personal communication). Moreover, the benefits of the floodplain to salmon are consistent with findings for other fish species. Sommer et al. (1997) found that the Yolo Bypass provides major spawning, rearing, and foraging habitat for the native cyprinid Sacramento splittail (*Pogonichthys macrolepidotus*). The spawning and rearing of fish on floodplains has been reported in diverse locations that range from small streams (Halyk and Balon 1983; Ross and Baker 1983) to large rivers (Copp and Penaz 1988) in both temperate (Gehrke 1992; Turner et al. 1994) and tropical (Winemiller and Jepsen 1998) locations. The growth ef-

Fig. 5. Feeding success results for Yolo Bypass (open bars) and Sacramento River (solid bars) juvenile salmon during 1998 and 1999. (a) Estimated prey weights in stomach contents. (b) Wet weight ration indices. Means and standard errors are shown.



fects of floodplain habitat have been described for several tropical locations (Welcomme 1979); however, the present study and the results of Gutreuter et al. (2000) represent the only examples from temperate rivers of which we are aware.

Differences between the invertebrate communities in floodplains versus river channels have been reported by Castella et al. (1991). The exceptional production of drift invertebrates on the Yolo Bypass floodplain is consistent with the results of Gladden and Smock (1990), who found that invertebrate production was one to two orders of magnitude greater on the floodplain than in adjacent streams. Although we did not monitor benthic invertebrates, results from other studies of large rivers indicate that benthic biomass may be up to an order of magnitude higher in the floodplain (Junk et al. 1989). The Yolo Bypass drift invertebrate results contrast with the results for zooplankton, which were not particularly abundant on the floodplain. This finding is comparable with that of Welcomme (1979), who reported that densities of zooplankton in natural floodplains are frequently low, except for low-water periods and localized concentrations near habitat interfaces such as shorelines.

The mechanism for greater abundance of drift invertebrates in the Yolo Bypass remains unclear, but is unlikely to be an artifact of land use on the floodplain. Possible explanations for increased drift abundance include increased food supply (e.g., primary production or detritus), more habitat, and longer hydraulic residence times. For each of these mechanisms, Yolo Bypass probably provides functions similar to more "natural" floodplains. Improved food supply is supported by the work of Jassby and Cloern (2000), whose

modeling studies suggest that the Yolo Bypass should have enhanced phytoplankton production as a result of its large surface area and shallow depth. Inputs of fertilizers from agriculture in the Yolo Bypass would not be important contributing factors, as nitrogen and phosphorous are rarely limiting to phytoplankton production in the delta (Ball and Arthur 1979). Like less-disturbed floodplains in other regions (Junk et al. 1989), invertebrate production in the Yolo Bypass may be stimulated by an increased availability of detritus in the food web. Alternatively, the trends in invertebrate abundance we observed may be a consequence of physical differences between floodplain and channel habitat. Inundation of the floodplain may increase the amount of habitat for benthic invertebrates, a major source of drift biomass. Given the larger surface area and lower velocities in Yolo Bypass, the floodplain probably has a much longer hydraulic residence time than the Sacramento River, reducing the rate at which drift invertebrates would be flushed out of the system. Increased habitat area and hydraulic residence time would also have been functional characteristics of the historical floodplain.

In the broader context, the results for salmon and drift invertebrates are consistent with the flood pulse concept, which predicts that floodplains should yield greater fish and invertebrate production than channel habitat (Junk et al. 1989). This finding is significant in that the flood pulse concept was developed primarily on the basis of relatively undisturbed rivers, whereas our study was conducted in a regulated river with a floodplain dominated by agricultural uses. Gutreuter et al. (2000) showed similar enhancements in fish growth from floodplain inundation in the Upper Mississippi River, another large regulated river. These studies suggest that floodplains can maintain important functional characteristics even in heavily modified rivers. In the case of the San Francisco Estuary and its tributaries, we do not claim that floodplain inundation is the primary factor regulating the productivity of the system. The Yolo Bypass floodplain may be seasonally more productive than the Sacramento River for some fish and invertebrates, but we have no data regarding its contribution during dry months or years. Nonetheless, the results of the present study and of Sommer et al. (1997) are sufficient to demonstrate that the floodplain represents one of the most biologically important habitat types in the region. We believe that proposed large-scale restoration activities in the San Francisco Estuary and its tributaries (Yoshiyama et al. 2000) that would increase the area and connectivity of the floodplain offer particular promise for native fish populations such as chinook salmon and Sacramento splittail.

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