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ANTARCTIC FISHES

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Introduction

Antarctica is a continental land mass much of which is covered by an ice cap, consequently the ichthyofauna is totally marine. Surrounding the continent is the Southern Ocean, approximately 36 M km^2, continuous with the Atlantic, Indian, and Pacific Ocean basins to the north and whose northern limit is generally taken as the Antarctic Polar Frontal Zone (APFZ). There is a clear separation between the Antarctic and the Southern Hemisphere continents; the nearest connection being with South America via the Scotia Arc, a series of islands, separated from each other by deep water.

The Antarctic Circumpolar Current (ACC) and the general oceanographic regime mean that marine isotherms are more or less concentric around the continent. Close to the continent the seasonal variation in temperature is rarely more than 1°C whilst even at the northern limit, as for example at South Georgia, the range is little more than 4°C.

These two factors, geographical isolation and constant low temperature, have a major effect on Antarctic fish.

Fish Fauna

The Southern Ocean ichthyofauna is relatively sparse and unusual in composition, consisting of 213 species belonging to only 18 families (**Table 1, Figure 1**). Nearly half the species belong to one group, the perciform notothenioids, which make up 45% of the fish fauna. Restricting consideration to the shelf, and particularly in the highest latitudes, nototheniods make up 77% of the species and 90–95% of the biomass of fish. Notothenioids are morphologically and ecologically diverse and have diversified into a wide variety of niches, mainly demersal, but also in the water column and even within sea ice. As a group this makes them more diverse than, for example, the finches of the Galapagos Archipelago. The concept of species flocks has been developed for freshwater fish to identify groups that have a close affinity; typically such flocks are to be found in ancient lake systems and it is extremely unusual for such a flock to be identified from a large marine environment. Antarctic notothenioids with their high species diversity

Table 1 Composition of Southern Ocean ichthyofauna

Taxon	*Benthic*	*Benthopelagic*	*Pelagic*
Agnatha	2		
Chondrichthyes	8	2	1
Osteichthyes			
Notacanthiformes		2	
Anguilliformes		2	
Salmoniformes	4		5
Stomiiformes			12
Aulopiformes			9
Myctophiforms			35
Gadiformes	9	11	1
Ophidiiformes	1		1
Lophiiformes			3
Lampriformes			2
Beryciformes			6
Zeiformes		1	
Scorpaeniformes	32		
Perciformes			
Zoarcidei	22		
Notothenioidei	95		
Blennioidei	1		
Scombroidei			2
Stromateoidei			1
Pleuronectiformes	4		

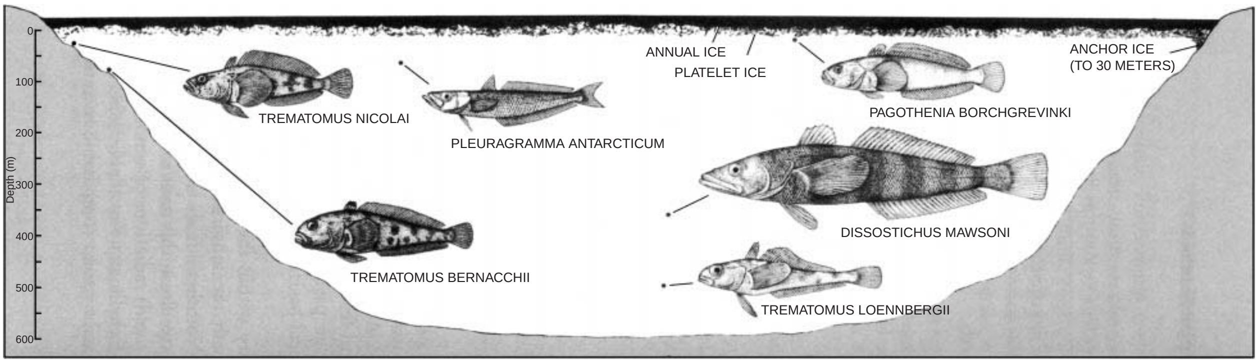

Figure 1 These six species from McMurdo Sound demonstrate some of the life history types included in the Nototheniidae. Pelagic, cryopelagic, epibenthic, and benthic species are illustrated. Dots indicate typical habitat, although most species have considerable depth ranges. (Modified from Eastman and DeVries (1986), copyright 1986 by Scientific American, Inc. All rights reserved.).

and endemism form a species flock comparable to that of Lake Baikal.

Adaptations

Cold Adaptation

Some of the earliest studies on the physiology of Antarctic fish concerned the measurement of oxygen uptake rates. Initially it had been assumed that, since many biochemical processes are temperature dependent, the metabolic rates of Antarctic fish might be very low. The initial experiments indicated that rates were substantially higher than those of temperate fish when studied at low temperature and the degree of elevation of the metabolic rate in Antarctic fish was attributed to a phenomenon termed ‘cold adaptation’. Subsequent studies demonstrated that the greater part of this elevation was caused by handling stress and the extended recovery time, of the order of 24 hours or more, following introduction into respirometers. In spite of this it is now accepted that some slight elevation of metabolic rate remains that cannot be explained wholly by experimental technique. Consideration of the phenomenon has raised some controversy between different workers. The existence of the phenomenon has been demonstrated experimentally, although it does not appear to confer any evolutionary advantage because it implies a higher energy requirement on the part of the fish. All these studies have been undertaken on whole fish; the overall oxygen uptake rate is the balance between all the component metabolic pathways that are present. As such it has been argued that the term ‘cold adaptation’ has little meaning and that it is more sensible to consider each component to provide an overall balance.

Antifreeze

Pure water freezes at 0°C, but the presence of salts causes the freezing point to be depressed such that normal sea water freezes at around $-1.85°\mathrm{C}$. At McMurdo Sound the annual mean water temperature is $-1.87°\mathrm{C}$ and varies within the range -1.40 to $-2.15°\mathrm{C}$. Body fluids, such as the blood plasma, of most teleost fish, have a freezing point of around $-0.7°\mathrm{C}$. Even though this difference is small it is important. Living in waters close to the freezing point of sea water Antarctic fish require some mechanism to prevent their body fluids from freezing.

In the absence of ice, fish could live in a supercooled state. Unfortunately this is not a stable state and some alternative adaptation is required. The ionic concentration of the blood of most marine teleosts is $320\text{–}380\,\mathrm{mOsm\,kg^{-1}}$, only about one third of that of Antarctic sea water ($1050\,\mathrm{mOsm\,kg^{-1}}$). The freezing point depression of some notothenioids at McMurdo Sound is $-2.2°\mathrm{C}$, although their blood osmolality is $550\text{–}625\,\mathrm{mOsm\,kg^{-1}}$, equivalent to a freezing point depression of -1.02 to $-1.16°\mathrm{C}$. Thus although there appears to be some compensation as measured by the osmolality it is insufficient to explain all of the depression in freezing point. Compensation for this difference comes in the form of antifreeze glycopeptides (AFGP) which exert their effect by a mechanism known as adsorption-inhibition (**Figures 2** and **3**). Even though ice crystals can form, their further growth is prevented when AFGPs are adsorbed onto them because the AFGP molecule prevents growth of the ice crystal along its main axis. Thus the AFGPs have exerted an antifreeze function. By this means the freezing point is lowered beyond that which would be expected

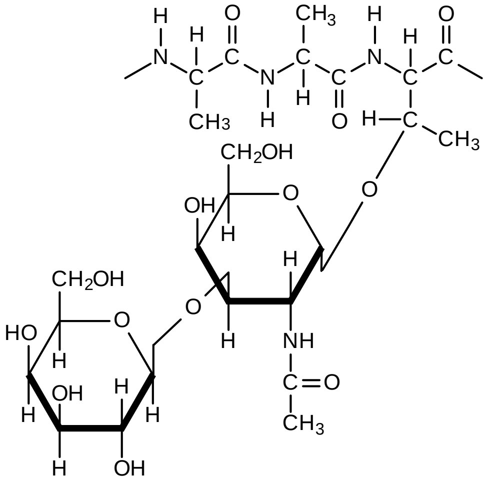

Figure 2 Basic repeating structural unit of the antifreeze glycopeptides (AFGPs) of notothenoids. The peptide consists of amino acids in the sequence [alanyl-alanyl-threonine]$_n$. Each threonine is joined to a disaccharide through a glycosidic linkage. In low molecular weight AFGPs 6–8, proline is periodically substituted for alanine at position one of the tripeptide. (Reproduced with permission from Eastman JT (1993) *Antarctic Fish Biology*, Academic Press.)

from the osmolality but not by reference to the melting point.

The AFGP molecules are of such a size that they would be lost through the glomeruli of normal teleost kidneys. In glomerular nephrons of normal teleosts molecules with a molecular weight of $< 68\,000$ Da pass through the filtration barrier. As the urine passes through the different parts of the nephron it is modified by reabsorption of nonwaste products and secretion of waste products. The AFGP molecules are of such a size that they would pass through the glomeruli but would need to be reabsorbed later on in the nephron. The kidneys of all Antarctic fish which possess AFGPs are aglomerular, obviating this requirement. Thus the evolution of the aglomerular trait in Antarctic fish complements that of the presence of antifreeze.

Cardiovascular

A continuous low water temperature means that the oxygen-carrying potential of sea water is high. Thus as long as the partial pressure of oxygen in the sea water remains high so will the available oxygen. It is against this background that further cardiovascular adaptations have evolved.

Early taxonomic studies relied on specimens preserved in alcohol or formalin, both of which affect the color of the fish. Because fish typically possess red blood no mention was made of the

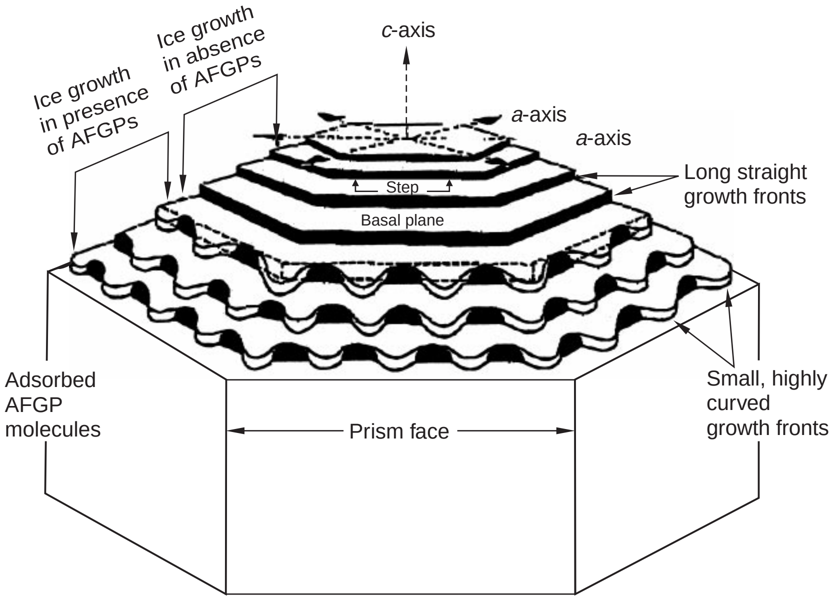

Figure 3 Model of an ice crystal depicting adsorption-inhibition as a mechanism for the freezing point depression of water by antifreezes. In the absence of AFGPs, ice crystal growth occurs as water molecules are added to the crystal in a regular fashion at steps on the basal planes. When the AFGPs are adsorbed, ice cannot propagate over them and long straight fronts become divided into many small curved fronts. (Reproduced with permission from Eastman JT (1993) *Antarctic Fish Biology*, Academic Press.)

anemic appearance of the gills of some species of Antarctic fish until the 1950s. At that time it was noticed that members of the Channichthyidae were white, as a result of which they were called 'white-blooded fish' or 'icefish'. The blood of channichthyids is devoid of hemoglobin, although small numbers of nonfunctional erythrocytes have been described in a few species.

Initial consideration was given to determine whether, because channichthyids do not possess scales, cutaneous respiration might be a major factor in oxygen uptake. However, the absorptive area and vascularization relative to the gills mitigated against that mechanism. Alternatively it was thought possible that channichthyids possessed either a more efficient oxygen utilization mechanism or else lowered oxygen requirement. This second consideration was being examined at a time when the concept of metabolic cold adaptation was under discussion.

Studies on oxygen uptake rates indicated that channichthyids utilized oxygen at a slightly lower rate as compared with equivalent red-blooded notothenioids. In the absence of hemoglobin, the oxygen-carrying capacity of channichthyid blood is only about one tenth that of red-blooded fish. Two mechanisms are possible to compensate for this effect; either channichthyid blood is circulated at a much faster rate or there is much more of it in the system. The latter has proven to be the case and channichthyid blood takes up 8–9% of the total volume of the fish (two to four times that of other teleosts), the heart rate and blood pressure are low but the stroke volume and resultant cardiac output are large. To reduce the resistance to flow the capillaries are larger than in other teleosts.

Even though the hemoglobinless condition is clearly effective it is a feature that confines the fish to areas of high oxygen tension such as are present in Antarctic waters. Experimental studies have demonstrated that channichthyids are particularly sensitive to hypoxia, indicating that in their natural habitat the oxygen saturation is always consistently high.

See also

Antarctic Circumpolar Current. Current Systems in the Southern Ocean. Weddell Sea Circulation.

Further Reading

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ANTHROPOGENIC TRACE ELEMENTS IN THE OCEAN

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Introduction

Human activities have increased the fluxes of several chemical elements into the ocean above natural levels. Despite convincing evidence for this enhancement of elemental fluxes (see Further Reading section for references relevant to the discussion in this article), there is only one element – lead (Pb) – where abundant evidence proves that open-ocean seawater concentrations are substantially higher than they were in preindustrial times. For a few other elements – e.g. cadmium (Cd) and mercury (Hg) – there is some evidence suggesting a detectable anthropogenic impact (or models indicating that an anthropogenic enhancement must exist even if it has not been observed). For most other elements, the size of the oceanic reservoir of these elements overwhelms relatively large anthropogenic fluxes, and it may require centuries of further inputs before the human impact can be discerned.

Anthropogenic Lead in the Ocean

Sampling and analysis for Pb have been difficult because of low concentrations and abundant con-