A Comparison of Adaptive Radiations of Antarctic Fish with those of NonAntarctic Fish

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Introduction

Antarctic biologists frequently emphasize the differences between the modern Antarctic environment and its fauna, and aquatic habitats and faunas elsewhere in the world. While it is valid to portray Antarctica as remote and its fauna as endemic and cold adapted, this approach tends to obscure broad scale similarities between Antarctic and non-Antarctic faunas. For example, the Antarctic fish fauna shares an evolutionary response to its habitat with fish in some tropical, temperate and boreal lakes. In this review we compare some well studied lacustrine radiations of fish with the two radiations of marine fish in the Antarctic Region of the Southern Ocean, notothenioids and liparids. We shall first make the case that, unlike other marine habitats, the Antarctic Region fulfills most of the essential parameters of lakes containing radiations of fish and that this large component of the world ocean is equivalent to a closed basin. Therefore in spite of its vastness, the Antarctic Region provides a comparable opportunity for studying evolutionary biology within a confined area. It is likely that notothenioids, and possibly liparids, are the first known examples of species flocks or radiations of marine fish. Thus the high Antarctic shelf and upper slope is an insular evolutionary site, with endemic faunas equally as interesting, but less well known, as those in ancient lakes throughout the world.

We use recent information to compare Antarctic and non-Antarctic radiations of fish with respect to age of habitat, species diversity, molecular divergence times, key innovations and degree of morphological and ecological divergence with respect to phyletic divergence. Also of interest are the geological, climatic and ecological factors that created the conditions leading to these radiations. The radiation of notothenioid and liparid fishes has taken place during a period of significant tectonic activity and substantial climatic change [1-6]. Furthermore the evolutionary history of one group, the notothenioids, has been elucidated by cladistic analyses employing both morphological [1,7] and molecular [8,9] techniques. Although the major features of the radiation of notothenioid fishes are now
reasonably well established, there remain critical areas of uncertainty. These include the nature of the parent stock, and the timing of key evolutionary events in relation to tectonic and climatic changes.

Species Flocks or Radiations of Fish

Evolutionary biologists have long been fascinated by the species flocks or adaptive radiations of organisms in isolated aquatic habitats, especially ancient lakes [10-16]. The distinguishing characteristics of ancient lakes are these: considerable age (5-20 Ma), great depth (permanence) and isolation. They also contain speciose and highly endemic faunas, sometimes including species flocks, and have been centers of evolution for a variety of organisms [15,16].

Species flocks usually exhibit monophyly, endemism and speciosity [15]. With respect to fish species flocks, the importance of monophyly has been considered either essential [17] or not a general criterion [18]. We follow Ribbink [18 p.24] in recognizing a species flock as "an assemblage of a disproportionately high number of closely related species which evolved rapidly within a narrowly circumscribed area to which all or almost all the member species are endemic."

The shelf and upper slope waters around Antarctica share many of the features of isolated aquatic habitats. Although large in size, the Antarctic shelf and upper slope is isolated from other shelf areas in the Southern Hemisphere by large areas of deep water, a major oceanographic feature (the Polar Front), and by being at subzero temperatures. In these respects the fish fauna of the Antarctic continental shelf is as isolated as a lacustrine fauna. The Antarctic continental shelf also resembles a lacustrine habitat in supporting a highly endemic fish fauna, although the species richness might be considered to be somewhat small for the size of the area. This fauna contains two groups which match Ribbink's [18] criteria for a species flock, the notothenioids and the liparids. In Table 1 we summarize the features of these groups with flocks of fish from ancient lakes.

The Fish Fauna of the Antarctic Continental Shelf and Upper Slope

The fish fauna of the Southern Ocean is small and limited in taxonomic diversity, containing only 274 species in 49 families [19]. Thus although representing 10% of the world's ocean, the Southern Ocean accommodates only about 1% of the world's fish fauna of 25,000 species. As will be seen below, however, a count of taxa leads to an underappreciation of the morphological and ecological diversity of the fauna. The fauna is highly
<table>
<thead>
<tr>
<th>Group &amp; Location</th>
<th>Habitat</th>
<th>Mean depth (m)</th>
<th>Age of habitat (my)</th>
<th>No. families/ genera/species</th>
<th>Species endemism</th>
<th>Nature of divergence</th>
<th>Key innovations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cichlids</td>
<td>African rift lake</td>
<td>572</td>
<td>5-20</td>
<td>1/50/185</td>
<td>99%</td>
<td>Trophic morph. Behavior/ecology</td>
<td>Modifications of pharyngeal jaw apparatus</td>
</tr>
<tr>
<td>Lake Tanganyika</td>
<td></td>
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<td></td>
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<td>Lake Malawi</td>
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<tr>
<td>Cichlids</td>
<td>African lake</td>
<td>40</td>
<td>0.0124</td>
<td>1/21/250</td>
<td>99%</td>
<td>Trophic morph. Behavior/ecology</td>
<td>Modifications of pharyngeal jaw apparatus</td>
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<tr>
<td>Lake Victoria</td>
<td></td>
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</tr>
<tr>
<td>Cottoids</td>
<td>Siberian rift lake</td>
<td>730</td>
<td>2-25</td>
<td>3/11/29</td>
<td>93%</td>
<td>Morphological Ecological Physiological</td>
<td></td>
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<tr>
<td>Lake Baikal</td>
<td></td>
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<td></td>
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<tr>
<td>Cyprinodontiids</td>
<td>Andean plateau lakes</td>
<td>105</td>
<td>0.8-2</td>
<td>1/1/43</td>
<td>&gt;50%</td>
<td>Head shape &amp; mouth position</td>
<td></td>
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<tr>
<td>Titicaca Basin</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Cyprinids (barbs)</td>
<td>Ethiopian lake</td>
<td>8</td>
<td>2</td>
<td>1/1/1?</td>
<td>0%</td>
<td>14 month/head shape morphs</td>
<td></td>
</tr>
<tr>
<td>Lake Tana</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Notothenioids</td>
<td>Antarctic shelf &amp; upper slope</td>
<td>&lt;500</td>
<td>12-22</td>
<td>6/40/95</td>
<td>97%</td>
<td>Morphological Ecological Physiological</td>
<td>AFQP derived from trypsinogen</td>
</tr>
<tr>
<td>Antarctic Region</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Liparids</td>
<td>Antarctic shelf &amp; upper slope</td>
<td>&gt;500</td>
<td>12-22</td>
<td>1/5/64</td>
<td>?</td>
<td>Phyletic</td>
<td></td>
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<tr>
<td>Antarctic Region</td>
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endemic, with 88% of the species confined to the Antarctic Region south of the Polar Front. If just notothenioids are considered, species endemism rises to 97% [20]. The major component of the fauna, that of the shelf and upper slope (Table 2), is represented by only 208 species and is unusual among marine habitats in containing radiations of two unrelated lineages, namely perciform notothenioids in shallower habitats and scorpaeniform liparids in deeper waters.

Table 2. Dominant families of benthic fishes inhabiting the continental shelf and upper continental slope of the Antarctic Region

<table>
<thead>
<tr>
<th>Taxon</th>
<th>No. of species</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myxinidae (hagfishes)</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Petromyzontidae (lampreys)</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Rajidae (skates)</td>
<td>8</td>
<td>3.8</td>
</tr>
<tr>
<td>Carapidae (pearlfishes)</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Moridae (deepsea cods)</td>
<td>4</td>
<td>1.9</td>
</tr>
<tr>
<td>Muraenolepididae (eel cods)</td>
<td>4</td>
<td>1.9</td>
</tr>
<tr>
<td>Gadidae (cods)</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Congiopodidae (horsefishes)</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Liparidae (snailfishes)</td>
<td>64</td>
<td>30.8</td>
</tr>
<tr>
<td>Zoarcidae (eelpouts)</td>
<td>23</td>
<td>11.0</td>
</tr>
<tr>
<td>Notothenioidei (includes six Antarctic families*)</td>
<td>95</td>
<td>45.7</td>
</tr>
<tr>
<td>Tripterygiidae (triplefins)</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Achiropsettidae (southern flounders)</td>
<td>4</td>
<td>1.9</td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td><strong>208</strong></td>
<td><strong>100.0%</strong></td>
</tr>
</tbody>
</table>

*Phylogenetic sequence according to [21].

Based on [19] with these exceptions: addition of two new nototheniids from Balushkin [22, 23], a number of liparids from Andriashev and Stein [4] and of zoarcids from Anderson [24].

*Balushkin [25].
Notothenioids

The perciform suborder Notothenioidei includes eight families and 121 species. All but 26 of these species are confined to the Antarctic Region. In the entire Southern Ocean, about 35% of species are notothenioids; in subzero shelf and slope waters 46% are notothenioids (Table 1). Here they occupy virtually all benthic and water column habitats, accounting for 90-95% of the biomass [26, 27]. In the eastern and southern Weddell Sea, for example, 94% of the specimens captured are members of the family Nototheniidae [28]. This exceptional degree of habitat saturation by a single taxonomic group is attributable to the fact that notothenioids occupy niches filled by taxonomically diverse groups of fishes in temperate and tropical oceans.

A simple count of taxa does not begin to adequately describe the nature of the nototheniid radiation. In addition to phyletic diversification, and unlike most other fish groups including some lacustrine radiations [29,30], notothenioids have also experienced substantial morphological and ecological diversification in that there are a number of distinct life history or ecological types. Notothenioids underwent a depth-related diversification centered on the evolutionary alteration of buoyancy and the morphology associated with swimming and feeding in the water column.

Although lacking swim bladders, some notothenioids diversified away from the ancestral benthic habitat toward pelagic or partially pelagic zooplanktivory and piscivory. Within the family Nototheniidae, for example, about 50% of the Antarctic species are pelagic, semipelagic, cryopelagic or epibenthic rather than benthic, the presumed ancestral type [1]. Referred to as pelagization, this ecomorphological trend toward life in the water column has arisen independently in at least two different nototheniid clades, although phylogenetically related species are not necessarily morphologically and ecologically similar [3].

Liparids

With the recent description of dozens of new species [4], it appears that a radiation of snailfishes of the scorpaeniform family Liparidae inhabits the deep shelf and upper slope of the Antarctic Region. The 64 liparid species from the Antarctic Region, mostly members of the genera Paraliparis and Careproctus [4], represent 31% of the 208 species of benthic fishes from the continental shelf and upper slope (Table 2). The Liparidae has surpassed the Nototheniidae as the most speciose fish family in the Southern Ocean.

Unlike notothenioids, liparids have a worldwide distribution and are one of the few fish families having both boreal and austral centers of species
diversity [31]. The family includes about 200 species living from the intertidal zone to depths of 7000 m [4,21,32]. Liparids probably originated and radiated in the North Pacific Region with subsequent dispersal southward along the western coast of the Americas [33,34]. In the deep waters of the Antarctic Region liparids underwent a secondary radiation complementing the shallow water radiation of perciform notothenioids. All known species are members of deep-water genera [35]; most are epibenthic at depths of 200-2000 m [4]. As the sea below 200 m is the largest living space on earth, it is reasonable to expect that it would be subject, with some constraints, to the same evolutionary processes occurring in other aquatic environments.

Although phyletically diverse, many Antarctic liparids are known from only a few specimens. They are taxonomically dominant in waters over 500-600 m deep, but may not be represented by large populations and biomass [4]. Liparids lack a swim bladder and phyletically primitive species are inshore benthic fish [36], but the liparid radiation in the Antarctic Region has centered on diversification into the water column, especially epibenthic niches. The amount of morphological divergence relative to lineage splitting reflects the degree of macroevolution and, if families are compared, this has been considerably less in liparids than in nototheniids.

Since they are few in number, deep-living and difficult to maintain in aquaria, we know little of the biology of Antarctic liparids. The sole exception is *Paraliparis devriesi* which lives at 500-650 m in McMurdo Sound. Although lacking a swim bladder, this species is neutrally buoyant through the combined effects of reduced skeletal ossification and expansion of a watery gelatinous subermal extracellular matrix consisting of glycosaminoglycans. This matrix serves as a low density buoyancy agent comprising about one-third of the body weight, the largest known proportion of any adult fish [37]. At nearly 78°S the population of *P. devriesi* in McMurdo Sound has the most southerly distribution of any known liparid, living in water with a temperature of about -1.9 °C and little seasonal variation. However only small amounts of antifreeze compounds have been inferred from the melting point-freezing point behavior of body fluids. Freezing avoidance in *P. devriesi* may therefore be the result of the combined effects of modest concentrations of a noncolligative antifreeze and elevated osmolality of body fluids [38].

**The Environmental Background to the Evolution of the Antarctic Continental Shelf Fauna**

The evolution of the Antarctic fish fauna can only be understood in relation
to the tectonic and climatic history of the area. We will discuss this before moving to a comparison of the radiations of Antarctic and lacustrine species flocks.

**Tectonic History**

Although Antarctica is presently covered by a single ice sheet, the underlying rocks comprise two crustal blocks of differing tectonic history: East Antarctica and West Antarctica. The latter includes the Antarctic Peninsula, whose position relative to East Antarctica has changed significantly through time. There is also a cluster of very small crustal plates (microplates) whose precise relationships and tectonic history are the subject of much debate.

The main block of what is now Antarctica includes Precambrian basement rocks, and in the Palaeozoic formed part of a single supercontinent, Pangea. As far back as the Cambrian the southern edge of East Antarctica and Australia supported a shallow-water marine fauna, with a defined trilobite faunal realm [39].

Following the inception of the present cycle of seafloor spreading in the Mesozoic, Pangea split into two major blocks, Laurasia and Gondwana, separated by the Tethys Sea. At this point there were two quite distinct areas of shallow water adjacent to the East Antarctic shield. One was the long coastline formed by South America and the southern/western coast of East Antarctica, facing the Pacific Ocean. The other was the northerly/eastern coast of the East Antarctic shelf and Australia, where they formed the southern boundary to Tethys. It is from the latter that the faunal elements defining the Weddellian Province of the later Mesozoic came. Since Gondwana remained as a single intact unit throughout the Palaeozoic and into at least the Jurassic, those proto-Pacific coastal habitats are considerably older than those around present-day East Antarctic (which faced the Tethys Sea).

It seems likely that the initial opening between Antarctica and South America/Africa was at about 150 Ma BP [40]. Initially this would have been a shallow epicontinental sea, evidence for which comes from the disjunct distribution of certain Jurassic endemics in both the southern Andes and East Africa/Madagascar [41-44]. Faunal exchange between the Pacific and Tethys/Weddellian Provinces could thus have started in the Jurassic, although it was not until much later that the Drake Passage opened sufficiently for deep-water circulation to start.

By the early Eocene, fragmentation of Gondwana was well underway, with Africa and India having moved substantially northwards. Australia was still attached to East Antarctica and there was no deep-water
separation of West Antarctica (the Antarctic Peninsula) from South America. Although faunal evidence suggests some shallow water faunal exchange, the deep water basins of the Atlantic/Weddellian Province and the Pacific Ocean were still separated.

The area of West Antarctica contains many microplates, the detailed movements of which have yet to be resolved. Nevertheless it is clear that the Drake Passage between South America and the Antarctic Peninsula first opened in the early Oligocene [45]. By this time Australia had already moved north from East Antarctica, and the Circumantarctic Current had probably started by about 25 Ma BP.

The movement of West Antarctic microplates and the fragmentation of the Scotia arc allowed a free exchange of fauna between the previously isolated Pacific and Weddellian (ex-Tethys) Provinces. Coupled with the oceanographic isolation of Antarctic by the inception of the Circumantarctic Current and the formation of the Polar Front, this also effectively reduced any exchange of shallow water faunal elements between West Antarctica and South America. The scene was therefore set for the continued evolution of the marine fauna of the Antarctic continental shelf in effective isolation from nearby faunas.

**Climatic History**

It is widely recognized that the waters around Gondwana in the late Cretaceous were mild, with bottom temperatures about 12 °C [46]. This was followed by a distinct warming phase in the early Tertiary, during which bottom temperatures may have reached 16 °C. After this warm period, which lasted through much of the Eocene, there started the sustained cooling which has dominated much (but by no means all) of the remainder of the Tertiary.

The first evidence of widespread sea-ice and continental glaciation appears in the late Eocene/early Oligocene [46]. This corresponds with a sharp drop in bottom temperature; the seawater temperatures are, however, cold rather than truly polar. The Oligocene appears to have been generally cool or cold at high latitudes, and this matches the time when the physical and oceanographic isolation of Antarctica became complete. This was followed, however, by a period of global warming in the middle Miocene, when Southern Ocean bottom temperatures may have reached 10 °C. High latitude seawater temperatures then fell in the mid to late Miocene, perhaps by as much as 4-5 degrees °C. This was accompanied by a switch from predominantly equatorial to strongly meridional circulation patterns in the large ocean basins, with major consequences for global heat transfer.

After brief periods of warming in the late Miocene and early Pliocene,
seawater temperatures then cooled to the present fully polar temperatures. There is some evidence for a general warming in the Pliocene, which may have led to some retreat of the ice-cap but this is still debated (see below).

**Key Problems in the Climatic History of the Antarctic in Relation to the Evolution of the Marine Fauna**

The broad features of the tectonic and climatic history of Antarctica during the Tertiary are now reasonably well established. Nevertheless there remain important unanswered questions in relation to the evolution of the Southern Ocean marine fauna.

**When Did Widespread Continental Glaciation Start?**

Prior to the establishment of a significant ice sheet in Antarctica, the continental shelves would have been shallower, shallow seas would probably have been more extensive, and there would have been a greater range of shallow-water habitats available including estuaries and mudflats. All of these are likely to have allowed a more diverse fauna than exists today, and fossil evidence indicates that early Tertiary fish fauna in Antarctica was indeed diverse, including many chondrichthyan and other groups not represented today [1,47]. Ancestral notothenioids probably inhabited the shelf of Gondwana, and later Antarctica, during the late Cretaceous or early Tertiary, although their representation in the late Eocene (40 Ma) fossil fish fauna from Seymour Island is debatable [47, 48].

Although there is evidence from glacial deposits of glaciers discharging at sea-level in the Eocene, these do not necessarily indicate the presence of ice sheets [46]. Evidence from sea-level changes suggests the growth and decay of substantial ice sheets in the Eocene, but isotopic data give no support to significant variations in ice volume prior to about 36 Ma BP.

On present evidence, there are thus indications that widespread continental glaciation started around the Eocene/Oligocene border. It is at this time that there may have been significant changes in habitat area, and many habitat types such as rivers and estuaries may have been eradicated, with consequent impacts on the diversity of the fish fauna.

**How Far Have Ice-Sheets Extended in the Past?**

The present ice-sheet covers over 99% of Antarctica, but does not extend over all of the continental shelf. Geophysical evidence has shown that in the past, ice-sheets have extended fully to the edge of the Antarctic continental shelf [49]. This would obviously eradicate all available habitat
for continental shelf organisms which would either become extinct, survive in refugia not covered by ice, or move into deeper water on the continental slope.

The critical piece of information in relation to the evolutionary history of the Southern Ocean marine fauna is whether during one or more glacial maxima in the past, the continental ice-sheet ever extended so far as to cover all of the Antarctic continental shelf at once. We cannot yet answer this question from geophysical or glaciological data. Nevertheless two pieces of ecological evidence suggest that previous glacial maxima may have covered a large proportion of the Antarctic continental shelf. The first is that the peak of species richness for notothenioid fishes in East Antarctica is at about 500-m depth [20]. The second is that the bathymetric ranges of many Antarctic marine organisms extended deeper than elsewhere on the globe [50].

Taken together this evidence suggests (but no more) that glacial maxima, perhaps as recently as the Pliocene or Pleistocene, may have severely reduced or even eradicated available habitat for fish living on the Antarctic continental shelf. If so, the radiation of notothenioid fish may be a much more recent event than traditionally has been thought to be the case.

**How Extensive Were Changes in Ice-Sheet Volume and the Extent of Shallow-Water Marine Habitat in the Pliocene?**

There has recently been considerable controversy over the extent, or even existence, of deglaciation in Antarctica during the Pliocene. Although the original evidence which came from diatom fossils has been shown to be unreliable [46,51], other evidence has suggested some limited deglaciation in Pliocene times (for example the Pecten conglomerate on Cockburn Island, dated at 3.5-5.3 Ma BP: [52]). Some highly speculative reconstructions of the Antarctic ice-sheet during the Pliocene suggest the presence of large shallow epicontinental seas, which would have increased greatly the habitat area available for shallow-water fish. On present evidence, however, we can only conclude that the evidence for Pliocene warming is suggestive. The possibility exists that shallow water habitats were more extensive in the Pliocene, but we cannot yet be sure.

**What is the Role of Milankovitch Cyclicity in the Evolution of the Southern Ocean Fauna?**

Gravitational interactions with other bodies in the solar system induce variations in the Earth's orbital parameters. The main cycles have periods of 23 kyr (precession), 41 kyr (obliquity) and ~100 kyr (eccentricity). It is
now recognized that the small variations in received solar radiation caused by these Milankovitch cycles are important drivers of climatic variability [53].

The strongest evidence that Milankovitch cycles induce changes in ice volume during glacial periods comes from the analysis of oxygen isotope fractionation in marine sediment cores. These show variability with strong signals at frequencies corresponding to cycles of 23 kyr and 41 kyr; recent studies have also demonstrated lower frequency cycles at ~100 kyr and ~400 kyr [54].

Although ice volume is only one factor influencing the marine sediment oxygen isotope signal, there is general agreement that orbital variations have been responsible for Milankovitch cycles in the volume of polar ice in the Pleistocene glaciation. Although it would seem reasonable to assume that similar Milankovitch cyclicity in ice volume will have occurred throughout the Cenozoic glaciation of Antarctica, evidence is hard to come by. There is, however, some evidence from varving in marine sediment cores for Milankovitch cyclicity in the Mesozoic [55].

We can therefore conclude that superimposed on large-scale changes in ice volume, such as that suggested for the Pliocene, will be shorter-term fluctuations on time-scales in the range 23 to ~400 kyr. If these fluctuations in ice volume were substantial it is possible that they may have driven significant changes in available shallow-water habitat. This in turn could be a mechanism for diversification through allopatric speciation, through a mechanism termed by Valentine [56] the climatic diversity pump [57].

Milankovitch-driven cycles in habitat area may have been a mechanism contributing to the high diversity of some taxa in the Southern Ocean [5,6,58]. At present, however, we do not have the evidence from the marine glacial record to determine the extent of high-frequency variations in the ice volume of Antarctica.

What Has Been the Role of Sudden Climatic Events in the Evolution of the Southern Ocean Fauna?

High resolution analyses of ice-cores from Greenland have shown that at certain periods, the regional terrestrial climate has changed very rapidly [59,60], confirming the rapid changes first demonstrated by climatic reconstructions from subfossil Coleoptera (beetles) [61,62].

What is not at all clear is the extent to which such rapid changes might occur in the sea. Whilst the thermal mass of water means that changes in the temperature of bulk seawater must inevitably be slow, it has become clear that climatic change in the sea may be exhibited through sudden changes in patterns of current flow. Evidence for such changes is
accumulating slowly. In the Southern Ocean the only evidence for rapid changes in temperature comes from the late Palaeocene where Kennett and Stott [63] have demonstrated a possible short-term warm event.

Although significant changes in circulation patterns clearly have the potential to influence distribution and evolutionary process through regional or wider-scale extinction, there is as yet no evidence that these processes have been important in the evolution of the Southern Ocean marine fauna.

The Evolution of the Antarctic Fish Fauna

The broad features of the evolution of the Southern Ocean fish fauna are now well established [1] and so will only be summarized here.

The vast ice-sheets of Antarctica limit the exposure of rock, and so our knowledge of the fossil history of the Southern Ocean fish fauna is frustratingly incomplete. Mesozoic fossils confirm the suggestion from tectonic reconstructions that the shallow waters around Gondwana were populated by faunas typical of the period [1]. Early Cenozoic fossils from Seymour Island indicate that prior to the oceanographic isolation of Antarctica, the fish fauna of Gondwana was diverse and contained representatives of many cosmopolitan taxa. The fauna appears to have been typical of the temperate seas of the time.

Unfortunately there are few postEocene fossil fish known from Antarctica and the modern fauna thus has no fossil record. We are therefore left with the intriguing observation that at some time between the Eocene and today, early Tertiary fish fauna of Antarctica largely disappeared. There was then a substantial radiation of notothenioid and liparid fish to produce the fauna we see today.

What Caused the Demise of the Early Tertiary Fish Fauna?

In the absence of a fossil record, we can only speculate on the causes of the extinction of the early Tertiary fish fauna of Antarctica. Nevertheless it is tempting to assume that a major factor must have been the severe reduction in the amount of shallow water and the loss of many habitats traditionally rich in fish consequent upon the major glaciation of Antarctica. This working hypothesis would then put the extinction event (if needed it can be regarded as a single event) around the late Eocene/early Oligocene (40-35 Ma BP). An explanation based on habitat loss also implies that the associated cooling was not necessarily the primary cause of extinction, but in truth there is no evidence to allow us to distinguish the two causes (which may have acted together).
The Origin of the Present Fauna

The modern Antarctic fauna of continental shelf and slope fishes is dominated in terms of species by liparids and notothenioids.

The liparids (snailfishes) appear to have their center of origin in the north Pacific. It is likely that they reached the Southern Ocean by range extension along the Pacific continental shelf and slope of the Americas, probably at a time when glacial maxima had pushed colder waters to lower latitudes. Once in Antarctica the group has radiated to produce over 60 species, though nowhere do liparids appear to be abundant [4]. The timing of the radiation is not known but if it was assumed to have taken place at the last glacial maximum then the radiation of liparids in the Southern Ocean must be a relatively recent affair.

The notothenioids have both radiated and become the dominant taxa of the Southern Ocean continental shelf fauna [1]. The notothenioids appear to be a monophyletic clade, though the ancestral stock cannot be identified with certainty [1]. Neither can we rely on fossil history, for as yet no unequivocal fossil notothenioids have been identified.

We must assume that the notothenioids evolved from a demersal perciform stock, and probably one which was already living in the shallow waters of Gondwana and probably in the Weddellian/Tethyan rather than the Pacific faunal province. Once the early Tertiary fauna became extinct the notothenioids were able to undergo a radiation to produce the fauna we see today. Diversification of the emerging notothenioid fauna was facilitated by the oceanographic and thermal isolation of Antarctica, by the increasing productivity of the Southern Ocean beginning about 22 Ma [64] and by the absence of competition from nonnotothenioids. This ecological space was filled by a diversifying notothenioid fauna tolerant of deeper and colder habitats, which poses the questions as to why it was the notothenioids that radiated, rather than some other group, and when did the radiation take place?

Why Notothenioids?

This is an impossible question to answer at present. It may be, however, that through an accident of history the notothenioids were simply the group that survived whatever caused the demise of much of the early Tertiary fauna. Certainly a number of features of their biology suggest that the notothenioids were in no way "pre-adapted" to radiate in the Southern Ocean. In particular the secondary loss of a functional swimbladder in the ancestral stock has limited their ability to move into the water column and
despite their evolutionary pelagization most species remain benthic or demersal [1].

**When Did the Radiation Take Place?**

Cladistic analysis of the notothenioids suggests that the suborder is monophyletic, though at present the topology of the split between Harpagiferidae and Artedidae is not resolved (Fig. 1). Recent molecular evidence from sequence analysis of 12S and 16S ribosomal RNA genes from 18 species spread across 5 families has broadly supported the analyses based on morphological data. It has, however, suggested that the most speciose family, Nototheniidae, may be paraphyletic [8].

The notothenioid diversification appears to have been protracted throughout much of the Tertiary, with the initial divergence of some of the basal families having taken place during the early fragmentation of Gondwana. At this time stocks appear to have become established in brackish water on isolated continental blocks (*Pseudaphritis* in Australia, and *Eleginops* in South America).

![Diagram of Notothenioid Phylogeny](image)

**Fig. 1.** Notothenioid phylogeny of Lecointre et al. [65] with familial nomenclature of Balushkin [25]. Hb, hemoglobin, AFGPs, antifreeze glycopeptides
McDonald and coworkers [66] used electrophoresis to examine variation at 30 protein-coding loci in six species of notothenioids from McMurdo Sound. Estimated divergence times within the Nototheniidae suggested that Dissostichus separated from Trematomus at about 28-20 Ma BP, and from Pagothenia at about 13 Ma BP. This would be consistent with the major phyletic divergence of notothenioids taking place after the isolation of Antarctica and after the initial period of cooling.

The traditional Bovichtidae is paraphyletic, with Pseudaphritis more closely related to nonbovichtid notothenioids than are Cottoperca or Bovichtus. The position of these latter two genera with respect to various notothenioid outgroups is uncertain [65]. Inference from mtDNA sequences implies that the radiation of the phyletically derived Antarctic notothenioids took place more recently than previously suspected, probably within the last 15 Ma [8]. Recent analysis of partial mitochondrial sequences from 12S and 16S rRNA genes and assuming a conventional rRNA molecular clock puts the average age of the trematomid radiation at only 3.4 Ma (mid-Pliocene). This is relatively recent, and it is intriguing that the age coincides so well with the timing of the controversial Pliocene warming event. If there was a significant warming event at around 2.5-5 Ma BP then this may have resulted in significant changes in available habitat and together with Milankovitch-driven variations in habitat extent may have prompted the radiation of trematomids.

The mapping of the presence of antifreeze glycoprotein onto the cladogram suggests that this feature evolved only once, after the divergence of the Bovichtidae. If the timing of the cooling of the Southern Ocean to subzero temperatures can be fixed precisely, then this in turn could fix the timing of the main diversification.

There are three main possibilities for the timing of Southern Ocean cooling to subzero temperatures. One is the sharp drop in surface temperatures at the start of the Oligocene, 35 Ma BP, the second is the marked cooling event at the middle of the Miocene at about 17 Ma BP, and the third is the final plunge to truly polar temperatures in the late Pliocene.

The third of these possibilities is not tenable on the grounds of biogeography, and all molecular evidence, and hence can probably be dismissed.

More intriguing, however, is the choice between the first two potential dates. The older date would be consistent with the combined evidence from biogeography and the cladistic analysis [1]. The molecular evidence, however, suggests a date for the main notothenioid diversification (after
separation of the bovichtid clade) of around 11 Ma BP [8]. If this later date is correct, it implies a much more rapid diversification than has traditionally been believed. It would also imply that either the first cooling event at the start of the Oligocene was not sufficient to require the evolution of antifreeze, or that antifreeze arose independently in several notothenioid clades.

The small degree of sequence divergence between the notothenioid antifreeze glycopeptide and trypsinogen genes suggests that antifreeze evolved somewhere between 5 and 14 Ma BP [67]. This is satisfactorily close to the entirely independent molecular evidence from mtDNA [8] and suggests strongly that the main diversification of the notothenioids has taken place in the past 10-15 Ma. This matches the end of the first phase of continental glaciation [46].

Comparison of the Radiation of Antarctic Fishes with Lacustrine Species Flocks

As a basis for comparison with notothenioids we will mention relevant aspects of the biology of the well studied flocks of fish in the East African Great Lakes and in Lake Baikal in Siberia.

East African Cichlids

Lakes Tanganyika, Malawi and Victoria differ greatly in morphometry, depth and age (Table 1). They have experienced climatic changes that affected both water levels and degree of isolation of their basins. Tanganyika and Malawi are old deep rift lakes that are permanently stratified and anoxic below 250 m. The rocky shorelines with isolated bays and islands provide a complex array of microhabitats. The present Lake Victoria, on the other hand, is a shallow depression variously dated from 750 000 [68] to 12 400 years old [69].

The perciform cichlids in Lakes Tanganyika, Malawi and Victoria (Table 2) are the most speciose and most extensively studied examples of fish species flocks [14,70,71]. The age of the various lakes is reflected in the higher level taxonomic complexity of the fauna. For example, the old flocks of cichlids in Tanganyika show more tribal and generic diversification than those in the other lakes. Furthermore, Tanganyika is home to small flocks of several catfish families and mastacembelids, and to an offshore fauna consisting of endemic clupeids and centropomids. Divergence times and phylogenetic relationships based on mtDNA sequences suggest that the cichlid flock in Tanganyika is polyphyletic, hence there are actually multiple flocks dating from 3.5 to 5 Ma. The
Malawi and Victoria flocks are closely related to one of the Tanganyikan lineages and are monophyletic and younger [71].

Although there has been behavioral and ecological differentiation, the amount of morphological differentiation has been relatively small, with species differences centering on head and tooth shape and body coloration. Modifications of the pharyngeal jaw apparatus, specifically the development of joints and the shift in muscle insertions, may have been a key evolutionary innovation in the radiation of these flocks. The pharyngeal jaws assumed the function of food mastication, freeing the oral jaws for extremely diverse collecting functions which lead to ecological differentiation [72]. Recent evaluation of the trophic diversity of the flocks in Tanganyiika lead to the conclusion that this diversity reflects historical (phylogenetic) factors rather than results of competition [73].

Periods of climatic change probably produced fluctuations in water level in all three lakes, and this was important in promoting microallopatric intralacustrine speciation [69,71,74]. This was likely the most important means of speciation in all cichlid flocks [71]. Speciation was also extremely rapid, hundreds to a few thousand years in some small lakes and in isolated parts of the three great lakes. This conclusion is based on the presence of endemic species in areas of some lakes known to be dry a few centuries ago. The youngest major flock, that in Victoria, is dated by molecular methods at 200 000 years [71]; however seismic reflection profiling and piston coring suggest that the lake dried completely 12 400 years ago [75]. This implies that the flock of 250 species evolved in this short period of time or that components of the flock survived in adjacent water and, after levels rose, repopulated Lake Victoria.

**Lake Baikal Cottoids**

With a maximum depth of 1620 m, Lake Baikal is the world's deepest and possibly oldest lake. The Baikal rift has contained a deep lake since the early Miocene (25 Ma), although the modern configuration was not acquired until 3.2-0.8 Ma [76]. The origins of the modern fauna date to the Miocene or Pliocene. Baikal holds the greatest animal species diversity of any extant lake [16, 76]. Unlike the East African lakes, Baikal is oxygenated to the bottom and therefore contains a significant deep-water fauna including fish that approach marine species in some of their adaptations to depth.

The fish fauna of Lake Baikal includes 56 species from 14 families [77,78]. Of the 50 native species, 29 (58%) are endemic sculpins (Cottoidae) belonging to the families Cottidae, Copephoridae and Abyssocottidae. The latter two are endemic to the lake. Although cottoids
are a marine group of North Pacific origin, they have colonized freshwaters in Eurasia and North America. Cottoïds from the freshwaters of Eastern Siberia may have been a source of the ancestral stock for the Baikal cottoids [77]. Recent molecular research has provided divergence times for a few species of the family Cottidae. Merged sequences from the cytochrome b and ATPase regions of mtDNA suggest that three species of Cottus and Cottocomorphus diverged 1-2 Ma [79].

Although lacking swim bladders, some Baikal cottoids diversified away from the ancestral coastal benthic habitat into water column habitats and deeper (abyssal) waters [77,80]. Species diversity peaks at 400-500 m [78]. In an interesting ecological and morphological parallel with the nototheniids Dissostichus and Pleuragramma [1], the two species of Comephorus have become secondarily pelagic. They are close to neutral buoyancy through a combination of reduced skeletal mineralization and increased levels of lipid [78]. Adaptation to deep water habitats in Baikal has involved modification of sensory systems similar to those seen in deep dwelling marine species. For example, in some Baikal cottoids the photoreceptors of the retina consist exclusively of rods [81,82], and canal neuromasts have been replaced by free neuromasts [78].

Final Remarks

Radiations or species flocks of fish are found in isolated aquatic habitats throughout the world, especially in geologically old lakes. The Antarctic shelf and upper slope, an isolated evolutionary site similar to ancient lakes, may also hold flocks of fish. The appearance of some species flocks is coincident with periods of climatic change and habitat instability that may have served as vicariant events. There is good documentation for the rise and fall of water levels in Lakes Malawi and Victoria. On the other hand, periods of habitat instability cannot be associated with the diversification of the deep living Antarctic liparids or Baikal cottoids. While flocks are a repeatable evolutionary response among phylogenetically diverse groups of fish, the size, age and nature of the diversifications are quite different (Table 1). In the Antarctic, notothenioids dominate the fish biomass of the shelf and their morphological and ecological diversity parallels their phylectic diversity. The deeper living liparids, on the other hand, are speciose but are not present in great numbers and are not morphologically diverse. Diversification in both groups has been keyed to underutilized water column habitats.

A key evolutionary innovation is a novel feature characterizing a clade (synapomorphy) and correlated with the adaptive radiation of the clade [29, p.181]. Innovations are the exception rather than the rule among flocks of
fish. It is likely that antifreeze glycopeptides are a key innovation in the Antarctic notothenioids [67,83]. Given their origin from a transformed trypsinogen gene, they are unique and distinct from the antifreeze glycopeptides in Arctic gadids. Their contribution to fitness or survival is obvious since diversification into subzero ice-laden water would have been impossible without them. A novelty or key innovation is responsible for a new evolutionary direction in a lineage. When mapped on the notothenioid cladogram, antifreezes have a single origin at the node for the Antarctic clade (the sister group of Eleginops). Based on ages inferred from the divergence of molecular sequences between trypsinogen and antifreeze, the appearance of genes responsible for the synthesis of antifreeze in the basal nototheniid (Disostichus) is coincident with the cooling and appearance of ice in the Southern Ocean 5-14 Ma [67]. This trait allowed considerably more diversification in the Antarctic clade (95 species) than in the nonAntarctic (26 species) clade.

As an independent test of antifreeze glycopeptides as a key innovation in notothenioids, we could ask whether the absence of high levels of antifreeze in Antarctic liparids has hindered their ecological diversification into shallow ice-laden waters. This may not be completely valid since Paraliparis and Careproctus are deep water genera and may have been unable to occupy niches already filled by the notothenioids which arrived on the Antarctic shelf and diversified before the liparids [4]. It is also interesting that whereas the Antarctic fish fauna is dominated by a single group of fish in which antifreeze capability evolved only once, the Arctic has a range of lineages in which antifreeze has evolved several times. Gadoids, for example possess an antifreeze glycoprotein (unrelated to that in notothenioids) and yet they have not radiated in the Southern Ocean.

In conclusion, the Antarctic shelf and upper slope is an insular evolutionary site, with radiations or species flocks of fish, equally as interesting as but less well known than the radiations in ancient lakes throughout the world. In spite of its vastness, the Antarctic Region provides an excellent opportunity for retrospective study of the evolution of an unusual fish fauna within a confined area during the latter part of the Tertiary.

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References

42. Mutterlose J (1986) Upper Jurassic belemnites from the Orville Coast, Western Antarctica, and their palaeobiological significance. Bull Br Antarct Surv 70:1-22