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"Physical Habitat Requirements for Adult Spawning and Juvenile Rearing Chinook Salmon in Tuolumne River"

Introduction

The Tuolumne River originates at an elevation of over 3,900 meters in the Sierra Nevada mountain range in Yosemite National Park. It drains an area of around 2,500 square kilometers into the San Joaquin River of the Central Valley and is home to a large population of anadromous Chinook salmon, *Oncorhynchus tshawytscha* (Kondolf et al. 1996). A series of dams built since the early 20th century have caused many changes to the instream habitat and cut off access to more than 90 hectares of native salmonid spawning habitat (McLain 2010). Since then, adult salmon have been forced to spawn in lower reaches of the Tuolumne River, and juveniles have been forced to rear in human-altered watersheds. Efforts to restore spawning grounds of these fish have been only marginally successful due to the inability to replicate natural geomorphic conditions on which spawning salmon rely (Kondolf et al. 1996). Understanding the spawning and juvenile habitat requirements of the Chinook salmon is necessary to maintain and restore healthy populations in the Tuolumne River.

Chinook Salmon Spawning History

Chinook salmon spring and fall spawning habitat has been heavily altered since dams were built on the Tuolumne River in the early 1900's. Historically, spring-run salmon migrated upstream in the high flows of snowmelt and remained in the high tributaries throughout the summer until they spawned in the fall (Kondolf et al. 1996). Fall-run salmon made the journey upstream in the fall and spawned between October and December (Moir and Pasternack 2008). Both spring- and fall-run juveniles appeared in early spring and grew to be smolts before they migrated downstream between the months of April and June. The construction of Don Pedro Reservoir in 1923 extirpated spring-run salmon from the Tuolumne River by increasing water temperatures and creating a physical barrier preventing salmon from migrating upstream (Kondolf et al. 1996). Dams and reservoirs have also dramatically reduced fall-run salmon populations by as much as 70% of 1945 population levels (Kondolf et al. 1996). Not only do the dams provide a physical obstacle for the fish, but they also create relatively warm-watered reservoirs that confuse seaward-migrating smolts and give predators, such as largemouth and smallmouth bass, a greater opportunity to feed on them. Historical Chinook habitat has been heavily altered, and now salmon must adapt to spawn in a dam-controlled novel river ecosystem.

Chinook Salmon Spawning Habitat

Habitat conditions where Chinook salmon choose to spawn generally include low order streams that are wide and shallow with riparian vegetation growing close to the riverbanks. Appropriate habitat complexity created by woody debris and riffle-pool sequences is necessary to reduce the social and environmental energy costs that may influence spawning success (Zeug et al. 2014). Ideal spawning areas are located where there are cold water temperatures and low instream vegetation. Chinook salmon typically choose to spawn in areas on the boundaries of different geomorphic structures like riffle-pool and riffle-run sequences (Zeug et al. 2014).

Spawning salmon have very specific velocity and depth requirements for where they build redds or nests. They typically prefer moderate water velocities ranging between 0.46-1.32 m/s (Moir and Pasternack 2008). These velocities are usually found in lateral bars, riffles, and riffle entrances and are essential to introduce oxygen into the sediment where salmon eggs are laid (McLain 2010). Similarly, salmon require a specific range of water depth for spawning, typically, 0.6 meters or shallower (Moir and Pasternack 2008). They seek out parts of a stream that have high width-to-depth ratios and commonly lay their eggs near the river edge or at a riffle entrance (Kondolf et al. 1996).

The sediment that salmon use to make redds is gravel-sized (6-102mm, D_{50}=24mm) and must be relatively stable, or not moved by flood events with a 1-2 year recurrence interval (Zeug et al. 2014). For this reason, the salmon usually spawn away from the thalweg where sediment transport and high flows are more common. Chinook salmon can only move sediment smaller than 10% of its body length (Kondolf 2000). Therefore, spawning reaches with relatively smaller substrates tend to support more redds since a higher proportion of spawning fish can move the substrate (Zeug et al. 2014). Although spawning salmon prefer a specific range of sediment sizes, there needs to be some heterogeneity of sediment size in spawning areas. As habitat restoration efforts have shown, salmon do not prefer a uniform distribution of gravel sizes, even if the gravel size is the appropriate spawning size (Kondolf et al. 1996). There needs to be enough sediment heterogeneity so that a diverse population of macroinvertebrates and primary producers can exist. If the gravel is too small, then salmon egg survival may be low if appropriate oxygen and temperature levels are not maintained due to low redd permeability (Zeug et al. 2014). Conversely, if the gravel is too large, then spawning salmon may not be able to move the substrate to build a high quality redd, resulting in shallow redds at risk of being scoured (Zeug et al. 2014).

Chinook salmon also need reaches of a river with high dissolved oxygen levels to spawn. Oxygen enters the water by physical aeration in riffles or rapids that absorbs the oxygen from the atmosphere and transfers it into the water (Moir and Pasternack 2008). Dissolved oxygen is also generated from some primary producers in the water via photosynthesis (Kondolf et al. 1996). Optimal dissolved oxygen level for spawning is 76% oxygen saturation at 16˚C, with a rapidly increasing demand for oxygen as temperature rises (Moir and Pasternack 2008).

Chinook Salmon Rearing Habitat

The general channel conditions required for juvenile Chinook salmon consist of a diverse stream reach with deep pools where there is abundant supply of benthic invertebrates (Williamson and May 2005). These anadromous fish rely on riparian floodplains to provide insects, shade, and refuge from predation during their younger years (Goertler et al. 2016). Dominant juveniles will reside near the bottom of pools where there is plenty of food, while non-dominant salmon will occupy the upper water of the pools or the pool margins where they can find cover essential for their survival (Williamson and May 2005).

Juvenile salmon require very different velocity conditions for rearing habitat than adult spawning salmon. Young fish need fairly low water velocities in pools to rear successfully (Williamson and May 2005). It has been observed that juvenile salmon rearing in slow and warm off-channel habitats generally grow at a higher rate than juveniles in fast and cool habitats (Jeffres et al. 2008). As underyearlings grow older, they occupy waters with increasing velocities and more variable flows (Williamson and May 2005).

Juvenile Chinook rear in freshwater pool habitat consisting of silty or sandy sediment (Williamson and May 2005). Floodplains are a depositional sink where small grains fall out of the water column as water velocity decreases (Jeffres et al. 2008). Sediment beds filter excess nutrients and chemicals in the water, increasing the water quality and reducing the effect of turbidity on juvenile Chinook (Lowe et al. 2015).

Dissolved oxygen content is highly variable in deep channel floodplain areas where juvenile salmon live. Oxygen enters the stream through photosynthesis by water plants and atmospheric diffusion by waves and wind (Goertler et al. 2016). Levels of dissolved oxygen vary seasonally with low levels in late summer months due to high temperatures and high levels in winter months due to colder temperatures (Goertler et al. 2016).

Salmon Habitat Restoration Efforts

Salmon spawning habitat restoration projects attempt to create areas with the specific physical characteristics needed for reproduction, but few have actually increased salmon spawning rates (Kondolf et al. 1996). It is relatively manageable to construct a river reach with the acceptable gravel size, river width, and water depth that Chinook need to spawn, but many projects fail because there are other important factors that impact redd selection (Kondolf et al. 1996). Researchers have found that incorporating friction slope into their considerations for spawning habitat restoration significantly increases the success rate of the project (Hauer et al. 2015).

In a study conducted in Western Norway on Atlantic Chinook salmon, researchers placed gravel into five historical spawning locations along a river in order to increase redd counts. In their findings, flux in friction slope proved to be the best predictor of redd formation; friction slope is a combination of flow velocity, Manning's roughness, and hydraulic radius, rather than just a single variable (Hauer et al. 2015). Essentially, spawning preference was highest among heterogeneous areas that were morphologically dynamic. At riffle entrances, water velocity rapidly increases, depth decreases, sediment size increases, and channel habitat fluctuates, thus creating good spawning conditions. Non-uniformity in sediment beds is also crucial for a successful salmon habitat restoration.

In a different project to restore rearing habitat for Chinook salmon in the Trinity River, researchers found that increasing both habitat quality and quantity was most optimal for increased rearing rates (Beechie et al. 2015). They quantified three alternative scenarios to increase salmon rearing consisting of increased habitat quality, increased habitat quantity, and increased both habitat quality and quantity (Beechie et al. 2015). To increase habitat quality, Beechie and his team constructed alcoves and created natural wood additions to the instream habitat. To increase habitat quantity, they increased sinuosity and side-channel length of a different stretch of river. They concluded that a combination of both habitat quality and quantity more than doubled the success of rearing salmon compared to the alternatives with just one variable increased (Beechie et al. 2015). Habitat complexity can be even more important than habitat availability for rearing Chinook salmon (Williamson and May 2005).

Restoration efforts have the potential to be successful in increasing salmon spawning rates. However, all important physical factors of spawning including velocity, depth, sediment, dissolved oxygen, channel habitat, and especially variable sediment beds must be considered to give projects the best chance at success.

Conclusion

Chinook salmon have specific requirements for spawning and rearing. Spawning salmon need low order streams with moderate velocity, low depth, coarse gravel sediment, and high dissolved oxygen levels. Rearing juvenile salmon need complex floodplain habitats with low water velocity, moderate depth, fine sediment, and moderate dissolved oxygen levels to grow into smolts and migrate to the ocean. In both cases, non-uniformity of physical conditions is crucial for productive Chinook salmon habitat. Utilizing these factors in restoration projects is important to rebuild lost spawning and rearing habitat as a result of dams or other human activity.

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