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Mini-Review

Physiological and Behavioural Adaptations of Arctic Fish to Their Aquatic Habitat

Émilie Ferguson[1]

[1]Clayton H. Riddell Faculty of Environment, Earth and Resources, University of Manitoba, Winnipeg, MB, R3T 2N2

Abstract

Arctic fish have evolved different physiological and behavioural mechanisms to survive the frigid waters of the Arctic Ocean. They synthesize antifreeze glycoproteins (AFGPs) that coat and inhibit the growth of ingested ice crystals and lower the freezing point of fish fluids. In addition, certain species of Arctic fish express different types of hemoglobins depending on the temperature of the water and oxygen availability. Some Arctic fish have also adapted anadromous life-history strategies to take advantage of the high summer primary productivity of the Arctic Ocean, and have modified their horizontal and vertical migration patterns based on the season. These physiological and behavioural adaptations have enabled Arctic fish to thrive in northern waters; however, the effect of climate change may induce further adaptations to their rapidly changing environment.

Keywords: Arctic, Cold Adaptation, Antifreeze Glycoproteins, Hemoglobin Multiplicity, Migration

Cold adaptations refer to physiological and behavioural changes that an organism has developed to survive in polar climates over evolutionary time[1]. Physiological changes occur when an organism alters its normal body functions to cope with environmental changes to maintain homeostasis. Organisms will alter their behaviour, the way they act in response to a stimulus, to ensure their survival. The Arctic Ocean is characterized by its extreme winters, wide range of temperatures that occur throughout the year[2,3], and high summer primary productivity[4]. Therefore, the ichthyofauna of the Arctic have developed cold adaptations that ensure their survival in the sub-zero and wide-ranging temperatures of the northern waters. Certain physiological adaptations such as, the presence of antifreeze glycoproteins in fish fluids[5] have allowed Arctic fish to cope with the freezing waters of the Arctic Ocean. For example, an average teleost fish will freeze at -0.8°C[5], but an Arctic fish can withstand water temperatures of -1.9°C[5]. Furthermore, some species have hemoglobin multiplicity[6], which enables fish to withstand the wide-ranging temperatures of the Arctic. Finally, some Arctic fish have developed anadromous life-history strategies and migratory patterns to take advantage of favourable ecological conditions[4,7]. Therefore, these behavioural adaptions have enabled these species to thrive and successfully reproduce.

Ice crystals can enter Arctic fish through their gills and intestinal tract[8], potentially damaging internal organs[9]. Therefore, they have developed antifreeze glycoproteins (AFGPs) to inhibit the growth of ice crystals in their systems[10]. AFGPs are synthesized in the liver and pancreas of fish and distributed in their blood and gastrointestinal fluids (Fig. 1)[9]. As ice crystals enter their body, they are coated with AFGPs, inhibiting ice crystal growth[11]. AFGPs are continuously recycled throughout the circulatory system and only excreted with feces (Fig. 1)[9]. Therefore, fish have a readily available supply of AFGPs to cope with the presence of ice crystals in their system.

AFGPs also lower the freezing point of the blood of Arctic fish due to their non-colligative properties[5]. This phenomenon is known as thermal hysteresis, which means that the freezing point of a substance is inferior to its melting point[10,5]. As AFGPs coat the surface of ice crystals, they lower the freezing point of the fish's blood and allow it to withstand waters with freezing temperatures. The winter flounder (*Pseudopleuronectes americanus*) is an example of a fish that was found to experience thermal hysteresis to cope with sub-zero water temperatures during the winter months[10]. In the winter, the freezing point of this species' serum is -1.37°C, and its melting point is -0.75°C[10].

AFGPs are a vital adaptation that have allowed Arctic fish to cope with the ingestion and formation of ice crystals within their system and prevent the freezing of their fluids. Recent studies have shown that there are five distinct antifreeze proteins (AFPs), namely ATGPs, Type I, Type II, Type III, and Type IV that are found in different species of fish[12,13]. These proteins have different structures and sequence compositions, but all have the same antifreeze functions[12]. Therefore, these proteins have convergently evolved the same antifreeze properties to survive freezing water temperatures.

Hemoglobin multiplicity has enabled Arctic fish to cope

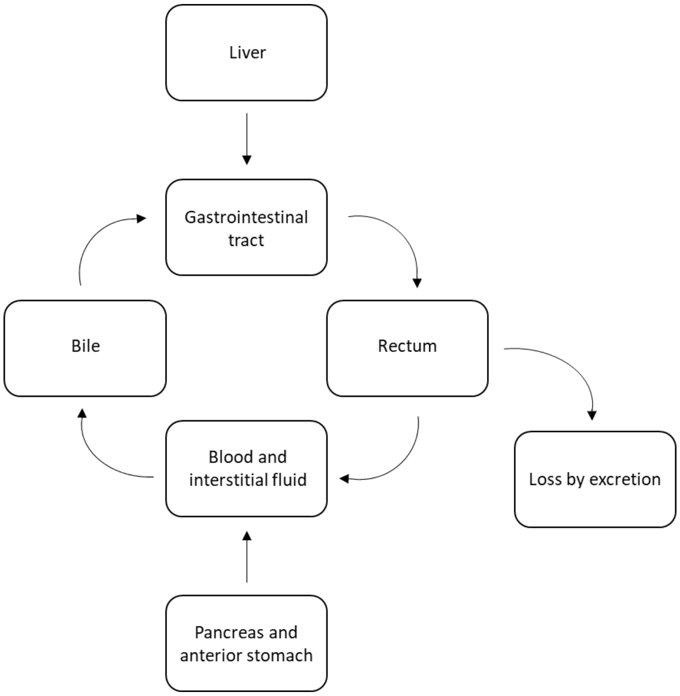

Figure 1: *Representation of antifreeze glycoprotein synthesis and recycling cycle in Arctic gadids (*Boreogadus saida*). The antifreeze glycoproteins are formed in the pancreas and liver. From the liver, they are released into the gastrointestinal tract. Those that are not excreted with the feces are resorbed by epithelial cells and transferred into the blood. Some are transferred into the bile and stored in the gall bladder, while others are released back into the gastrointestinal tract.*

with the wide-ranging temperatures of the Arctic Ocean[14]. Hemoglobins are proteins that are found in the blood of fish that increase the transportation of oxygen from the gills to the tissues[15, 6]. Hemoglobin multiplicity refers to the ability of hemoglobins to display different oxygen affinities depending on the temperature of the water[3]. For example, three major hemoglobins (Hb 1, Hb 2, and Hb 3) were found in the blood of the spotted wolffish *(Anarhichas minor)*[14], and three species of cods: the polar cod (*Arctogadus glacialis*); Arctic cod (*Boreogadus saida*); and the Atlantic cod (*Gadus morhua*)[6]. Hb 1 and 2 displayed a low Bohr effect, or low oxygen affinity, while Hb 3 displayed a high Bohr effect[14]. In other words, these species have the ability to acclimatize to waters with high and low concentrations of oxygen, and therefore waters of different temperatures.

Furthermore, hemoglobin multiplicity is often associated with fish that have a dynamic life-history[15]. For example, the Arctic charr (*Salvelinus alpinus*) and the Atlantic salmon (*Salmo salar*) are species that migrate to different tempered waters throughout their lives[4, 15]. Ten different hemoglobins were identified in the blood of the Arctic charr[16], whereas the Atlantic salmon is known to possess more hemoglobin genes than any other teleost[15]. Therefore, hemoglobin multiplicity has allowed these species to cope with the different levels of oxygen present in their migratory waters.

Arctic fish species have developed behavioural adaptations that allow them to best utilize the environmental conditions of the Arctic Ocean. For example, certain populations of Arctic charr have developed an anadromous life-history[17, 4], which means they migrate from salt water to freshwater to spawn. More specifically, they overwinter in northern freshwater lakes, migrate to the Arctic Ocean to feed in the nutrient rich waters during the spring and summer months, and then return to their freshwater habitat to spawn[4]. Arctic charr that have developed an anadromous life-history can grow to be more than 70 cm in length at maturity, while those that occupy freshwater year-round only measure up to 20 cm[4]. Hence, it is likely that the anadromous life-history strategy of the Arctic charr is advantageous because the ocean offers a richer supply of food than the freshwater habitat, which allows the fish to grow to larger sizes.

Furthermore, recent research has identified the horizontal and vertical movements of the migratory pattern of the Arctic charr[7]. They were found to occupy higher latitudes in the summer and fall months, than during the winter and spring[7]. The study also revealed that they mostly occupied surface waters during the winter and early spring, and deeper waters during the summer and fall[7]. It is likely that the migratory behaviour of the Arctic charr reflects its preferred water temperatures and the availability of nutrients in the water column.

Conclusion

Fish have adapted to the extreme winters and wide range of temperatures that characterize the Arctic Ocean. Physiological adaptations include the presence of antifreeze glycoproteins that allow fish to prevent the growth of ice crystals and lower the freezing point of their body fluids, and hemoglobin multiplicity, which allows fishes to cope with the fluctuating oxygen concentrations of different tempered waters. Behavioural adaptions include migratory strategies that allow the ichthyofauna to take advantage of the nutrient rich Arctic waters during the summer months, as well as horizontal and vertical displacements that allow them to best utilize their preferred aquatic environments. These adaptations have allowed species to survive and thrive in northern waters; however, with the warming climate Arctic fish may need to further adapt to their changing environment. The Arctic Ocean is experiencing warming temperatures and consequently, longer periods of stratification and lower levels of available oxygen[18]. In addition, marine species and boreal fish are expanding their distributional ranges[19, 20]. Therefore, the warming climate is disrupting normal ecological interactions[18], which will greatly influence population sizes and the overall health of Arctic fish species[18].

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