Spring-run and fall-run Chinook salmon aren't as different as they seem

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Spring-run Chinook salmon, like these in Butte Creek, migrate from the ocean into freshwater early in the year and spend the summer in cool, deep pools near their spawning habitat before spawning in the fall. Credit: Allen Harthorn

Historically, spring-run and fall-run Chinook salmon have been

considered as separate subspecies, races, ecotypes, or even as separate species of fish. A new genetic analysis, however, shows that the timing of migration in Chinook salmon is determined entirely by differences in one short stretch of DNA in their genomes.

The new findings, published October 29 in *Science*, mean that within a drainage basin like the Klamath River, the different runs of Chinook salmon are all part of a single diverse population.

"It's like blue and brown eye color in humans—it just depends on what genotype you inherit from your parents," said corresponding author John Carlos Garza, adjunct professor of ocean sciences at UC Santa Cruz and a research geneticist with NOAA's Southwest Fisheries Science Center.

The study has profound implications for conservation and management of Chinook salmon, the largest species of salmon, and makes restoration of the beleaguered Klamath River spring run more feasible if plans for the removal of dams on the river move forward.

"We view this as very good news," Garza said.

Garza's team began by sequencing the complete genomes of 160 Chinook salmon from the Klamath River and Sacramento River drainages. The only consistent differences they found between spring-run and fall-run fish occurred within a single region on chromosome 28. Within that region, they identified a shorter "Region of Strongest Association" (RoSA) that occurs in two versions, "E" for early migration and "L" for late migration.

RoSA includes parts of two genes and the stretch of DNA between them. The E and L versions differ in multiple places, making them "haplotypes," the term for a set of DNA variations that are inherited together. Salmon, like all vertebrates, inherit two sets of chromosomes,

one from each parent, so their RoSA "genotype" can be either EE, LL, or EL.

Armed with genetic markers for the E and L haplotypes, the researchers sampled 502 Chinook salmon harvested by the Yurok Tribe in the Klamath River Estuary. For fish with the "homozygous" EE and LL genotypes, there was no overlap in the timing of migration, when the fish leave the ocean to swim up the Klamath and spawn. EE fish migrate early (spring run), and LL fish migrate later (fall run).

Fish with the "heterozygous" EL genotype had intermediate migration times, overlapping with those of the homozygous genotypes. The migration times of EL salmon were skewed toward the spring run, but some overlapped with fall-run salmon.

According to Garza, these results show that seasonal differences in migration are completely attributable to the RoSA genetic variants. "That was an extraordinary finding," he said. "I know of no other gene region that so completely determines a complex migratory behavior in the wild in a vertebrate."

This finding is especially striking because people have long noted differences between spring-run and fall-run salmon in their fat content and other features, which were presumed to be part of a suite of heritable traits characterizing the different runs. But in fact, Garza said, all those differences are tied to the timing of migration as determined by the RoSA genotype.

Spring-run salmon enter freshwater early in the year, where they encounter different environmental conditions, notably warmer water, which likely accelerates their maturation. The fish spend the summer in cool, deep pools near their spawning habitat before spawning in the fall.

"Spring-run and fall-run fish all start maturing at the same time in the ocean, but during that period after the spring run enters freshwater, they experience different environmental conditions, leading to differences in where and when they spawn," Garza said. "Also, people notice differences in fat content and body condition because they are encountering spring-run fish earlier in the maturation process than fall-run fish."

When the researchers sampled the carcasses of salmon that had died after spawning in the Salmon River, a major tributary of the Klamath, they found evidence that the spring-run and fall-run salmon were freely interbreeding. The ratios of EE, LL, and EL genotypes were close to what would be expected for random mating patterns. Garza noted that if two EL fish mate, their offspring will include EE, LL, and EL fish.

In other words, a spring-run salmon can have a fall-run sibling.

"It's hard to come up with any scenario where you could classify individuals from the same nest as belonging to different populations," he said. "For me, one of the underlying messages is that, in our attempt to categorize things, we've overlooked the fact that these are fundamentally the same animal."

The researchers extended their survey of post-spawning carcasses to rivers throughout northern California and the Siletz River in Oregon. Again, they found that heterozygous (EL) fish were widespread where early-migrating fish occur and suitable habitat for them exists.

The researchers also found that the RoSA haplotypes are the same in all the Chinook salmon lineages found in different rivers, indicating that they predate the evolution of genetically distinct lineages adapted to specific drainages along the coast.

"Those haplotypes are ancestrally the same everywhere, which is good news because it means that there are no variants related to the spring-run migration trait that have been lost with the extirpation of the historically abundant spring run in the upper Klamath River," Garza said.

Dams have blocked migrating salmon from the upper reaches of the Klamath River since 1912. Salmon lineages that used to spawn in the upper Klamath now stop at the Iron Gate Dam and spawn below there. The dams also reduced the cool-water habitat needed by spring-run salmon to survive during the summer, selecting against the EE and EL genotypes. But Garza's team found that Chinook salmon with the genetic traits for local adaptation to the upper Klamath still persist below the dam.

"It highlights the importance of taking those dams out, because descendants of the historic upper Klamath spring run are still there—they've just lost the E haplotype," Garza said. "Simple crossing with other populations in the Klamath to put the E haplotype back into the genetic background of upper Klamath Chinook salmon could restore that spring run."

More information: N.F. Thompson el al., "A complex phenotype in salmon controlled by a simple change in migratory timing," *Science* (2020). science.sciencemag.org/cgi/doi … 1126/science.aba9059

"Should I stay or should I go?" science.sciencemag.org/cgi/doi … 1126/science.abe9169

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