



Genetic insights into the past, present, and future of a keystone species

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In a new paper in PNAS, Thompson et al. (1) examine the genetic legacy of a struggling keystone species—and the implications for a phoenix-like recovery from its genetic remnants. For thousands of years before European contact, indigenous peoples of the Pacific Northwest of North America eagerly anticipated a critical spring event: the return migration of Chinook salmon (*Oncorhynchus tshawytscha*) into freshwater (Fig. 1). Early-migrating Chinook travel farther upstream than typical fall-migrating Chinook and are highly valued for their superior nutritional value and for providing an influx of protein and fat during a critical period (2). The importance of these salmon is highlighted by numerous traditional celebrations and ceremonies that mark their return. Colonizing Europeans also valued these early-returning salmon, which were heavily harvested, so much so that they began to show signs of depletion as early as the 1870s in the Columbia River (3, 4). Early-migrating Chinook also played an important role in terrestrial ecosystems by providing predators with longer access to salmon resources and transporting marine-derived nutrients farther upstream—and earlier (3). It is safe to say that these early-migrating salmon, or “spring Chinook,” were a keystone species for peoples and ecosystems.

However, this is no longer the case. Human activities, including extensive dam construction, fishing, and water diversion for agriculture, have caused widespread population declines and the loss of an estimated 54% of spring Chinook populations from the contiguous United States (5). In US endangered species legislation, spring Chinook populations are usually not considered separately from fall Chinook populations within the same watershed (6). In some watersheds, struggling spring Chinook populations are not listed because their fall counterparts are abundant. Spring Chinook spend much longer in freshwater than their fall counterparts, making them more vulnerable to anthropogenic habitat alteration, especially dams that limit habitat access and change downstream temperatures

and flow regimes (3, 6). In short, a keystone species has been extirpated from much of its range—but will its extirpation be forever?

In recent years, extensive effort has been put into Chinook salmon recovery: Dams are being removed, catches are carefully regulated, and water withdrawals are closely controlled. However, the recovery of spring Chinook following these efforts will depend critically on the biological basis for early migration. If migration timing is plastic (environmentally determined or behaviorally flexible), then recovery could be extremely rapid. If migration timing is genetic, then recovery could be much slower and dependent on particulars of its genetic basis, such as how many genes and what types of alleles are involved. Theory generally predicts that the simpler the genetic basis for a trait (e.g., two alleles at a single locus) the more rapid its evolution. Yet, this very property can be a double-edged sword for recovering populations; rapid evolution during the last few centuries of disturbance might have led to the loss of simple genetic variation necessary for recovery.

Genetic Control of Migration Timing

Recent research suggests that early migration in Chinook does indeed have a simple genetic basis, strongly influenced by the gene *GREB1L* (7, 8). Thompson et al. (1) advance our understanding of the role *GREB1L* in migration timing by collecting detailed phenotypic and genetic data, which confirm a robust association between *GREB1L* and migration timing. Furthermore, they show that heterozygotes exhibit intermediate summer migration timing that is unlikely to be maintained in fall-run populations.

Given these results, the potential for recovery of spring Chinook would benefit from an “evolutionary impact assessment”—how much genetic variation remains, where it is, and what are the implications for the probability and speed of recovery (6)? Thompson et al. (1) provide such an assessment for the Klamath watershed in Oregon and California, where the largest dam removal project ever (scheduled to begin in

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Fig. 1. Adult Chinook salmon spawning in freshwater. Adult salmon are sensitive to freshwater temperatures and spring Chinook are impacted by changes in temperature regimes downstream of dams.

2021) will restore access to historic spring Chinook habitats. The authors use current and historical samples, the latter from archeological excavations of indigenous fishing sites, to provide baseline assessments that inform the likelihood of restoration of former spring Chinook populations from nearby contemporary fall Chinook populations. First, they show that the contemporary association between *GREB1L* and migration timing was likely also present in historic Klamath spring-run populations. Second, they sampled fall Chinook from three contemporary Klamath populations and showed that the spring-run allele is currently found in all three populations: at very low frequencies in two populations (Shasta and Scott Rivers) and at higher frequencies in the river with the lowest abundances (Salmon River). The authors conclude that reevolution of spring Chinook from these fall Chinook populations and, by extension, others in the area, is unlikely. However, a recent survey of a broader geographic area (8) showed that the spring-run allele is much more common in some watersheds outside the Klamath basin, especially in parts of Oregon, Washington, and Idaho, potentially providing a source of spring-run alleles for recovery, either through natural colonization or recovery actions.

Conservation Controversy

Thompson et al. (1) present their findings as further evidence for a single evolutionary origin of the spring-run allele in Chinook salmon, a theory that has important implications for conservation (6, 9). Early genetic studies concluded that the spring-run phenotype arose repeatedly and independently in multiple

watersheds, because spring-run populations are more closely related to fall-run populations in the same watershed than to spring-run populations from other watersheds (10). Recent studies confirm that spring Chinook arose repeatedly but have argued that, because multiple spring-run populations share the same mutations of *GREB1L*, the spring-run allele likely arose a single time and was maintained in the standing genetic variation of ancestral Chinook salmon (7, 8). It follows that, if lost, the spring-run phenotype would be unlikely to reevolve, so conservation efforts to maintain the allele itself might be needed. How to incorporate such results into conservation work has been controversial, not least because of fears that policies based on single genes could fail to protect important variation at the organismal or population level (11). In a recent perspective, Waples and Lindley (6) argue that a realistic mechanism that could lead to the pattern described by the single origin theory is needed. Perhaps one analog might be the loss of armor plates in threespine stickleback (*Gasterosteus aculeatus*) upon freshwater colonization via selection for a single allele at the gene *EDA*. The majority of global freshwater stickleback populations (outside Japan) share the same *EDA* allele that seems to have evolved once and been maintained at low frequency in the marine metapopulation—rising to high frequency each time freshwater is colonized (12).

Ultimately, we cannot know whether extirpated spring Chinook populations will reevolve for several reasons. First, given the existing habitat, the loss of the spring-run phenotype could have been adaptive—and remain so into the future.

Thompson et al. (1) show that downstream of the dam in the Rogue River, the spring-run allele has been selected against. In an ideal world, dam removals would restore habitats that once again favor spring migration, but freshwater habitats face other stressors, including climate change. Second, the repeatability of evolution is unclear even in the absence of anthropogenic pressures. Recent reviews of parallel evolution have shown that our expectations should not be for perfectly parallel evolutionary outcomes (13). Third, we cannot know the exact selective regimes, phenotypes, or genetic architectures of the populations that gave rise to spring Chinook, or how they differ from current conditions. In marine stickleback populations, *EDA* heterozygotes exist at frequencies around 1%, which has facilitated repeated (12) and rapid (14) freshwater colonization. Except in the small population in the Salmon River, the *GREB1L* heterozygote frequencies sampled by Thompson et al. (1) were lower, at around 0.5%. The dam removals scheduled for the Klamath Basin will provide a fascinating test of the whether sufficient standing genetic variation exists in anthropogenically impacted Chinook populations to recover historical spring-run populations. This system has the potential to inform future restoration efforts, not only for salmon and dam removals but for other populations that have undergone anthropogenic evolution.

Rapid evolution in response to human activities has been previously demonstrated, including in salmon migration timing (3). Evolution of migration timing downstream of a dam led to loss of the valuable spring-run phenotype in the Rogue River Chinook Thompson et al. (1) studied, but it likely also facilitated their persistence in altered habitats. Viewed in this light, rapid evolution might be considered promising evidence that populations

can respond quickly to unintentional anthropogenic selection, even in relatively small populations. Similarly, in pink salmon (*Oncorhynchus gorbuscha*), evolution of migration timing in response to climate change has been determined to be genetic, at least in one population (15). In both cases, genetic change appears to have come at the cost of phenotypic variation, such that salmon migrate over a shorter window of time. Life-history diversity is part of the biocomplexity that promotes resilience in salmon (16). Loss of phenotypic variation could thus hinder their ability to respond to future stressors, anthropogenic or otherwise.

Thompson et al. (1) provide timely evidence for strong association of a single gene with an important life-history morph in response to anthropogenic pressures. In doing so, they have addressed several outstanding questions critical to Chinook salmon conservation (6). The results suggest that hopes for recovery of spring Chinook may rely on the evolutionary history of a single gene. How genetic studies that point to single genes with outsized effect should be incorporated into endangered species legislation is a current challenge for conservation scientists and policymakers (6, 11). Spring Chinook and *GREB1L* are at the forefront of this debate. Thus, the work of Thompson et al. (1) is relevant not only for a highly contentious conservation debate over salmon conservation, but also to legislation in the United States and beyond. Whether spring Chinook can, like a phoenix, reevolve from remnants remains to be seen.

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