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[Article]

Habitat Use and Stranding Risk of Juvenile Chinook Salmon on a Seasonal Floodplain

TED R. SOMMER,* WILLIAM C. HARRELL, AND MATTHEW L. NOBRIGA

California Department of Water Resources, Sacramento, California 95816, USA

Abstract.—Although juvenile Chinook salmon *Oncorhynchus tshawytscha* are known to use a variety of habitats, their use of seasonal floodplains, a highly variable and potentially risky habitat, has not been studied extensively. Particularly unclear is whether a seasonal floodplain is a net ''source'' or a net ''sink'' for salmonid production. To help address this issue, we studied salmon habitat use in the Yolo Bypass, a 24,000-ha floodplain of the Sacramento River, California. Juvenile salmon were present in the Yolo Bypass during winter–spring; fish were collected in all regions and substrates of the floodplain in diverse habitats. Experimental releases of tagged hatchery salmon suggest that the fish reared on the floodplain for extended periods (mean = 33 d in 1998, 56 d in 1999, and 30 d in 2000). Floodplain rearing and associated growth are also supported by the significantly larger size of wild salmon at the floodplain outlet than at the inlet during each of the study years. Several lines of evidence suggest that although the majority of young salmon successfully emigrated from the floodplain, areas with engineered water control structures had comparatively high rates of stranding. Adult ocean recoveries of tagged hatchery fish indicate that seasonal floodplains support survival at least comparable with that of adjacent perennial river channels. These results indicate that floodplains appear to be a viable rearing habitat for Chinook salmon, making floodplain restoration an important tool for enhancing salmon production.

A large downstream movement of fry to provide dispersal to rearing areas is typical of ocean-type Chinook salmon *Oncorhynchus tschawytcha* (Healey 1991). Rearing areas include channel and off-channel habitat in natal and nonnatal streams and their estuaries (Bjornn 1971; Kjelsen et al. 1982; Levy and Northcote 1982; Swales et al. 1986; Swales and Levings 1989; Healey 1991; Shreffler et al. 1992). Recently, Sommer et al. (2001b) observed that juvenile Chinook salmon also live on seasonal floodplains. Large rivers and streams typically have dynamic floodplains varying in size from several to thousands of hectares, unless their channels are heavily confined by topography (e.g., streams at high elevation or confined by canyons or levees). Floodplains are known to be of major importance to aquatic ecosystems in most regions; large rivers typically favor the development of a fauna adapted to colonize this habitat (Welcomme 1979; Junk et al. 1989; Sparks 1995). As a result, it is reasonable to expect dispersing salmonid fry show some ability to use seasonal habitat. In support of this hypothesis, Sommer et al. (2001b) reported that food resources and water temperatures on the seasonal floodplain of a large river were superior to those in an adjacent perennial channel, resulting in enhanced growth rates of young salmon. Despite some evidence that enhanced growth on the floodplain improved fry–smolt survival in the estuary, Sommer et al. (2001b) did not address any effects on adult production.

Intuitively, rearing in seasonal floodplains or intermittent streams seems risky because these habitats are among the most dynamic on earth (Power et al. 1995). It is still unknown whether seasonally dewatered habitats are a net ''source'' or a ''sink'' for salmonid production relative to production in permanent stream channels (Brown 2002). In particular, the high degree of seasonal flow fluctuation characteristic of floodplain habitat could cause major stranding events and increase mortality rates of young salmon (Bradford 1997; Brown 2002). For resident taxa in intermittent streams, the benefits of very large flow fluctuations appear to outweigh costs associated with a variable environment (Spranza and Stanley 2000). This issue continues to be a key concern for regulatory agencies that evaluate off-channel restoration projects or proposed flow fluctuations for possible effects on fishes (Brown 2002; Bruce Oppenheim, NOAA Fisheries, personal communication).

Here, we describe spatial and temporal trends in juvenile Chinook salmon habitat use and stranding in a large California river floodplain. Our study was conducted in the Yolo Bypass, the primary floodplain of the Sacramento River, the major pro-

* Corresponding author: tsommer@water.ca.gov

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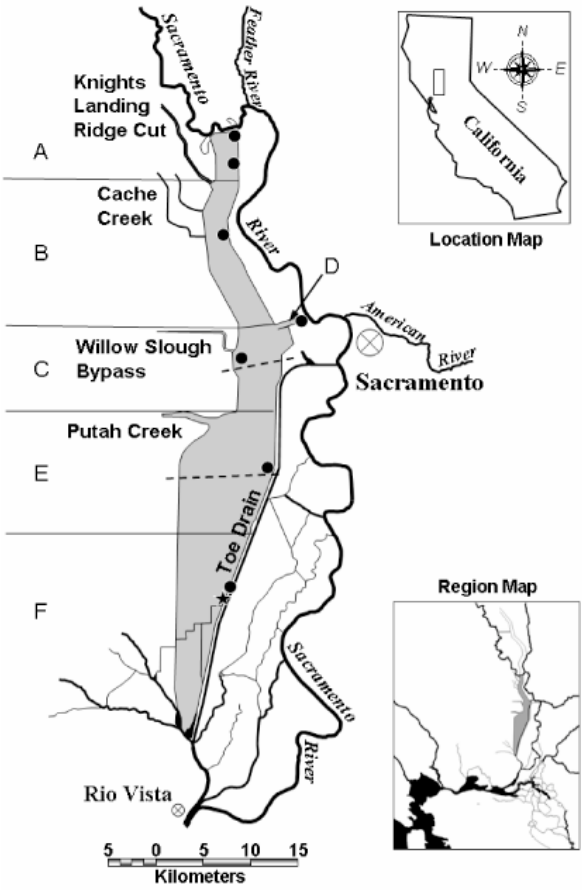

FIGURE 1.—Location of Yolo Bypass in relation to the San Francisco Bay–Delta and its tributaries. Fremont Weir is the upper (northern) edge of the Yolo Bypass. The major regions of the floodplain are delineated from north to south and correspond to the following codes: (**A**) Fremont Weir; (**B**) Cache Creek sinks; (**C**) Yolo Bypass Wildlife Area; (**D**) Sacramento Bypass; (**E**) Putah Creek Sinks; and (**F**) Liberty Island. The sampling locations are identified as follows: beach seine sites (solid circles); screw trap (star); and purse seine transects (dotted lines).

ducer of salmon in the San Francisco estuary (Figure 1). Because the Yolo Bypass can convey 75% or more of the total flow from the Sacramento River basin (Sommer et al. 2001a), this floodplain can be expected to be a migratory pathway for a substantial number of juvenile Chinook salmon. A major objective of our study was to collect basic information about the timing, duration, and habitat use of salmon on floodplains. We hoped that these data would provide insight into whether a floodplain is a net source (i.e., with rearing benefits) or a net sink (i.e., with high mortality because of stranding or predation) for salmon populations. The major hypotheses evaluated were as follows: (1) salmon occur in all major habitat types and geographic regions; (2) floodplains provide rearing habitat for salmon and are not simply a migration corridor; and (3) stranding of juvenile salmon does not have a major population-level effect on survival of the fish that use floodplain habitat. We addressed these hypotheses by sampling wild fish throughout the floodplain, experimentally releasing tagged fish, and using hydrologic modeling and measurements of physical conditions to describe how habitat varied over the study period.

Study Area

The San Francisco Estuary and its two component regions, Sacramento–San Joaquin Delta and downstream bays (Figure 1), make up one of the largest estuaries on the Pacific coast of North America. Major changes to the system have included diking and isolation of about 95% of the wetlands, introduction of exotic species, channelization, sediment inputs from hydraulic mining, and discharge of agricultural and urban chemicals (Nichols et al. 1986; Kimmerer 2002). The Estuary receives most freshwater via the Delta, which drains approximately 100,000 km^2. Most precipitation occurs upstream of the Delta during winter and spring, resulting in a greater than 10-fold seasonal range of daily freshwater flow into the estuary. However, the hydrograph is substantially altered by dams on each of the major rivers. Peak flow pulses typically occur during winter, but dam operations can reduce the magnitude of the pulses, particularly in dry years, when much of the inflow is captured behind reservoirs (Mount 1995; Kimmerer 2002). The historically prominent spring flow pulse from snowmelt is at present muted except during heavy, late-season storms. For the past several decades, much of the spring snowmelt has been stored in reservoirs and released during summer and autumn, periods of historically lower flow. As much as 65% of the net Delta flow during summer and autumn is diverted from the channels by two large water diversions (the State Water Project and the Central Valley Project); additional water is diverted by 2,200 pumps and siphons for irrigation (Kimmerer 2002).

The 24,000-ha Yolo Bypass is the primary floodplain of the Delta (Sommer et al. 2001a). The majority of the floodplain is leveed to protect surrounding cities from floodwaters, but levees confine flow through the bypass only under very high flow events. The Yolo Bypass currently floods an average of every other year, typically under high-flow periods in winter and spring. The Yolo Bypass has a complex hydrology, with inundation possible

from several different sources. The floodplain typically has a peak inundation period during January–March but can flood as early as October and as late as June. The primary input to the Yolo Bypass is through Fremont Weir in the north, which conveys floodwaters from the Sacramento and Feather rivers. During major storm events (e.g., >5,000 m^3/s), additional water enters from the east via the Sacramento Weir, adding flow from the American and Sacramento rivers. Flow also enters the Yolo Bypass from several small streams on its western margin, including Knights Landing Ridge Cut, Cache Creek, and Putah Creek. During much of the winter, water-suspended sediment levels in the Yolo Bypass and Sacramento River are high, generally resulting in secchi depths of less than 0.25 m. However, hydraulic residence times are typically longer in the Yolo Bypass than in the Sacramento River (Sommer et al. 2004). Floodwaters recede from the northern and western portions of the bypass along relatively even elevation gradients of 0.09% west–east and 0.01% north–south into a perennial channel on the eastern edge of the Bypass; they then rejoin the Sacramento River near Rio Vista. The majority of the Yolo Bypass is at present managed for wildlife in a mosaic that includes riparian, wetland, upland, and perennial pond habitats; however, a dominant land use during the past two decades, agriculture has decreased in recent years because of habitat restoration activities.

Our data collection focused on the fall-run juvenile Chinook salmon, currently the numerically dominant race in the Sacramento Valley (Yoshiyama et al. 2000). There are four races of Chinook salmon in the Sacramento Valley: winter, spring, late-fall, and fall-run. Like many other native fish, Chinook salmon in the San Francisco estuary and its tributaries have been adversely affected by such factors as habitat loss, water diversions, and species introductions (Bennett and Moyle 1996); as a result, the Sacramento River winter and spring run Chinook salmon are protected under the Federal Endangered Species Act. The typical life history pattern is for young fall-run salmon fry (approximately 35–70 mm fork length) to migrate from the tributaries during winter and spring to the estuary (Brandes and McLain 2001).

Methods

Physical habitat.—Because seasonal hydrologic variability is a key characteristic of floodplain habitat, we reasoned that detailed data on changes in physical habitat would be necessary to evaluate the responses of young salmon. Daily flow data were obtained from gauging stations in the floodplain, and temperature data were collected using continuous temperature recorders (Sommer et al. 2001b). However, the vast area of Yolo Bypass made it impractical to directly measure other parameters, such as depth and surface area. As an alternative, we used a hydrologic model to estimate these parameters (Sommer et al. 2004). To summarize, the model treated Yolo Bypass as a ''reservoir'' described by (1) basin geometry and (2) flow and stage time series. The Yolo Bypass floodplain geometry was developed from 200 cross-sections with data collected at 300-m intervals by standard rod and level survey techniques. Mean daily stage and flow data were obtained from five gauging stations in the Yolo Bypass. For each date in the time series, we used linear interpolation between the gauging stations to estimate the stage at each cross-section. The estimated stage value was then used to calculate conveyance characteristics of each cross-section: area, width, and wetted perimeter. The daily results for each cross-section were used to estimate total surface area and mean depth. The large scale of the study reach did not allow validation of the depth estimates. As a partial validation of the model, Sommer et al. (2004) estimated total inundated area for the Yolo Bypass by using aerial photographs on days when the floodplain was inundated (February 8 and March 2, 1998) and when the floodplain was draining (April 28, 1998). To provide additional information about areas where fish stranding and consequent losses could occur, we estimated the portion of the area that was isolated ponds versus inundated area that was actively draining to the Delta (i.e., perennial channels and adjacent inundated area) on April 28, 1998.

Fish habitat use.—We used beach seine sampling to examine which regions and substrates of the floodplain were used by young salmon (hypothesis 1). During January through April of each year, a 15-m seine (3.2-mm mesh) was used to sample six regions of the Yolo Bypass (Figure 1). Fixed stations were used in each region during flooded periods. After floodplain drainage, samples were collected randomly within each region. For all periods, the primary substrate type of the habitat (sand, mud, gravel, pavement, or vegetation), fish species and size, and an estimate of the surface area swept by the seine were recorded. Habitat use during flood events was summarized in terms of the percentage of samples that contained salmon for each region and substrate type.

To provide additional information about habitat use, we conducted purse seine sampling along two transects (Figure 1). This sampling, performed in 1998 when the Yolo Bypass flow was relatively high (>850 m^3/s), used purse seines (30.5 m × 4.6 m, 4.75-mm mesh) set from a jet boat. Purse seining was conducted at 1–2 transects up to five times weekly, depending on hydrology. Hauls were made at random points in each of three habitat types (riparian, agricultural fields, and wetlands), the boundaries of which were established from aerial photographs taken before the Bypass was inundated. In the case of riparian habitat, hauls were made in clearings adjacent to trees to avoid snagging. We also recorded transect side (east or west half) for each haul because the western side of the Yolo Bypass was shallower and flow was dominated by inputs from westside streams rather than from Fremont or Sacramento weirs (Sommer et al. 2004). Most of these hauls were performed in areas exposed to at least a modest current. Additional limited paired sampling was conducted to examine possible differences between areas with and without velocity refuges. Low-velocity habitats sampled included downstream edges of levees, islands, and clusters of trees. Water velocities in randomly selected areas were approximately 0–0.05 m/s compared with greater than 0.33 m/s in adjacent exposed areas. Water depths were similar for each sampling pair. Differences in salmon densities for each habitat type were examined by using a Kruskal–Wallace test. A randomization *t*-test with 1,000 iterations (Haddon 2001) was used to compare salmon density on the east and west sides of the floodplain.

Migration trends.—To examine temporal trends in salmon migration through the floodplain (hypotheses 2 and 3), we operated a rotary screw trap (EG Solutions, Corvallis, Oregon) near the base of the Yolo Bypass during each study year. This technique was intended to provide an indication of the timing and duration of migration, rather than an absolute measure of the number of salmon emigrating the floodplain. During much of the sampling period the inundated width of the floodplain was 1–5 km, an area we considered too large for the traditional mark–recapture evaluations required to measure trap efficiency and total emigration (Roper and Scarnecchia 1996). A 1.5-m-diameter trap was used for the first 3 weeks of sampling in February 1998, after which a 2.4-m trap was used for all other sampling. We operated traps as often as 7 days each week, the daily effort varying from 1 to 24 h, depending on debris load and safety considerations. Fish number and size were recorded in all years. In 1998, young salmon were classified as fry (prominent parr marks) or transitional fish/smolts (faded parr marks, silver appearance).

Floodplain residence time and growth.—We used experimental releases of salmon with coded wire tags (CWTs) as our primary method to evaluate fish residence time on the floodplain (hypothesis 2). Fry (mean size = 57 mm fork length) from the Feather River Fish Hatchery (Figure 1) were tagged by using coded-wire half tags (Northwest Marine Technologies) and released in the Yolo Bypass below the Fremont Weir on March 2, 1998 (53,000 fry); February 11, 1999 (105,000 fry); and February 22, 2000 (55,000 fry). We assessed residence time in the Yolo Bypass from recoveries of tagged fish in the screw trap at the base of the floodplain.

We also examined, using the previously described beach seine data, whether there was evidence of long-term rearing of wild salmon in the floodplain. We compared the slopes of weekly fork length measurements for the two northern beach seine regions (''North'') to the southernmost region (''South''), using a generalized linear model (GLM) with a Poisson distribution and log link variance function. We reasoned that major significant differences between the sizes of fish in the two areas provided evidence of extended rearing and growth of fish in the floodplain.

Salmon survival and stranding.—We used several independent data sources to examine whether salmon successfully emigrated from the floodplain (hypothesis 3). First, we compared survival of each of the Yolo Bypass CWT hatchery-reared salmon release groups with the survival of parallel CWT groups containing the same number of fish released into the Sacramento River (Sommer et al. 2001b). Recapture rates at the smolt stage of the 1998 and 1999 release groups had previously been analyzed by Sommer et al. (2001b); in the present study, we evaluated adult recoveries in the commercial and recreational ocean fisheries through 2003. Second, we examined stranding by using beach seine data (described previously) collected within a few weeks after the Sacramento River stopped flowing into the Yolo Bypass. Densities of salmon were compared with a randomization *t*-test (Haddon 2001) for (1) isolated earthen ponds (2) perennial channels, and any sites immediately adjacent to these water sources. The results for all years were pooled because of relatively low sample sizes for individual years. Data for each year

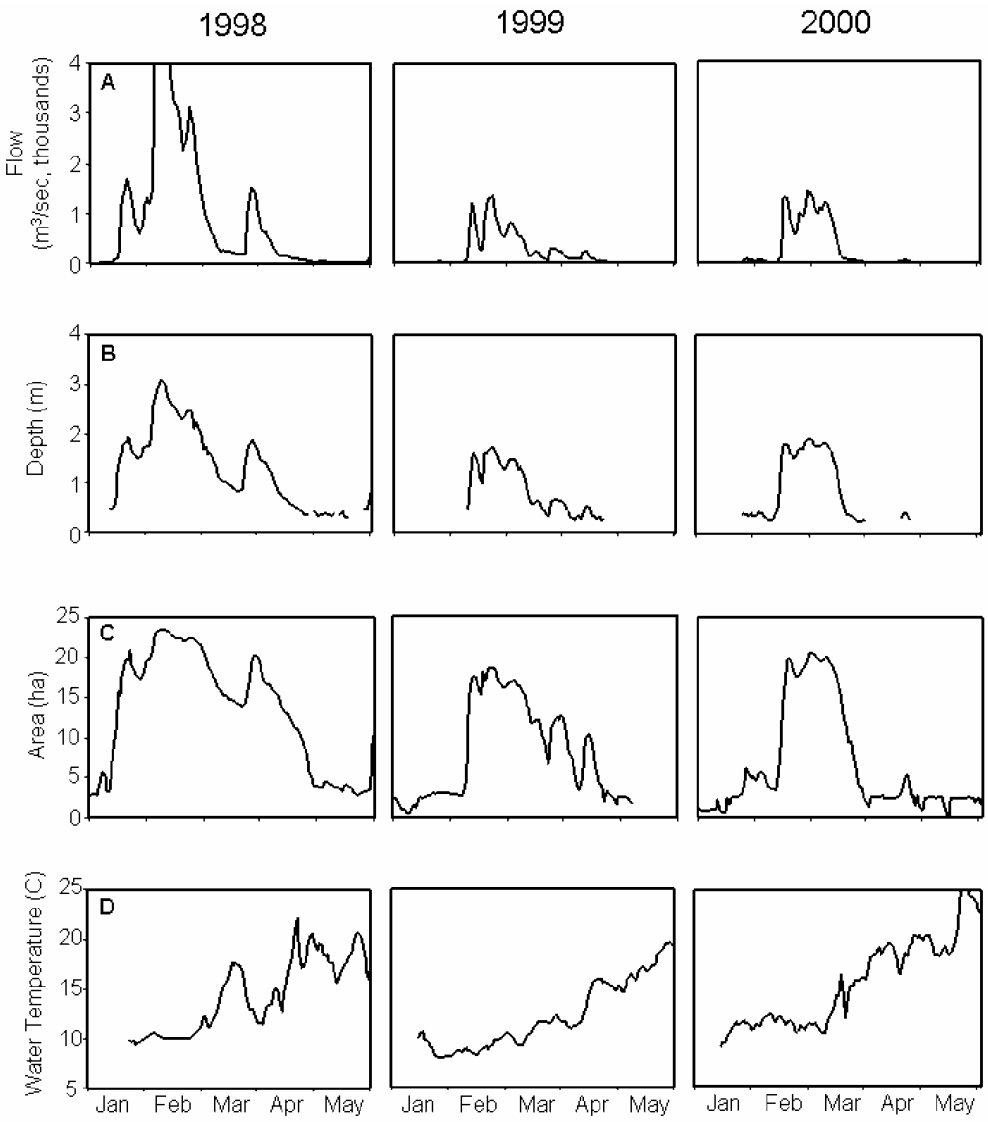

FIGURE 2.—Trends in physical variables for January–June 1998–2000: (**A**) mean daily flow in the Yolo Bypass; (**B**) simulated mean daily depth; (**C**) surface area; and (**D**) daily mean water temperature. The surface area data for 1998 and 2000 are from Sommer et al. (2004).

were first standardized for possible annual differences in abundance by conversion to *z*-scores; we then ran the randomization analysis using 1,000 iterations. We hypothesized that abundance of salmon would be equal in isolated ponds and contiguous water sources; that is, they would show no distinct ''preferences.'' Our reasoning was that similar abundance levels would indicate successful emigration, because most of the water drains from the floodplain. To further understand factors that could affect stranding, we also used a randomization *t*-test to compare densities of fish in two types of isolated ponds: isolated earthen ponds and concrete weir scour ponds at Fremont and Sacramento weirs (Figure 1). Sampling effort was much greater in the isolated earthen ponds, so the randomization *t*-test was performed after randomly subsampling the earthen pond data from throughout the floodplain to provide equal sample sizes. We predicted that flood control structures would cause higher stranding than ''natural'' ponds. In addition, we examined trends in the catch of salmon in the screw trap data. We predicted that salmon catch would increase substantially during drainage because fish successfully emigrated the floodplain.

Results

Physical Habitat

The hydrographs varied substantially during the years of study (Figure 2A). In 1998 the hydrology

was wet (4.4-year recurrence flood event) and the Yolo Bypass was inundated during mid-January through mid-April and again in early June. The flow was lower in the other 2 years, when inundation occurred between mid-February and mid-March, peak flood events being at the 1.7-year recurrence interval in 1999 and at the 2.4-year recurrence interval in 2000. Surface area in the Yolo Bypass closely followed the flow peaks, the amounts of inundated area being successively smaller in each of the study years (Figure 2C). For the April 28, 1998, photographs, the total surface area of 5,050 ha was slightly lower than the model estimate of 6,700 ha. Based on the aerial photographs, we estimated that only 600 ha of the 5,050 ha comprised isolated ponds, the remainder being water that drained to the Delta. For all but peak flood events, mean water depth remained less than 1 m (Figure 2B). During peak flood events, mean depths did not exceed 2 m except in February 1998. Water temperature showed gradual increases throughout each study year (Figure 2D).

Fish Habitat Use

We captured salmon in all regions of the floodplain and on all substrate types. During 1998–2000 flood events, salmon were captured in a high percentage of samples in each region (Figure 1) of the floodplain: (1) Fremont Weir (100%, $n = 13$ samples); (2) Cache Creek Sinks (50%, $n = 16$ samples); (3) Yolo Bypass Wildlife Area (77%, $n = 22$ samples); (4) Sacramento Bypass (100%, $n = 7$ samples); (5) Putah Creek Sinks (94%, $n = 11$ samples); and (6) Liberty Island (100%, $n = 7$ samples). Similarly, during 1998–2000 flood events we collected salmon on a high percentage of substrate types: (1) mud (70%, $n = 47$ samples); (2) sand (100%, $n = 3$ samples); (3) pavement (100%, $n = 8$ samples); (4) vegetation (97%, $n = 32$ samples); and 5) gravel (89%, $n = 9$ samples).

Salmon densities as estimated by purse seine sampling were not significantly different between riparian (mean abundance = 46.9/ha, SE = 10.4, $n = 23$), agricultural (mean abundance = 20.9/ha, SE = 6.1, $n = 35$), or natural vegetated habitat types (mean abundance = 27.5/ha, SE = 5.6, $n = 31$) based on a Kruskal–Wallis test ($H = 4.38$, df = 2, $P = 0.112$). There was also no statistically significant difference between the east (mean abundance = 29.5/ha, SE = 6.0, $n = 53$) and west (mean abundance = 29.9/ha, SE = 6.7, $n = 36$) sides of the Bypass as shown by a randomization t-test ($P = 0.95$). Salmon were collected in six hauls in low-velocity habitat (mean abundance = 189/ha, SE = 24/ha), but none were collected in adjacent areas exposed to a current.

Floodplain Migration Trends

Salmon migration as indicated by trends in screw trap catch was highly variable over the course of the study, but there were prominent peaks in Chinook salmon catch coincident with floodplain drainage during late March–April (Figure 3B). Additional smaller peaks in salmon catch also paralleled flow, mostly during February and March. The life history stage of salmon during 1998 was exclusively parr through the end of March, after which the majority showed signs of smoltification.

Floodplain Residence Time

Based on recoveries of tagged fish in the screw trap, the mean residence time of CWT salmon was 33 d (range, 16–46 d; $n = 10$) in 1998, 56 d (range, 4–76 d; $n = 49$) in 1999, and 30 d (range, 28–37 d; $n = 25$) in 2000. The size of fish was significantly larger ($P < 0.001$; GLM) at the outlet of the floodplain than at the top (Figure 3C) during each of the study years.

Salmon Survival and Stranding

The numbers of CWT fish recovered for the Yolo Bypass were higher than in the Sacramento River in 1998, similar in 1999, and lower in 2000 (Table 1). Densities of wild Chinook salmon were highly variable during floodplain drainage events, with no statistically significant difference between densities in isolated earthen ponds and contiguous water sources (Table 2). However, densities of salmon were significantly higher ($P < 0.0001$; randomization t-test) in concrete weir scour ponds than in isolated earthen ponds (Table 3).

Discussion

Research on migratory fishes reveals that these species frequently have alternative life histories that may be influenced by habitat use at early life stages (Clark 1968; Secor 1999). Under Clark's (1968) ''contingent hypothesis,'' migratory taxa have divergent migration pathways that could help the species deal with environmental variability and heterogeneity. This theory is consistent with our understanding of Chinook salmon, which are adapted to the extreme hydrologic variability in western North America and show a range of life histories (Healey 1991; Bottom et al. 2005). In this context, the use of multiple habitats—including natal and nonnatal streams (Bjornn 1971; Scriv-

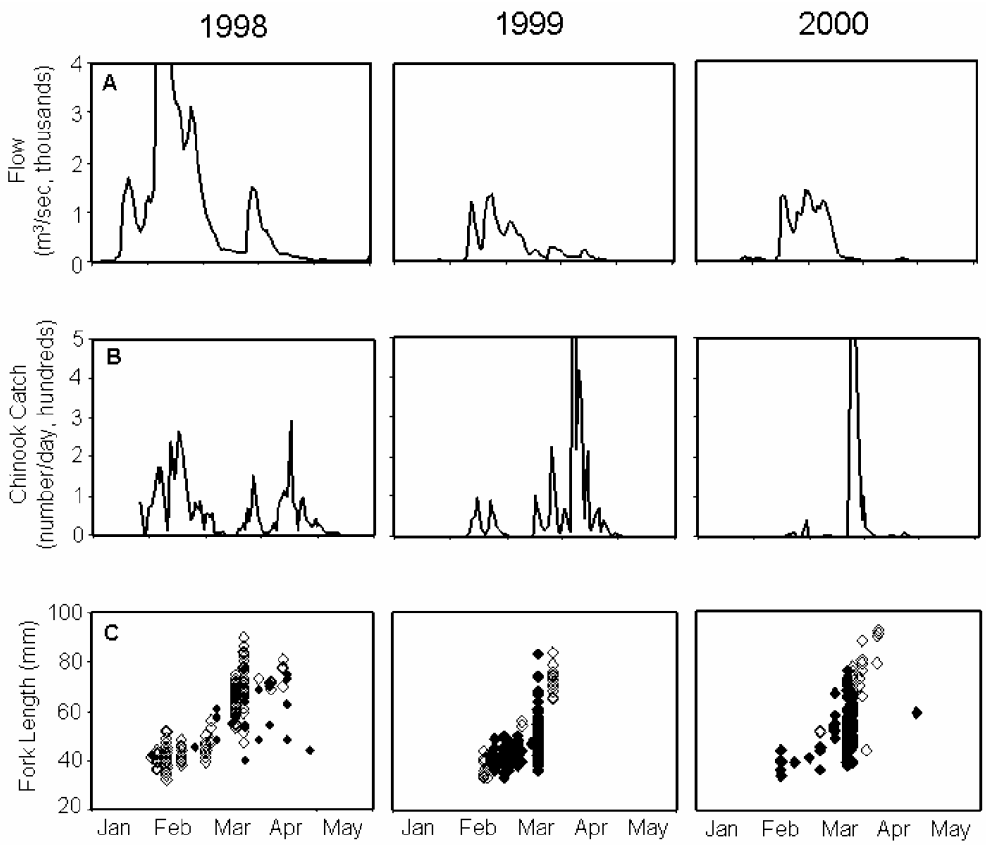

FIGURE 3.—Chinook salmon results during winter and spring 1998–2000: (**A**) mean daily flow; (**B**) salmon catch rates in screw trap sampling; and (**C**) salmon size for beach seine samples near the Yolo Bypass intake (solid symbols) and outlet (clear symbols).

ener et al. 1994), side channels and off-channel ponds (Swales et al. 1986; Swales and Levings 1989), low-elevation rivers (Kjelsen et al. 1982; Brown 2002), and estuaries (Healey 1991; Shreffler et al. 1992)—can be considered as part of an overall ''bet-hedging'' strategy that spreads risk across a variable environment. Despite the fact that seasonal floodplain represents perhaps the single most variable habitat available to salmon, our study suggests that floodplains are a viable rearing location for young fish.

TABLE 1.—Number of coded wire tags recovered in the ocean and commercial fisheries for Chinook salmon released in the Yolo Bypass and Sacramento River. The total number of tagged fish released in each location for each year is shown in parentheses. The survival ratio is calculated as the number of Yolo Bypass recoveries divided by the number of Sacramento River recoveries.

Release group	1998 (53,000)	1999 (105,000)	2000 (55,000)
Yolo Bypass	75	136	27
Sacramento River	35	138	47
Survival ratio	2.14	0.99	0.57

At the beginning of our study, our conceptual model for floodplain habitat use was that young salmon move into the floodplain during high-flow events and spread throughout the broad expanse of seasonally inundated habitat. Among the wide variety of suitable substrates and habitat types for rearing, young salmon appear to seek out low-velocity areas. Moreover, floodplain habitat apparently is not simply a migration corridor; many young salmon actively rear on the highly productive floodplain habitat for extended periods of time, resulting in high growth rates. Our findings suggest that salmon emigrate from the seasonally inundated habitat both during flood events and during drainage. Juvenile Chinook salmon do not appear to be especially prone to stranding mortality; indeed, survival may actually be enhanced by floodplain rearing in some years. Our conceptual model was supported by our results and has a variety of management implications.

Salmon were present in a broad range of habitat and substrate types and were collected in all regions and sides of the Yolo Bypass floodplain. The

TABLE 2.—Densities of Chinook salmon (number/ha ± SE, with sample size in parentheses) collected in beach seine sampling during drainage events in 1998–2000. The sample locations are divided into isolated earthen ponds and contiguous water sources. Density differences were not statistically significant between the two pond types based on a randomization *t*-test of the pooled data for all years ($P = 0.79$; $n = 43$ for isolated ponds; $n = 59$ for contiguous water sources).

Location type	1998	1999	2000
Isolated ponds	206 ± 112 (30)	890 ± 491 (8)	126 ± 65 (5)
Contiguous water sources	167 ± 79 (33)	310 ± 104 (13)	463 ± 123 (13)

fact that they were present on the western half of the Bypass, where flows are dominated by Knights Landing Ridge Cut and Cache and Putah creeks, suggests that salmon spread throughout the floodplain after entering the basin by way of Fremont and Sacramento weirs. A few of these fish may have originated from a modest spawning population in Putah Creek (Marchetti and Moyle 2001). The fact that salmon were present in a wide range of habitat and substrate types and in different regions of the Yolo Bypass indicates that many areas of habitat were suitable, although this does not mean that there were no habitat preferences. Like many young fishes, much of the distribution of juvenile Chinook salmon can be explained by their association with shallow depths and low velocities (Everest and Chapman 1972; Roper et al. 1994; Bradford and Higgins 2001). The physical modeling indicated that mean depths were generally 1 m or less during all but peak flood periods, so much of the thousands of hectares of inundated habitat was probably within the shallow range typically preferred by young Chinook salmon (Everest and Chapman 1972). Our limited purse seine sampling suggested that young salmon were most abundant in low-velocity areas, which is consistent with previous studies in river and stream habitat (Everest and Chapman 1972; Roper et al. 1994; Bradford and Higgins 2001). We did not directly simulate water velocity in the present study; however, the relatively shallow water depth during flood events reflects the broad area of low-velocity rearing habitat created during flood events. We expect that this increase in rearing habitat in the Yolo Bypass provides foraging opportunities (Sommer et al. 2001b), reduced energy expenditure, and perhaps reduced probability of encounter with a predator (Ward and Stanford 1995).

Our results also suggest that fish rear in the system for extended periods rather than simply using it as a migration corridor. The mean residence time of 30–56 d for the 44-km reach between the floodplain release location and the screw trap is substantially longer than one would expect, given that (1) fingerlings are capable of migrating at rates of at least 6–24 km/d in low-elevation reaches of other large rivers (Healey 1991) and (2) one of our 1999 CWT fish was recovered just 4 days after being released, having traveled an estimated rate of 11 km/d. The fish were significantly larger at the base of the Yolo Bypass, suggesting that their period of residence in the floodplain was long enough to support substantial growth. Similarly, Sommer et al. (2001b) found that salmon showed higher growth rates in the Yolo Bypass than in the adjacent Sacramento River, primarily because of higher levels of invertebrate prey in the floodplain. A long period of rearing is also supported by the screw trap data, which showed that the densities of salmon were greatest during drainage of the floodplain. We believe that these peaks are a result of rearing salmon being forced off of the floodplain by receding flows. Temperature and salmon life history stage do not provide good alternative explanations for the emigration trends. In 1998, for example, water temperatures were relatively high by late March and salmon began smoltification shortly thereafter; yet the screw trap data indicate

TABLE 3.—Densities of Chinook salmon (number/ha ± SE, with sample size in parentheses) collected in beach seine sampling for earthen ponds and adjacent concrete weir ponds. Density differences were statistically significant between the two pond types based on a randomization *t*-test of the pooled data for all years ($P < 0.0001$; $n = 26$ for each pond type). Note that we used a randomly sampled subset of the earthen pond data to provide equal sample sizes for the comparison.

Location type	1998	1999	2000
Earthen ponds	186 ± 67 (63)	531 ± 200 (21)	369 ± 97 (18)
Concrete weir ponds	2,717 ± 1,115 (14)	14,208 ± 3,898 (12)	4,181 ± 1,275 (3)

that emigration did not peak until the end of April, when the floodplain drained. Perhaps the emigration trends are partially confounded by seasonal variation in salmon abundance. In the absence of trap efficiency data, we cannot estimate the proportion of the population that emigrated in winter versus spring events.

Several lines of evidence suggest that the majority of fish successfully emigrated from the floodplain. One important observation was that the area of isolated ponds was small relative to the overall area of the floodplain during both peak flood and drainage periods. As an example, in 1998, the wettest year we studied, the peak area of inundation was 24,000 ha, but the total inundated area dropped to 5,000 ha by late April. Of the 5,000 ha remaining at this point, our estimates from aerial photographs showed that isolated ponds took up only 600 ha. Put another way, isolated ponds represented just 12% of the wetted area in April and only 2.5% of the peak inundated area in winter. The same trend is evident in the area simulations for 1999 and 2000, when the peak area was 20,000 ha, but dropped to about 2,000 ha within a month. These results demonstrate that the Yolo Bypass drains fairly efficiently, leaving little isolated area where stranding can occur. This finding was somewhat unexpected, because many parts of the Yolo Bypass have natural topographic features or agricultural levees that could potentially impede drainage and fish emigration. Even if the area of isolated ponds is low, stranding could still be a substantial source of mortality if densities of fish in the remaining ponds were very high. However, we found no evidence that densities of fish stranded in isolated ponds were significantly higher than those in contiguous water sources that were draining to the Delta. The key point here is that most of the water drains from the floodplain and apparently the majority of the fish are leaving with the receding floodwaters. To help illustrate this issue, if we assume that mean densities of fish observed in Table 2 were representative of the entire wetted area of floodplain in April 1998, then the total number of fish in the 600 ha of isolated ponds would have been 123,600 salmon, lower than an estimate of 835,000 fish in the 5,000 ha of contiguous water sources. This conservative estimate also does not include the large numbers of fish that emigrated from the floodplain before April.

In addition to the beach seine and surface area data, we believe that trends in screw trap data support the hypothesis that stranding is not consistently a major problem on the floodplain. The screw trap data are somewhat ambiguous, because the large area of the floodplain makes it unreasonable to measure the efficiency of the trap. Therefore, we cannot accurately estimate the absolute number of salmon emigrating from the floodplain. However, we can at least examine the patterns of trap catch to evaluate likely mechanisms. Some of the possible patterns that we would expect to see for different factors are summarized in Figure 4. First, under the ''trap efficiency'' model, we would have expected dual peaks in the earliest and latest portions of flood events, when the screw trap would be sampling the highest portion of total flow (Figure 4A). If young salmon follow the ''go with the flow'' model, catch and flow peaks should be well-correlated (Figure 4B). Alternatively, if floodplains represent an important rearing habitat, we would expect catch trends to follow the ''loitering'' model, in which catch does not increase until drainage, when fish are forced from their rearing habitat by receding floodwaters (Figure 4C). Finally, if stranding were a major factor controlling catch trends, we would expect an early increase in catch as fish moved through the floodplain during inundation, but then catch should drop earlier than flow as young salmon became isolated from draining floodwaters (Figure 4D; ''bathtub'' model). Of these patterns, our data for the Yolo Bypass provide the strongest support for both the ''go with the flow'' and ''loitering'' models. In each year we saw obvious screw trap catch peaks associated with flow events, and additional prominent peaks associated with drainage. To summarize, apparently some of the fish move

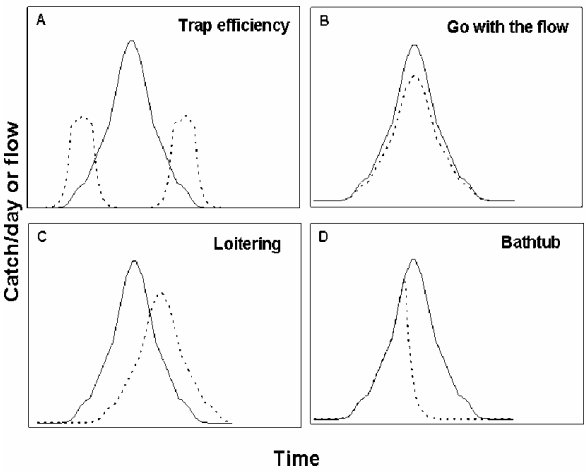

FIGURE 4.—Four conceptual models of expected screw trap catch (dotted line) relative to flow (solid line). See the Discussion for further details about each model.

through the floodplain in direct association with flow, whereas others remain as long as possible to rear on the floodplain. The screw trap trends show no evidence that stranding had a major influence on patterns of emigration.

Relatively low stranding rates on the Yolo Bypass floodplain are supported by observations from other seasonal floodplain habitat in the San Francisco estuary (Peter Moyle, University of California−Davis, personal communication) and other studies. Higgins and Bradford (1996) and Bradford (1997) report that juvenile salmonids are relatively mobile and that most avoid being stranded during moderate rates of stage change. Higgins and Bradford (1996) state that maximum recommended stage reduction levels for gravel bars of regulated rivers are typically 2.5–5 cm/h, much more than the 1 cm/h or less rates of change in mean water depth we observed during drainage in the present study. In his review of the ecology of fishes in floodplain rivers, Welcomme (1979) noted that the majority of fish emigrate from floodplain habitat during drainage.

Even if stranding is not a major source of mortality, this does not necessarily mean that floodplains are not sinks for salmon production. Of the possible sources of mortality, birds and piscivorous fishes may have benefited from stranded salmon (Brown 2002). As noted by Sommer et al. (2001a), major avian predation is unlikely because densities of wading birds are low relative to the thousands of hectares of rearing habitat available during flood events. We did not measure densities of fish predators, but believe that the creation of large areas of rearing habitat should create more refuges for young fish and decrease the probability of encounter with a predator.

Ultimately, it is survival data that allow us to differentiate source from sink habitat. The size and complexity of the San Francisco estuary made it very difficult to directly measure survival rates with statistical rigor (Newman and Rice 2002); however, our CWT release studies at least provide an indication of whether survival rates in the Yolo Bypass were substantially different from those in the Sacramento River, the adjacent migration corridor. The limited results suggest that fry–adult survival rates were at least comparable in the Yolo Bypass and the Sacramento River. Moreover, the 1998 results suggest that in some years, survival may actually be substantially higher for salmon that migrate through the floodplain. Although none of these CWT releases were replicated, the fact that Sommer et al. (2001b) reported similar results for fry-to-smolt survival for the same releases in 1998 and 1999 increases our confidence that the survival data are not spurious.

Our data indicate that floodplains are a viable rearing habitat for juvenile Chinook salmon. Hence, the most important management implication of our study is that seasonal habitat should be considered as part of restoration plans for this species. Despite frequent concerns that off-channel habitat could increase stranding mortality (Brown 2002; Bruce Oppenheim, NOAA Fisheries, personal communication), our results for a hydrologically variable seasonal floodplain suggest that one should be able to design restoration projects that do not create a population sink because of excessive mortality. This is not to say, however, that stranding mortality is never an issue on floodplain habitat. For example, in the Yolo Bypass we saw significantly higher stranding rates in the concrete weir scour ponds of Fremont and Sacramento weirs than in earthen ponds. This finding suggests that artificial water control structures can create unusual hydraulics that promote stranding. However, the total area of these concrete weir ponds was only 3 ha, much smaller than our estimate of 600 ha for total isolated pond area for April 1998 and insignificant compared with the peak inundated area of 24,000 ha area. Fixing the poor hydraulics at these water-control structures may, nonetheless, be an attractive option, particularly if the cost of the solution is relatively low or if it helps to address other fisheries issues such as adult fish passage. In the Yolo Bypass, the concrete weirs not only create stranding problems for juveniles but also frequently block upstream passage of adult salmon, sturgeon, and steelhead trout (Sommer et al. 2001a), thus creating an incentive to resolve both issues simultaneously.

Finally, we wish to acknowledge that even natural floodplain or well-designed restored floodplain habitat could at least occasionally be a population sink because of stranding or predation losses. Our study was conducted over 3 years for a single, large floodplain; we cannot rule out the possibility that floodplains may not have net benefits in other years or locations. As an example, fish densities in the Yolo Bypass were relatively low compared with those reported in some other studies (Levy and Northcote 1982; Swales et al. 1986; Swales and Levings 1989); perhaps young salmon behavior could be different at higher densities. However, the potential for such losses can still be consistent with effective management of salmon populations. Diverse life history strategies

provide bet-hedging for salmon populations in the highly variable environment of coastal tributaries (Secor 1999; Bottom et al. 2005). We therefore expect that young salmon will not thrive in all habitats in every year. In the case of highly variable seasonal environments such as floodplains, stranding losses might cause excessive mortality in some years, but the risks may be offset by increased rearing habitat and food resources in other years (Sommer et al. 2001b; Brown 2002).

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