Environ Biol Fish (2008) 83:449–458
DOI 10.1007/s10641-008-9367-1

Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river

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Received: 13 November 2007 / Accepted: 19 May 2008 / Published online: 6 June 2008

Abstract We reared juvenile Chinook salmon for two consecutive flood seasons within various habitats of the Cosumnes River and its floodplain to compare fish growth in river and floodplain habitats. Fish were placed in enclosures during times when wild salmon would naturally be rearing in floodplain habitats. We found significant differences in growth rates between salmon reared in floodplain and river enclosures. Salmon reared in seasonally inundated habitats with annual terrestrial vegetation experienced higher growth rates than those reared in a perennial pond on the floodplain. Growth of fish in the non-tidal river upstream of the floodplain varied with flow in the river. When flows were high, there was little growth and high mortality, but when the flows were low and clear, the fish grew rapidly. Fish displayed very poor growth in tidally influenced river habitat below the floodplain, a habitat type to which juveniles are commonly displaced during high flow events due to a lack of channel complexity in the main-stem river. Overall, ephemeral floodplain habitats supported higher growth rates for juvenile Chinook salmon than more permanent habitats in either the floodplain or river. Variable responses in both growth and mortality, however, indicate the importance of providing habitat complexity for juvenile salmon in floodplain reaches of streams, so fish can find optimal places for rearing under different flow conditions.

Keywords Juvenile Chinook · Floodplain · Rearing · Growth · Restoration

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Introduction

Temperate rivers and their floodplains have been heavily altered to meet demands of an expanding human population (Richter et al. 2003). Dams store water for purposes of flood protection and agricultural and municipal water supply and thereby reduce or eliminate natural flood flows. Many rivers have been channelized and are flanked by levees, which reduces connectivity between river and floodplain except during extremely high discharge events (Mount 1995; Tockner and Stanford 2002).

In the last two decades, numerous studies have demonstrated that both aquatic and riparian ecosystems benefit from dynamic connectivity between rivers and their floodplains. Riparian species benefit from nutrients mobilized by inundation of floodplain areas (Junk et al. 1989), while riverine species benefit by having access to the floodplain for foraging, spawning, and as a refuge from high velocities found in the river during high flow events (Moyle et al. 2007). Fish yields in watersheds generally increase when water surface area in floodplains is increased (Bayley 1991). In the Central Valley of California, USA, significant resources are being invested in floodplain restoration (CALFED 2004) and thus, information is needed on the ecological benefits associated with various types of floodplain habitat (e.g., annual vegetation, forest, seasonal wetland, permanent pond/wetland). Further, many physical parameters (i.e. temperature, water depth, water velocity, hydrologic connectivity, etc.) ultimately determine what habitats are available to the many species that rely on floodplains for growth, reproduction and survival (Moyle et al. 2007).

Floodplains can be particularly beneficial to juvenile anadromous salmonids, which use floodplains for foraging and refuge during their downstream migrations (Brown and Hartman 1988). Thus, Sommer et al. (2001) found that juvenile Chinook salmon rearing on a large, fairly uniform engineered floodplain of the Sacramento River (the Yolo Bypass) had higher rates of growth and survival than fish that reared in the river channel. In this study, we build on the work of Sommer et al. (2001) and examine juvenile Chinook salmon growth in different habitats on the complex river-floodplain system of the Cosumnes River. The Cosumnes River, within the San Joaquin River watershed, is an undammed river flowing out of the Sierra Nevada Mountains, into California's Central Valley. In this river, the first major rains in the fall allow adult fall-run Chinook salmon to migrate upstream to spawn. Salmon fry emerge from the gravel during winter when flows are elevated from frequent precipitation events (Florsheim and Mount 2002). With the increase in flow, fry both actively and passively migrate downstream (Healey 1980; Kjelson et al. 1981). In the lower reaches of the river, a large portion of the total river flow enters the floodplain during high river stages (Ahearn et al. 2006). Flows from both the river and floodplain then enter the intertidal waters of the Sacramento-San Joaquin Delta (Fig. 1; Swenson et al. 2003). Thus, juvenile Chinook rear in three primary habitat types of the lower Cosumnes: river, floodplain, and tidal delta. We compared growth rates of juvenile Chinook salmon in enclosures placed in these three primary habitats as well as in enclosures placed in three distinct habitats (a permanent pond and two ephemeral habitats) on the floodplain itself. Our hypothesis was that juvenile salmon in floodplain habitats experience higher growth rates than juvenile salmon in adjacent river or tidal habitats.

Methods

Study area

The Cosumnes River is the only major California Central Valley river draining the Sierra Nevada that lacks major dams and thus retains a relatively natural hydrology. The Cosumnes River watershed encompasses ~2,000 km^2 and originates at an elevation of 2,357 m and flows into the Mokelumne River in the Sacramento-San Joaquin Delta (Fig. 1). The majority of the lower river is leveed with the exception of sections in the lowest five km within the 18,615 ha Cosumnes River Preserve (CRP) managed by The Nature Conservancy and multiple government agencies. Within the CRP, four intentional breaches in the levee allow connection between the river and its floodplain. The breaches are part of a project that has restored former farmland to various floodplain habitats through active and passive approaches (Swenson et al. 2003). Floodplain habitats include terrestrial herbaceous vegetation, ephemeral ponds, permanent ponds and forest. Water flows into the floodplain through the four breaches and exits the floodplain through one small breach and a slough used in summer as a source of water for a local farm (Fig. 1).

Enclosure fish growth study

For two independent winter flood seasons (2004 and 2005), six enclosures were placed in each of three different habitat types in the floodplain and two locations in the river (30 enclosures total) (Fig. 1). Floodplain habitats included an ephemeral pond (Upper Pond), flooded terrestrial herbaceous vegetation (FP Veg), and a pond that was permanent during the first year of the study and ephemeral during the second (Lower Pond). The ephemeral pond became completely dry by late summer and supported annual grasses and other herbaceous vegetation. The pond became inundated when river flows increased as a result of rains in late December or early January. The

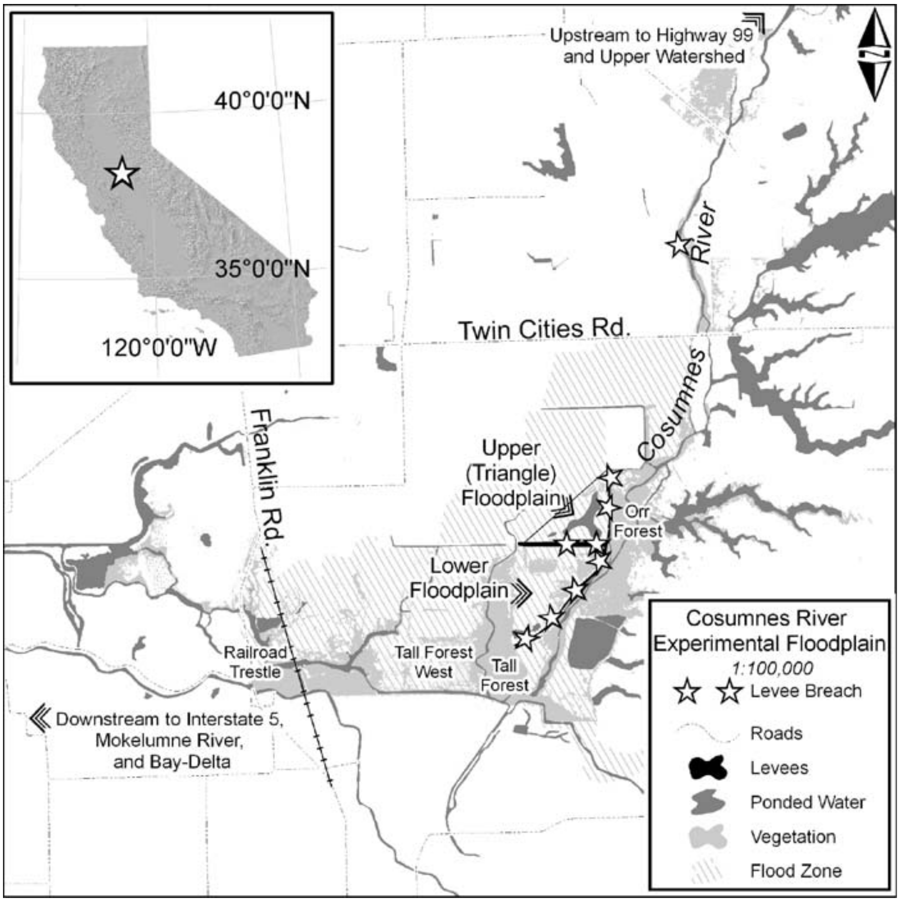

Fig. 1 Location of the studied habitat types within the lower Cosumnes River

terrestrial vegetation enclosures were in the area surrounding the ephemeral pond and the habitat was covered with annual herbaceous vegetation interspersed with young oak, willow and cottonwood trees. The lower pond was connected to a slough that had a temporary dam across from which water could be pumped for irrigation. As water level in the slough was raised during the summer months, water level in the pond was subsequently raised. This created a pond with a fine, muddy, anoxic substrate and very little rooted vegetation. During the second year of the study, the hydrologic connection between the lower pond and the agricultural slough was closed and the pond dried out during the summer months, allowing grasses and other herbaceous vegetation to grow in the bottom of the pond. Thus, the vegetation characteristics of this pond differed between years. The two river locations were the river channel above the floodplain (above FP) and the river channel below the floodplain (below FP). The river location above the floodplain was in a non-tidal portion of the river with a sandy substrate under a bridge. The river location below the floodplain was in a freshwater tidal area, with a substrate of small gravel from a nearby bridge abutment and fine muddy sediment. Enclosures in the river below the floodplain were placed within three meters of the shore, which are similar to areas generally selected by juvenile Chinook salmon during migration (Beechie et al. 2005).

We obtained approximately 500 juvenile Chinook salmon in February 2004 and 2005 from the Mokelumne River Fish Hatchery and placed them in a 142-l cooler filled with water from the hatchery raceway. The fish were progeny of fall-run Chinook salmon collected at the hatchery during the previous fall. All juvenile Chinook collected for the experiment were the same age and from within the same raceway at the hatchery and were of similar size to wild fish collected on the floodplain (Jeffres, unpublished data). An aerator was placed in the cooler to maintain dissolved oxygen levels. The fish were transported to the Cosumnes River Preserve where they were placed into 0.6×0.6×1.2 m enclosures. The frames of the enclosures were constructed from 19 mm polyvinyl chloride (PVC) pipe with 6.3 mm extruded plastic netting fitted around the frame. The 6.3 mm netting allowed the free movement of zooplankton, benthic macroinvertebrates, larval fish and other food items to enter the enclosure. The netting was held in place by plastic cable ties placed at regular intervals to keep the netting close to the frame.

At each location we randomly selected ten fish by sweeping a net through the cooler, measured their fork length, and then placed them in the enclosure. There was natural variation in the size of the fish, but the average size of the selected fish was statistically similar across all habitats. We then secured the enclosure by tying a rope from the outside corner of the enclosure to a cinder block. Then the remaining opening in the netting was closed with plastic cable ties. We then placed the enclosure on the substrate with its longest part horizontal to the ground. The depth of water at the cages varied with changes in river flows. The cages were within a meter of the water surface during all but the highest flows. Cages in the ephemeral pond and lower pond were in similar depths throughout the study.

In 2005, fish placed in two of the six floodplain vegetation enclosures immediately displayed erratic opercular movements and swam rapidly in circles. Within 5 min, all of the fish placed in both enclosures were dead. A concurrent water quality study indicated that dissolved oxygen levels in the local area had dropped from a 3-day mean of 60% saturation (6.2 mg l^{-1}) to approximately 30% saturation (3.0 mg l^{-1}) 2 days prior to the fish being placed in the enclosures (Ahearn et al. 2006). The enclosures were moved to a location closer to the center of the floodplain, but still in flooded vegetation and 10 more fish were placed in each enclosure. Eleven of the fish in this new location survived for 11 days, and then all of the fish died on 3 March, most likely due to low dissolved oxygen levels. Lengths of the fish that died as a result of low dissolved oxygen were not used in the analysis of growth rates between habitats. We did not include these fish in the analysis because we wanted to compare growth rates between habitats that provided tolerable conditions for rearing, in other words, habitats representative of those that wild salmon would have actively selected or within which they would have chosen to remain.

Due to variability in river flows, fish sampling occurred when conditions allowed for enclosure location and retrieval. During high flows, high water depth and velocity did not allow access to the enclosure locations. In 2004, fork lengths were measured 17, 28 and 32 days after initial deployment of the enclosures. Each time fish were measured, they were taken out of the enclosure, measured and then placed into an aerated cooler until all fish were measured. They were then placed back into the enclosure and the opening was closed with cable ties. The last time that the fish were measured, they were killed by a quick blow to the head and placed in a cooler with dry ice. In 2005, fork lengths were measured 6, 19, 41 and 56 days after the initial deployment of the enclosures. Weights of the fish were not taken during each sampling due to inclement weather conditions (wind and rain) that would not allow the scale to work properly.

We preformed diet analysis on randomly selected individuals from all floodplain and the upstream river habitats only to determine potential prey items, not to quantify feeding rates or prey selection throughout the length of the study. Fish from enclosures in the below floodplain river habitat had already been utilized in a concurrent study, and were not available for gut content analysis. Stomachs of selected fish were removed and weighed, then contents of the stomach were removed and the stomach was weighed again. Stomach contents were identified to the lowest taxonomic level using a dissecting microscope. Percentage of each prey type was visually estimated and that number was used to determine relative abundance of each prey item. For analysis, we grouped stomach contents into order and prey type; contents that could not be identified were labeled as miscellaneous.

Temperature data were recorded every 15 min with Onset stowaway tidbit temperature loggers placed on the floodplain and in the river channel. We obtained flow data from the Michigan Bar stream flow gauging station (gauge number 11335000) operated by the United States Geological Survey. The Michigan Bar gauge is located 50 km upstream of the study site. River discharge data was collected every 15 min throughout the study. Through previous studies, it was determined that when discharge at Michigan Bar reached 22.6 $m^3 s^{-1}$, the river and floodplain became hydrologically connected.

Fish fork lengths were analyzed at deployment to determine if they were all statistically the same length using a two-way ANOVA. After the initial measurement, the two years were analyzed separately where the effect of habitat type on mean fork length was analyzed using a linear mixed effects model with habitat, time, and habitat by time interaction as fixed effects and with compound symmetry to account for possible time dependence. Model fit was assessed using graphic analysis of residuals and the Shapiro–Wilks test for normality. Post hoc comparisons were performed using the Tukey–Kramer for multiple testing. Above floodplain habitat was excluded from the second year analysis due all of fish not surviving throughout the experiment. Statistical significance was declared at the 0.05 level. Analysis was performed using JMP version 5.1.2.

Results

Physical parameters

In 2004, we placed salmon on the floodplain while it was connected with the river and during the descending limb of a small flood (45 m^3 s^{-1}) on 20 February. A week after the fish were placed in the enclosures, the largest flood (108 m^3 s^{-1}) of the year occurred. The river and floodplain remained hydrologically connected for 14 days from the time the enclosures were deployed and was disconnected for the final 19 days of the study (Fig. 2). As the floodplain drained, water levels decreased at some enclosure

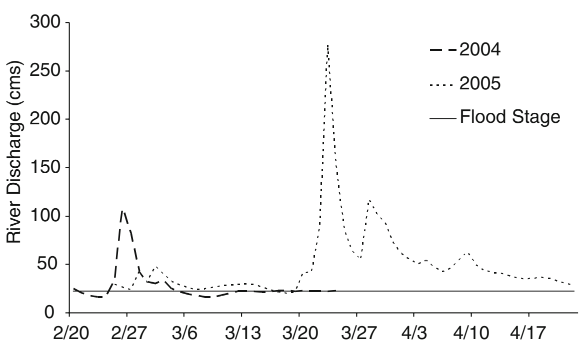

Fig. 2 Comparison of the difference in magnitude of river flows during each of the two flood seasons. Hydrographs of the Cosumnes River at the USGS Michigan Bar gauge during the time when experiments took place in 2004 (*heavy dashed line*) and 2005 (*light dashed line*). Flood threshold (*solid line*) is the flow at which the river and the floodplain become hydrologically connected. The duration of each years experiment is shown by the duration of the hydrograph

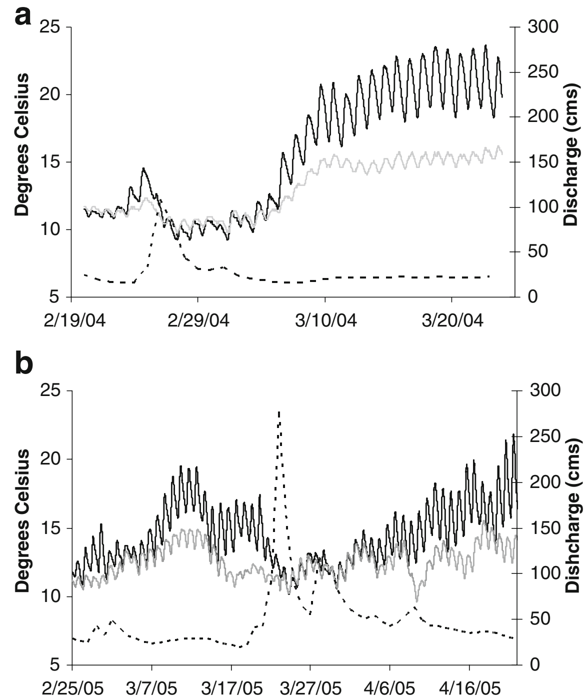

Fig. 3 Water temperature of floodplain (*dark line*) and river (*light line*) in relation to river discharge (*dashed line*) in 2004 (**a**) and 2005 (**b**). Note that when the river is low and not fluctuating, floodplain water temperature is often warmer than water in the river channel

locations. As the water stage lowered and air temperature increased, water temperature on the floodplain increased (Fig. 3).

In 2005, we placed salmon on the floodplain 5 days after a peak flow (50 m^3 s^{-1}) on 25 February. The floodplain became disconnected from the river, and had begun draining by the time the enclosures were deployed. Small floods maintained hydrologic connection between the river and the floodplain for the next 23 days. On day 24, flows increased to 368 m^3 s^{-1} and the floodplain remained connected to the river for the remaining 30 days of the study (Fig. 2). Temperatures on the floodplain increased during stable flows in the river after the large flow event (Fig. 3).

Fish growth

In 2004, fish length was the same for all of the enclosures at the initial deployment (55.0±0.6 mm; ANOVA: P=0.95; Fig. 4). After 17 days, average lengths of the fish in the flooded vegetation site and upper pond were significantly greater than those of

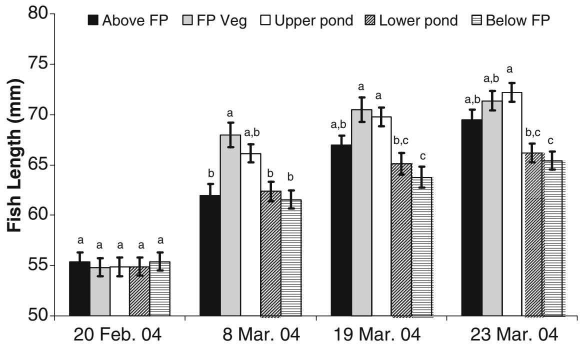

Fig. 4 Mean (±standard error) fork lengths of juvenile Chinook placed among various habitats over four sampling sessions during the 2004 flood season. "FP Veg", "Upper Pond", and "Lower Pond" are floodplain habitats while "Above FP" and "Below FP" are river channel sites above and below the floodplain respectively. Habitats *not connected by the same letter* are statistically different

fish in the other three locations (Tukey–Kramer HSD: $\alpha<0.05$, $Q=3.66$; Fig. 4). After 26 days, fish in the flooded vegetation habitat and the upper pond were still significantly longer than those in the lower pond and the river location below the floodplain (Tukey–Kramer HSD: $\alpha<0.05$, $Q=3.66$). However, lengths of fish in the river site above the floodplain increased rapidly and were intermediate between the ephemeral floodplain habitats and the lower pond and river location below the floodplain (Fig. 4). The final time that the fish were sampled, 32 days after deployment, fish in the river site upstream of the floodplain were statistically grouped with the fish in ephemeral floodplain sites, with greater lengths than fish placed in both the lower pond and river below the floodplain habitats (Tukey–Kramer HSD: $\alpha<0.05$, $Q=3.66$; Fig. 4).

In 2005, mean fork length of the fish was the same for all enclosures at initial deployment (54.2±0.2 mm; ANOVA: $P=0.89$; Fig. 5). The first time that all of the locations were sampled, 20 days after initial deployment, fish in the flooded vegetation, upper pond, and above the floodplain had increased in length significantly more than fish in the lower pond and below the floodplain (Tukey–Kramer HSD: $\alpha<0.05$, $Q=3.57$; Fig. 5). We were unable to sample the fish again for 22 days (41 days after initial deployment), due to high river discharge. When next sampled, enclosures in the river above the floodplain had no fish in them. The enclosures were all structurally sound and four were partially buried in sand. It is likely that the fish perished from the effects of suspended particles during the previous high flow event. Fish in all three habitats on the floodplain experienced more growth relative to fish in the river below the floodplain, which showed little growth from the previous sampling (Tukey–Kramer HSD: $\alpha<0.05$, $Q=3.57$; Fig. 5). The final sampling took place after 56 days. Fish in all three floodplain habitats continued to grow at similar rates. Fish in the river below the floodplain did increase in length, but growth relative to floodplain fish was still small (Figs. 5 and 7).

Gut contents

The majority of food items found in fish reared in floodplain ponds were zooplankton (Fig. 6). Gut contents of fish placed in herbaceous vegetation habitat on the floodplain consisted primarily of benthic macroinvertebrates, larval fish, and zooplankton (Fig. 6). In the river site above the floodplain, gut contents showed that fish were feeding on benthic macroinvertebrates and terrestrial invertebrates (Fig. 6).

Discussion

Juvenile Chinook salmon placed in ephemeral floodplain habitats grew larger than fish placed in the intertidal river site below the floodplain; these results were similar to those found by Sommer et al. (2001) (Figs. 4 and 5). Sommer et al. (2001) suggested that increased growth on the floodplain was a result of

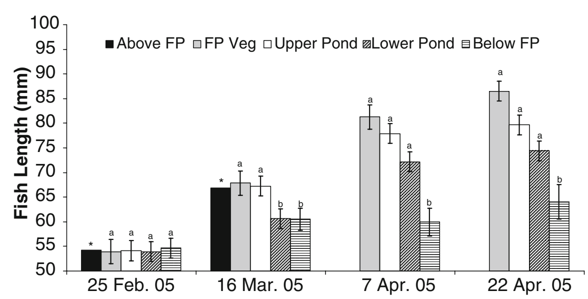

Fig. 5 Mean (±standard error) fork lengths of juvenile Chinook placed among various habitats over four sampling sessions during the 2005 flood season. "FP Veg", "Upper Pond", and "Lower Pond" are floodplain habitats while "Above FP" and "Below FP" are river channel sites above and below the floodplain respectively. Habitats *not connected by the same letter* are statistically different. *Asterisk* indicates that the habitat type was not included in the statistical analysis

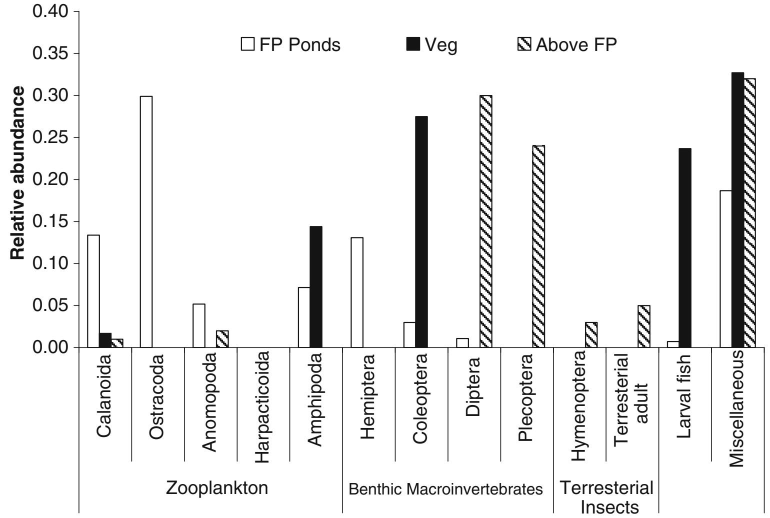

Fig. 6 Relative abundance of prey items found in gut contents of fish from floodplain ponds (*open boxes*), floodplain vegetation (*filled boxes*) and river channel above floodplain (*cross hatched boxes*)

higher temperatures and higher productivity relative to the adjacent main-stem river habitat. We hypothesize that along with increased temperature and productivity, ephemeral floodplain habitat is also important for increased growth of juvenile salmon throughout a variety of flow conditions (Fig. 7).

During the first year of the study, fish in the lower pond grew slow relative to those in other floodplain sites, but growth rates were similar to those found in the river site below the floodplain. The lower pond had filled nine years earlier and remained wet the entire time. During the nine years of inundation, no vegetation had grown in the pond. After the first year of the study, land managers closed the gate that connected it with a slough used as a source of water for irrigation, resulting in the pond drying out and herbaceous vegetation growing in the substrate. Grasses and cockleburs were the predominant plants, similar to the ephemeral pond. During the second year of the study, fish in this pond area had significantly longer fork lengths than those in the river site below the floodplain (Fig. 5). Thus when the lower pond lacked vegetation, the fish in this habitat had similar, low fork lengths as in the river below the floodplain. This provides support for the importance of vegetative structure for promoting primary and secondary production (Dodds et al. 1996; Baranyi et al. 2002).

Magnitude, duration and timing of flows that enter the floodplain are factors that drive primary production on the Cosumnes River floodplain (Ahearn et al. 2006). At high flows, the floodplain carries the majority of flow that comes down the river (Ahearn et al. 2006). Due to the relatively large surface area and abundant vegetation, velocities are much lower on the floodplain, which provides refuge for fish and other fauna moving down the river. As river stage falls, floodplain water velocity decreases and clarity increases as suspended sediments fall from the water column. Floodplain water temperature increases with declining flow and turbidity (Fig. 3), creating ideal conditions for the growth of phytoplankton (Ahearn et al. 2006), as well as for zooplankton and other animals that feed on phytoplankton (Grosholz and Gallo 2006). Grosholz and Gallo (2006), studying the

Fig. 7 Comparison of a single enclosure of fish reared in intertidal river habitat below floodplain (*left*) and a single enclosure of fish reared in the floodplain vegetation (*right*) after 54 days in respective habitats at the end of the second year of the study

same floodplain area in which our cages were located, found that zooplankton biomass was 10–100 times greater in floodplain sites than in river sites. The periods of floodplain-river connection and disconnection create an abundant food source for juvenile Chinook salmon on the Cosumnes River floodplain and provide a possible explanation for the observed fork lengths in our study.

Food sources for juvenile salmon vary both temporally and spatially in the Cosumnes River and associated floodplain. Flood pulses that enter the floodplain create ideal conditions for primary and secondary production and ultimately provide an abundant food source for juvenile Chinook (Ahearn et al. 2006; Grosholz and Gallo 2006). While gut contents of fish collected at the end of a study do not describe diet throughout the study, they do indicate the types of food juvenile salmon were willing and able to consume while enclosed in their respective habitats. Food items found in juvenile Chinook gut contents were typical of what would be found in each habitat type. Fish in the river habitat fed on benthic macroinvertebrates often found in moving waters, while fish in floodplain habitats fed primarily on pelagic zooplankton and macroinvertebrates (Fig. 6). These data show a diversity of prey items among the various habitats available to juvenile Chinook rearing in the lower Cosumnes River.

Higher water temperature is one of the factors that distinguished floodplain habitat from the river habitat (Fig. 3). The optimum temperature for growth of juvenile salmon is dependant on food availability. Temperatures from 14°C to 19°C provide optimal growing conditions for juvenile Chinook salmon fed at 60% to 80% of satiation (Marine and Cech 2004; Richter and Kolmes 2005). In habitats where food is abundant and fish are satiated, temperatures for optimum growth may be higher than those observed in studies where food is limited (Myrick and Cech 2004). Temperatures on the floodplain for a 1-week period had a daily average of 21°C and reached a daily maximum of 25°C and fish continued to grow rapidly. Continued growth at high temperatures implies that food is not limiting during warm water conditions.

In the second year of the study, fish in the river channel above the floodplain grew rapidly during the first part of the study, when flows were low and clear. Flows in the river then increased and remained high for the remainder of the study, killing all fish in the river cages above the floodplain. The fish most likely died because there was no escape from high velocities where the enclosures were located. During high flow events, wild salmon in the river would likely move downstream to the restored floodplain, where rearing conditions are favorable, or to intertidal habitat where rearing conditions are less favorable. Wild juvenile salmon in the river may have been able to avoid the high velocities. However, the Cosumnes River for much of its length is incised and lacks channel complexity, similar to other rivers in the Central Valley. Therefore, during a high flow event such as the one during the second year of the study, wild juvenile Chinook salmon would likely have been displaced downstream to either the floodplain or the intertidal river below the floodplain. This enclosure study highlights the importance of off-channel rearing habitat for juvenile salmon during high flow conditions.

Rearing on a floodplain is a balance of risk and reward for juvenile salmon. Growth rates can be very high on the floodplain, but fish risk stranding and periods of stagnation, which can also create conditions lethal to juvenile salmon. However, natural floodplains tend to be heterogeneous in terms of water quality (Ahearn et al. 2006) and fish can avoid stressful conditions and seek more favorable habitats (Matthews and Burg 1997). The risk of stranding merits further study in this and other systems although preliminary observations suggest that wild salmon generally leave the floodplain prior to complete disconnection and that most non-salmonids that are stranded on the floodplain are non-native fish (Moyle et al. 2007).

Conclusion

Restoration of floodplains and other off channel habitats is potentially important for increasing production of juvenile salmonids in California's Central Valley. When juvenile salmon are migrating down from upstream spawning grounds during high flow events, migration is more passive than active (Healey 1980; Kjelson et al. 1981) and they are essentially entrained in the water column until they find slower water velocities where active swimming becomes possible. The Cosumnes River is similar to most rivers in the Central Valley in that it is incised and lacks channel complexity. Because other Central Valley rivers also lack access to floodplains – with the notable exception of the Yolo Bypass for the Sacramento River (Sommer et al. 2001) – juvenile salmon in these systems are frequently displaced to the intertidal delta during high flows. Our study indicates that off-channel floodplain habitats provide significantly better rearing habitat, supporting higher growth rates, than the intertidal river channel. Variable responses in both growth and mortality in the habitats investigated, however, indicate the importance of providing habitat complexity for juvenile salmon in floodplain reaches of streams, so fish can find optimal places for rearing under varying flow conditions.

When juvenile Chinook salmon leave fresh water at a larger size, as seen in fish reared on floodplains, overall survivorship to adulthood is increased (Unwin 1997; Galat and Zweimuller 2001). Restoration of river-floodplain connectivity should thus prove to be an effective part of any salmon conservation strategy. This study and that of Sommer et al. (2001) show that restoring floodplain habitats in Central California should have major benefits to Chinook salmon populations.

Acknowledgements We thank the California Bay Delta Authority Science Program and The David and Lucile Packard Foundation for financial support of this project. We are grateful to the Cosumnes River Preserve for their support and access to the preserve. We would also like to express our appreciation for their help in the study design and field assistance to Wendy Trowbridge and Alicia Gilbreath. We thank the reviewers and the editor for their comments.

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