Evolution of the Antarctic fish fauna with emphasis on the Recent notothenioids

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Abstract: The composition of the Antarctic fish fauna has undergone remarkable changes through time. Fossil fishes are known from Devonian, Jurassic, Cretaceous and early Tertiary deposits of the region. The Recent fauna does not appear to be derived from any part of any of the known fossil faunas. The Devonian fish fauna includes agnathans, placoderms, acenthodonts, chondrichthyes and osteichthyes all belonging to families now extinct. The Jurassic fauna is known by only one species, a neopterygian of the now extinct family Archacomaenidae. Both the Palaeozoic and early Mesozoic fish faunas known from Antarctica indicate Australian biogeographic affinities based on other (i.e., non-Antarctic) known Palaeozoic and Mesozoic fish faunas. Late Cretaceous and early Tertiary species from the Antarctic region (Seymour Island) belong largely to families of fishes that today live in other regions of the world, but are extinct in the Antarctic region. The Recent (extant) fish fauna is drastically different from any of the fossil faunas and is dominated by perciforms of the suborder Notothenioidei. To date the fossil record has provided no fossils identifiable as notothenioids, or even species closely related to the group. It is unlikely that low water temperatures were directly responsible for the local extinction of the Tertiary Seymour Island ichthyofauna or for the lack of diversity in the Recent fauna. The decline of suitable substrate and trophic factors may have been more important in changing the composition of the fish fauna. There is considerable morphological, physiological and ecological diversification within the Notothenioidei. Although the emergence of this group was probably not a direct response to cooling, the subsequent radiation of notothenioids was associated with a variety of specializations related to low water temperature.

The Recent Antarctic fish fauna is neither speciose nor diverse, unlike the situation in the shelf waters of other southern continents. Most species belong to the highly endemic perciform suborder Notothenioidei that dominates Antarctic waters. For decades ichthyologists surmised that the notothenioid stock had been isolated on the continental shelf of Antarctica for most of the Tertiary; and that the fauna had evolved in situ and in isolation, adapting gradually to cooling conditions in the Southern Ocean (Regan 1914; Norman 1938; DeWitt 1971). The only modification of this scenario has been recognition of a possible role for tectonic movements in notothenioid evolution (Andersen 1984; Miller 1987).

There is unfortunately no Antarctic fossil record known for the Notothenioidei. There are taxonomically diverse fossil fishes from Antarctic deposits formed about the time the notothenioid stock probably emerged (late Cretaceous or early Tertiary). These fishes are not closely related to notothenioids, and are not unlike any other component of the Recent fauna. In addition, the ichthyofauna shows an Australian biogeographic affinity during the Palaeozoic and early Mesozoic that is not evident in the Cenozoic and Recent faunas. This paper is a primarily theoretical consideration of the evolution of notothenioids. While this will be our focus, we also have broader goals, including (1) briefly reviewing the Antarctic fish fauna through the Phanerozoic, (2) considering the importance of temperature and other factors in producing faunal change and (3) discussing the diversification of notothenioids.

Palaeontological history of the Antarctic fish fauna through the Phanerozoic

In their review of the Antarctic fossil fish fauna, Grande & Eastman (1986) indicated that the biogeographical significance of the fauna is variable through geological time. Their conclusions are briefly summarized below and updated with recent additions to the fauna.

Palaeozoic

All Palaeozoic fishes from Antarctica are in Devonian rocks. These fishes inhabited freshwater ecosystems that were free of ice (Tass 1977). Several diverse groups are represented: the thelodont agathan Parnia sp., placoderms, acanthodians, xenacanthid elasmobranchs, osteolepid crossopterygians and palaeonisciform actinopterygians. Most of these specimens are too fragmentary for use in phylogenetic analysis. The placoderm Antarcaspis muelleroeisis and the xenacanthid Antarticnassa prasca reflect an Antarctic–Australian biogeographical relationship during the Devonian, a period predating the breakup of Gondwana.

In evaluating all vertebrate faunas from Palaeozoic Gondwana, Young (1987) refined biogeographic relationships for fishes. He recognizes strong biogeographic affinities between faunas in southeastern Australia and Victoria Land, Antarctica, and between faunas in South Africa–South America and the Ohio Range, Transantarctic Mountains, Antarctica. Young (1989) also indicates that, as the most persistent Palaeozoic continental region, initial colonization of non-marine aquatic environments took place in Gondwana.

Mesozoic

Lower Jurassic (179–161 Ma) fishes consist of several complete individuals of the osteichthyan pholidophoriform Oreoichima elliotti from lacustrine interbeds in the Transantarctic Mountains, Victoria Land (Schaeffer 1972). A member of the freshwater family Archaeoceramidae, O. elliotti also has Australian affinities as all other species in this family are confined to Australia.

Seymour Island, near the tip of the Antarctic Peninsula (Fig. 1), has been an exceptionally rich locality for late Cretaceous fishes. Late Cretaceous material consists largely of fragmentary elasmobranch teeth and undetermined vertebral centra. Based on teeth, Grande & Eastman (1986) recognized the lamnid shark Isurus sp., and Grande & Chatterjee (1987) reported hexanchiform sharks including Notidanodon sp. and possibly Sphenodus sp.

A specimen from the late Cretaceous of Seymour Island also provided Grande & Chatterjee (1987) with material for a description of the oldest teleost from Antarctica. This species, Antarcicichthys seymouri, is a member of the beryciform family Trachichthyidae, an extant group with a wide marine distribution. Although modern representatives of this group are restricted to deep-sea habitats, late Cretaceous beryciform fishes may have been present in inshore waters – the ecological equivalents of modern Perciformes (Moyle & Cech 1988).

The late Cretaceous was an important time in the evolutionary history of fishes with teleosts radiating during this time. Unlike the situation hypothesized for some invertebrate groups from Seymour Island (Zinsmeister & Feldmann 1984), we see no evidence suggesting that Seymour Island served as a centre of origin and dispersal for fishes that later occupied deep and shallow water ecosystems at lower latitudes.

Cenozoic

All known Antarctic Cenozoic fishes are from Seymour Island. Most fossils are confined to the late Eocene or early Oligocene La Meseta Formation, a relatively shallow water beach (Woodburne & Zinsmeister 1984) or deltax (Pezzetti & Krisske 1986) deposit c. 40 Ma. Included in this material are a diverse array of chondrichthyans including sharks, saw sharks, rays and ratfish. The sharks were cosmopolitan in temperate oceans during the mid-Eocene to early Oligocene. A ratfish, mentioned by Grande & Eastman (1986) as a new addition to the Antarctic fauna, is being described by Ward and Grande.

Teleosts are represented in the La Meseta Formation by a siluriform pectoral spine, by a variety of fragmentary and unidentifiable vertebral centra and by unidentifiable jaw bones from large and small individuals. Thus the Cenozoic material contributes little biogeographic information as the represented taxa have wide distributions outside Antarctica.

Woodward (1908) described isolated vertebral centra from Eocene deposits on Seymour Island. He attributed these to the Notosthenidae; however his identification is probably not accurate. Centra are not diagnostic for most nototheniids, and furthermore the centra described by Woodward are indistinguishable from those of a majority of teleosts. Sinton's (1957) report of Notosthena from the mid–late Miocene of New Zealand is also a misidentification (Fordyce 1982). Thus while over 70 distinct perciform families are recognizable in Eocene deposits around the world (60 reported by Romer 1966, and several others since then in various publications), fossil notothenioids have not yet been discovered.

Grande & Chatterjee (1987) indicated that artificial preservation is probably responsible for the greater diversity of chondrichthyans relative to osteichthyans in the late Cretaceous/early Tertiary Seymour Island fauna. Most of
the fish fossils known from Seymour Island are preserved as isolated teeth, vertebrae, spines and other fragments. Isolated teeth are diagnostic for both fossil and Recent chondrichthians, but not for most teleosts. Therefore the teleost fauna appears less diverse as isolated teeth (and other isolated bone bits) are assigned to indeterminate species.

Recent
In summarizing information concerning the distribution and endemism of the Recent Antarctic fish fauna, DeWitt (1971) notes that the fauna comprises 120 species including about 80 species of the highly endemic perciform suborder Notothenioidei. Since 1971 many new taxa have been described; there are now 203 species (including about 110 notothenioids) representing 28 families in the Antarctic region (Andriashev 1987). Andriashev mentions that discovery of many new non-notothenioid species has reduced the dominance of notothenioids; however they still constitute 53% of the species in the Antarctic region. He notes that endemism is also high within the Notothenioidei; 97% for species and
85% for genera.

The Recent Antarctic fauna is therefore less diverse than might be expected given the considerable age (discussed below) and large size of the marine ecosystem. This fauna is also markedly different in composition from the fauna that preceded it in geologic time. The Tertiary marine fauna of Australia, for example, is similar to the Recent fish fauna (Long 1982). This is not true in the Antarctic as formerly diverse and abundant groups such as the Chondrichthyes are represented today by only a few species of rajids. Moreover, the Recent fauna is unusual in that it is dominated by a single perciform suborder, the Notothenioidei.

**Taxonomy and systematics of notothenioids**

The classifications of Regan (1914) and Norman (1937, 1938) persisted largely intact until recently. Today the systematic relationships of notothenioids are areas of active research (Eakin 1981; Andersen 1984; Balushkin 1984; Iwami 1985). Monophyly had been assumed but not proven until Iwami (1985) used cladistic methodology to evaluate phylogenetic relationships among notothenioids (Fig. 2). The notothenioid sister group has not been definitely identified among the Perciformes, although blennioids are generally thought (Gosline 1968; Eakin 1981) to be closely related to them, and a likely candidate. No unambiguous character evidence has been presented to clearly establish blennioids or any other perciform subgroup as the sister group. Eakin (1981) presents a good discussion of the problems encountered in separating convergences from true relationships and in searching for a notothenioid sister group.

**Cenozoic geology and palaeoclimatology**

**Breakup of Gondwana**

The breakup of Gondwana and the subsequent development of cold ocean currents around Antarctica certainly influenced the composition of the Antarctic fish fauna. These events also provide a time frame for considering the evolution of notothenioids. Key elements may be briefly summarized as follows (Cradock 1982; Woodburne & Zinsmeister 1984; Zinsmeister 1987). Antarctica, at the centre of the Gondwana landmass, attained a south polar position during the Cretaceous. During the late Cretaceous, South America, Antarctica, New Zealand and Australia were still continuous, although there were prominent breaks between all crustal blocks. Separation of Australia from East Antarctica may have begun by the late Jurassic, with the development of deep-sea conditions in this narrow trough c. 80 Ma. Final separation took place between late Eocene and early Oligocene (38 Ma). Separation of West Antarctica from South America occurred during the early Tertiary, however deep-sea conditions have prevailed in the Drake Passage only since the Oligocene/Miocene boundary 23.5 Ma. Once Antarctica was fully isolated by seafloor spreading, the unrestricted circum-Antarctic current began to reach full development. By decoupling warm subtropical gyres from the continent, this current served as a barrier to heat flow and thermally isolated Antarctica. Thereafter glaciers developed, the polar ice cap began to form and the Antarctic Convergence formed and expanded northward (Kennett 1978, 1980). The most recent data suggest that the ice cap may have initially appeared 30 Ma, disappeared, and then reformed 13 Ma to persist to the present (Kerr 1984, 1987).

**Antarctic Convergence**

The Antarctic Convergence, located between 50° and 60° S (Fig. 1), represents an approximate northern boundary for the Antarctic Ocean. Here cold, north flowing Antarctic surface water meets and sinks beneath warmer, less dense Subantarctic water. While there are few physical barriers to migration and dispersal
in marine fishes, the Convergence delimited, at least for the Recent fauna, a natural biogeographic province. The Convergence is characterized by a 3° to 4° change in water temperature, as well as by changes in a number of other oceanographic parameters. This region of abrupt thermal change has had a marked effect on the shallow water fauna by preventing southern migration and colonization of Antarctic waters by most pelagic fishes.

**Southern Ocean palaeotemperatures**

Although there is not complete agreement on all details, Southern Ocean palaeotemperatures during the Cenozoic provide a basis for discussion of water temperatures in relation to the changing Antarctic fish fauna and the emergence of notothenioids. Palaeotemperature variations are inferred from the isotopic ratio of $^{18}O$/$^{16}O$ in the calcium carbonate of foraminiferal tests obtained from cores of the ocean bottom (Kennett 1977). The amount of $^{18}O$ in the tests is dependent on the temperature of seawater at the time tests were formed.

Clarke (1983) has given a summary of palaeotemperature information as it relates to the physiological adaptation of Antarctic marine organisms. He indicates that, based on isotopic data, during the late Cretaceous and Paleocene Antarctic waters were considerably warmer than they are today. A general cooling trend began in the late Paleocene/early Eocene and has continued into the Recent. During this period of c. 50 Ma, water temperatures fell from c. 15°C to less than 0°C. This trend has been interspersed with periods of warming, and there have been occasional drops in water temperature that deviated sharply from the general decline. For example, over a period of a few million years at the Eocene/Oligocene boundary, temperatures declined from 10°C to 6°C. Bottom temperatures have been less than 5°C for c. 12 Ma. Shelf waters today are below 0°C and in some areas, McMurdo Sound for example, the mean annual water temperature is only −1.8°C.

**Factors producing faunal change or limiting diversity**

Comparison of the early Tertiary temperate fauna from Seymour Island with the Recent fauna conveys the impression of marked change in species composition. While in part artifactual, as explained previously, it is true that the Seymour Island fossil faunas have no representatives among the Recent fauna. Furthermore, the Recent fauna is not diverse considering the large size of the ecosystem. Unfortunately there is no fossil record from the late Tertiary, leaving a gap of 38 Ma between the Eocene/Oligocene and the present, and no direct knowledge of the transition fauna (from late Tertiary to Recent).

**Low water temperature**

It is tempting to attribute change in the fish faunal composition to low water temperature, perhaps the most obvious environmental feature of the ecosystem. It is unlikely, however, that this parameter was directly responsible for the disappearance of the Seymour Island fauna or the lack of diversity in the Recent fauna. Low temperature should not have been an insurmountable problem in the evolutionary adaptation of fishes given a decrease of 15°C over a period of c. 50 Ma. When averaged out, the change is 0.03°C per 100 000 years. Even the sharp drop of 5°C over 2 million years at the Eocene/Oligocene boundary amounts to only 0.25°C per 100 000 years. Schoel (1980, p. 246) considers a change of 1°C per 100 000 years as ‘well within the adaptive capabilities for every species ever examined’.

On page one of his thought-provoking monograph, Dunbar (1968) cautions against ‘preoccupation with temperature’ when considering the evolution of polar ecosystems. He notes (1968, p. 56) ‘that adaptation to low temperature as such presents few evolutionary difficulties and has been accomplished by thousands of species’.

Clarke (1983) has also argued convincingly that low temperature is not a limiting factor for biosynthetic processes, that evolutionary adaptation to low temperature has occurred repeatedly and that the majority of life history patterns observed in invertebrates and fishes are reflections of ecological constraints rather than low temperature.

We think that both these viewpoints are valid in considering the evolution of the Antarctic fish fauna. Low water temperature cannot singularly account for the disappearance of the Seymour Island fauna or for the paucity of non-notothenioids among the Recent fauna. Factors in the realm of ecological constraints (Clarke 1983) provide suitable alternative hypotheses relating to available substrate and to food supply.

**Limited habitat**

As a result of isostatic depression of Antarctica by the ice sheet, the average depth of the conti-
nental shelf is 500–900 m. This is four times greater than that of the other continents, and twice as great as that of the Arctic (Johnson et al. 1982). As a result of glacial erosion the shelf is also narrow. Furthermore, Antarctica lacks the extensive archipelagos characteristic of many continents. Thus with deep water close to the continental margin (Fig. 1), the prime habitat for fish diversity is limited.

Glaciation also eliminated existing riverine and estuarine habitats on the continent. These habitats have not existed since the onset of glaciation c. 25 Ma (Johnson et al. 1982). In addition, glaciation on the shelves reduced potential marine habitat for shallow water benthic species (Miller 1987).

Trophic considerations
In considering the pattern of diversification in fossil and Recent fishes, Thomson (1977) suggested that there may be a ceiling on diversity imposed largely by trophic resources. Although Antarctic waters are productive during the summer, seasonal oscillation in the food supply is marked in some areas and may have constrained the evolution of certain trophic types among fishes. There are, for example, no phytobenthic feeders or obligate mass consumers of planktonic crustaceans. Filter feeders might not be able to tolerate the low productivity in the ecosystem during the austral winter. Since seawater has a high kinematic viscosity at low temperatures (Vogel 1981), it is also possible that the evolution of continuously swimming, filter feeding fishes was hampered by the energetic cost of these activities in subzero seawater.

Benthos is a seasonally stable resource that is theoretically available to fishes at all times of the year. On the east side of McMurdo Sound infaunal densities are among the highest in the world (Dayton & Oliver 1977). However in some areas the Antarctic benthos consists largely of sessile particle feeders or scavengers (Hedgpeth 1969; Dell 1972) that are mostly inedible (sponges, barnacles, sedentary polychaetes, sea urchins, sea stars, sea spiders and brittle stars). The taxonomic composition of the invertebrate fauna may also contribute to a reduced number of niches for fishes. Grande & Eastman (1986) suggested that the diversification of rajas in the Recent chondrichthyan fauna may have been restricted by the absence of suitable food. Molluscs, an important food group for many rajas, are poorly represented in the Antarctic fauna (Dell 1969; Dayton & Oliver 1977).

Many aspects of the trophodynamics of the Antarctic marine ecosystem are poorly understood, and the food web itself is more complex than previously realized (Clarke 1985). Another level of complexity is added in attempting to assess the influence of trophic factors on the evolution of the fish fauna. Some research, for example, indicates that the distinction between the midwater and benthic productivity may be artificial. At McMurdo Sound, near the southerly limit of marine life, Berkman et al. (1986) found bottom sediments containing viable algal material throughout the period of winter darkness. They suggested that such primary detritus, when resuspended by currents, could serve as a 'food source for planktonic herbivores feeding during the austral winter in nearshore environments'.

Origin of notothenioids
Nonexistent fossil record
Identification of fossil notothenioids would probably be based on only osteological evidence. Unfortunately there is not a unique osteological feature known that characterizes the suborder. A morphological diagnosis of the Nototheniidae includes (Eakin 1981): (1) three flat, plate-like pectoral radials, (2) pleural ribs poorly developed and floating or absent, (3) one nostril on each side of the head, (4) non-pungent fin spines, (5) no swim bladder, (6) two or three lateral lines, occasionally one, (7) jugular pelvic fins and (8) usually fewer than 15 principal caudal rays (10–19). Individually none of these characters is unique to notothenioids and therefore as characters they are somewhat ambiguous. The group is diagnosed by a proposed unique combination of characters rather than by one or more synapomorphies. Hence it will be difficult to recognize a notothenioid any specimen not possessing the entire suite of characters. Also some are features of the soft anatomy that will not be represented in the fossil record.

Traits essential for survival at low temperature
We have advanced the hypothesis that low water temperature was not primarily responsible for either eliminating the Seymour Island fish fauna or for constraining the diversity of the Recent fauna. Similarly the emergence of notothenioids was probably not a direct response to cooling, but the subsequent radiation of this group under cold conditions was necessarily associated with
a variety of specializations related to low water temperature.

Antifreeze. The acquisition of antifreeze glycopeptides by notothenioids was absolutely essential for survival in certain habitats in the Southern Ocean. Over the past 20 years DeVries (1982) has elucidated the structure, mode of action and distribution of antifreezes in notothenioids.

Nothing is known about the evolutionary origin of antifreezes. Surface mucus may have acted as an antifreeze by preventing propagation of ice across the thin epithelial surfaces of the gills. This may have provided adequate protection before waters reached temperatures below the body’s freezing point. As climatic cooling continued, more effective internally synthesized and systemically distributed antifreezes may have become necessary.

While antifreezes were probably not present (or at least not necessary for survival) in the ancestral notothenioids living in the warmer waters of the late Cretaceous/early Tertiary, the acquisition of antifreezes allowed the radiation of some notothenioids into ice-laden habitats later in the Tertiary. Not all Recent notothenioids require antifreezes, only those species living in portions of the water column colder than −0.8°C and where ice is present, or species liable to encounter ice during latitudinal or vertical migrations. Notothenia kempi, for example, inhabits a +1°C layer of water near the Balleny Islands and does not possess antifreezes (DeVries & Lin 1977). The New Zealand black cod (Notothenia angustata) does not have antifreeze translation products and does not synthesize antifreezes (DeVries et al. 1982). While cold resistance is ancestral for the suborder (Andriashev 1987), the possession of definitive antifreeze glycopeptides may be a derived condition associated with other derived conditions such as agglomerular kidneys (Eastman & DeVries 1986b).

We do not agree with the theory of Scott et al. (1986) that antifreezes first appeared in notothenioids as the stock responded to the Eocene/Oligocene cooling event at 38 Ma. Waters at this time were simply too warm (5°–7°C) to require the presence of definitive antifreezes in a benthic stock not likely to be exposed to sea ice. Water temperatures did not approach 0°C until the late Miocene, c. 10 Ma. As the notothenioid stock diversified, cryopelagic offshoots like Pagophilus borchgrevinki might have required antifreezes early in their evolutionary history as they became associated with ice. On the other hand, some benthic species, confined to ice-free habitats or to Subantarctic waters, might never require antifreezes. We suspect that antifreezes evolved rapidly in various notothenioids during the past 10 Ma. They have been isolated in only 15 species to date (Ahlgren & DeVries 1984; Eastman & DeVries 1986).

Enzyme adaptations. Low environmental temperatures have a rate-depressing effect on biochemical processes in poikilotherms. Notothenioids are stenothermal with some species from McMurdo Sound having upper lethal temperatures of +6°C (DeVries 1977). Since upper and lower lethal temperatures cannot be raised or lowered by warm or cold acclimation, notothenioid enzyme systems are obviously specialized for function under constantly cold conditions. While far from complete, research on notothenioids to date suggests that only one set of isozymes is necessary for an unchanging thermal environment like McMurdo Sound (Clarke 1987). Clarke also indicates that notothenioid enzyme systems function at constantly low temperatures through genetic expression of enzyme variants with lower free energies of activation and by fine control of the enzyme microenvironment.

Membrane adaptations. Normal function of plasma and organelle membranes is necessary for survival of notothenioids at low temperatures. That vital functions like ionic transport and synaptic transmission occur is evidence that there has been adaptation in the membrane systems of these fishes. Conservation of the physical state of membrane lipids and proteins in poikilotherms is known as homeoviscous adaptation (Hochachka & Somero 1984). The fluidity of membranes is influenced by the ratio of saturated/unsaturated fatty acids in membrane phospholipids (Prosser 1986). Increased unsaturation of fatty acids ensures membrane fluidity at low temperatures. Work on notothenioids indicates that both sensory and motor nerves are resistant to blockade at low temperatures, and show compensatory increases in excitability and conduc tion velocity compared with values extrapolated from temperate fishes (Macdonald 1981; Montgomery & Macdonald 1984).

Conclusion

Biochemical specializations have predominated over gross morphological specializations in allowing notothenioids to successfully exploit this environment. Recent work on the eyes of notothenioids is a case in point (Eastman 1988b).
McMurdo Sound notothenioids are subject to a unique photic regime. Four-month periods of continual darkness in the winter and continual light in the summer are separated by two month transition periods. However, there is no obvious correlation between the unusual light conditions in McMurdo Sound and ocular morphology among ecologically diverse notothenioids. The key evolutionary adaptations for visual function in this habitat are biochemical. Antifreeze glycopeptides prevent freezing of ocular fluids, while homeoviscous adaptations allow normal cellular function, including synaptic transmission in the retina and eye muscle contraction, at subzero temperatures. Apparently light penetration in McMurdo Sound is sufficient to permit ocular function in cold adapted, but morphologically unspecialized, eyes.

**Diversification of notothenioids**

The Antarctic continental shelf is 400–500 m deep at the edge and also contains inner shelf depressions 1000 m deep (Andriashev 1965). When compared to the depth distribution of temperate fishes, species diversity among Recent notothenioids is greatest at 300–600 m rather than 100–200 m (Andriashev 1965, 1987; DeWitt 1971). This pattern of distribution, known as glacial submergence, may be attributable to destruction of bottom habitat by continental glaciers and ice shelves (Andriashev 1987). This habitat and fault destruction may have caused the local extinction of most of the early fish fauna, leaving an ecological void which was filled by a notothenioid fauna tolerant of deep water conditions.

Most Recent notothenioids are bottom fishes confined to waters less than 1000 m deep, although the depth range of individual species may be considerable (DeWitt 1971). There is no reason to suspect that the ancestral notothenioid stock lived any deeper than 1000 m because closely related perciform groups like blennies are coastal fishes. Notothenioids lack swim bladders, are usually denser than seawater and commonly feed and reproduce on the substrate. The midwaters of the Southern Ocean are underutilized by fishes, in an ecological sense, and could theoretically support more species. The waters south of the Antarctic Convergence are productive during the summer, but contain relatively few non-notothenioid fishes. There is evidence of a trend toward diversification, particularly of pelagic species, among notothenioids (Nybelin 1947; Andriashev 1970; DeWitt 1970; Eastman 1985a; Hubold & Ekau 1987). For example, Dissostichus mawsoni Pleuragramma antarcticum and Aethenia mitopteryx are neutrally buoyant, permanent members of the midwater community (Eastman 1985a, 1988a).

Another factor that may have facilitated diversification of notothenioids is the tendency for the young of some species to pass through a distributive life history stage. Young of the boviichthyid Boviichthys variegatus, for example, are common near the surface in the outer shelf waters off New Zealand (Robertson & Mito 1979). Adults, however, are typical heavy bottom dwellers in shallow coastal and intertidal habitats. The evolution of neutrally buoyant species like Pleuragramma antarcticum could have been the result of neoteny.

The absence of competition and the isolation of Antarctica have provided the opportunity for speciation within this group. Thus notothenioids fill ecological roles normally occupied by taxonomically diverse fishes in temperate waters. There has obviously been evolutionary diversification in this basic notothenioid body plan (Fig. 3). Work over the last 10 years has revealed the morphological basis for the diversification in buoyancy and body types in the family Nototheniidae (Eastman & DeVries 1981, 1982, 1985, 1986a; DeVries & Eastman 1978, 1981; Clarke et al. 1984). This family contains 16 genera and about 50 species, including a variety of ecological types (Fig. 3).

(1) **Large, pelagic midwater predator.** Averaging 127 cm in total length and 28 kg in weight, Dissostichus mawsoni is six times longer and 250 times heavier than most other notothenioids. In McMurdo Sound Dissostichus live at 300–500 m and can be considered the ecological equivalent of a shark.

(2) **Shoaling midwater zooplanktivore.** Pleuragramma antarcticum has a depth range of 0–900 m and is found in both open water and beneath ice. A vital component of the food web in the Southern Ocean, it is an especially numerous and ecologically important nototheniid (Eastman 1985b). Although not a filter feeder, Pleuragramma may be ecologically equivalent to a herring.

(3) **Cryopelagic species.** Pagothenia borchgrevinki are specialized for swimming and feeding near the undersurface of the sea ice (Eastman & DeVries 1985).

(4) **Benthopelagic species.** Although they live close to the bottom, their streamlined appearance and lack of substrate contact adaptations indicate that they do not actually live on the substrate. In McMurdo Sound Trematomus loemnbergi inhabits depths of at least 450 m.
(5) Benthic species. Like their ancestors, most nototheniids are benthic, spending their lives on or near the substrate. There is a greater variety of food and micro-habitats available to bottom dwelling fishes than to midwater fishes, consequently bottom dwelling communities are more diverse (Roberts 1982).

(6) Generalized species that are difficult to classify ecologically. Cryothenia peniuviae exhibits morphological characteristics of both pelagic and benthic species. It may be an ecological generalist living and feeding in the mid-waters or on the bottom.

(7) Species with an ontogenetic change in life cycle. In Notothenia rossii marmorata fingerlings are pelagic, nearshore juveniles are demersal and offshore adults are both demersal and pelagic. These changes in habitat are accompanied by changes in colour, caudal fin shape and body shape (Burchett 1983).

Final Remarks

The diversification and dominance of Recent notothenioids probably indicate that the Southern Ocean is, in an ecological sense, underutilized by fishes and theoretically capable of supporting more species. Notothenioids fill roles occupied by taxonomically diverse fishes at lower latitudes. Since fossil notothenioids have not been discovered, we can say little about the prior distribution of this group. The fossil record does indicate, however, that a reasonably diverse fish fauna was present in the temperature waters near Seymour Island about the time notothenioids are suspected to have originated. We have discussed the disappearance of the Seymour Island fauna, the emergence of notothenioids and the lack of diversity among Recent non-notothenioid fishes. Further studies in Antarctic fish biology and additional palaeontological work at Seymour Island will contribute to the resolution of these intriguing issues.

Fig. 3. These seven species of notothenioids from McMurdo Sound demonstrate some of the morphological and ecological divergence mentioned in the text. Pelagic, cryopelagic, benthopelagic and benthic species are illustrated. All are members of the family Nototheniidae except Gymnodraco acuticeps which is a bathydraconid. Dots indicate typical habitat; however most species have considerably wider depth ranges. From Eastman & DeVries (1986w), copyright © 1986 by Scientific American, Inc. All rights reserved.
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EVOLUTION OF ANTARCTIC FISHES


