



Fishes on the Antarctic continental shelf: evolution of a marine species flock?*

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Distance, currents, deep water and sub-zero temperatures isolate the waters of the Antarctic continental shelf from other shelf areas in the Southern Hemisphere. The Antarctic shelf is an insular evolutionary site for a variety of marine organisms. The fish fauna is relatively small and unusual in composition, consisting of 213 species with higher taxonomic diversity restricted to 18 families. Ninety-six species of perciform notothenioids comprise 45% of the fish fauna. However in many areas of the shelf, including the highest latitudes, notothenioids make up 77% of the species and 90–95% of fish abundance and biomass. Notothenioids are morphologically and ecologically diverse and have diversified into niches in the water column. Antarctic notothenioids were evaluated using criteria employed for assessing freshwater species flocks. Although monophyly is in question, notothenioids exhibit the disproportionate speciosity (5.6-fold more Antarctic than non-Antarctic species) and high endemism (97%) characteristic of a species flock. Notothenioids are one of the first recognized examples of a species flock of marine fishes. Notothenioids are compared with some freshwater species flocks and calculations made of the time required for speciation (TFS) for notothenioids of the family Channichthyidae. Estimates of TFS are slower than for most lacustrine species flocks but similar to estimates for island radiations of birds and arthropods.

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INTRODUCTION

The polar regions and their faunas are commanding attention as biodiversity, environmental change and resource management are viewed increasingly in a global context. Since climatic change is a stimulus for evolution, contrasting and explaining polar marine biodiversity has intrigued biologists working in polar regions (Dunbar, 1968, 1977, 1989; Hempel, 1985; Dayton, 1990; Clarke & Crame, 1992, 1997; Dayton *et al.*, 1994; Crame, 1997). In the case of fishes, there have been evolutionary responses to the polar environment at levels of organization from the molecule to the community (Eastman, 1997). For example, freezing resistance adaptations involving elevated osmolality and the acquisition of antifreezes have appeared among unrelated fishes from both poles (DeVries & Cheng, 1992; Davies *et al.*, 1993; Chen *et al.*, 1997*a,b*; Cheng, 1998*a,b*), and a cryopelagic community, composed of unrelated fishes, resides at the undersurface of the pack ice at both poles (Andriashev, 1970). However, fishes in the two polar regions have been subject to different regional histories that have influenced the evolution of faunal diversity. The key distinguishing feature of the

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Antarctic fish fauna relative to the northern polar fauna, is that the long isolated Antarctic shelf harbours an endemic radiation of notothenioid fishes.

Other endemic radiations of fishes, usually within a freshwater lake, have been termed species flocks (Echelle & Kornfield, 1984). Such species flocks, especially those in ancient African and Siberian rift lakes, have engendered great interest (Brooks, 1950; Myers, 1960; Kozhov, 1963; Fryer & Iles, 1972; Echelle & Kornfield, 1984; Meyer, 1993; Martens *et al.*, 1994; Sturmbauer, 1998; Stiassny & Meyer, 1999). Species flocks are also represented as fossils in Jurassic and Pliocene rift lakes (McCune, 1987*a,b*, 1990; Smith, 1987). The possible existence of flocks in the marine realm has received less attention; candidates include Antarctic perciform notothenioids (Eastman, 1993; Clarke & Johnston, 1996; Eastman & Clarke, 1998; Johns & Avise, 1998) and North-eastern Pacific scorpaenids of the genus *Sebastes* (Johns & Avise, 1998). In this paper Antarctic fish diversity is reviewed at the species level, and it is suggested that the dominant notothenioids are comparable to lacustrine species flocks in many respects. The Antarctic continental shelf is contrasted with other continental shelves of the world and with the isolated lake basins inhabited by more familiar fish species flocks. The distinctive taxonomic composition of the fish fauna and the morphological and ecological divergence of notothenioids on the shelf are outlined. The data are examined suggesting that the Antarctic notothenioids are similar in many respects to the species flocks of freshwater fishes. Evolutionary time scales for channichthyid notothenioids and freshwater species flocks are compared, employing calculations of the time required for speciation (TFS). It is concluded that, when assessed using the criteria of Ribbink (1984), notothenioids appear to be the marine equivalent of a freshwater species flock.

THE ANTARCTIC CONTINENTAL SHELF AS AN EVOLUTIONARY SITE

CONTINENTAL SHELVES

Continental shelves are shallow extensions of continental landmasses into the sea. The shelf break, the transition to the continental slope, averages 130 m deep over most of the world ocean (Kennett, 1982). Although shelves represent only *c.* 7% of the ocean's surface and 0.2% of the ocean's volume (Postma & Zijlstra, 1988), they are sites of high biodiversity and centres of evolution in some areas of the world. The world's fish fauna includes 24 618 species in 484 families (Nelson, 1994). About 60% are marine species and about 46% of the total number live on the continental shelf at depths of <200 m (Cohen, 1970). Certain small areas of the shelf are sites of especially high species diversity. For example, although coral reefs occupy only 0.1% of the earth's surface (Kohn, 1997), they present topographically and trophically complex habitats that harbour high fish biodiversity: *c.* 25% of all marine fish species (Ormond & Roberts, 1997). Such high biodiversity in a small area is atypical, so as a basis for comparison with the Antarctic, a description of species diversity among other cold and cold-temperate shelves of the world should be informative. The fish fauna of the Arctic Region, as delimited by Andriashev & Chernova (1995), includes 96 families containing 416 species, 358 marine and 58 freshwater (Andriashev & Chernova, 1995). There are no up-to-date figures for endemism, although Briggs (1974) cites

20–25% for marine species. The North Sea fish fauna includes 170 species from 69 families (Zijlstra, 1988), and there are similar numbers off the north-east coast of the United States: 180 species and 82 families (Sherman *et al.*, 1988). The Tasmanian fish fauna includes 459 species in over 150 families (Last *et al.*, 1983). The territorial waters of New Zealand contain 1008 species in 208 families (Paulin *et al.*, 1989). Endemism is 11% at the species level.

THE ANTARCTIC SHELF

The Antarctic shelf is not contiguous with other shelf areas of the Southern Hemisphere, and is isolated from other landmasses by deep water. Another characteristic feature of the Antarctic shelf is its great depth: at 500 m it is eight times the world average (Anderson, 1999). The depth is due to downwarping caused by the weight of the ice sheet on the continent, by glacial erosion and by absence of sedimentation from fluvial discharge (Anderson, 1999). The Antarctic shelf also differs from other shelves in characteristics related to its polar locality including sub-zero temperatures, pack ice and a highly seasonal light regime. Water temperatures in high latitude shelf areas are between -1.5 and -1.9°C .

During the last glacial maximum, ice shelves extended to the outer continental shelf of the Ross and Weddell Seas (Anderson, 1999). In the Ross Sea, grounded ice occupied most of the continental shelf as recently as the late Pleistocene, about 34 000 years BP (Anderson, 1999). The shelf is deeply eroded in many areas, so topography and bathymetry are irregular, there are ridges and banks as well as troughs, or inner shelf depressions, with depths to 1400 m. The troughs are eroded by ice discharged from outlet glaciers (Anderson, 1999). There are few wave dominated coastal zones and beaches since coasts are covered by glacial or pack ice. Finally tidal currents are sluggish and terrigenous sediment supply is restricted to glacial processes since the shelf receives no fluvial discharge. The biological consequences are that potential sites of high fish diversity are non-existent or limited on the Antarctic shelf, due to an absence of shallow water in general, and estuaries, reefs and intertidal zones in particular. Furthermore, shallow benthic habitats are covered with anchor ice to a depth of about 30 m and are scarred by icebergs to depths of several hundred metres. These near-shore environments are therefore permanently in a state of change or recovery (Barnes, 1999). Shallow habitats are not as limited in the lower latitude shelf areas of the Scotia Arc and Antarctic Peninsula.

SIMILARITIES BETWEEN ANCIENT LAKES AND THE ANTARCTIC SHELF

At first glance there seem to be few similarities between ancient, isolated lake basins and an extensive area of continental shelf seemingly without physical boundaries. The Antarctic shelf, however, is isolated from other shelf areas in the Southern Hemisphere by distance, current patterns and sub-zero temperatures. The Antarctic shelf is also an evolutionary site and it shares some characteristics of rift lakes holding species flocks of fishes (Table I). Certain rift lakes, Lake Tanganyika for example, are *c.* 10 million years older than the typical post-glacial lake (Martens, 1997). The Antarctic shelf has existed under polar conditions for 14–12 My (Kennett, 1982); it supports a highly endemic fauna and has been a centre of evolution for a variety of aquatic organisms. The

TABLE I. Comparison of features of lakes containing flocks of fishes (Martens *et al.*, 1994) and the Antarctic shelf

Characteristics of lakes	Applicable to the Antarctic shelf?	Comments
Great age (20–5 My)	Yes	Low temperatures and ice for 14–12 My
Considerable depth (permanence)	Yes	500 m deep, as old as many ancient lakes
Isolation	Yes	Geographic, oceanographic, bathymetric and thermal isolation
Speciose fauna	Possibly	Given that certain prime inshore habitats do not exist
Highly endemic fauna	Yes	97% for notothenioid fish species
Centre of evolution for a variety of organisms	Yes	Isopods, amphipods, fishes, penguins, lobodontine seals

Antarctic shelf has been subject to repeated grounding of the ice sheet (Anderson, 1999). Although ice disrupts habitat and faunal stability (Dayton, 1990; Barnes, 1999), this may have presented a stimulus for evolution in the same way that the fluctuations in levels of some African Great Lakes may have promoted the development of species flocks of cichlids (Fryer & Iles, 1972). For example, advances of the ice sheet probably led to regional extinctions of the fish fauna, with populations being forced into refugia near coastal or sub-antarctic islands followed by recolonization after glacial retreat. As a specific example, the Antarctic Polar front advanced 300 km to the north during the late Miocene (6.5–5.0 My) and cold water reached as far north as New Zealand (Kennett, 1982).

HISTORICAL PERSPECTIVE: EVOLUTION ON THE ANTARCTIC SHELF

The Antarctic shelf offers several examples of faunal replacement and radiation among marine groups, including gastropods, echinoids, cirripedes, bryozoans, amphipods and isopods (Brandt, 1992; Brandt *et al.*, 1999). In the case of fishes, during the past 38 My the fauna changed from taxonomically diverse, cosmopolitan and temperate to taxonomically restricted, endemic and polar (Eastman, 1993, 2000).

The cool temperate fish fauna is represented by fossils in the late Eocene (38 My) La Meseta Formation on Seymour Island near the Antarctic Peninsula (Eastman, 1993, 2000). With the tectonic and oceanographic changes in the Tertiary, the Antarctic shelf became isolated, colder and subject to ice scour. Especially important was sea floor spreading that opened the Drake Passage to deep water, and the subsequent development of the Antarctic Circumpolar Current and Antarctic Polar Front at 25–22 My (Kennett, 1982). Conditions and climate on the shelf became polar with the formation of sea ice at 14–12 My (Kennett, 1982). It is not known when the Eocene fauna became extinct or whether there were transitional faunas, but there was little carryover of genera and families from the Eocene into the modern fauna. The faunal replacement was attributable to a variety of factors including destruction of inshore habitats

TABLE II. Families of benthic fishes in the Antarctic Region

Taxon ^a	Number of species ^b	Percentage of fauna
Myxinidae (hagfishes)	1	0.5
Petromyzontidae (lampreys)	1	0.5
Rajidae (skates)	8	3.7
Carapidae (pearlfishes)	1	0.5
Moridae (deepsea cods)	4	1.8
Muraenolepididae (eel cods) ^c	4	1.8
Gadidae (cods)	1	0.5
Congiopodidae (horsefishes)	1	0.5
Bathylutichthyidae ^d	1	0.5
Liparidae (snailfishes)	67	31.5
Zoarcidae (eelpouts)	23	10.8
Notothenioidei (includes five Antarctic families)	96	45.1
Tripterygiidae (triplefins)	1	0.5
Achiropsettidae (southern flounders)	4	1.8
Totals	213	100%

^aArranged phylogenetically with sequencing according to Nelson (1994).

^bBased on Gon & Heemstra (1990); notothenioids updated by Eastman & Eakin (2000) and these additions among non-notothenioids: number of liparids from Andriashev & Stein (1998) plus three from Matallanas (1998, 1999) and number of zoarcids from Anderson (1994).

^cThere may be an additional species of *Muraenoelpis* near South Georgia (Kompowski & Rojas, 1993).

^dBalushkin & Voskoboinikova (1990).

by ice and changing trophic conditions; new ecological niches became available and the notothenioids were able to adapt to these.

FISH FAUNA OF THE ANTARCTIC SHELF

Unlike other oceans, the Southern Ocean surrounding Antarctica is not a distinct basin but is delimited by an oceanographic feature, the Antarctic Polar Front. The vast area of cold ocean south of the Polar Front is the Antarctic Zoogeographic Region. Compared with other large marine ecosystems, the fish fauna of the Southern Ocean is limited in both species and higher taxonomic diversity. The Southern Ocean contains only 313 species in 50 families (Gon & Heemstra, 1990; Eastman, 2000). Thus the Southern Ocean, representing 10% of the world's ocean, contains only 1.3% of the world's fish fauna. Benthic fishes are the major component of the fauna on continental shelf and upper slope of the Antarctic Region (Table II). There are 213 species and higher taxonomic diversity is confined to 18 families (Gon & Heemstra, 1990; Eastman, 2000). Two perciform groups, the Notothenioidei (notothenioids) and the Zoarcidae (eelpouts), and the scorpaeniform family Liparidae (snailfishes) are the most speciose taxa, accounting for 87.4% of the species. Such restriction of higher taxonomic diversity is unusual among shelf faunas.

NOTOTHENIOID DIVERSITY

The fish fauna in general is highly endemic, with 88% of the species confined to waters south of the Antarctic Polar Front (Andriashev, 1987). If just

TABLE III. Fishes collected in 19 bottom trawls at depths of 107–1191 m on the shelf of the southwestern Ross Sea (73–77° S), cruises 96-6 and 97-9 of the RV ‘Nathaniel B. Palmer’^a

Family	Percentage by:		
	No. of species ^b	No. of specimens ^c	Weight (station 119 only) ^d
Rajidae	6.4	0.7	
Muraenolepididae	2.1	1.6	
Liparidae	6.4	0.8	
Zoarcidae	8.5	5.3	8.8
Nototheniidae	14.9	50.1	16.8
Arteidraconidae	27.7	14.5	15.1
Bathydraconidae	19.1	18.9	30.1
Channichthyidae	14.9	8.1	29.2
Totals	100%	100%	100%

^aData from Eastman & Hubold (1999).

^bNumber of species is 47.

^cNumber of specimens is 979.

^dNumber of specimens at station 119 (77°19' S, 165°41' E; 900–910 m deep) is 83.

notothenioids are considered, endemism rises to 97% (Andriashev, 1987). This is high for a marine group, as specific endemism of only 10% is sufficient for recognition of provinces (Briggs, 1974). In other isolated marine shelf habitats the rate of endemism for fishes is considerably lower; examples include Hawaii at 25%, Easter Island at 23.2% (Briggs, 1995) and the Galápagos at 9.4–16.7% (Grove & Lavenberg, 1997).

The high latitude (71–78° S) embayments of the Ross and Weddell Seas are the largest areas of the Antarctic continental shelf and are representative of the High Antarctic Zoogeographic Zone (Kock, 1992). Here waters are covered by ice for most of the year, water temperatures are nearly constant, usually < –1.5° C, and the fish fauna includes 12 families and about 80 species (Hubold, 1992; Eastman & Hubold, 1999). Midwater and benthic trawling in the Ross and Weddell Seas indicates that notothenioids are dominant in terms of species, abundance and biomass (Table III) (DeWitt, 1970, 1971; Ekau, 1990; Hubold, 1992; Eastman & Hubold, 1999). *Trematomus* is important among nototheniids, and there are larger proportions of artedidraconids, bathydraconids and channichthyids than farther north (Kock, 1992). Notothenioids are dominant because they occupy niches filled by taxonomically diverse groups of fishes in temperate and tropical oceans, groups not represented on the Antarctic shelf.

Further north, the Seasonal Pack-ice Zoogeographic Zone extends between the maximum limit of pack-ice in winter/spring and the minimum limit in autumn/summer (Kock, 1992). The shelf near Elephant Island (61°10' S, 55°14' W), one of the South Shetlands, is typical of this zone. Twenty-one families and 65 species compose the fish fauna (Kock & Stransky, 2000). Elephant Island is an area of faunal overlap; notothenioid species with High Antarctic distributions still dominate species diversity but they account for only 1% of abundance and biomass (Tiedtke & Kock, 1989; Kock & Stransky, 2000).

Instead Lesser Antarctic notothenioids, especially nototheniids of the genera *Gobionotothen*, *Notothenia* and *Lepidonotothen* and a few channichthyids, dominate abundance (91–98%) and biomass (Tiedtke & Kock, 1989; Kock & Stransky, 2000). Harpagiferids are present but there are lower proportions of artedidraconids, bathydraconids and channichthyids than further south (Kock, 1992). Although fish biomass is higher in the Seasonal Pack-ice Zone, indices of species diversity and evenness are lower than for comparable depths on the High Antarctic shelf (Tiedtke & Kock, 1989).

MORPHOLOGICAL AND ECOLOGICAL DIVERSIFICATION IN NOTOTHENIOIDS

The sub-order Notothenioidei includes eight families and 122 species. Five families and 96 species are Antarctic whereas three families and 26 species are non-Antarctic (Eastman & Eakin, 2000). In contrast to many other fish radiations, which may show phyletic diversity but little morphological and ecological diversity (Brooks & McLennan, 1991; Mayden, 1992), notothenioids exhibit substantial morphological and ecological diversification. The diversification relates to niches in the water column, especially those involving pelagic or partially pelagic zooplanktivory and piscivory (Eastman, 1993). The large stocks of Antarctic krill *Euphausia superba* are an exceptionally important resource for many of the Lesser Antarctic notothenioids that consume this species throughout their life (Kock, 1992). Notothenioids fill water column niches but are also the dominant benthic group. The family Nototheniidae is a case in point: about one-half the species occupy the ancestral benthic habitat, but others are semipelagic, epibenthic, cryopelagic and pelagic (Eastman, 1993). This type of radiation, known as pelagization or pelagicism, has arisen independently in different nototheniid clades (Klingenberg & Ekau, 1996). Morphological diversification centred on features associated with buoyancy control. Although notothenioids lack swim bladders, density reduction to neutral buoyancy has been achieved in some species through a combination of reduced skeletal mineralization and lipid deposition (Eastman, 1993).

Unlike some other radiations of fishes, especially cichlids (Fryer & Iles, 1972), there has been only modest diversification in trophic morphology and no fine scale partitioning of trophic resources among notothenioids. Some niches have remained unfilled—there are no continuously swimming filter feeding zooplanktivores (Eastman, 1993). Some pelagic species that permanently inhabit the water column are relatively sedentary. *Pleuragramma antarcticum* Boulenger, for example, is a discriminate zooplanktivore that spends much of its time motionless in the water column, something that is possible because its buoyancy is attributable to static rather than dynamic mechanisms.

ANTIFREEZE AS A KEY INNOVATION CREATES ECOLOGICAL OPPORTUNITY

A key innovation is a uniquely derived feature, or synapomorphy, characteristic of a clade and correlated with the radiation of that clade (Brooks & McLennan, 1991). Notothenioid antifreeze glycopeptides, which arose from a related pancreatic trypsinogen-like protease (Chen *et al.*, 1997a; Cheng & Chen, 1999), are distinct from all other types of fish antifreezes, including the

glycopeptides of Arctic gadids (Chen *et al.*, 1997b; Cheng, 1998a). Only *c.* 20–25% of the species and three of the five families in the Antarctic notothenioid clade have been surveyed for the presence of antifreezes (Eastman, 1993), so it may be premature to designate these compounds formally as a synapomorphy for the group. Nevertheless this is likely, since the antifreezes are essential for life and would be expected to be present in all notothenioids living in subzero waters where contact with ice is likely (DeVries, 1988).

The notothenioid antifreeze gene sequence began as an integral part of the ancestral protease gene, underwent expansion and then shed most of the protease sequence (Cheng & Chen, 1999). Based on the 14–5 My age inferred from the divergence of molecular sequences between trypsinogen and antifreeze (Chen *et al.*, 1997a), the acquisition of antifreeze genes was coincident with the appearance of ice on the Antarctic shelf. When mapped on the notothenioid cladogram, antifreeze glycopeptides have a single origin at the node for the Antarctic clade: the sister group of the non-Antarctic Eleginopidae (Eastman & Clarke, 1998). The Antarctic notothenioid clade of 95 species (excluding the Bovichtidae, and the non-Antarctic Pseudaphritidae and Eleginopidae), characterized by antifreeze glycopeptides, is nearly six times more diverse than its non-Antarctic sister group.

Notothenioid antifreeze meets the criteria of a key innovation as defined by Brooks & McClennan (1991), but according to others, a key innovation must also aid entry to a new ecological habitat (Grant, 1998). It has been suggested that a key innovation in the feeding mechanism of cichlid fishes facilitated evolution of trophic specializations characteristic of the African cichlid radiations (Liem, 1973), but key innovations seem to be the exception rather than the rule among species flocks of fishes. What *does* seem to be characteristic of many lacustrine species flocks is the colonization of unoccupied habitat, for example, a newly formed lake, preceding the diversification of a lineage. Antifreeze glycopeptides of Antarctic notothenioids are a key innovation which allowed either continued existence in or colonization of sub-zero ice-laden water during episodes of ice sheet expansion onto the Antarctic shelf, and this created ecological opportunities for subsequent diversification.

NOTOTHENIOID MONOPHYLY AND DIVERGENCE TIMES

A well-resolved cladogram for the entire notothenioid suborder is not available, although there are cladograms for some smaller taxonomic units. At least two described families are paraphyletic. The monophyly of notothenioids has not been established firmly on the basis of morphological data; the presence of three plate-like pectoral radials is a possible synapomorphy (Eakin, 1981; Iwami, 1985; Lecointre *et al.*, 1997). Molecular sequence data, available for *c.* 30% of the species in the suborder, are also equivocal with regard to monophyly. This work has utilized DNA from mitochondrial genes (Bargelloni *et al.*, 1994, 1997, 2000; Ritchie *et al.*, 1996, 1997), nuclear genes (Lecointre *et al.*, 1997) or a combination of both (Bargelloni & Lecointre, 1998; Chen *et al.*, 1998). The most recent analyses have not supported monophyly (Lecointre *et al.*, 1997; Bargelloni & Lecointre, 1998). Lecointre *et al.* (1997) suggest that early cladogenesis within notothenioids was simultaneous with the explosive diversification of perciforms.

Consequently with little time for differences to accumulate, it is difficult to resolve outgroup nodes.

Divergence times for the shelf-dwelling Antarctic notothenioids have been inferred from molecular sequence data. Most estimates for the age of the radiation of the five families with antifreeze glycopeptides are in the range of 16–10 My. Inference from mitochondrial DNA sequences implies that the radiation took place within the last 15 My (Bargelloni *et al.*, 1994) or 16–10 My (Bargelloni & Lecointre, 1998). In the family Nototheniidae, the average age of the trematomid radiation is only 3.4 My (Ritchie *et al.*, 1996). Again dealing with phyletically derived clades, Bargelloni *et al.* (2000) suggest that the trematomid and channichthyid radiations occurred 8–2 Mya.

One additional point is noteworthy because it influences the number of recognized species in the notothenioid flock. Molecular phylogenetic studies indicate that the family Bovichtidae is paraphyletic and that the newly defined Bovichtidae (*Bovichtus* with nine species and *Cottoperca* with one species) is no more closely related to other notothenioids than are several non-notothenioid outgroups (Lecointre *et al.*, 1997). The divergence of this basal clade probably preceded the radiation of notothenioids on the Antarctic shelf, so a case can be made for removing these ten species from the number included in the notothenioid flock. This reduces the size of the non-bovichtid notothenioid clade to 112 species, 95 Antarctic and 17 non-Antarctic.

HOW RAPID WAS SPECIATION IN NOTOTHENIOIDS?

Often speciation in insular habitats and lakes is thought to be relatively rapid. How do notothenioids compare with other species flocks? To make explicit comparisons of the time required for speciation (TFS) in different lacustrine species flocks of fishes, McCune (1997) defined TFS_{ln} as the average doubling time for number of species in a clade, so that $TFS_{ln} = t(\ln 2)(\ln n)^{-1}$, where t is the age of the clade and n is the number of species.

Clade-level estimates of TFS for notothenioids overall cannot be made given the uncertainty concerning the monophyly of the sub-order and several constituent families. However, estimates of TFS can be made for the monophyletic clade of Antarctic notothenioids using the origin of antifreeze to date the origin of the clade (Chen *et al.*, 1997a) and for Channichthyidae (icefishes), based on nucleotide sequences from the cytochrome b gene (Chen *et al.*, 1998). These data (Table IV) allow comparisons of TFS with lacustrine species flocks and island radiations.

For the 95 species of Antarctic notothenioids, estimated TFS is 0.76–2.1 My, the range of the estimate reflecting the range of estimated time of divergence (5–14 My) of the antifreeze and trypsinogen genes (Chen *et al.*, 1997a). Clade level estimates of TFS, based on cytochrome b (Chen *et al.*, 1998), for channichthyids vary from about 1–6 My per divergence event, depending on the calibration used (0.4, 1.0, 2.5% sequence divergence per million years; Table IV). None of these calibrations are ideal, given that they are not specific for notothenioids and cytochrome b, but all have been used to calibrate sequence divergence in teleost fishes. In his review of mitochondrial DNA evolution, Rand (1994) reports a rate of mitochondrial DNA evolution in carp *Cyprinus carpio* L. of about 0.4–0.7% My⁻¹. Martin & Palumbi (1993) estimated a rate

TABLE IV. Estimated divergence times for some species of the notothenioid family Channichthyidae^a

Sister species pair ^b or clade level average ^c (TFS _m)	Cytochrome b, no. of base pairs	% seq. div.	TFS estimated with different calibrations	
			2.5% My ⁻¹	1% My ⁻¹ — 0.4% My ⁻¹
<i>Neopagetopsis ionah</i> and <i>Pseudochaenichthys georgianus</i>	752	4.3	1.72 My	4.3 My
<i>Pagetopsis macropterus</i> and <i>P. maculatus</i>	752	1.9	0.76 My	1.9 My
<i>Chionobathyscus dewitti</i> and <i>Cryodraco antarticus</i>	722	2.1	0.84 My	2.1 My
<i>Chionodraco rastrispinosus</i> and <i>C. hamatus</i>	752	2.3	0.92 My	2.3 My
Clade level estimate of TFS ^c	722	9.3	0.95 My	2.4 My

^aBased on Figure 1 (parsimony tree) and sequence data in Chen *et al.* (1998).

^bSpecies pairs comparisons were made for the four pairs of sister species shown in the parsimony tree from Chen *et al.* (1998). Cytochrome b sequences for those eight species were obtained from GENBANK. Sequences were aligned and uncorrected % sequence divergence computed using DNAsStar.

^cThe clade level estimate is computed for the 15 species of Channichthyidae using the maximum pairwise % sequence divergence reported in Chen *et al.* (1998) to estimate divergence time for the clade (see text). Because this average estimate is based on a sample of 14 of the 15 species in the clade, the estimate assumes that the unsampled species would be nested somewhere inside the phylogeny given by Chen *et al.* and its sequence would not differ from any other species by more than 9.3%.

of 0.9–1.0% My^{-1} based on RFLP data for salmonids and Meyer *et al.* (1990) used 2.5% My^{-1} for cichlids, a calibration that was based on mammalian divergence data. Of the three suggested calibrations for divergence of mitochondrial DNA, the two faster calibrations gave better agreement between clade age of endemic fishes and the most refined geological dates for the origin of the lakes which they inhabit (McCune, 1997). Similarly, these two faster calibrations for mitochondrial DNA divergence, 1% or 2.5% My^{-1} , yield estimated values of TFS for channichthyids (0.95 and 2.4 My) which are in reasonably good agreement with TFS (TFS=0.76–2.1 My), based on divergence of antifreeze and trypsinogen genes, for Antarctic notothenioids overall.

TFS can be approximated for pairs of sister species using maximum time since divergence, computed as the product of % DNA sequence divergence between sister species and a calibration factor. However this estimate may be confounded by variation that preceded divergence and include differences that have accumulated since divergence (McCune & Lovejoy, 1998). Such values for maximum time since divergence can be estimated for four pairs of sister species within the Channichthyidae (Table IV), given the nearly complete species sampling in Chen *et al.* (1998). These maximum values of divergence time between sister species (0.8–1.7 or 1.9–4.3 My, depending on calibration) are in good agreement with the clade level estimate of TFS for channichthyids, and both are in agreement with the TFS estimated for Antarctic notothenioids using the higher calibrations of 1–2.5% My^{-1} (Table IV).

A review of TFS in lacustrine species flocks of fishes (using a calibration of 2.5% My^{-1}) showed that in most lacustrine species flocks, TFS is <0.3 My, except for Lake Tanganyikan cichlids which may be slower (McCune, 1997). For selected island radiations of Galápagos finches as well as Hawaiian arthropods and birds, TFS is 0.6–1.3 My. Estimated TFS for icefishes (0.8–1.7 My) is similar to the estimated TFS for these island faunas if the same 2.5% My^{-1} calibration is used. But if this calibration is too fast, then speciation in icefishes may be considerably slower than in these other groups. McCune & Lovejoy (1998) suggested that the apparently slower rate of speciation within island faunas relative to lacustrine species flocks might be a reflection of the allopatric mode of speciation in island faunas being slower than the sympatric mode of speciation among lacustrine fishes. This difference can also be seen simply as a difference in degree of sequence divergence, independent of calibration. If there is any validity to this difference in rates (or sequence divergence) between allopatric and sympatric speciation, then speciation in icefishes would appear to be consistent with an allopatric mode, both in terms of rate and in terms of environmental fluctuations.

ANTARCTIC NOTOTHENIIDS AND OTHER SPECIES FLOCKS

SPECIES FLOCKS

Most species flocks of fishes are confined to lakes, and these flocks are usually <3 My old (Echelle & Kornfield, 1984; McCune, 1997). The Antarctic shelf is not yet widely recognized as an insular evolutionary site. However, given the parallels between the shelf and lacustrine habitats, and the characteristics of notothenioids, there is a rationale for evaluating the five Antarctic families as a

species flock. Ribbink's (1984) definition of a species flock is: 'an assemblage of a disproportionately high number, relative to surrounding areas, of closely related species which apparently evolved rapidly within a narrowly circumscribed area to which all the member species are endemic'. Greenwood (1984) employs a more restrictive definition: 'its members are endemic to the geographically circumscribed area under consideration and are each others' closest living relatives'. The importance of monophyly is thus either essential (Greenwood, 1984) or not a general criterion (Ribbink, 1984). Flocks are a noteworthy biological phenomenon because of the large number of species in a given locality relative to the number of species in surrounding areas, not because of the recent pattern of speciation or monophyly (Ribbink, 1984). If antifreeze glycopeptides are a synapomorphy for the Antarctic notothenioids, then this group would qualify as a species flock under either definition.

One element in both Ribbink's (1984) and Greenwood's (1984) definitions of a species flock does not appear applicable to Antarctic notothenioids. Since notothenioids inhabit the waters of a continent twice the size of Australia, they are not confined to a 'narrowly circumscribed area', and such geographic localization is an essential feature in recognising species flocks. However both definitions were formulated with lake faunas in mind. The Antarctic shelf is isolated, so in this respect the notothenioid fauna of the Antarctic shelf is nearly as discrete as that of a lake. Antarctic notothenioids fulfil the most important criteria of a species flock on the basis of Ribbink's (1984) definition: disproportionate speciosity. Excluding the bovichtids, there are 5.6-fold more Antarctic than non-Antarctic species.

COMPARISON WITH THE COTTOID SPECIES FLOCK FROM LAKE BAIKAL

Among the major lacustrine species flocks (Echelle & Kornfield, 1984), the notothenioid habitat and aspects of their diversification are most similar to the cottoid flock of Siberian Lake Baikal (Smith & Todd, 1984). These similarities include the sparsity of the general fish fauna in the two regions, the appearance of endemic families within each flock, the eurybathy of the flocks and the nature of the morphological diversification necessary for habitation of the water column.

The fish fauna of Lake Baikal includes 56 species from 14 families (Sideleva, 1994, 1996). Of the 50 native species, 29 (58%) are a flock of endemic sculpins of the families Cottidae, Comephoridae and Abyssocottidae. The latter two families are not found outside the lake. Although lacking swim bladders (like notothenioids), some Baikal cottoids diversified away from the ancestral coastal benthic habitat into deeper (abyssal) waters and water column habitats (Smith & Todd, 1984; Sideleva, 1994). In an interesting ecological and morphological parallel with the nototheniid genera *Dissostichus* and *Pleuragramma* (Eastman, 1993), two species of the genus *Comephorus* have also become secondarily pelagic. As is the case in these nototheniids, *Comephorus* are brought close to neutral buoyancy by a combination of reduced skeletal mineralization and increased levels of lipid (Sideleva, 1996).

Recent molecular research has provided an age for the Baikal cottoid flock. Hunt *et al.* (1997) obtained nucleotide sequences of the nuclear rod opsin gene for 12 Baikal species representing all three families and for one non-Baikal

marine species. With the molecular clock set for this gene, they inferred ages of 29.9 My for separation of the Baikal cottoids and the marine outgroup species from a common ancestor, and 4.9 My for the origin of the flock or beginning of the radiation. This age for the origin of the flock is at least 3 My older than that inferred from mitochondrial DNA sequences of a more limited sample of species (Slobodyanyuk *et al.*, 1995). The phylogenetic trees of Hunt *et al.* (1997) also indicate that the adaptation to deep water was a relatively recent event and was confined to the more derived lineages.

RECOGNISING MARINE SPECIES FLOCKS

Ribbink's (1984) criteria identify Antarctic notothenioids as a species flock because this group inhabits one of the few shelf regions that is geographically, oceanographically and thermally isolated. Confinement to a discrete area, exclusive of some oceanic islands, is not a general feature of marine faunas, so it may prove difficult to identify other marine fish groups as species flocks using Ribbink's definition. However, other approaches may be used for the initial recognition of possible marine species flocks. Johns & Avise (1998), for example, employed statistical signatures of non-random cladogenesis contained in molecular sequence data. This approach is objective and applicable to groups where comprehensive molecular data sets are available. It requires no presumptions about what constitutes adequate species or morphological diversity for recognition of a species flock. However, it does not address the critical requirement of geographic localization.

Johns & Avise (1998) sought to identify phylogenetic footprints characterizing ancient marine species flocks when viewed at the present time. Using molecular phylogenetic data, they tested null theoretical models that assume random temporal placement of phylogenetic nodes. The null model is rejected if speciation is non-random and if there is significant clustering of cladogenic events in time. Their analysis detected a marine species flock, with an estimated age 8.5–3.6 My, among the 65 species of North-eastern Pacific scorpaeniform rockfishes of the genus *Sebastes*. This cold temperate shelf dwelling group inhabits the East Pacific Boreal Zoogeographic Region. It is difficult to assign an age to their extensive modern habitat, however the East Pacific Region began to cool with the onset of glaciation in the late Pliocene at 3 My (Briggs, 1995).

Johns & Avise (1998) also conducted a similar analysis using the notothenioid molecular data of Bargelloni *et al.* (1994) and Ritchie *et al.* (1996). When bovichtids were excluded, statistical tests of nodal placements in the notothenioid phylogeny suggested that speciation events were non-random, with significant clustering of cladogenetic events in time—the hallmark of a species flock. This was true for the Antarctic notothenioid families in general, and for the nototheniid trematomids in particular. Research on marine species flocks is in its infancy; so far notothenioids are unique in extending the occurrence of species flocks into a high latitude marine environment.

FINAL REMARKS

Antarctica is a continental island and the waters of its shelf form an insular evolutionary site. These waters resemble a closed basin, isolated from other shelf

areas in the Southern Hemisphere by distance, current patterns and sub-zero water temperatures. As these isolating conditions developed during the past 25 My, the fish fauna adapted to the new shelf habitat and their ranges became highly circumscribed. Notothenioids are the dominant fish group in terms of species, abundance and biomass. In the absence of competition from other fish groups, their morphological and ecological diversification resulted in occupation of under-utilized niches in the water column. They are probably a species flock, comparable to those in some ancient lakes such as Lake Baikal. The existence of a notothenioid species flock reinforces the observation that the formation of fish species flocks is a repeatable evolutionary event. Finally, the Antarctic fauna occupies an extreme in the spectrum of habitats where fishes are found—it provides a glimpse of the scope of adaptation and evolution in one of the world's most isolated and unusual habitats.

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