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Mini-Review

Adaptive Radiation in Antarctic Notothenioids

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Abstract

With the formation of the Antarctic Polar Front 30-35 million years ago, the Antarctic notothenioids have undergone adaptive radiation in order to survive. Many of the traits were evolved with respect to their frigid, sub-zero environment. This paper explores the mechanisms currently used by the Notothenioidei to survive the frigid Antarctic waters. With climate change threatening to warm their formerly stable environment, the phenotype-environment correlation that has allowed them to dominate the Southern Ocean may become their downfall in a changing environment.

Keywords: Antarctic, Notothenioidei, Southern Ocean, Adaptive Radiation, Climate Change

All around the world, numerous species will need to adapt to changes in their environment as the effects of climate change, such as warmer temperatures, become increasingly apparent. Species that live in thermally stable environments, such as deep in the Southern Ocean near Antarctica, are vulnerable to minute changes in temperature and the rates at which they occur[1, 2]. The Antarctic Polar Front (APF), an oceanographic barrier running between 50°S and 60°S, has thermally and geographically isolated the Antarctic waters for 30 to 35 million years[3]. The APF has made the Antarctic waters a more constant, extreme, and isolated environment than the Arctic waters, which has led to distinct differences among the marine fauna[4]. Of the 25,000-28,000 fish species globally, there are only 322 recognized species of fish that live in the Southern Ocean, due to the extinction event caused by the formation of the APF[5, 6]. Of these, 101 species are from five of the eight families under the suborder Notothenioidei, and they compose 92% of the fish abundance in Antarctica[5, 6]. These bony, perch-like fish have undergone adaptive radiation in the Antarctic, where many distinct species with a common ancestor rapidly diversify to fill the ecological niches left by an extinction event[5, 7]. Another major component of adaptive radiation are the features a species develops as a result of interactions with their environment[7]. For the Notothenioidei, this is seen through the development of antifreeze glycoproteins, and the loss of various cells in blood, heat shock protein (HSP) expression, and swim bladder to survive in the sub-zero Antarctic environment.

The most revolutionary mechanism the Notothenioidei evolved is the creation of antifreeze glycoproteins (AFGPs), which prevents internalized ice by lowering internal freezing points[8, 9]. Ice enters the fish via ingestion or absorption through the skin, then internal AFGPs can adsorb to the ice crystals in the gastrointestinal tract and spleen, likely excreting the complex in the feces[6]. The hyposmolarity of the stomach, intestinal, and pancreatic fluids determines the difference between melting and freezing points, which, if large, indicates a large presence of AFGPs in the organs[8]. Many larval Notothenioidei do not have AFGPs, instead relying on physical barriers from undeveloped gills and intact outer layers to prevent ice crystals entering the body in the first place[10, 3]. The eight types of AFGPs are now known to be constantly synthesized in the exocrine pancreas at approximately three months post-hatching, evolving from a trypsinogen-like protease[11, 8, 3, 9]. AFGPs are crucial to survive in a subzero environment, but as water temperatures warm, they will eventually no longer be needed.

Another adaptation of the circulatory system is the absence of erythrocytes, myoglobin, and haemoglobin (Hb) in the most derived Notothenioidei family, Channichthyidae, or "icefish"[12, 13]. Channichthyidae compensate for this loss through increased blood volumes and larger hearts[14]. The other families within Notothenioidei have reduced levels of Hb with low oxygen affinities and reduced levels of erythrocytes[3, 13]. These are energy-saving changes required by the increased viscosity of blood at cold temperatures, and are feasible due to the high solubility of oxygen at low temperatures[3]. Most of the Notothenioidei are known to have reduced metabolisms and slower heart rates from the frigid environment, which would reduce their oxygen requirements, further enabling this adaptation[15, 13]. With the potential for climate change warming the waters and decreasing the oxygen solubility, the loss of oxygen-carrying blood cells would become detrimental. Antarctic fishes also have enzymes that are more efficient due to the flexibility of the proteins and membranes from changes in the intramolecular bonds at low temperatures[16, 17]. This would further aid in cold-adaptation at the cellular and tissue-levels.

In addition to losses within the circulatory system, most notothenioids do not see expression of HSPs[18]. HSPs were believed to have been lost from the notothenioids, Antarctic fish are now known to have retained these genes, and are unable to upregulate the gene in response to increased temperatures as they are extremely stenothermal, only being able to tolerate a very small range of temperatures, resulting from living in constant conditions[19]. The inability to respond to heat stress will be damaging with the imminent threat of climate change and its increasing temperatures. This is particularly documented in the emerald rockcod, *Trematomus bernacchii*, as this organism is highly acclimatized to its environment and is consequently under constant cold-stress, likely causing constant upregulation of the stress protein, hsp70[18, 19, 20]. In the non-Antarctic notothenioids, hsp70 is an inducible protein, typically seeing upregulation due to increases in temperature[19]. This protein assists in repairing thermally denatured proteins, and may be permanently activated in the Antarctic specimens in order to maintain appropriate protein levels due to cold denaturing the proteins, among other environmental stressors[19, 20].

Antarctic fishes also see adaptations to the environment at the tissue and organ level. All notothenioids have lost the swim bladder, a characteristic likely derived from their benthic ancestors[5, 6]. Some notothenioid species, for example the Antarctic silverfish, *Pleuragramma antarcticum*, have achieved neutral buoyancy in their role as secondarily derived pelagic sit-and-wait predators, eliminating the need for continuous uplift to stay in the suspended in the water column as an energy-conserving measure[21, 5, 6]. Neutral buoyancy is achieved in these species by high lipid contents, and reduced ossification[6]. Some species, for example *P. antarcticum*, have additional specializations for buoyancy, such as lipids sacs instead of adipose cells, reduced mineralization of scales, and the retention of larval characteristics, a feature which may also provide additional benefits such as camouflage in the pelagic environment[22, 21, 6]. As climate change causes sea ice and glaciers to melt, the ocean will experience a dilution effect, causing the water to become less dense, making neutral buoyancy challenging[1]. Other organ specializations in Notothenioidei, excluding the basal family Bovichtidae, are aglomerular kidneys, where the lack of capillaries likely evolved to prevent the loss of AFGPs through urine and to minimize the energetic costs of resynthesizing these glycoproteins[23]. Bovichtidae have a largely temperate distribution, with only one species in Antarctica[13]. They do not have AFGPs or aglomerular kidneys, which suggests that these are derived characters in the Antarctic notothenioids[23].

Given the unique Antarctic environment created by the APF, the Notothenioidei have had many diverse adaptations arise within the past 30 to 35 million years[3]. This suborder is a prime example of adaptive radiation, with the majority of the group rapidly diversifying and modifying its phenotype to survive in this extreme environment[23, 6]. However, with warmer water temperatures in the future, many of these once-crucial adaptations will become disadvantageous. The production of AFGPs will become unnecessary and a waste of energy, the loss of oxygen-carrying blood cells would become detrimental due to increased metabolisms and decreased oxygen solubility in warmer water, the inability to respond to heat shock would likely be lethal, and the loss of a swim bladder would be energetically inefficient with less dense water. When the Southern Ocean became hostile to most species with the formation of the AFP, the Notothenioidei rose to the challenge. When the effects of climate change hits, will the Notothenioidei be able to survive or will the ecosystem of Southern Ocean once again change drastically?

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