Life history diversity emerges in salmonids repopulating tributaries of the undammed Elwha River

A fundamental concept in ecology is that diversity stabilizes natural systems. The world is an unpredictable place with opportunities and disasters scattered through space and time. Diversity is a way for natural systems to spread risk amidst this uncertainty – if functionally similar parts of a system do things in different times and places or respond differently to shared disturbances, then wholesale catastrophe is less likely. Unfortunately, human stressors tend to simplify biological systems, which undermines their stability.

Anadromous salmonids translate this idea into a real-world application. Salmonids run a gauntlet of habitats whose conditions change unpredictably – droughts happen, predators come and go, and plankton can bloom early or late. In the face of these hazards, populations express diverse life histories. For example, a juvenile cohort may swim to sea at different ages, and if one year's outmigration conditions are poor, this will only impact a portion of the cohort. In this way, diversity increases the chances that some juveniles will find a favorable path to adulthood. The result is reliable fish production, which is important to people and many other species that interact with salmonids.

Life history diversity is generated in large part by the landscape. Basic attributes such as temperature and flow regimes can vary tremendously within landscapes. Different species or life histories of salmonids are adapted to – or are generated by – these physical differences. For example, warm environments can accelerate metabolism and lead to faster incubation and growth compared to colder areas, and the physiology of various species may be better suited to some environments compared to others. Diverse parts of the landscape can thus create diverse assemblages of species and life histories that are nested across watersheds.

However, many human stressors erode this diversity. Habitat loss and simplification leads to watersheds that produce salmonids from similar environments and thus express similar life histories. Dams can prevent juveniles from rearing, or adults from holding, over summer by blocking access to cold, high elevation habitat. Ocean fisheries can select against older ages at maturity. Hatcheries are constrained by economies of scale that do not apply to nature and face an uphill battle to produce diverse fish. Ultimately, centuries of human stressors can erode diverse habitats and

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fish genes, which diminishes the reliability of formerly resilient fisheries. This can result in commercial fishery closures when unfavorable conditions occur.

Dam removal on the Elwha River therefore represents an exciting opportunity to understand how life history diversity can recover as human stressors are alleviated. My colleagues and I, in a collaboration among the Lower Elwha Klallam Tribe, Conservation Angler, and NOAA, recently published a paper called "Dam removal enables diverse juvenile life histories to emerge in threatened salmonids repopulating a heterogeneous landscape" that investigated this process. I will describe it here.

The Elwha River flows within the Olympic Peninsula in the northwest corner of Washington. As has been covered previously, dams without fish passage were built on its lower mainstem beginning in 1912 and removed beginning in 2012. Thus, for a century, anadromous fish could not access its tributaries, but that access is now restored. While not pristine, the forest landscape that surrounds the river is relatively undeveloped and located in Olympic National Park.

Two tributaries enter the Elwha River next to each other and provide very different physical environments. Indian Creek is warm and gently sloped while Little River is cool and steep. Their temperature differences are attributable to Indian Creek's lower maximum elevation, beaver activity, and upstream lake, in contrast to Little River's higher elevations and connections to snowmelt. In light of these environmental differences, we hypothesized that Indian Creek and Little River would support different salmonid species and life histories. This would be consistent with prior research that shows that the physical environment is often related to life history variation and species composition.

To test this hypothesis, we captured and quantified smolts as they emigrated from Indian Creek and Little River. From 2016-2021, we used screw traps to capture smolts so that we could identify, count, and measure the length of the fishes. Then we analyzed the data.

One difference between these tributaries was that Indian Creek produced juveniles that grew faster. Differences in growth were easiest to discern in juvenile Chinook salmon because nearly all of them emigrated in their first year and thus we knew that each individual's growth happened that year. At the Life history diversity was apparently generated by diverse physical conditions across the landscape. And, presumably, it enables the combined populations of the tributaries to spread risk – disasters and opportunities should befall the two tributaries' cohorts unevenly and thus catastrophe in both tributaries should be less likely.

beginning of April, which represents a middling emigration date, juvenile Chinook salmon from Indian Creek were ~53 mm while those from Little River were ~47 mm.

Another difference was that juveniles from Indian Creek emigrated earlier. For this analysis, we compared median annual emigration dates of species and age classes between the tributaries. We made comparisons for species and age classes for which numerous individuals were observed in the same year in both rivers. This led us to examine six total cohorts of age-0 Chinook and age-0 coho salmon. While accounting for effects of year and species, we found that juveniles emigrated from Indian Creek ~25 days earlier than Little River.

Finally, we found that species composition and age classes differed between Indian Creek and Little River. Both tributaries produced predominantly Chinook salmon, but Indian Creek produced proportionally more coho salmon and steelhead. Also, coho salmon and steelhead that emigrated from Indian Creek were generally older. A clear difference was that age-0 juveniles comprised almost 90% of the coho salmon that emigrated from Little River, but only about 50% of the juveniles that migrated from Indian Creek.

Uniquely, Indian Creek produced coho salmon that were quite large. Indeed, some

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Proportional composition of salmonid assemblage compared between Indian Creek and Little River for all years (left) and individual years (right).

individuals exceeded 200mm in length, roughly double the length of a typical conspecific. We assigned these juveniles to age 2, but without otolith or scale analyses to confirm, they may have been age-1 juveniles that grew remarkably fast.

To summarize, Indian Creek and Little River supported diverse salmonid life histories in the years immediately after dam removal. Life history diversity was apparently generated by diverse physical conditions across the landscape. And, presumably, it enables the combined populations of the tributaries to spread risk - disasters and opportunities should befall the two tributaries' cohorts unevenly and thus catastrophe in both tributaries should be less likely. While we have no pre-dam observations to compare to, it is likely that the general pattern of different environments giving rise to different salmonid life histories is a feature that the Elwha River system historically - and now presently - expresses. Likewise, we only examined salmonids in two of the Elwha River's tributaries, but we may expect similar diversity to emerge throughout the landscape's diverse habitat mosaic.

Looking forward, these results are promising in the context of other dam removals. In particular, dams were recently removed on the and opened vast expanses of previously



Juvenile Chinook salmon in Little River, a cold tributary to the Elwha River. Photo credit: John R. McMillan

blocked habitats to anadromous fish. Like the Elwha (and rivers generally), the Klamath River generates diverse physical environments that provide important fish habitat. As the restoration process unfolds, we may expect salmonids to repopulate its now-accessible upper landscape and express diverse life histories across the basin. Ideally, this will bolster the stability of its fishery amidst the many challenges posed by the Anthropocene.

Suggested reading

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Editors Note:

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