Steelhead Persistence and Adaptation in a Warming World

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With a geographic range that once extended as far south as Baja, California, the broadest range of life histories and highest thermal tolerance of any Pacific salmon, *Oncorhynchus mykiss* is arguably the most diverse and adaptable of the six Pacific salmon species (*Oncorhynchus spp.*) native to the U.S. As climate change progresses and aquatic environments adjust, the ecological and genetic diversity of steelhead will likely prove decisive in facilitating this species' persistence. Like other salmon, they excel at colonizing newly created habitat and adapting locally to complicated dynamics. However, 11 out of 14 populations of steelhead on the West Coast are already listed as threatened or endangered under the Endangered Species Act, and thus additional stress from climate change poses a more ominous challenge. How will steelhead respond to climate change? Our discussion complements a recent review of ocean stages by Kate Myers and Nate Mantua ("Climate Change and Ocean Ecology of Northwest Steelhead," *The Osprey*, May 2013); we here focus on climate impacts and responses expected in freshwater life stages.

> ***Rising temperatures are the greatest risk for fish populations that already experience near-lethal summer temperatures.***

Projected Climate-Induced Changes in Freshwater Habitats

Rising year-round temperatures and shifts in hydrological regimes are the major climatic changes to freshwater that will impact salmon life history and individual fitness in the coming decades. Under a business-as-usual carbon emissions scenario, air temperatures in the Pacific Northwest are expected to rise 2.3-9.2°F in winter and 3.4-9.4°F in summer within the next 50 years. Water temperatures will likely warm at about 80% of the rate of air temperature. Reduced snowpack at higher elevations will also produce an earlier and smaller spring freshet. Changes in precipitation are far less certain, and variability in historical precipitation has always been very high, extending the time horizon further into the future when mean changes due to climate change will be detectable.

Nonetheless, many climate models project more extreme storm events in the cool season, while drier summers become the norm. Increased winter flooding and summer drought may thus pose increasing threats to salmon freshwater stages.

How will these physical changes affect steelhead? Rising temperatures present the greatest direct risk for populations that already experience near-lethal summer temperatures. These include steelhead in warmer streams in California, southern Columbia and Snake Rivers, and western Oregon. High temperatures limit survival of adult migrants, especially those that migrate long before spawning, "summer-run" fish, and juveniles that typically spend one or more summers in freshwater.

More than other salmon, adult steelhead in the Columbia River use cool tributaries as thermal refugia along their migration route. In general, the more time they spend in these refugia, the lower their survival. Seeking headwater tributaries in Idaho, however, is also associated with lower survival. The primary reason thought to explain these observations is that steelhead concentrated in smaller refugia or tributaries become more vulnerable to harvest. Importantly, even catch-and-release fishing causes far higher mortality for salmon in warm conditions, and females are more likely to die after handling than males.

Exposure to high water temperatures and low flow is often punctuated by disease outbreaks, which can lead to dramatic fish kills. In 2002, roughly 70,000 Chinook salmon died in the Klamath Basin when gill rot disease flourished. The warm temperatures

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and low flows caused by the combination of a drought year and human water diversion provided perfect conditions for the disease to spread quickly and reach epidemic status. Warming can increase virulence of a variety of diseases by accelerating population growth rates and movement of disease agents. Disease transmission among fish also increases when fish are tightly concentrated into limited pools. Furthermore, salmon immune systems are compromised by thermal stress. Thus high temperatures and close concentrations of salmon are very strong predictors of high mortality.

Sub-lethal temperatures are just as important as lethal temperatures in shaping population response to climate change. Exposure of adults to sub-lethal temperatures during migration may impair egg viability, either through reduced egg provisioning or direct thermal stress in utero. Developmental temperatures can affect skeletal and muscle morphology, as well as fin position. However, the influence of temperature on rates of growth and development is perhaps most important of all.

Metabolic rates increase exponentially as temperatures rise, affecting development and energy balance at all life stages. For example, in warmer water, fry emerge earlier and smaller, with smaller yolk reserves. These smaller reserves increase the urgency of switching to an external food supply in early winter or spring. Historically, natural selection has favored emergence timing that matches the availability of food, leading to highly population-specific spawn timing. Changes in thermal regimes will alter both of these processes, potentially resulting in a mismatch between fish needs and prey availability. This in turn will direct pressure on and possibly drive evolution in spawn timing.

Once they reach the juvenile stage, growth rates have an optimum temperature that reflects the trade-off between increased food consumption and the acceleration of metabolic rates at warmer temperatures. At warmer temperatures, food is usually more abundant; however, prey quality can also decline, and fish need more food to sustain minimum functioning. The optimal temperature for growth is therefore higher in very productive environments with few fish and lower in more nutrient-poor environments with higher density. Thus, a web of interactions affects juvenile steelhead physiology.

Winter water temperature also has important ramifications. Food is scarce in winter, placing a priority on minimizing energetic expenses over prey capture. Shorter, warmer winters could bring higher energetic costs and higher mortality. Come spring, juvenile steelhead "determine" whether and when to smolt, based in large part on growth rates and lipid reserves. If juveniles grow quickly enough to lower their mortality risk in the ocean, but not so quickly that conditions in freshwater favor skipping the ocean stage altogether, they will smolt.

Salmon are carried downstream by the spring freshet during their juvenile migration, and lower flows (resulting from reduced snow accumulation over winter) typically lead to lower smolt survival. Migration timing also plays an important role in smolt survival, and will likely advance earlier in the year with warmer, smaller and earlier spring flows. Ocean arrival timing profoundly influences marine survival; however, it is not clear whether changes in ocean conditions will shift the optimal arrival time.

In mid-elevation basins, peak flows might shift from spring to winter, with potential effects on egg survival, growth, and migration timing. More intense storms in fall and winter are likely and would result in floods of greater magnitude and frequency during these seasons. These drivers are expected to negatively influence fall-spawning salmon and trout. However, rainbow trout and steelhead might be better suited for this hydrological regime because they spawn after winter flooding. The effects on adult migration might be population-specific, with access to spawning areas dependent on migration timing that is appropriately matched to adequate flows for passing over physical barriers. In some cases, the current migration timing might be less successful due to the new combination of thermal stress during migration, low flows, and winter flooding. However, these consequences are highly site specific.

In sum, most projections indicate that salmon habitat will decline with climate changes anticipated during the 21st century, although *O. mykiss* suffers less than other salmon because they spawn in the spring. Despite this general pattern of habitat decline across salmon species, growth will likely improve in some cases, such as warming of relatively cool habitat. Similarly, streams with low flows tend to improve with projections of increased fall and winter rain, although these projections are uncertain.

Negative effects of warming often appear in summer and winter, when consumption cannot compensate for increased metabolic demands. Reduced precipitation in summer exacerbates the risks posed by extremely low flows. Changes in growth rate also affect the timing of vulnerability to predators such as bass, which are size selective.

A specific analysis of vulnerability for Pacific Northwest steelhead found that populations in the southern part of the region face greater threats from temperature, while those in the interior and northern parts will likely confront substantial flow changes. Unfortunately, many populations that already face severe conservation challenges also face the greatest threats from climate change.

Anthropogenic Stressors

The direction of these impacts is similar to that of many anthropogenic effects already confronted by salmon populations. Many habitat modifications raise stream temperature, increase the intensity of flooding and reduce summer minimum flows. Loss of shading from riparian vegetation and interchange of flows between the channel and subsurface flows, for example, raise stream temperature. Water that transits through the ground is cooler and more consistent than water exposed directly to radiative heating.

Barriers, armoring, and incised channels all reduce connectivity between streams and their floodplain, limiting the natural ability to maintain diverse stream habitats that would otherwise

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provide refugia from high temperatures and flooding. Irrigation withdrawals exacerbate low flows, leaving some streams completely dry in summer.

Construction of dams and storage reservoirs for flow control and year-round power production has altered both the thermal and hydrological regime of regulated rivers. These effects are similar to climate change effects in some cases, but opposite in others. In the Columbia and Snake Rivers, freshets are much smaller and peak earlier in the year than would occur in a free-flowing river.

Reservoirs typically increase summer temperatures by lengthening the time for equilibration between water and air temperature, and increase transit time for smolts. However, some dams are managed to release water that is cooler in summer and warmer in winter than a free flowing river. Targeted releases of deep, cool water from stratified reservoirs such as Dworshak Reservoir in Idaho can lower temperatures in some reaches. These cases present opportunities for mitigating some effects of climate change.

Adapting to Climate Change: Plasticity and Genetic Change

In response to all of these environmental changes, organisms can alter their exposure or sensitivity to unfavorable conditions by changing behavioral or physiological traits. Phenotypic traits, such as migration timing or thermal tolerance vary in how "plastic" they are. Plastic traits change systematically with environmental conditions within the lifetime of an individual. This relationship is called a "reaction norm." Highly plastic traits that have shifted quickly in response to recent climatic changes include age at juvenile migration, growth rate, size at age, seasonal timing of adult migration and spawning, and fecundity.

Evolutionary adaptation, on the other hand, reflects selection acting on a trait, and occurs over generations. Thermal tolerance, for example, is strongly genetically determined, and will likely require strong selection in order to change. Nonetheless, *O. mykiss* contains genetic variability for this trait, as shown by rapid laboratory selection of rainbow trout with greatly enhanced heat tolerance. Similarly, developmental sensitivity to temperature is generally considered to have low plasticity, although exposure to warm temperatures during particular developmental windows has been shown to alter these responses in some fish. Like heat tolerance, developmental responses in *O. mykiss* have adapted locally to natural habitat heterogeneity using genetic variation that exists in many populations, and hence could theoretically evolve in response to climate change. In fact, many traits involved with juvenile growth and development, age at smolting and age at maturity have successfully adapted in less than 30 generations to new habitat after Chinook salmon were introduced in the southern hemisphere.

> *The complexities of climate change make it difficult to predict the rate of genetic response to a changing environment.*

Although historically, genetic adaptation to local environments clearly has occurred in nearly all traits, it is difficult to predict rates of response to future climate change because of the complex selection landscape in the wild. Many traits are tied together physiologically or temporally. For example, if you change migration timing, the subsequent life stage may face a total different set of conditions. Our predictive ability is further hampered because it is usually not possible to employ standard methods for demonstrating evolutionary change in response to recent climate change in salmonids, because we cannot directly compare modern and ancestral populations under the same conditions, nor can we usually identify the parentage of all individuals in a population. Nonetheless, some examples of genetic change have been shown in migration timing.

Serendipitously, several decades ago researchers in Auke Bay, Alaska inserted molecular markers into the genome of pink salmon to differentiate between early and late modes of a naturally migrating population. One marker specifically identified the late migrants, while neutral markers tracked levels of genetic drift in the population to separate natural selection from random processes.

Frequencies of these early vs. late migration markers have been independently monitored for both odd- and even-year populations of pink salmon since the 1970s. In both populations, the late-migration mode disappeared in the early 1990s, coincident with some unusually warm years in the stream. Loss of the molecular marker indicated that the entire late-migrant segment of the population had disappeared rather than their descendants having shifted to an earlier migration (a plastic response).

Migration timing, like most traits, incorporates both plastic and genetic components. In the Columbia River basin, steelhead, sockeye, and Chinook salmon have also shifted their migration timing since the 1950s. Most adult sockeye and spring/summer Chinook salmon stocks migrate prior to warm summer temperatures, and they now migrate earlier than in the 1950s. Conversely, many fall Chinook and steelhead stocks migrate after summer temperatures decrease, and they have shifted their migration date later in the year. Both responses allow fish to avoid peak temperatures in the mainstem, which now consistently hover over 20°C for much of the summer.

Later migration appears especially advantageous for steelhead adults because it reduces the bioenergetic cost of holding over the entire winter. This cost increases exponentially with temperature, so a difference of even 1°C in mean temperature entails loss of precious reserves that will not then be available for reproductive activity. In the Columbia River basin, these shifts are likely a plastic response to environmental cues used by individu-

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als to modulate their behavior, at least in part. However, evidence from an analysis of sockeye salmon migration survival suggests that selection may have acted on these populations as well.

Selection has acted by shifting the reaction norm for migration timing over the past 60 years. Steelhead and other salmonids have been well served by a combination of genetic and plastic responses that have allowed them to occupy diverse habitats and conditions. They can respond quickly to changes in the environment, but natural selection refines the response over time. Thus evolution and plasticity act together to shape the behaviors that support anadromy in Pacific salmon and that allow them to respond to a changing world.

However, populations must persist in order to adapt. A primary concern regarding modern climate change is that depressed populations may lack sufficient genetic variation to provide the raw material for rapid evolution. This would mean salmon populations are closer to going extinct in response to strong selection or chance events simply because they have a smaller starting point. Thus, a process that might have eventually produced a better-adapted phenotype could die out before it has time to spread within or among populations. Nonetheless, in natural populations, some traits have already adapted in response to recent climate change.

What Can We Do?

In summary, the major climatic change to the freshwater environment that will impact steelhead in the coming decades is rising temperature. Risk of increased mortality is greatest in summer, but shifts in flow regime may increase winter flows and storm intensities, resulting in decreased snowpack with an earlier spring freshet and lower minimum flows.

Despite the high adaptability and flexibility of steelhead, long histories of salmon abundance from the paleological record and historical documentation reveal large swings in population size over time. Not all of these fluctuations are climate-driven, nor do all populations respond similarly to a given climate. Nonetheless, many of these swings do correlate with major changes in climate, from regime shifts of the Pacific Decadal Oscillation to the Little Ice Age. Generally, warmer climates have been less favorable for salmon, demonstrating limits in the ability to compensate for climate change.

These impacts are similar in direction to many anthropogenic impacts already confronted by salmon. On the plus side, the similarity between anthropogenic and climate change impacts provides an advantage: restoration to mitigate anthropogenic impacts can also lessen many impacts of climate change. Tim Beechie and his colleagues have laid out a clear framework for conducting restoration to mitigate for climate change. Their guidelines for conservation prioritize restoring natural processes that keep waters cool and habitats diverse. Restoration of these processes will require maintenance of natural flow regimes, reconnection of streams with their floodplains, and expansion of riparian vegetation.

Like other salmon, adult steelhead can be most vulnerable when they seek thermal refuge in deep pools or headwater tributaries. Fish hold in these pools and are relatively easy to catch during such periods. Even if released after catch, steelhead and other salmonids experience high rates of mortality after handling. Thus, protection of thermal refugia in general and from fishing in particular is a key component of preserving a successful summer-run life cycle.

Steelhead face many challenges in the coming years as temperatures continue to rise, stream flows change, and humans demand more of limited freshwater. The odds of persistence for this species are enhanced by a natural ability to adapt to variable environments. However, to foster this resilience, we must ensure that populations remain abundant and that heterogeneous habitats remain accessible to the greatest extent possible.

Further reading

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Web Resources

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