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

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Abstract

We reared juvenile Chinook salmon for two consecutive flood seasons within various habitats of the Cosumnes River and its floodplain (California) to compare growth rates of in river and newly created floodplain habitats. Fish were placed in enclosures in several different habitat types on the floodplain and in the river during times when wild salmon would naturally be rearing in floodplain habitats. We found significant differences in growth rates between salmon rearing in floodplain and river sites. Salmon reared in seasonally inundated habitats with annual terrestrial vegetation showed higher growth rates than those reared in a perennial pond on the floodplain. Growth of fish in the river upstream of the floodplain varied with flow and turbidity in the river. When flows and turbidity were high, there was little growth and high mortality, but when the flows were low and clear, the fish grew rapidly. Fish in tidal river habitat below the floodplain in showed very poor growth rates. Overall, ephemeral floodplain habitats supported higher growth rates for juvenile Chinook salmon than more permanent habitats in either the floodplain or river.

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 further 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 terrestrial organisms as well as ecosystems benefit from dynamic connectivity between rivers and floodplains. Floodplain species benefit from nutrients mobilized by inundation of riparian 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. submitted). Fish yields in watersheds generally increase when water surface area in floodplains is increased (Bayley 1991). Floodplains have also been shown to be beneficial to species that use the main stem of the river primarily as a migration corridor and secondarily as a rearing area, such as juvenile anadromous salmonids (Brown and Hartman 1988). Sommer et al. (2001) found that Juvenile Chinook salmon that reared within a large, engineered floodplain of the Sacramento River (the Yolo Bypass) had higher rates of growth and survival than fish that reared in the main-stem river channel during their migration.

In this study, we build on the work of Sommer et al. (2001) and experimentally compare juvenile Chinook salmon growth between different habitat types of a more complex natural river-floodplain system. We examine in detail how different floodplain and riverine habitats influence the growth of juvenile salmon in the Cosumnes River, an undammed river flowing out of the Sierra Nevada, in central California. 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. Flows from both the river and floodplain then enter the intertidal waters of the Sacramento-San Joaquin Delta (Figure 1)(Swenson et al 2003). Thus, juvenile Chinook rear in three primary habitat types of the lower Cosumnes: the main-stem river channel, the floodplain, and the tidal Delta.

Sommer et al. (2001) demonstrated that temporarily flooded habitat in an artificial floodplain in the Central Valley produced superior growth of juvenile Chinook salmon compared to river habitats. Here we evaluate how differences in growth occur in different habitats in more complex natural floodplains and their associated rivers. Land managers and government agencies are investing significant resources in floodplain restoration (CALFED 2004) and, thus, require information 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 ultimately determine what habitat is available to the many species that rely on floodplains for growth, reproduction and survival. Factors such as magnitude and duration of floods play an important role in determining quality and accessibility of various floodplain habitats. We compared growth rates of juvenile Chinook salmon in enclosures placed in different habitats within the Cosumnes River floodplain, as well as in adjacent river and intertidal habitats, during two years with different flooding regimes. Our basic hypothesis was that juvenile salmon in ephemeral floodplain habitats experience higher growth rates than juvenile salmon in other floodplain habitats or in adjacent river or tidal habitats.

Methods

Study Area

The Cosumnes River watershed is unusual for a Sierra Nevada river because there are no major dams on the main-stem and the river is relatively free flowing (Figure 1). The Cosumnes River watershed encompasses ~2000 km^2 and originates at an elevation of 2357 m and flows into the Mokelumne River in the Sacramento-San Joaquin Delta. During the summer months in a typical water year, the lower 36 km of the river channel is dry due to the lowering of the water table from municipal and agriculture water demands (Fleckenstein et al. 2004). The majority of the lower river is leveed with the exception of sections in the lowest 5 km of the river 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). The floodplain habitat includes terrestrial herbaceous vegetation, ephemeral ponds, permanent ponds and forest. Water flows into the floodplain through 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 (Figure 1).

Enclosure Fish Growth Study

For two 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 (Figure1). Floodplain habitats were an ephemeral pond, flooded terrestrial herbaceous vegetation, and a previously permanent pond. The ephemeral pond became completely dry by late summer and supported annual grasses and other herbaceous vegetation. It became flooded when river flows increased as a result of rains in late December or early January. The flooded upland vegetation was in the area surrounding the ephemeral pond. It was covered with annual herbaceous vegetation interspersed with some young oak, willow and cottonwood trees. The lower pond was connected to a slough that had a temporary dam across it so water could be pumped from it for irrigation. As the slough elevation was raised during the summer months, the elevation of 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 river locations were the river channel above the floodplain and the river channel below the floodplain. 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 an 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 in edge habitat, which is similar to habitat that is 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-liter cooler filled with water from the hatchery raceway. 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 0.6m x 0.6m x 1.2m. 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 6.3mm netting allowed the free movement of zooplankton, 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, fish were haphazardly selected by sweeping a net through the cooler. Ten fish were selected and their fork length measured. After the fish were placed in the enclosure, a cinder block was tied with rope to the outside corner of the enclosure to keep it from floating away. Then the remaining opening in the netting was closed using plastic cable ties. The enclosure was placed 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. The cages in the ephemeral pond and lower pond were in similar depths throughout the study.

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 flood season 2004, the first year of the study, fork lengths were measured 17, 28 and 32 days after initial deployment of the enclosures. Weights were only measured on the initial deployment and the final day of the experiment to reduce stress on the fish. 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 enclosure was closed with cable ties. The last time that the fish were measured, they were weighed and then killed by a quick blow to the head and placed in a cooler with dry ice.

In flood season 2005, second year of the study, fork lengths were measured 6, 19, 41 and 56 days after the initial deployment of the enclosures. Weights were not taken so that fish would be handled as little as possible.

Temperature data was recorded using Onset stowaway tidbit temperature loggers. Flow data was obtained from the Michigan Bar stream flow gauging station 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 minutes throughout the length of the study. When discharge at Michigan Bar reached 22.6 m^3s^{-1}, the river and floodplain became hydrologically connected.

We analyzed differences in fish length between habitats using one-way analysis of variance (ANOVA). Tukey-Kramer honestly significant difference (HSD) tests were preformed to determine which habitats showed significant differences in lengths at the intervals that fish were sampled. ANOVA and Tukey-Kramer tests were assessed for significance at α=.05.

Results

Physical parameters

In 2004, salmon were placed on the floodplain while it was connected with the river and during the descending limb of a small flood (45 m^3s^{-1}) on 20 February. A week after the fish were placed in the enclosures, the largest flood (108 m^3s^{-1}) of the year occurred. The river and floodplain remained hydrologically connected for 14 days from the time the enclosures were deployed and were disconnected for the final 19 days of the study (Figure 2). As the floodplain drained, water levels decreased at some enclosure locations. As the water stage lowered and air temperatures increased the temperature of the water on the floodplain also increased (Figure 4).

In 2005, salmon were placed on the floodplain 5 days after a peak flow (50 m^3s^{-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^3s^{-1} and the floodplain remained connected to the river for the remaining 30 days of the study (Figure 3). The temperatures on the floodplain increased during the stable flows in the river after the large flow event (Figure 4).

Fish Growth

In 2004, the length of the fish was the same for all of the enclosures at the initial deployment (55.0 ± 0.6 mm; ANOVA: $p=0.95$; Figure 5). The first time that the enclosures were checked, after 17 days, the average lengths of the fish in the flooded vegetation site and the ephemeral pond were significantly greater than those of fish in the other 3 locations (ANOVA: $p<0.0001$; Tukey-Kramer HSD: $P<0.05$, $q=2.75$) (Figure 2). The second time that the enclosures were sampled, after 26 days, fish in the flooded vegetation site and the ephemeral pond were still significantly longer than those in the lower pond and the river location below the floodplain (ANOVA: $p<0.0001$; Tukey-Kramer HSD: $P<0.05$, $q=2.76$). However, lengths of fish in the river site above the floodplain increased rapidly and were intermediate between the two floodplain habitats and the lower pond and river location below the floodplain (Figures 2 and 4). The final time that the fish were sampled, 32 days after deployment, the fish in the river site upstream of the floodplain were statistically grouped with the fish in the ephemeral floodplain sites, with longer lengths than the fish in the lower pond and the river below the floodplain. (ANOVA: $p<0.0001$; Tukey-Kramer HSD: $P<0.05$, $q=2.76$; Figure 5).

In 2005, the mean fork length of the fish was the same for all enclosures at the initial deployment (54.2 ± 0.2 mm; ANOVA: $p=0.89$; Figure 6). When the fish were placed in enclosures 1 and 2 of the flooded vegetation site, they immediately displayed erratic opercular movements and swam rapidly in circles. Within 5 minutes, all of the fish placed in the enclosures were dead. A concurrent water quality study indicated that the dissolved oxygen levels in the area had dropped from a three day mean of 60% saturation (6.2 Mg L^{-1}) to approximately 30% saturation (3.0 Mg L^{-1}) two days prior to the fish being placed in the enclosures (Ahearn et al. in press). The enclosures were moved to a location closer to the center of the floodplain and ten more fish were placed in each enclosure. Eleven of the fish in this location survived for eleven days, and then all of the fish died on 3 March, most likely due to low dissolved oxygen levels. The lengths of the fish that died as a result of low dissolved oxygen were not used in the analysis of growth rates between habitats. Due to high water levels in the river, the first time that the enclosures were checked was seven days after the initial deployment and only the enclosures on the floodplain could be accessed. The fish in the lower pond showed slower growth than fish in the ephemeral pond and submerged herbaceous vegetation. The first time that all of the locations were sampled, 20 days after initial deployment, the fish in the terrestrial vegetation, ephemeral pond and above the floodplain showed growth that was significantly higher than that of fish in the lower pond and below the floodplain (ANOVA: $p<0.0001$; Tukey-Kramer HSD: $P<0.05$, $q=2.75$; Figures 3 and 5). We were unable to sample the fish again for 22 days, 41 days after initial deployment, due to the high discharge in the river. The 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. The fish in all three habitats on the floodplain showed high growth relative to fish in the river below the floodplain, which showed little growth from the previous sampling (ANOVA: $p<0.0001$; Tukey-Kramer HSD: $P<0.05$, $q=2.60$; Figure 6). The final sampling took place after 56 days. The fish in all three of the floodplain habitats continued to grow with similar growth rates. Fish in the river below the floodplain did show an increase in length, but length relative to floodplain fish was still small (Figures 3, 5 and 6).

Discussion

Juvenile Chinook salmon placed in ephemeral floodplain habitats grew more than fish placed in the intertidal river site below the floodplain; these results were similar to those found by Sommer et al. (2001) (Figure 7). The river site above the floodplain showed relatively high growth during the first year of the study, but was lethal to the fish during high flow events in the second year (Figure 5). Sommer et al. (2001) suggested that increased growth on the floodplain was a result of higher temperatures and higher productivity relative to the adjacent main-stem river habitat. Our findings suggest that along with increased temperature and productivity, flooded terrestrial herbaceous vegetation is also important for increased growth of juvenile salmon throughout a variety of flow conditions.

During the first year of the study, fish in the lower pond showed slower growth rates 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 9 years earlier and remained wet the entire time. During the 9 years of inundation, no vegetation had grown in the pond. After the first year of the study, the 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 showed significantly higher growth rates than those in the river site below the floodplain (Figure 6). This is presumably because of the abundant zooplankton that formed a major part of the salmon diet (unpublished data). Other studies have shown that in floodplain habitats, zooplankton abundance and biodiversity are closely associated with vegetation (Baranyi et al. 2002).

Temperature is an important physical parameter that influences the growth of juvenile Chinook salmon on floodplains (Sommer et al. 2001). Temperatures from 14^0 C to 19^0 C have been shown to provide optimal growing conditions for juvenile Chinook salmon fed at 60% to 80% of satiation (Marine and Cech 2004; Richter and Kolmes 2005). The optimum temperature for growth is dependant on the amount of food that is available to juvenile salmon. 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 reached a daily maximum of 25^0 C and fish continued to grow rapidly. The continued growth at high temperatures implies that food is not limited during warm temperatures. Higher temperature is one of the factors that distinguish the floodplain habitat from the river habitat (Figure 4). When the river stage is high and the floodplain and river are hydrologically connected, there is little difference in temperatures between the floodplain and the river habitats. When flows are lower or the river is not connected with the floodplain, temperatures on the floodplain are warmer than those of the river (Figure 4). The differences in temperature closely track the observed differences in growth noted among the different habitats used in the study.

Magnitude and duration of flows that enter the floodplain are factors that drive primary production on the floodplain (Ahearn et al. in press). At high flows, the floodplain carries the majority of flow that comes down the river. During these high flow events, water chemistry is virtually identical on the floodplain and river. 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. It is not until flows in the river begin to subside that water on the floodplain looses velocity completely. As the water velocity on the floodplain is reduced, water begins to clear as suspended sediments fall from the water column. As the water level lowers and clears, it warms (Figure 4), creating ideal conditions for the growth of phytoplankton (Ahearn et al. in press), as well as for zooplankton and other animals that feed on phytoplankton.

These periods of floodplain river disconnection provide the best growing conditions for juvenile Chinook salmon on the Cosumnes river floodplain.

Fish placed in the channel above the floodplain in the first year of the study showed varying growth depending on magnitude of river flows. When flows were high and turbid, fish showed similar growth to those in the intertidal channel site below the floodplain, which was significantly lower than growth observed in the ephemeral floodplain. When river flows were low and water clear, fish in the channel above the floodplain showed similar growth to fish in the ephemeral floodplain. Fish in the intertidal channel below the floodplain showed slow growth throughout both years of the study, with no correlation to river discharge. Water in the river site below the floodplain remained cold and turbid throughout the study and changed very little with river discharge. In the second year of the study, fish in the 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 and turbid for the remainder of the study. There was a 100% mortality rate for fish in the river site above the floodplain during high discharges. The fish most likely died because there was no escape from high velocities where the enclosures were located. During high flow events, wild salmon migrating downstream would not be able to rear in the incised main channel, but would likely rear in the restored floodplain, where rearing conditions are favorable, or intertidal habitat where rearing conditions are less favorable. This shows the importance of off-channel rearing habitat for juvenile salmon during high flow conditions. Likewise, periods of water stagnation on floodplains can also create conditions lethal to enclosed fish due to low dissolved oxygen. These data show how variable a single habitat can be depending on changing physical conditions. Natural floodplains tend to be heterogeneous in terms of water quality, and during stressful conditions, fish will seek out more favorable physical conditions for rearing (Matthews and Burg 1997, Ahern et al. in press).

Restoration of floodplains and other off channel habitats is potentially important for increasing production of juvenile salmonids in central California. 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). Juvenile fish are essentially entrained in the water column until they find slower water velocities where active swimming becomes possible. The Cosumnes river is highly incised and channelized upstream of the restored floodplain, which is directly above the tidally influenced portion of the river. During all but the highest flow events, fish migrating downstream have little access to off-channel or floodplain habitat until they reach the restored floodplain in the last five km before the river becomes tidal. Fish in the river above the floodplain showed highest growth rates when water conditions were low and clear. However, when discharge was high, fish in the channelized portion of the river above the floodplain showed decreased growth rates and high mortality. Juvenile Chinook salmon in our study also showed slow growth in the tidal fresh waters below the floodplain. Overall, our study suggests that if more off channel floodplain habitat were available to juvenile Chinook during downstream migration, fish would be larger when they reached estuarine and marine waters, which has been found to increase overall survivorship (Unwin 1997; Galat and Zweimuller 2001).

Figure 1. Location of the studied habitat types (solid circle).

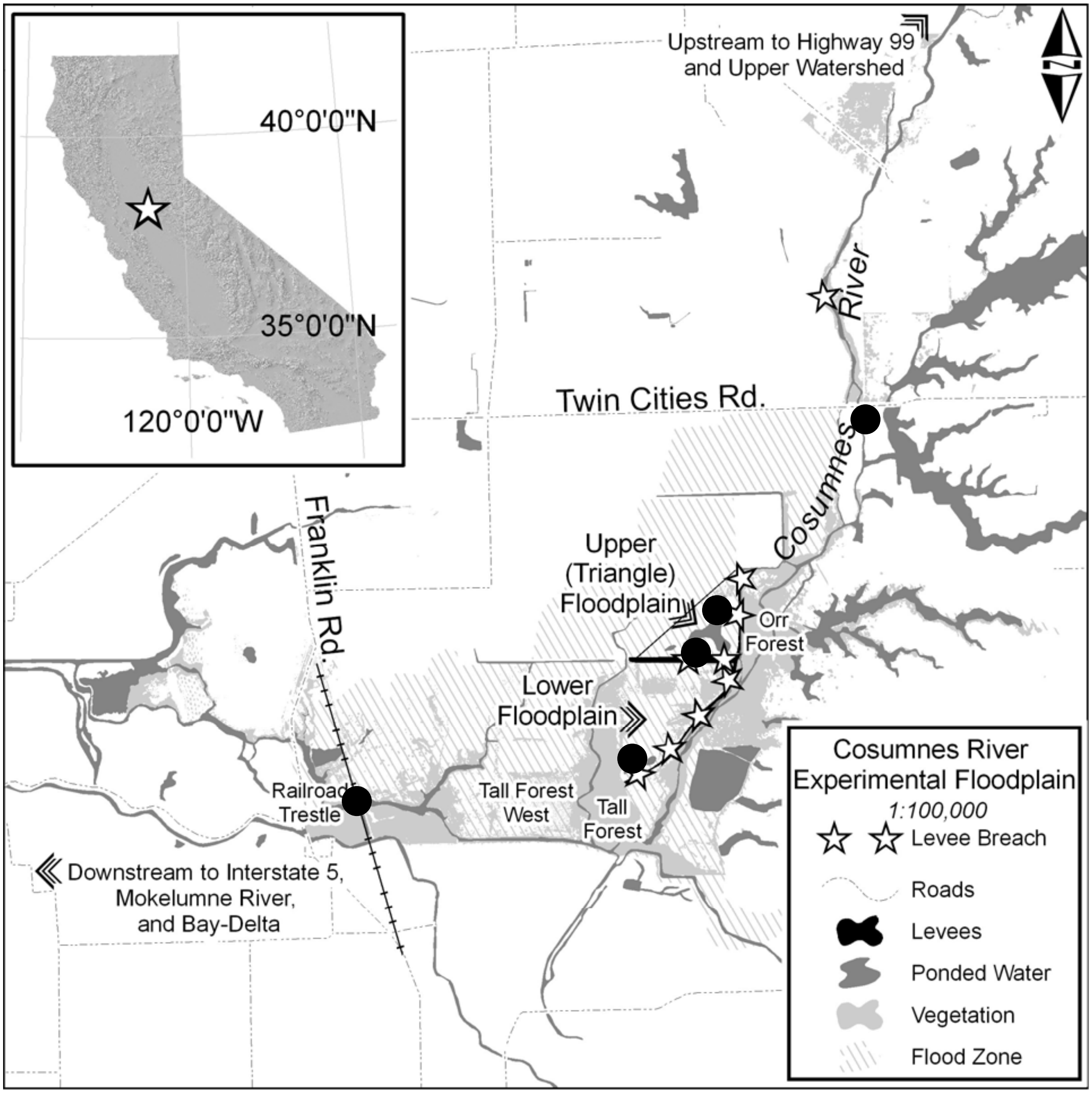


Figure 2. Mean length (+/- SE) of juvenile Chinook salmon in various habitats plotted with river discharge during 2004 sampling season. Tri Veg = flooded terrestrial vegetation, Tri Pond = ephemeral pond, Lower pond = permanent pond during the first year and ephemeral pond in the second year, Below FP = intertidal river channel below restored floodplain, Above FP = main-stem river channel above floodplain.

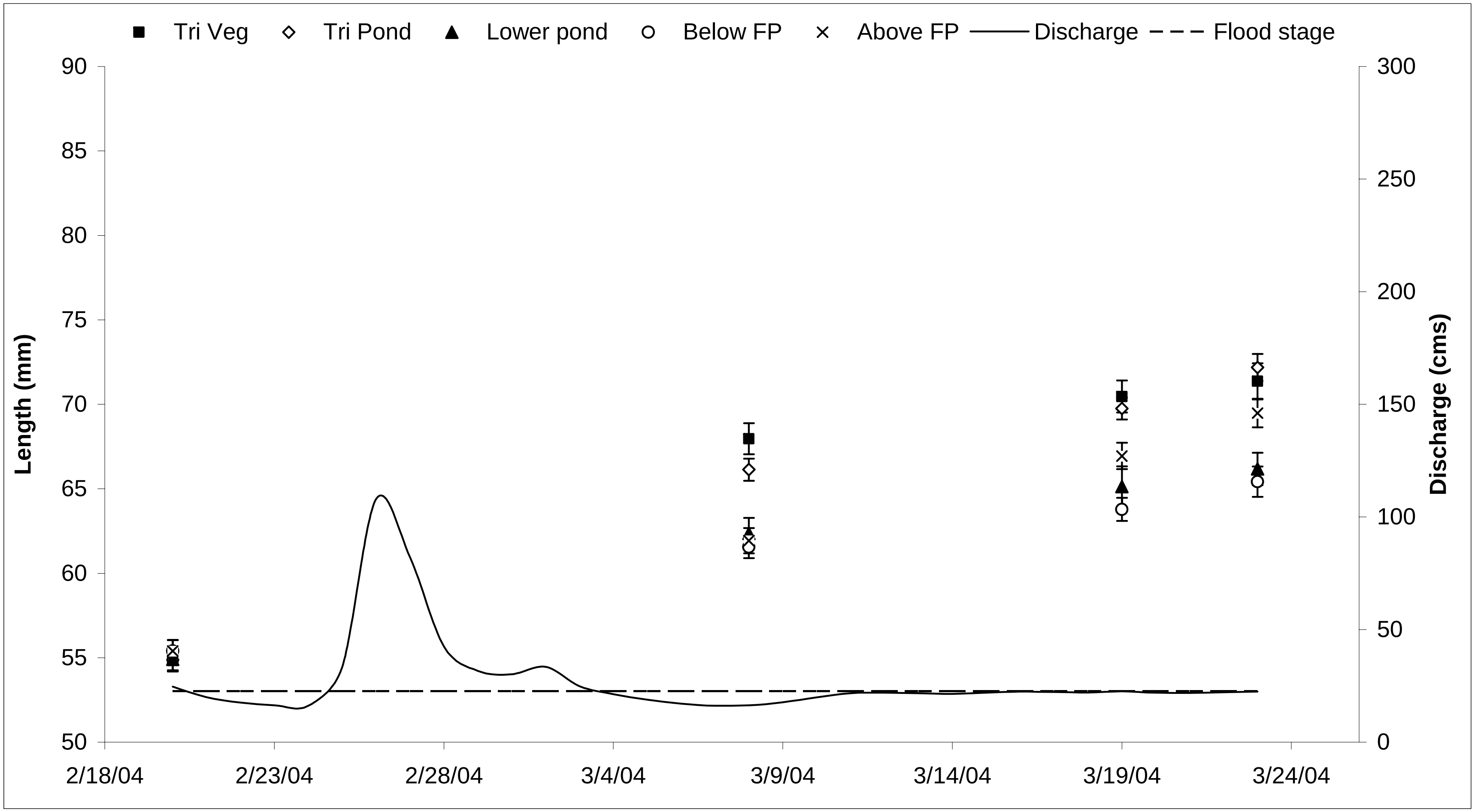


Figure 3. Mean length (+/- SE) of juvenile Chinook salmon in various habitats plotted with river discharge during 2005 sampling season. See figure 2 for habitat descriptions.

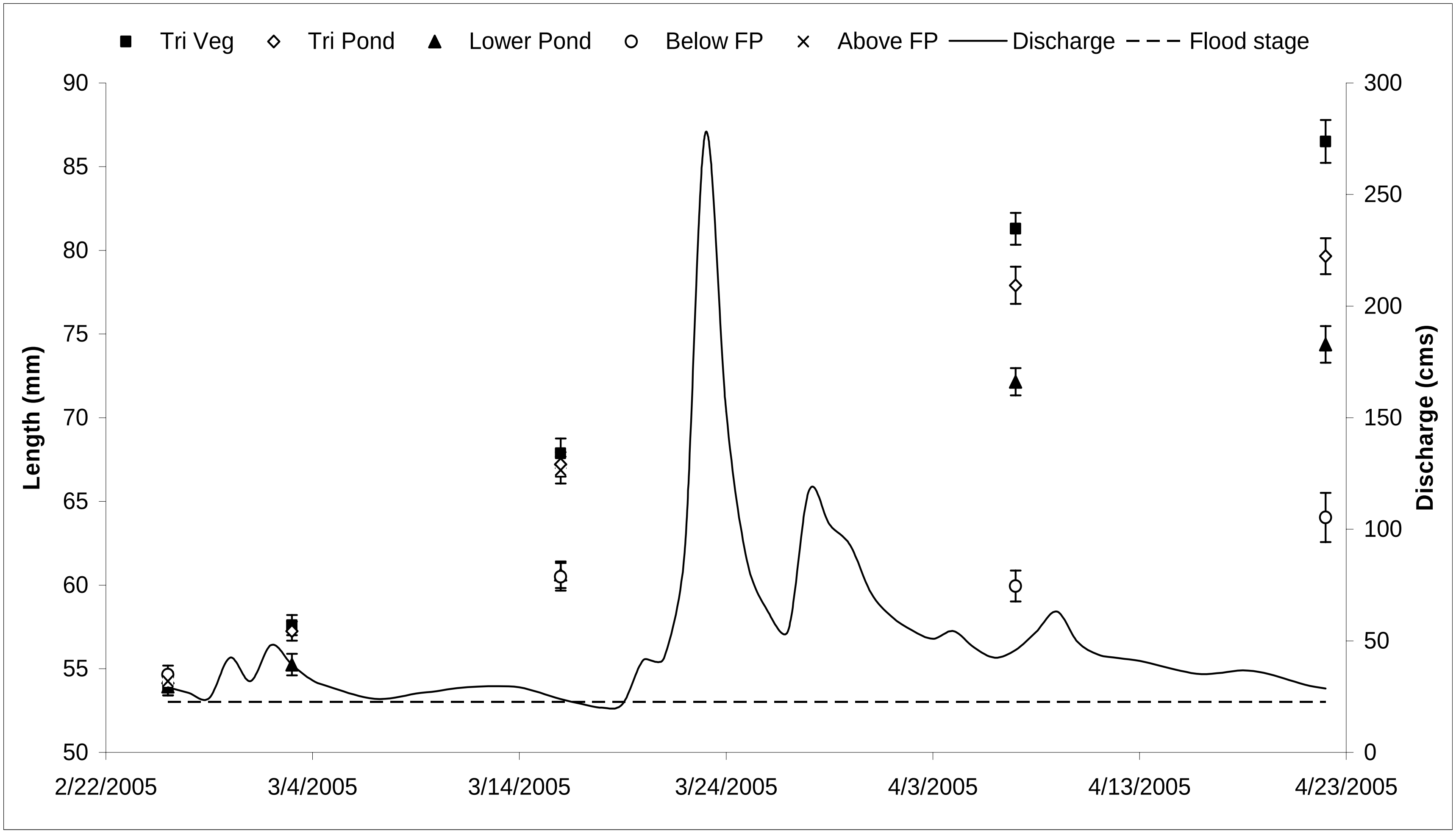
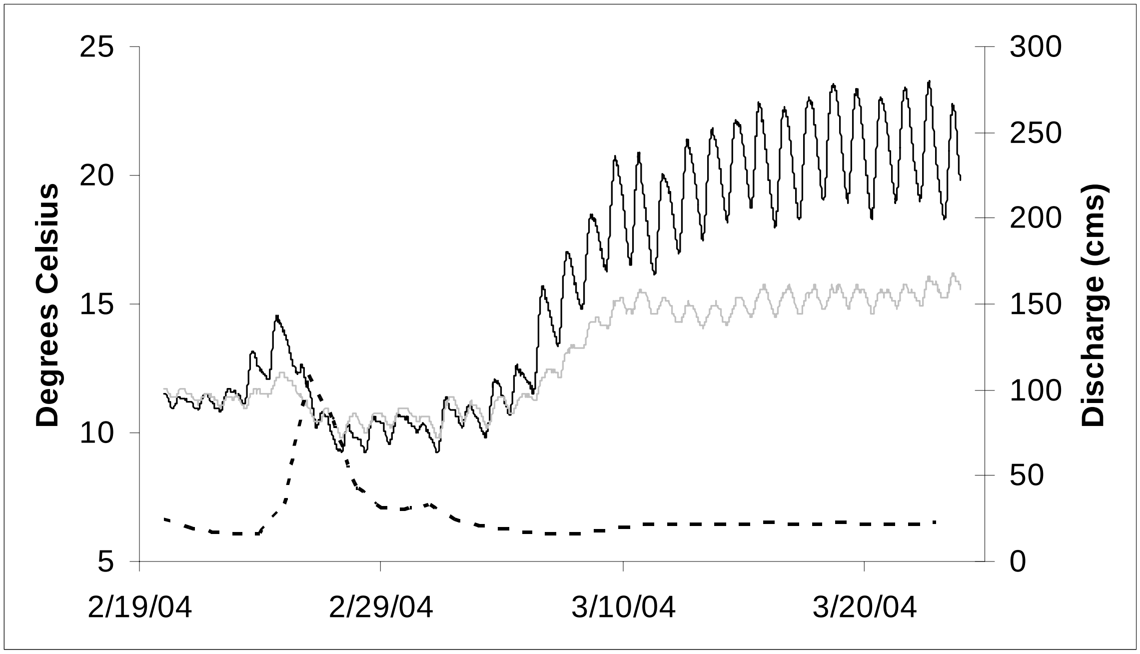


Figure 4. Water temperature of floodplain (dark line) and river (light line) in relation to river discharge (dashed line) in 2004 (a) and 2005 (b).

a)



b)

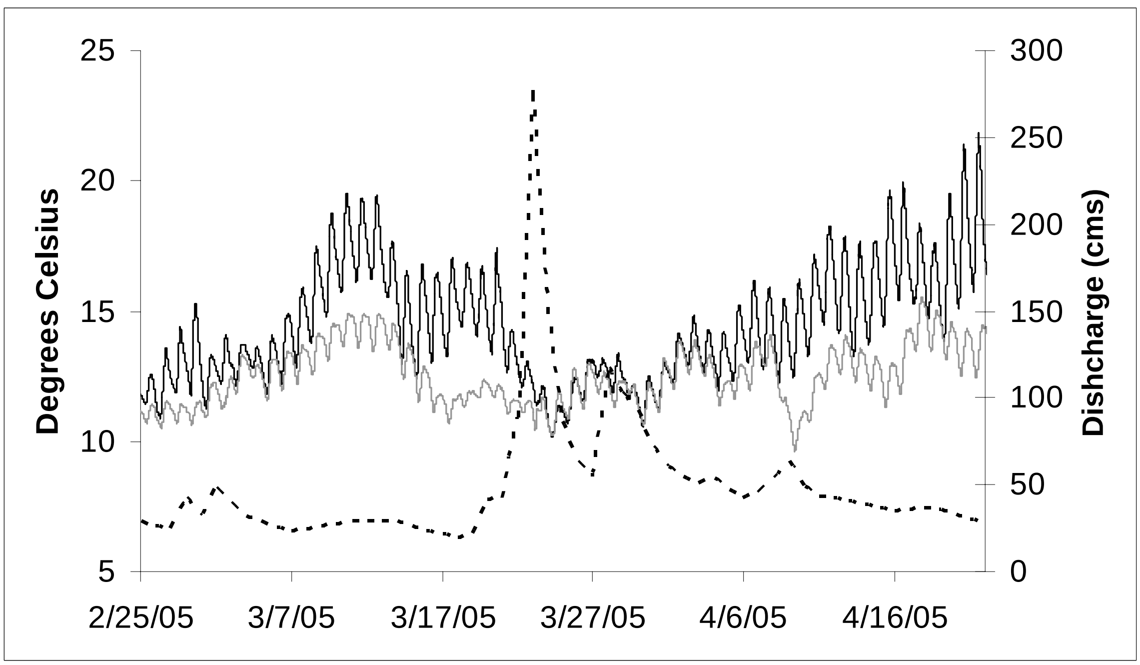


Figure 5. Length of juvenile salmon in various locations in 2004. Different letters denote significant differences in length (Tukey-Kramer HSD: $P<0.05$, $q=2.76$,). See figure 2 for habitat descriptions.

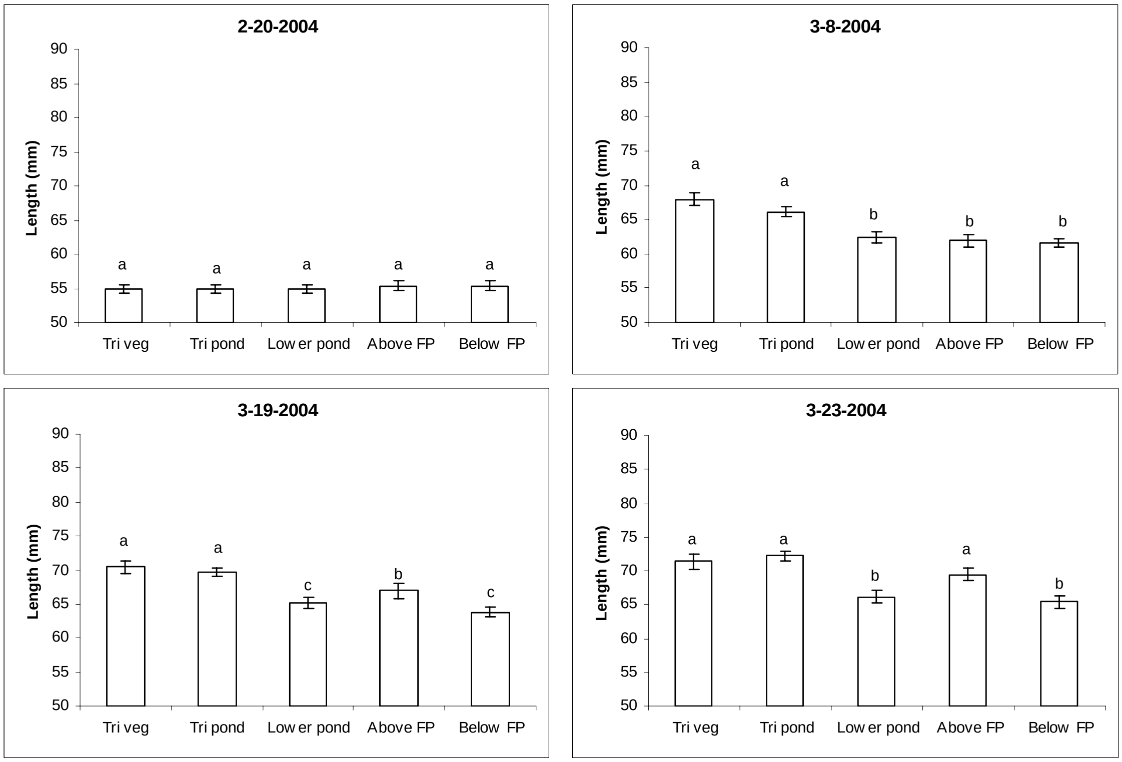


Figure 6. Length of juvenile salmon in various locations in 2005. Different letters denote significant differences in length (Tukey-Kramer HSD: P<0.05, q=2.59,). See figure 2 for habitat descriptions.

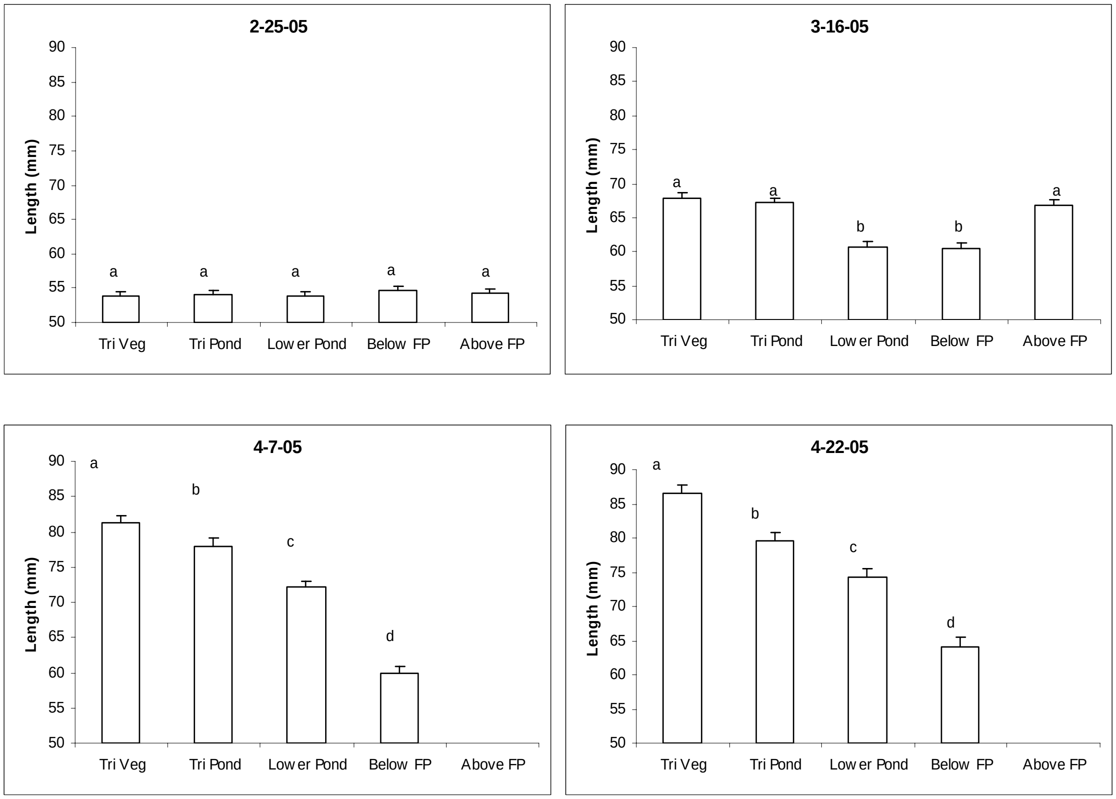


Figure 7. Comparison of a single cage of fish reared in intertidal river habitat below floodplain (left) and a single cage of fish reared in the triangle vegetation (right) after 54 days in respective habitats.

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