A cold-specialized icefish species underwent major genetic changes as it migrated to temperate waters, new study finds

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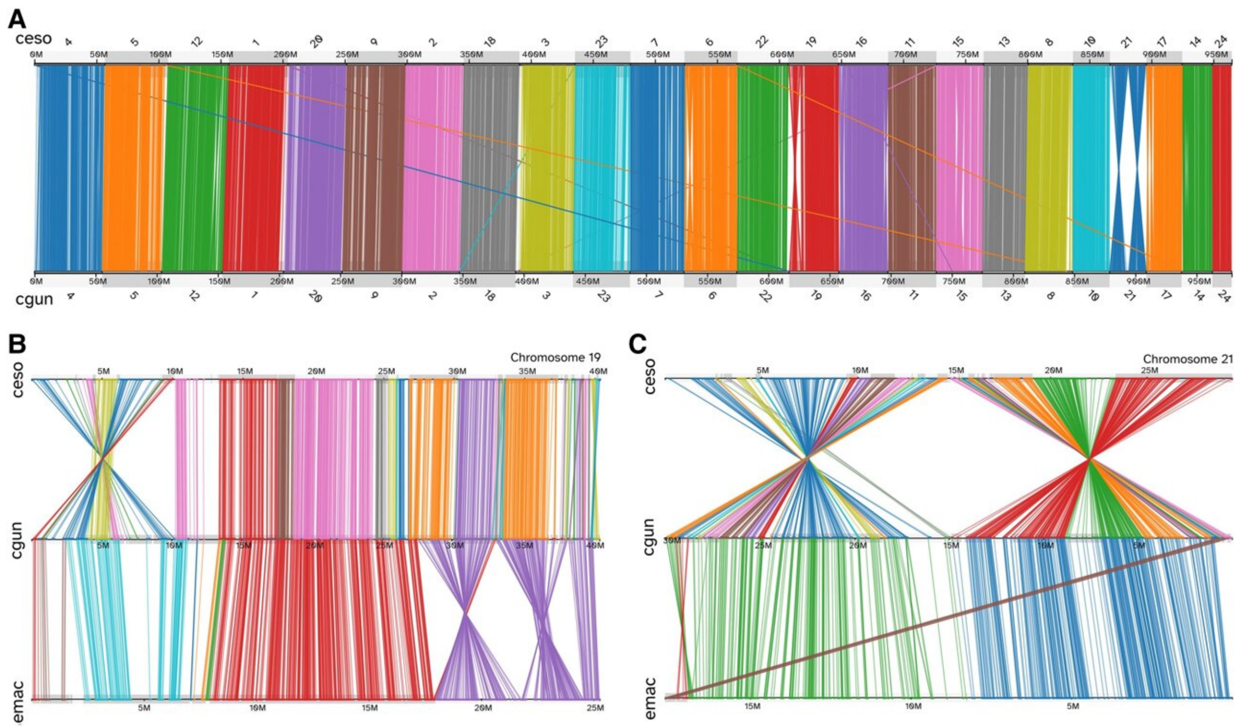

Patterns of conserved synteny between the genomes of temperate and Antarctic icefish species. Credit: *Molecular Biology and Evolution* (2023). DOI: 10.1093/molbev/msad029

Many animals have evolved to tolerate extreme environments, including being able to survive crushing pressures of ocean trenches, unforgiving heat of deserts, and limited oxygen high in the mountains. These animals are often highly specialized to live in these specific environments, limiting them from moving to new locations.

Yet, there are rare examples of species that once lived in harsh environments but have since colonized more temperate settings. Angel Rivera-Colón, a former graduate student now postdoc in the lab of Julian Catchen (CIS/GNDP), an associate professor in the department of Evolution, Ecology, and Behavior at the University of Illinois Urbana-Champaign, explores the genetic mechanisms underlying this anomaly in Antarctic Notothenioid fish.

Antarctic notothenioids, or cryonotothenioids, have evolved to live in freezing waters around Antarctica, where most fish would otherwise freeze solid if exposed to such cold temperatures. However, cryonotothenioid fish are able to survive in these waters due to antifreeze glycoproteins they produce in their cells. The AGFPs bind to any ice crystals that form, preventing them from growing and the cells from freezing.

Antarctic icefishes, a family within cryonotothenioids, are even more specialized to live in the icy waters. Icefishes also are the only vertebrate that has adapted to live without hemoglobin in their blood cells, causing their cells and tissues to be translucent/white in color. Hemoglobin is a protein in blood cells that helps increase oxygen uptake and results in the red coloration of cells. Normally animals need hemoglobin to get enough oxygen, but in the cold, oxygen-rich waters around Antarctica, icefishes have developed morphological changes, such as bigger hearts for pumping blood, that they no longer need hemoglobin to get enough oxygen.

Despite this extreme specialization, one species of icefish called Champsocephalus esox, or the pike icefish, has escaped Antarctica and now lives in warmer, less oxygenated, South American waters. "The movement of this species to warmer waters posed an interesting evolutionary mystery that I wanted to try to solve," Rivera-Colón said. "If you're specialized to only live in very cold environments, how do you survive and adapt to this new warmer environment?"

To understand how the genome of the fish changed as it migrated into warmer waters, Rivera-Colón compared the genetics of the pike icefish to that of an Antarctic species of icefish, C. gunnari. The team took tissue samples collected by collaborators and fishermen from southern Chile, South Georgia, and the Sandwich Islands to sequence the genomes.

"This is the first time we've looked at a genome of a notothenioid species that escaped Antarctica into this new temperate environment. A big part of that is because the pike icefish is very rare and elusive, so the help of these fishermen as well as collaborators for gathering samples was indispensable," Rivera-Colón said. The researchers used continuous long read sequencing to generate a chromosome-level genome for each fish species.

After comparing the genomes, they found that while the genome was highly conserved between the species, there was divergence in areas of the pike icefish genome associated with the physiology that would need to change as the fish moved to warmer waters. Surprisingly, the pike icefish genome still contained multiple copies of the gene that codes for AGFPs, but the genes were full of mutations that may render it non-functional.

"Most of the genes had stop codons inserted in," Catchen explained. "Assuming everything works as we'd expect, we wouldn't see them transcribed into AGFPs. But the genes are still there and presumably could still active. We're not sure." The researchers say that while mutations in this gene in cold water cryonotothenioids could spell death if the gene no longer works, in warmer waters the selection on this gene in pike icefish would've loosened, as the fish would no longer need to prevent themselves from freezing.

Researchers also found the pike icefish genome displayed chromosomal inversions—when part of the chromosome becomes flipped in orientation. "We know that inversions and other chromosomal changes can be very important for mediating adaptive processes as well as creating barriers between species," explained Rivera-Colón. "So finding them here suggests that they could be important for adaptation to the warmer environment in South America." Rivera-Colón further explained that inversions could make it more difficult for the two species to mix, speeding up speciation between the sister species, despite only splitting less than 2 million years ago.

In addition to evolving to live in warmer waters, the pike icefish would've also needed to adapt to a different light environment. The sea around the Antarctic is dark much of the year, and the surface ice blocks much of the light. But in temperate waters, pike icefish experience a more normal day-night cycle. The team is currently examining gene expression in related fish to see how their physiology and circadian rhythms have adapted to these new light cycles.

The researchers also plan to look at the genomes and mitochondria of another pair of related species, Trematomus borchgrevinki and Notothenia angustata. Similar to this study, T. borchgrevinki lives in the cold Antarctic waters, while N. angustata has secondarily transitioned to live in warm waters on the coast of New Zealand. The current study, as well as this planned study on the other species pair, will help researchers better understand how species highly specialized to live in certain environments can escape and adapt to new environments.

"I think one of the really interesting aspects of this study is that it challenges how we tell stories about 'why evolution acted the way it did,'" Catchen described. "We use the classic story of the icefish to explain loss of hemoglobin due to the cold, oxygenated waters it specializes in, but then you have this species that escaped back to normal temperatures and is managing fine. Selection pushed an organism to the extreme in this direction, and then the environment shifted, and now it's being pushed in a different direction."

Rivera-Colón added "Our study just goes to show that this specialization for extreme cold is not an evolutionary dead end, and it helps explain how these transitions happen in nature."

The study, titled "Genomics of secondarily temperate adaptation in the only non-Antarctic icefish," is published in *Molecular Biology & Evolution*.

More information: Angel G Rivera-Colón et al, Genomics of Secondarily Temperate Adaptation in the Only Non-Antarctic Icefish, *Molecular Biology and Evolution* (2023). DOI: 10.1093/molbev/msad029

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