The nature of the diversity of Antarctic fishes. Pol Biol

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REVIEW

Joseph T. Eastman

The nature of the diversity of Antarctic fishes

Abstract The species diversity of the Antarctic fish fauna changed notably during the ≈40 million years from the Eocene to the present. A taxonomically restricted and endemic modern fauna succeeded a taxonomically diverse and cosmopolitan Eocene fauna. Although the Southern Ocean is 10% of the world's ocean, its current fish fauna consists of only 322 species, small considering the global diversity of ≈25,000–28,000 species. The fauna is "reasonably well-known" from a taxonomic perspective. This intermediate designation between "poorly known" and "well-known" indicates that new species are regularly being described. A conservative estimate of the number of undescribed species is ≈30–60; many of these may be liparids. On the Antarctic continental shelf and upper slope the fauna includes 222 species from 19 families of benthic fishes. The most speciose taxa are notothenioids, liparids and zoarcids, accounting for 88% of species diversity. Endemism for Antarctic species is also, coincidentally, 88%, at least threefold higher than in faunas from other isolated marine localities. Eight notothenioid families, including five that are primarily Antarctic, encompass a total of 44 genera and 129 species, 101 Antarctic and 28 non-Antarctic. The 101 Antarctic species make up 45% of the benthic species diversity in the Antarctic region. However, at the highest latitudes, notothenioids contribute 77% of the species diversity, 92% of the abundance and 91% of the biomass. Although species diversity is low compared to other shelf habitats, the nature of the adaptive radiation in organismal diversity among notothenioids is noteworthy in the marine realm. In some notothenioid clades phyletic diversification was accompanied by considerable morphological and ecological diversification. The exemplar is the benthic family Nototheniidae that underwent a habitat or depth related diversification centred on the alteration of buoyancy. They occupy an array of pelagic and benthopelagic habitats at various depths on the shelf and upper slope. Diversification in buoyancy is the hallmark of the nototheniid radiation and, in the absence of swim bladders, was accomplished by a combination of reduced skeletal mineralisation and lipid deposition. Although neutral buoyancy is found in only five species of nototheniids some, like *Pleuragramma antarcticum*, are abundant and ecologically important. Much work remains to be done in order to frame and to use phylogenetically based statistical methods to test hypotheses relating to the key features of the notothenioid radiation. To reach this analytical phase more completely resolved cladograms that include phyletically basal and non-Antarctic species are essential.

Introduction

Biologists have discovered and described only about 10% of the species diversity of the earth's biosphere (Wilson 1992; Brooks and McLennan 2002). Since the world ocean occupies nearly 70% of the earth's surface, documenting and explaining large-scale patterns of marine diversity is an especially challenging task (Committee on Biological Diversity in Marine Systems 1995). Knowledge of species composition in an area or ecosystem is a fundamental prerequisite for subsequent work in evolutionary biology, ecology, biogeography and conservation. Fortunately, after a century of exploration and taxonomic work, fish species diversity in the 10% of the world's ocean around Antarctica, the Southern Ocean, is sufficiently well-known to allow us to note some unusual aspects of its composition and to begin to recognize macroevolutionary events such as radiations in certain components of the fauna.

There are currently 322 recognized species of Antarctic fishes, a small number considering the global diversity of fishes (≈25,000–28,000 species) and the large

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size of the Southern Ocean. But the relatively low species diversity should not lead us to dismiss the fauna as uninteresting or unimportant in comparison to the speciose faunas of tropical lakes, rivers and coral reefs. Here, I will suggest that numbers of species are not all that counts and that, when considering the Antarctic shelf, the nature of the fish diversity overshadows the absolute numbers. By this, I mean that the high latitude shelf waters of Antarctica might be considered an evolutionary hot spot (here meaning a concentration of diversity found nowhere else) in the sense that the abundance and biomass as well as the morphological and ecological diversity of the dominant notothenioid fishes eclipses the rather small number of species. Notothenioids have radiated in the subzero waters of the continental shelf (Eastman 1993, 2000; Clarke and Johnston 1996) and may form a special type of adaptive radiation known as a species flock (Eastman and Clarke 1998; Eastman and McCune 2000). A species flock is an assemblage of a disproportionately high number of closely related species that have evolved rapidly within a circumscribed area where most species are endemic (Ribbink 1984). In this respect the Antarctic fish fauna resembles those from some of the well-studied hot spots, especially Lake Baikal, an ancient rift lake in Siberia. This macroevolutionary aspect of Antarctic biology, involving faunal radiation, has not received the attention of comparable events in non-Antarctic localities and is under appreciated by most evolutionary biologists not working in Antarctica. Surrounding an isolated continental island, the cold shelf waters of Antarctica form a unique evolutionary site.

As the twenty-first century begins, evolutionary research on Antarctic fishes is growing and thriving in the sense that more scientists have become involved, research output is increasing and new methodology is being applied to longstanding enigmas. Knowledge of genomic organization and the techniques of molecular biology have provided evolutionary insights into adaptational processes, providing mechanistic answers to "where did this come from" and "how did this happen"—questions that, not too long ago, might have seemed nave to ask and unlikely to be answerable. Examples I have in mind are the origin and acquisition of antifreeze glycopeptides, a key innovation in notothenioids (Chen et al. 1997a, b; Cheng and DeVries 2002), and the loss of erythrocytes and haemoglobin (Cocca et al. 1995; Zhao et al. 1998; Detrich 2000; di Prisco et al. 2002) and the variable patterns of myoglobin expression in muscle tissues (Sidell et al. 1997; Moylan and Sidell 2000) of white blooded channichthyids. The growing database of nucleotide sequences is also contributing more characters for phylogenetic analysis and our knowledge of phylogenetic relationships of notothenioids has been expanding rapidly (Chen et al. 1998; Bargelloni et al. 2000; Derome et al. 2002; Near et al. 2003a, 2004). There has also been progress in narrowing down the sister group of notothenioids (Chen et al. 2003; Detta and Lecointre 2004). For example,

molecular phylogenetics has identified a large acanthomorph clade, referred to as "clade X" (Detta and Lecointre 2004), containing 88% of the benthic fish fauna of the Antarctic shelf and upper slope including percids, notothenioids, zoarcoids, cottoids, serranids, gasterosteids, scorpaenids, trachinids and triglids. This analysis rejects a number of taxa traditionally considered as the sister group for notothenioids, including zoarcoids and trachinoids, and supports percids as the sister group (Detta and Lecointre 2004). It is possible, however, that this finding is an artefact of sampling since percids are a Northern Hemisphere freshwater group and the dataset did not include sequences from marine perciforms living in the Southern Hemisphere (Chen et al. 2003). Additional details and insight will certainly be forthcoming.

The editors of *Polar Biology* invited me to contribute an article in the form of a review and essay. They allowed me to choose a topic reflecting my interests and also encouraged personal reflection and insight. I am an anatomically oriented ichthyologist and work exclusively on Antarctic fishes. However, I wanted to consider a topic broader than morphology and have settled on diversity—here meaning number of species or species richness—and the nature of the radiation in organismal diversity that makes the Antarctic fish fauna unique and different from other marine faunas. I will consider these topics: diversity of fossil fishes, size and taxonomic composition of the modern fauna, estimates of undiscovered species, endemism, aspects of the notothenioid radiation relating to buoyancy and general aspects of adaptive radiation pertinent to notothenioids. I have attempted to enhance readability by writing in a more conversational tone than is typical for scientific papers.

Changes in diversity through time: historical perspective on the Antarctic fish fauna

Evolutionary research at the faunal and organismal levels is frequently retrospective, investigating the modern outcome of historical processes. So in attempting to understand the diversity and composition of the modern Antarctic fish fauna, we are confronted with the results of a series of evolutionary events that have proceeded through the Cenozoic, first in the coastal waters of Gondwana and later on the Antarctic shelf. Therefore, I thought it would be worthwhile to begin by briefly summarizing what is known about the antecedents of the fishes now living in Antarctica.

The major and most extensively studied Cenozoic fossil fish fauna from Antarctica is unlike the modern fauna that replaced it and the modern Antarctic fauna is unlike the shelf faunas of other southern continents. This middle to late Eocene ($\approx$40 million years ago) fossil fauna from the La Meseta Formation on Seymour Island, near the tip of the Antarctic Peninsula, provides a glimpse of what a high latitude ($\approx$60°S) shelf fauna was

like at this time (Fig. 1). The taxonomically diverse La Meseta fish fauna was cool temperate in character, living in waters like those found today around Tasmania, New Zealand and southern South America. As biogeographic provinciality was less evident at high latitudes in the Eocene, the fauna was cosmopolitan rather than endemic to the Antarctic component of Gondwana. The known fauna consists of at least 29 taxa, including 21 chondrichthyans and eight actinopterygians. It has been summarized recently (Eastman 2000 and references therein) so here I will simply use Fig. 1 to emphasize a few points. The figure shows all known actinopterygian fossils, but only some of the chondrichthyans. The apparent dominance by chondrichthyans is artifactual and attributable to the distinctiveness of their preserved teeth making the various taxa identifiable, frequently to species, unlike the case with most actinopterygian remains (Grande and Chatterjee 1987). Nevertheless, shark diversity and abundance was especially high, and coastal upwelling probably supported the extensive fish and invertebrate biomass that would have been necessary to maintain these shark populations (Case 1992). Rajids and gadiforms are the only taxa unequivocally represented in both the Eocene and modern faunas. The presence of notothenioids in the fossil fauna is open to

question because the partial dorsal cranium originally described as a gadiform (Eastman and Grande 1991) has been reinterpreted as a basal notothenioid of the family Eleginopidae (Balushkin 1994). It would be useful for someone with "fresh eyes" to step forward and provide additional perspective on this fossil. In summary, the Eocene fauna is not ancestral to most of the modern fauna and most components of the modern fauna do not have a fossil history in Antarctica. As we will see below the modern fauna is also unlike its predecessor in having restricted taxonomic composition and high endemicity.

I should mention briefly that additional Eocene fossil fishes have recently been discovered in Antarctica, in this case on Mount Discovery in East Antarctica on the opposite side of the continent from Seymour Island (Long and Stilwell 2000). To date the known fossils consist of two taxa of sharks and one gadid (cod). Together with those from Seymour Island, these new fossils suggest the presence of a circum-Antarctic fish fauna during the Eocene.

Beginning in the early Miocene (25–22 million years ago) the Antarctic shelf was subject to a series of tectonic and oceanographic events that probably altered faunal composition. Antarctica gradually became isolated and colder, and expansion of the ice sheet led to

Fig. 1 Synopsis of diversity of some chondrichthyan and all known actinopterygian taxa of the Middle to Late Eocene (≈40 million years ago) fossil fauna from the La Meseta Formation on Seymour Island, Antarctic Peninsula. Additional information and discussion is in Eastman (2000). The Xiphiorhynchid is a recent addition to the fauna (Cione et al. 2001) and the *dagger* indicates that this family is extinct. Outline drawings from Nelson (1994), Smith and Heemstra (1986) and Norman (1937) show modern representatives of fossil groups
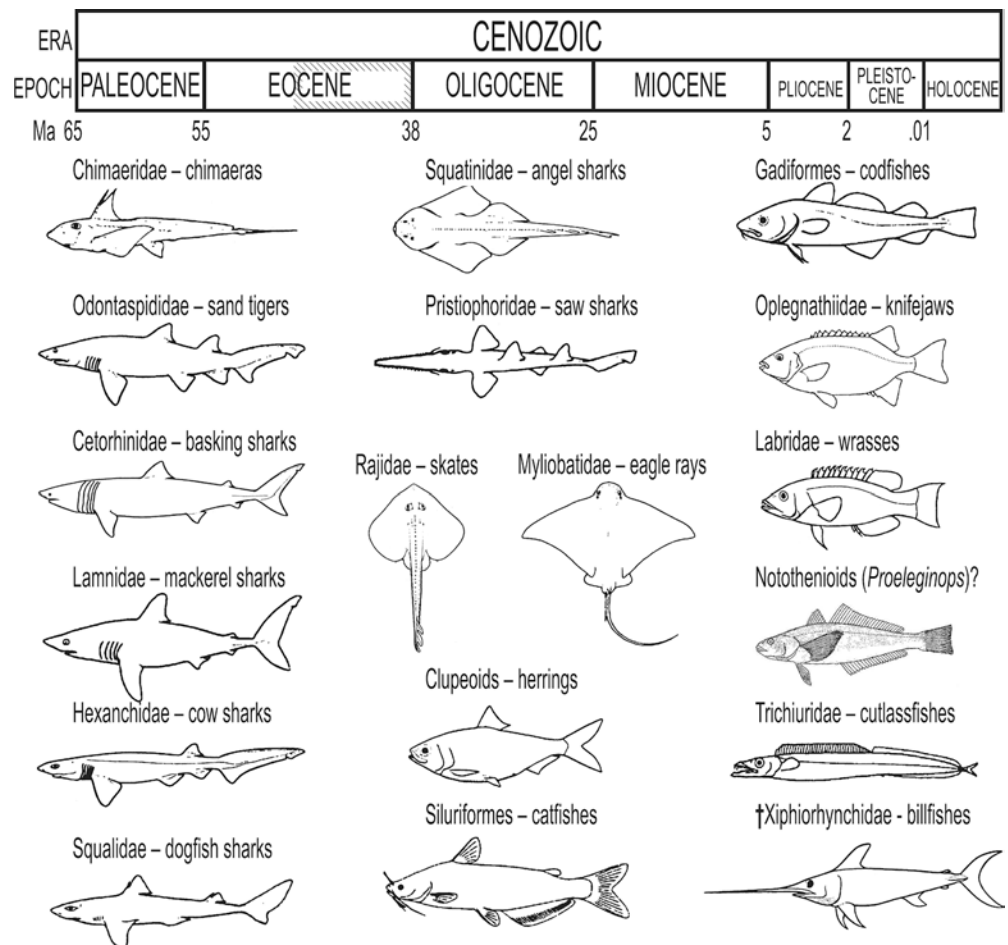
destruction and disturbance of inshore habitat by ice, with repeated groundings of parts of the ice sheet as far as the shelf break (Anderson 1999). Loss of habitat and changes in the trophic structure of the ecosystem probably led to the local extinction of many of the Eocene components of the fish fauna. Thus the diversity of the fauna was reduced and, as Antarctica became increasingly isolated, new niches became available to other groups that were diversifying in situ (notothenioids) or immigrating into (liparids and zoarcids) this developing cold-water ecosystem. We do not know when the fauna became modern in taxonomic composition.

Diversity of the Antarctic fish fauna

A remote but moderately well-known fauna

The Southern Ocean surrounding Antarctica is unlike other oceans in that it is not contained in a distinct basin, but is instead delimited and defined by an oceanographic feature—the Antarctic Polar Front located between ≈50°S and 60°S. That area between the Polar Front and the continental margin, encompassing about 10% of the world's ocean (Laws 1985), is the Antarctic Zoogeographic Region and focus of our interest here. Although extensive and remote from population centres, even the high latitude waters of the region have been explored for more than a century and the fish fauna has been the subject of two taxonomic treatises (Gon and Heemstra 1990; Miller 1993) as well as treatments from a fisheries (Kock 1992) and evolutionary (Eastman 1993) perspectives. Thus, unlike the poorly known fish faunas of tropical freshwaters (Greenwood 1992; Berra 1997; Lundberg et al. 2000) and the deep-sea (Greenwood 1992; Merrett and Haedrich 1997; Roberts 2002), the fish fauna of the Southern Ocean falls into an intermediate category termed "moderately well-known" on the basis of a set of subjective criteria outlined by Clarke and Johnston (2003). To understand this designation I should mention that the other categories are "poorly known" and "well-known", and that the Southern Ocean fauna is not "well-known" because new species are still being regularly described. I will make an attempt to estimate the number of undescribed species in a section below.

The fauna consisted of 274 species from 49 families at the time Gon and Heemstra (1990) were compiling *Fishes of the Southern Ocean*. Since the publication of this book there have been a number of additions—a combination of new species, new records for the region and taxa that were inadvertently missed. I have tracked these additions and place the current size of the fauna at 322 species from 50 families. Although *Fishes of the Southern Ocean* is still in print, we are fortunate that a second edition is in the planning stages and by the end of the decade we will again have an up to date and comprehensive summary of the fauna at our fingertips.

Low diversity and restricted taxonomic composition

The relatively small number of species and the restriction at higher taxonomic levels, again viewed against a global fish diversity of ≈25,000 species and 482 families (Nelson 1994), are distinctive features of the fish fauna of the Southern Ocean. Excluding the epi-, meso- and bathypelagic components of the fauna and focusing on the benthic fishes that constitute the major component on Antarctic continental shelf and upper slope, we see that there are 222 species with higher taxonomic diversity confined to 19 families (Table 1). Two perciform groups, the Notothenioidei (notothenioids) and the Zoarcidae (eelpouts), and the scorpaeniform family Liparidae (snailfishes) are the most speciose taxa, accounting for 87.8% of the species. It is interesting that a recent molecular phylogenetic analysis indicates that all three of these groups are members of the same clade: acanthomorph "clade X" (Detta and Lecointre 2004).

Notothenioids are the indigenous Southern Hemisphere component of the fauna that evolved in situ (Andriashev 1965) whereas the ancestors of the modern Antarctic liparids likely originated in the North Pacific and dispersed into the Antarctic via the west coast of South America, possibly during the Miocene (Andriashev 1991). Zoarcids also have a North Pacific origin, dispersed to the Southern Hemisphere during the Miocene and subsequently radiated in Antarctica where

Table 1 Families of benthic fishes in the Antarctic Region

Taxon[a]	No. of species[b]	Fauna (%)	
Myxinidae (hagfishes)	1	0.5	
Petromyzontidae (lampreys)	1	0.5	
Rajidae (skates)	8	3.6	
Carapidae (pearlfishes)	1	0.5	
Moridae (deepsea cods)	4	1.7	
Muraenolepididae (eel cods)	4	1.7	
Gadidae (cods)	1	0.5	
Congiopodidae (horsefishes)	1	0.5	
Bathylutichthyidae[c]	1	0.5	
Liparidae (snailfishes)[d]	70	31.5	87.8
Zoarcidae (eelpouts)[e]	24	10.8	
Notothenioidei (with representatives from six families)[f]	101	45.5	
Tripterygiidae (triplefins)	1	0.5	
Achiropsettidae (southern flounders)	4	1.7	
Total	222	100	

[a] Arranged phylogenetically with sequencing according to Nelson (1994)
[b] Based on Gon and Heemstra (1990); footnotes provide updates and additions for various groups
[c] Balushkin and Voskoboinikova (1990)
[d] Additional liparids from Andriashev and Stein (1998), Matallanas (1998, 1999), Matallanas and Pequeño (2000), Chernova and Eastman (2001) and Chernova and Duhamel (2003)
[e] Additional zoarcids from Anderson (1991)
[f] Notothenioids from Eastman and Eakin (2000) with subsequent additions of Antarctic species from Prirodina (2000, 2002, 2004) and La Mesa et al. (2002)

they exhibit a major area of endemism (Anderson 1994). The molecular phylogenetic studies identifying "clade X" also infer at least three distinct origins for the Antarctic components of the clade, as well as indicating that while the Antarctic groups lack swim bladders, their respective sister groups all have them (Detta and Lecointre 2004).

On the High Antarctic shelf, waters are covered by ice for most of the year and water temperatures are nearly constant, usually $< -1.5°C$. Here, there are larger proportions of artedidraconids, bathydraconids and channichthyids than farther north (Kock 1992), components of the phyletically derived Antarctic clade of notothenioids. In the high latitude (71°S–78°S) embayments of the Ross and Weddell Seas, the largest areas of the Antarctic continental shelf, diversity is about 80 species from 12 families (Hubold 1992; Eastman and Hubold 1999). These numbers, however, do not convey the unusual nature of the diversity as revealed by the results of midwater and benthic trawling in the Ross and Weddell seas (DeWitt 1970, 1971; Ekau 1990; Hubold 1992; Eastman and Hubold 1999). As shown by the pie charts in Fig. 2, notothenioids are overwhelmingly dominant, not just in terms of number of species, but they also dominate abundance and biomass at levels > 90%. Such dominance by a single taxonomic group is unique among shelf faunas of the world. Notothenioids filled the ecological void left by the eradication of most of the Eocene fauna.

Another perspective on diversity

Although the number of fish species is low given the large size of the Southern Ocean, we could view this situation from another perspective and say that the number of species could be considered reasonably high given the absence of some key benthic habitats on the Antarctic shelf. In general, the availability of substrate is an especially important aspect of fish diversity, in part due to the wider array of food and microhabitats available on or near the bottom than in the water column (Roberts 1982). Anchor ice covers the bottom to depths of 30 m and icebergs scar the substrate to depths of 100–200 m on the Antarctic shelf. Furthermore, glacial and pack ice occupy and scour most coastal areas to the extent that beaches, intertidal and subtidal zones, reefs and estuaries are limited or absent. Glacial isostasy, glacial erosion and the absence of fluvial sedimentation also serve to deepen the continental shelf so that in most areas it averages 500 m in depth—about eight times the world average (Anderson 1999). Hence shallow inshore habitats, the prime areas for marine fish diversity elsewhere in the world, are restricted in the High Antarctic. When viewed in this light we could turn things around and say that, given the restriction in the availability of key shallow water habitats, it is amazing that there are as many fishes as there are in Antarctica.
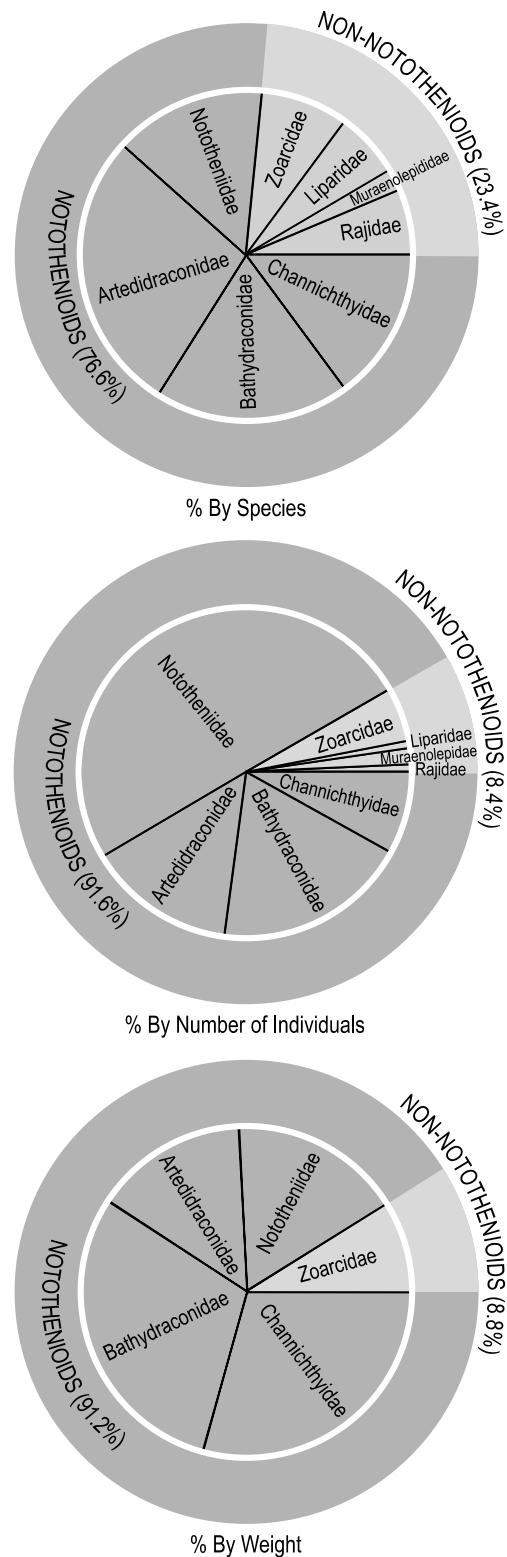

Fig. 2 Pie charts showing the dominance of notothenioids by diversity, abundance and biomass on the Antarctic shelf. Data summarize a catch of 47 species and 979 specimens in 19 bottom trawls at depths of 107–1,191 m in the southwestern Ross Sea (73°S–77°S). Biomass data based on a single trawl that captured 83 specimens at a deep (900–910 m) extremely high latitude (77°19′S, 165°41′E) site. Data from Eastman and Hubold (1999)

Notothenioids dominate diversity

A reasonably up to date synopsis or list of currently recognized notothenioid species and a generally accepted taxonomic scheme is available in Eastman and Eakin (2000). This was the third iteration in the sense that *Fishes of the Southern Ocean* was the initial source (Gon and Heemstra 1990) and there were slight subsequent modifications by Eastman (1993). Since the publication of Eastman and Eakin (2000), five new species have been described (Prirodina 2000, 2002, 2004; Last et al. 2002), one species has been resurrected from synonymy (La Mesa et al. 2002) and the known but previously overlooked South American species *Patagonotothen trigramma* (García and Menni 1996; Ojeda et al. 2000), described in 1913 by Regan, should probably be added to the list. Thus, the eight notothenioid families now encompass a total of 44 genera and 129 species, 101 Antarctic and 28 non-Antarctic. The 101 Antarctic species make up 45% of the benthic fish species from the Antarctic Region (Table 1).

Taxonomy is a complex and somewhat controversial field of biology and there are different approaches to identifying species. Therefore I would be remiss in not mentioning that Balushkin's (2000) "take" on notothenioid taxonomy recognizes more genera (48) and species (139) than do most other workers. The difference in taxonomic approach between lumping and splitting accounts for the differences, most of which are confined to the families Nototheniidae and Channichthyidae. Here, we see that the mindset and modus operandi of the taxonomist can positively influence species richness in notothenioids, in this case by about 9%.

Figure 3 is a cladogram of relationships among notothenioid families and also indicates the number of species in each of the eight families while highlighting the extent to which the Antarctic clade has diversified. In order to accentuate the diversification of certain genera,
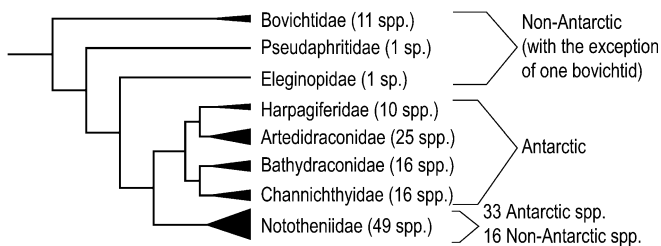

Fig. 3 Cladogram of relationships among notothenioids (Near et al. 2004), pruned to the level of family. Original cladogram is a strict consensus of four trees resulting from maximum parsimony analysis of the complete gene 16S rRNA dataset and the analysis of this data demonstrates monophyly for both the suborder and the dominant family Nototheniidae (Near et al. 2004). Pruning and use of currently recognized family names obscure the paraphyly in the Bathydraconidae. Wedges are proportional to species diversity in each family; geographic distributions also indicated with Gon and Heemstra (1990) taken as authoritative for species with Antarctic distributions. Non-Antarctic species have distributions exclusively outside the Antarctic and Subantarctic Regions

I also provide a histogram of the frequency distribution of species per genus values (Fig. 4). The histogram is most easily understood by first reading the vertical axis-values of the bars from left to right. Thus, there are 26 monotypic genera (the tall left-most bar), seven genera containing two species, one genus with three species, one so on. The pattern seen here for notothenioids is considered typical, with a more or less regularly arranged series of bars falling off in height to the right. If a line were drawn connecting the bars, it would be in the shape of an inverse asymptotic curve (the expected "hollow curve of distribution" as defined by Willis 1922, who first employed these graphs). However, outliers on the right, those speciose genera that have undergone phylogenetic diversification, interrupt the smooth decline in the curve. Our attention is especially drawn to *Pogonophryne* with 17 species and *Patagonotothen* with 15 species. It is interesting that there have been bursts of diversification in both the high latitude shelf waters and in non-Antarctic localities. In the case of *Pogonophryne*, we are dealing with a sedentary, benthic Antarctic group showing little morphological and ecological diversification. The mental barbel, once thought to be specifically distinct and a reliable taxonomic character, has subsequently proven to be highly variable in some species, *P. scotti* for example (Eakin et al. 2001). The species of *Pogonophryne* probably present the greatest taxonomic challenge in the suborder and may be a recent radiation. We do not have much of a feel for the nature of the radiation of *Patagonotothen*. With the exception of one species, all have non-Antarctic distributions in South America and the Falkland Islands. In recent molecular
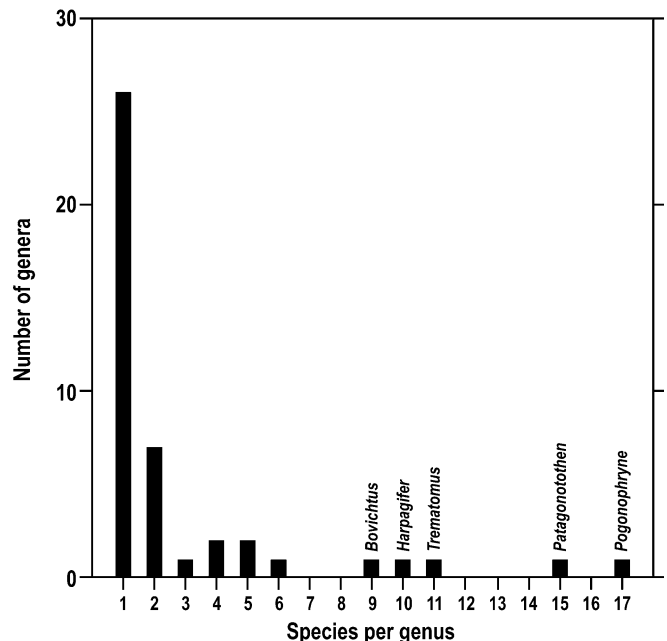

Fig. 4 Frequency distribution of species per genus values for notothenioids based on 44 genera and 129 species. Monotypic genera represented by *tall left bar*, the most speciose genera are outliers on the *right*

phylogenetic analyses, the few species of *Patagonotothen* studied are the sister group of the peripheral Antarctic genus *Lepidonotothen* (Bargelloni et al. 2000; Stankovic et al. 2002; Near et al. 2004; G. Lecointre, personal communication), with the divergence time between the two genera estimated at 6.6–7.1 million years ago, well after the formation of the Antarctic Polar Front (Stankovic et al. 2002). Thus, while *Patagonotothen* is hypothesized to have an Antarctic origin and to have dispersed northward, the only species studied to date (*P. tessellata* and *P. guntheri*) appear to lack antifreeze glycoprotein sequences in their genomes (Cheng et al. 2003). Assuming the possession of antifreeze genes is an accurate predictor of evolutionary history, this is a puzzling finding.

Documenting the diversity of the Antarctic fish fauna: undiscovered species

The temporal pattern in the description of species

In this section, I will attempt to answer the seemingly straightforward question: how well-known is the Antarctic fish fauna? One way to approach this question is to look retrospectively at the history of species descriptions. Figure 5 summarizes the cumulative trends in the descriptions of new species for notothenioids, liparids and zoarcids—the dominant components of the Antarctic fauna. In spite of heavy ice cover and lack of motorized winches, collectors associated with the vari-

ous national Antarctic expeditions early in the twentieth century did a thorough job in obtaining many of the shallow inshore species. These were mostly notothenioids and, as shown by the line in Fig. 5, about 62% of the currently recognized 129 species were described by 1916. The rate has accelerated again in the past 30 years and the curve gives no indication of having reached an inflection point. Most zoarcids and liparids live at greater depths and were less accessible to early collectors. The parallel and nearly horizontal lines in Fig. 5 indicate that the Antarctic representatives of these two families were poorly known until they became the objects of collection and study in the last 30 years, exemplified by major taxonomic works of Anderson (1988, 1994) for zoarcids and of Andriashev (1986, 2003), Stein and Tompkins (1989) and Andriashev and Stein (1998) for liparids. This burst of activity elevated liparids to the status of the most speciose Antarctic fish family. Returning to Fig. 5, we see that the curve for zoarcids has begun to plateau and the expert on this group, M. Eric Anderson (2004, personal communication), has indicated that he does not expect to see new zoarcids from the Antarctic region except at depths exceeding 2,000 m, particularly in western Antarctic regions. The curve for liparids, on the other hand, is still rising steeply. David Stein (2004, personal communication), who specializes on this group, expects this trend to continue and the Southern Ocean to yield additional new species into the foreseeable future. In support of his prediction he notes that there has been comparatively little exploration of isolated islands and banks in the region, and that there has also been little deep-water trawling in the Southern Ocean. A final general reason for expecting the discovery of new taxa is that new technology, such as remotely operated vehicles and manned submersibles, has been slow to be employed in the search for undocumented fish diversity in the Antarctic.
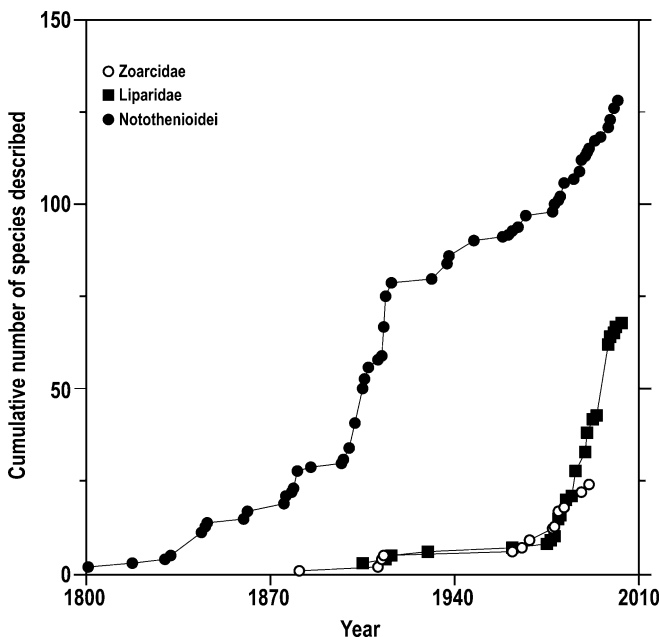
What remains: estimated numbers of unknown species

New fish species are being described at the rate of between 130–160 (Berra 1997) and 200–250 (Eschmeyer 1998, 2003) species per year. Furthermore, the Census of Marine Life (O'Dor 2003) reports the addition of 600 marine fish species just since 2000. Given the information in the previous section, it is clear that the numbers of notothenioid and especially liparid species are still rising and that the Southern Ocean fauna is not completely documented. Is it possible to estimate what remains to be discovered? I will make an attempt, but first some prerequisite information is necessary. There are between 24,618 (Nelson 1994) and 28,000 (Eschmeyer 2003) known and 5,000–7,000 unknown (or taxonomically undescribed) fishes in the world today (Eschmeyer 1998, 2003), and marine fishes account for 58% of the fish fauna (Cohen 1970). We could therefore assume that the total number of unknown marine fishes represents 58% of the 5,000 unknown species, or

Fig. 5 Two-century time course for the description of species in the three most speciose taxa of benthic fishes from the Antarctic Region. *Line* for notothenioids includes all 129 currently recognized species both Antarctic and non-Antarctic; *plots* for liparids and zoarcids based only on Antarctic species

approximately 3,000 species if rounded off. Three thousand is a conservative figure as other estimates place the number of undescribed marine species at 5,000 (O'Dor 2003). Using the 3,000 figure, I have estimated the number of unknown Antarctic fishes in three different ways:

– The Southern Ocean is 10% of the world's ocean and if species were homogeneously distributed, a simplistic estimate suggests there could be 300 unknown species in the Southern Ocean. However, species are not evenly distributed in the ocean or anywhere else, and regional differences in biodiversity can vary by an order of magnitude (Wilson 2002). An Indo-Pacific coral reef could easily harbour 150 fish species, whereas a sponge bed in the Ross Sea has only 15 species (Eastman and Hubold 1999). Therefore, it is justifiable to reduce this estimate from 300 to 30 *unknown species*.
– Since Southern Ocean fishes are 2.1% (322/15,000) of the known marine fishes, they represent a similar percentage of the unknown fauna: 2.1% of 3,000 species = 63 *unknown species*.
– Since the unknown marine fish fauna is 20% (3,000/15,000) of the known fauna, they also compose a similar percentage of the Southern Ocean fauna: 20% of 322 species = 64 *unknown species*.

Much of the Southern Ocean is deep-sea and therefore offers relatively little habitat diversity; as indicated above nearly 70% of the known Antarctic fishes are benthic shelf and slope species. Thus, it could be argued that the percentage of world habitat available to these fishes should be smaller than the 10% used in one of the calculations above. However, the Antarctic continental shelf is slightly over 11% of the world's total shelf area (Clarke and Johnston 2003) so substituting this figure in the calculation would slightly inflate rather than reduce the estimated number of new species.

These estimates of ≈30–60 undescribed species seem reasonable in light of recent discoveries in the Ross Sea where a small scale trawling operation, consisting of only 10 successful trawls out of a total of 19, turned up two new notothenioids and two new liparids (Eastman and Hubold 1999). In what types of habitats might we expect to find new species? Prime locations for benthic species on the Antarctic shelf are sites where an organic matrix has developed (Emery 1978), for example sponge beds with elaborate spicule mats and bank tops with macrophyte cover. Inner shelf depressions (1,000–1,200 m) are another possible site. North of the shelf break, deep water in general and trenches and sea mounts in particular are localities where new species might be encountered.

We must note that, on the basis of David Stein's comments above, Antarctic liparids are still something of an unknown and my estimate of 30–60 undescribed species may be low given the high probability that additional new liparids will come to light. There are many deep areas and trenches that have not been explored. Furthermore, many liparids are linked to the substrate by the lack of larval pelagic stages, and hence tend to become isolated and form endemic species (Chernova et al. 2004). For instance, in the past 30 years hundreds of *Paraliparis devriesi* have been collected, but this species has never been taken outside the Erebus Basin near McMurdo Sound and is likely endemic to this locality. Although known only from the holotype, the same can be said for *P. macrocephalus* from the 1,200 m deep Drygalski Basin 200 km north of McMurdo Sound (Chernova and Eastman 2001). Furthermore, instead of appearing in ones and twos, new species of liparids have been materializing, at least in non-Antarctic areas, in lots of ten (Chernova 2001) to 30 (Stein et al. 2001). There is still much to be learned about the most basic aspects of the natural history of Antarctic liparids. Nothing is known about the abundance and biomass of most species since they have been collected in such small numbers. It is also likely that there are symbioses or other complexities in the life cycles of some species. Near South Georgia, for example, a species of *Careproctus* has been discovered living commensally with and hitching rides on a lithodid crab, raising the possibility that snailfish eggs are being incubated in the gill cavity of the crab (Yau et al. 2000).

High endemism: Antarctica has "the world's most distinctive marine biota"

John C. Briggs, an eminent marine biogeographer, made this statement with reference to the modern Antarctic fauna. He was using data on endemicity in fishes in developing his argument that Antarctica is an evolutionary centre of origin for marine organisms (Briggs 2003). A high level of endemism is a distinguishing feature of the Antarctic fish fauna. Among the benthic fishes of the Southern Ocean, those confined to waters south of the Antarctic Polar Front (Table 1), rates of endemism are 88% for species and 76% for genera (Andriashev 1987). If only notothenioids are considered, endemism rises to 97% for species and 85% for genera (Andriashev 1987). The large size of the Antarctic region, especially the continental shelves, and geographic and thermal isolation of the fauna contribute to these high rates (Clarke and Johnston 2003). The larger the area of a region, the less likely it is that a given species will be found outside that region. However, the endemism of Antarctic fishes is exceptionally high for a marine group, as species level endemism of only 10% is sufficient for recognition of biogeographic provinces (Briggs 1974, 1995). For comparison, rates of species level endemism for various Antarctic invertebrate groups are also high: 51% for sponges, 57% for polychaetes, 72% for amphipods, 75% for molluscs, 88% for isopods and 91% for pycnogonids (Arntz et al. 1997; Brandt 1999).

How do species diversity and rates of endemism for Antarctic fishes compare to those for faunas from adjacent areas of the Southern Hemisphere? In Chile, there are 162 species between 18°S and 56°S and the rate of endemism is 18%, but these figures only include species living at depths < 60 m (Ojeda et al. 2000). New Zealand has 1,008 species with 11% endemism (Paulin et al. 1989). What about rates of endemism among marine fishes from more isolated areas? Among the best examples of isolated islands are Hawaii with 566 species and Easter Island with 126; associated rates of endemism are 23 and 22%, respectively (Randall 1998). The number of Hawaiian species is high and endemism is low compared to the Antarctic, yet McDowall (2003) considers the Hawaiian marine biota "impoverished", at least compared to the Indo-west Pacific, and the rate of endemism as high. Obviously everything is relative to the standard of comparison. But the 88% endemism for Antarctic fishes is unmatched in the marine realm and certainly sets Antarctica apart as a distinctive evolutionary site.

The nature of notothenioid diversity

It is not the large number of species but the nature of the fish biodiversity that distinguishes the Antarctic from all other shelf areas in the world. We have seen that notothenioids dominate the fauna in terms of diversity, abundance and biomass. But another important aspect of the "nature of the biodiversity" is that in contrast to many other fish radiations, which may show phyletic diversity but little ecological and morphological diversity (Brooks and McLennan 1991; Mayden 1992; Near et al. 2003c), some components of the notothenioid radiation, nototheniids for example, exhibit considerable ecological and morphological diversity. In the absence of competition from a taxonomically diverse fauna, they underwent a habitat or depth-related diversification keyed to the utilization of unfilled niches at various depths in the water column, especially pelagic or partially pelagic zooplanktivory and piscivory. Notothenioids filled these niches as well as remaining the dominant benthic group. Their diversification centred on the alteration of buoyancy and, 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 (DeVries and Eastman 1978; Eastman and DeVries 1981, 1982; Eastman 1993). The five families comprising the Antarctic clade of notothenioids (Fig. 3) have undergone different degrees of ecological and morphological diversification, with some showing little. The large dominant family Nototheniidae is the most extreme case, so we will consider them in more detail in the next section after a few comments about the other four families:

– Harpagiferids, consisting of a single genus of nine ecologically and morphologically similar species, have undergone primarily phyletic diversification. Most are inshore benthic fishes that could even be termed cryptobenthic because they are small, disruptively coloured and inconspicuous. Harpagiferids have largely non-overlapping distributions at the various islands near the periphery of the Antarctic Region. The recent discovery of new species at depths of up to 320 m (Prirodina 2000, 2002, 2004) indicates that the slight ecological diversification in this group extends into deeper waters and that some islands have both shallow and deep living species.

– Artedidraconids are modestly diverse with respect to size, ranging from small (some *Artedidraco*) to large (some *Pogonophryne*), and the family and some species are eurybathic. They are not ecologically or morphologically diverse as all are sedentary benthic fishes with a mental barbel of uncertain function. *Pogonophryne*, the most speciose genus in the suborder, contains 17 morphologically similar species that, because of their similarity, are the most taxonomically difficult notothenioid group. We may cite this genus as an example of a radiation within the larger notothenioid radiation; in this instance *Pogonophryne* have experienced primarily phyletic diversification.

– Bathydraconids have an elongated body and show moderate diversification in form, ranging from moderately robust and well-muscled to thin and delicate. They are less reliant on benthic food sources than are harpagiferids and artedidraconids. The genus *Bathydraco* includes the deepest-living species (DeWitt 1971, 1985), with *B. scotiae* recorded from 2,950 m (Gon 1990), deeper than any other notothenioid. Since the family also contains shallow-living species, bathydraconids have the greatest overall depth range among notothenioid families.

– Channichthyids are fusiform pike-like fishes with large heads and depressed, elongated snouts. All species lack haemoglobin and, as a family, they are the largest notothenioids, with adults ranging in size from 25 to 75 cm total length (Iwami and Kock 1990). Most live at depths of less than 800 m. Channichthyids are similar in morphology, ecology and behaviour and most have combined pelagic-benthic life styles, exhibiting an active vertical migration to feed on pelagic prey, especially fish and krill. With its reduced density and pelagic lifestyle, *Dacodraco hunteri* is somewhat more specialized than other channichthyids (Eastman 1999). As the ascending process of the premaxilla has been lost (Iwami 1985), there are no obligatory benthivores in the family (Voronina and Neelov 2001) and although some may rest on the substrate they are less reliant on it for food than are the other Antarctic families.

Nototheniids: ecological and morphological diversification related to buoyancy

This family of 49 species has undergone the most substantial ecological and morphological diversification in

the suborder. About one-half of the 33 Antarctic species occupy the ancestral benthic habitat, but others are semipelagic, epibenthic, cryopelagic and pelagic (Eastman 1993) and, as far as I am concerned, this diversification in buoyancy is the hallmark of the radiation from an organismal perspective. They range from relatively heavy benthic species to those that are neutrally buoyant and spend their entire lives in the water column. A large intermediate group, sometimes subdivided as semipelagic, epibenthic and cryopelagic species, could also be grouped and considered benthopelagic since they are ecologically and trophically plastic. For example, a high degree of planktivory has been documented in benthic nototheniids (Foster and Montgomery 1993). This type of radiation, termed pelagisation or pelagicism, has occurred independently in different nototheniid clades (Klingenberg and Ekau 1996; Bargelloni et al. 2000), but usually not to the point of neutral buoyancy. We should also note that ecological diversity is further enhanced by the ontogenetic habitat shifts experienced by some species during transition from fingerling or juvenile to adult stages. Examples include a pelagic → benthic shift in *Notothenia rossii* (Burchett 1983) and a benthic → pelagic shift involving considerable changes in buoyancy and habitat depth in *Dissostichus mawsoni* (Near et al. 2003b).

Neutral buoyancy is rare

Weighing fish in water (W_{WATER}) and in air (W_{AIR}) provides a measurement of buoyancy expressed as percentage buoyancy (%B), the percentage of weight in air supported when the fish is in the water:

$$\%B = W_{\mathrm{WATER}}/W_{\mathrm{AIR}} \times 10^2$$

These measurements for notothenioids range from 0 to about 6%. Neutral buoyancy (%B = 0.0–0.5%)—the extreme end point of pelagisation—is rare among notothenioids. How many nototheniids have undergone a reduction in density to the point of neutral buoyancy? Freshly captured specimens of adult *Pleuragramma antarcticum* (DeVries and Eastman 1978) and *Dissostichus mawsoni* (Eastman and DeVries 1981) have been measured as having negligible weight in seawater. So we are sure that these two species are neutrally buoyant as adults, but beyond this everything is based on inference. For example, on the basis of morphological study of preserved specimens, *D. eleginoides* (Oyarzún et al. 1988) and *Aethotaxis mitopteryx* (Eastman and DeVries 1982) have been inferred as neutrally buoyant. *Aethotaxis* has an extremely high lipid content, 61.4% of dry weight, among the highest of any fish studied to date (Hagen et al. 2000), and this adds credence to the circumstantial case for neutral buoyancy in this species. Finally, *Gvozdarus svetovidovi*, a meter-long predator on *Pleuragramma*, could be neutrally buoyant on the basis of its water column habitat and diet of *Pleuragramma* (Balushkin 1989; DeWitt et al. 1990; Shandikov and Kratkiy

1990). Since it is represented in museum collections by only two specimens, little else is known about its biology.

Thus, at most only 4% (5/129) of the species in the suborder are or are likely to be neutrally buoyant, but this does not mean they are insignificant oddities. *P. antarcticum*, for example, is abundant and ecologically important. Given the morphological constraints imposed by a benthic heritage, the energetic constraints of life at subzero temperatures and the patchy distribution of zooplankton on the Antarctic shelf, evolution has not managed to produce an aerobic herring or anchovy equivalent from the notothenioid body plan—*Pleuragramma* is as close as it gets. Video images from "critter cameras" provide some insight into their mode of life. Unlike the typical continuously swimming filter feeder, *Pleuragramma* are relatively inactive. They shoal in loose aggregations with individuals spaced 2–4 m apart (Fuiman et al. 2002). Their neutral buoyancy allows them to hang almost motionless, in a sit-and-wait fashion, to monitor the water for visual and vibrational signals and then to discriminately feed on zooplankton. The eminentia granulares and crista cerebellares, areas of the brain involved with mechanoreception, are large and the cerebellum is small in comparison to those of other nototheniids (J.T. Eastman and M.J. Lannoo, unpublished data). *P. antarcticum* is the dominant species in the water column and the key species in the food web of the high Antarctic shelf where *Euphausia superba* are absent (DeWitt 1970; Hubold 1984; Eastman 1985; La Mesa et al. 2004).

There is one final point I would like to make concerning neutral buoyancy in the family Nototheniidae. When the phylogenetic hypotheses of either Balushkin (2000) or Near et al. (2004) are employed, neutral buoyancy is confined to a single clade containing *Pleuragramma*, *Aethotaxis* and *Dissostichus* (and also *Gvozdarus* in the case of Balushkin's data). However, some molecular sequence data does not recover a neutrally buoyant clade, nor is it rejected (G. Lecointre, personal communication). I think there is sufficient variability in the morphological mechanisms of buoyancy that it is not necessary to hypothesize a single origin for neutral buoyancy, and that this important aspect of the biology of these fishes could have evolved in parallel.

Inferring buoyancy from appearance is sometimes unreliable

I have long suspected that neutral or near neutral buoyancy might be discovered in nototheniids other than those mentioned above, and possibly in some channichthyids as well. *Lepidonotothen larseni* and *Champsocephalus gunnari* were the prime candidates I had in mind. Appearance and ecomorphological measurements are sometimes sufficient to identify a species adapted to life in the water column but, as I was to learn,

this is not necessarily accompanied by neutral buoyancy or measurements even close to neutral buoyancy. During a recent cruise in the South Shetland Islands, Bruce Sidell and I were able to determine buoyancies for both these species (Eastman and Sidell 2002). Surprisingly, in spite of its compressed fusiform body and general appearance of a pelagic or semipelagic species, *L. larseni* was among the heaviest species that we measured, with a %*B* = 5.62%. In this case, a streamlined body shape neither predicts nor is associated with a low percentage weight in water. Nor is a benthic body shape necessarily associated with a high percentage weight. We found that *Gobionotothen gibberifrons*, the classic example of a benthic nototheniid with a depressed body suited to browsing on the substrate, had a %*B* = 4.54%, less than *L. larseni*. At a %*B* = 3.07% *Champsocephalus gunnari* did prove to be the lightest species in our sample of 13 species, but it was not close to neutral buoyancy and its buoyancy was not significantly different from that of *Chionodraco rastrospinosus*, a less streamlined and presumably more benthic channichthyid. The conclusion here is that, in spite of their seemingly specialised external morphology and differences in buoyancy, all four of these species are sufficiently opportunistic that they are capable of feeding in the water or on the substrate and could be considered benthopelagic.

In addition to documented neutral buoyancy and besides ecomorphological measurements and indices suggesting a pelagic life, what are the major morphological changes accompanying neutral buoyancy in nototheniids? My current hypothesis on the incidence of neutral buoyancy is that it is possible only when there is: (1) marked skeletal paedomorphy and (2) substantial accumulation of somatic lipid within the white axial musculature and/or in an adjacent subcutaneous layer. As we have seen above, such modifications have been achieved infrequently in the suborder. The best examples of skeletal paedomorphy include the persistence of cartilage in the skull to the extent that some of the bones of the skull are merely thin lamina sheathing an extensive cartilaginous core (*Dissostichus*, *Pleuragramma*) and unconstricted (*Pleuragramma*) or partially constricted (*Aethotaxis*) vertebral centra with a persistent or partially persistent notochord. Heterochrony, and especially paedomorphy, has been important in the evolution of notothenioids in general (Balushkin 1984; Voskoboinikova 1994, 2001).

Do notothenioids form an adaptive or a nonadaptive radiation?

Tectonic, oceanographic and climatic changes during the past ≈40 million years isolated the Antarctic shelf, lowered its water temperatures, introduced habitat-altering ice shelves and changed trophic conditions. Over the same period of time, the fish fauna also changed, from diverse, cosmopolitan and cool temperate to taxonomically restricted, endemic and polar (Eastman

1993, 2000). Although their fossil record is questionable, notothenioids were likely a component of the Late Eocene fauna. They persisted after the elimination of most of the non-notothenioid fauna and what was to become the Antarctic clade acquired antifreeze glycopeptides, a key innovation that allowed colonisation of subzero ice-laden water (DeVries 1988; Chen et al. 1997a, b; Cheng 1998). With the elimination of most of the Eocene fauna, competition was reduced and ecological opportunities became available. Notothenioids diversified to fill a variety of niches and became the dominant fish group on the Antarctic shelf.

The notothenioid radiation was a macroevolutionary event that resulted in diversification at the level of the family although, as we have seen, some genera have radiated as well. The notothenioid radiation, especially that of the Antarctic nototheniids, is likely an adaptive radiation as it satisfies most of the criteria outlined by Schluter (2000): common ancestry, phenotype-environment correlation, trait utility and rapid speciation. However, the overall notothenioid radiation may also include nonadaptive radiations (Schluter 2000) such as that of the genus *Pogonophryne* where diversification of the 17 species was accompanied by negligible ecological differentiation. The rapidity of the speciation has not been established in most notothenioid clades, but this is less of an issue in notothenioids since we are dealing with the divergence of five Antarctic families, and this would not be as rapid as the species that Schluter (2000) used in his examples. Much work remains to be done in order to frame and to use phylogenetically based statistical methods to test hypotheses relating to the key features of the notothenioid radiation. At this stage our knowledge of the notothenioid radiation is still in the discovery phase; it is not sufficiently advanced to serve as a case study in a book like Schluter's (2000) *The Ecology of Adaptive Radiation*.

Evolutionary trajectories of radiations: how far advanced is the notothenioid radiation?

I found two recent papers by Streelman et al. (2002) useful in evaluating the nature of the notothenioid radiation and in comparing it with other radiations. In the first paper, they focused on testing hypotheses concerning the evolution and diversification of another perciform group, the 90 species of parrotfishes of the family Scaridae. They found that the initial divergence of lineages was along an ecological axis, in this case between seagrass and coral reef associated clades, and this was accompanied by changes in the oral jaw apparatus related to feeding preference and performance in the two habitats. Subsequent diversification in certain clades was triggered by variation in colour and breeding behaviour and was decoupled from the initial divergence. They concluded that the most diverse clades resulted from sexual selection along axes of color and/or communication.

In a later more general paper, Streelman and Danley (2003) develop the argument that different vertebrate radiations follow similar evolutionary trajectories or proceed in similar stages. Divergence frequently occurs sequentially along axes of habitat, trophic morphology and communication in that order. Within the radiation clades proceed to different stages, with the endpoint correlated with species diversity. They suggest that divergence along axes of habitat and trophic morphology follow ecological selection models whereas diversification along the axis of communication proceeds according to sexual selection models. Diversification along the communication axis is exemplified by male nuptial coloration, territoriality and haremic mating systems. They also hypothesize that extensive species richness, as seen in African cichlids or coral reef-dwelling parrotfish, results only when this final stage in attained.

Can the stages of radiation outlined by Streelman and Danley (2003) be recognized in Antarctic notothenioids? In overview it appears to me that Antarctic notothenioids have diverged along the habitat axis into a variety of benthic to semipelagic to permanently pelagic habitats, with the superimposition of a depth related gradient as they occupy inshore to upper slope depths. The morphological alteration of buoyancy, through skeletal reduction and lipid accumulation, to the point of neutral buoyancy is the most extreme departure from the ancestral condition and, as we have seen, is rare. Divergence along the axis of trophic morphology is not conspicuous and is probably confounded by the ecological and dietary plasticity of many species. In an ecosystem with relatively low species diversity and reduced competition, fine division of trophic resources is unlikely. A case in point is the heavy (%$B = 4.15$) benthic nototheniid *Notothenia coriiceps*, a general ambush predator, with an extremely diverse diet that reflects its ability to move up and down in the water column to feed opportunistically on pelagic and benthic prey (North 1996; Casaux et al. 2003; Fanta et al. 2003). In spite of its weight, ungainly body shape and inactivity as documented by video of free-living specimens (North 1996), it shows a preference for feeding in the water column on krill although it switches to macroalgae and the associated amphipod fauna when krill are sparse (Fanta et al. 2003). As far as diversification along Streelman and Danley's (2003) third axis, little is known about communication in notothenioids. Colors are usually muted, sexual dimorphism is modest and to date nesting and possible altruistic behaviour in guarding eggs is known only in *Harpagifer antarcticus* (Daniels 1978, 1979) and in *Lepidonotothen nudifrons* (Hourigan and Radtke 1989). Thus, the most prominent aspect of the radiation of Antarctic notothenioids is the divergence in habitat (from substrate to various levels in the water column with a superimposed shallow to deep gradient), with a lesser amount of divergence along the axis of trophic morphology. As far as our knowledge extends, the radiation has not progressed to the communication stage.

Final remarks

Remoteness and climate have not been obstacles to documenting Antarctic fish diversity, which I have characterized here as relatively low given the large size of the Southern Ocean and moderately well-known. Our knowledge of the diversity of the Antarctic fish fauna is more complete than is that for some more accessible regions, tropical freshwaters for example, because Antarctic ichthyologists have not been confronted with the taxonomic problems posed by the hundreds or thousands of species of siluriforms, characiforms and cichlids. Snailfishes are the Antarctic equivalent in terms of speciosity and taxonomic difficulty, and new species will certainly be discovered. We have seen that the nature of Antarctic fish diversity involves taxonomic restriction of most non-notothenioids and radiation of notothenioids. Liparids have also radiated, but we know so little about their biology that this is not yet a topic for detailed discussion. Notothenioids may be unique among fishes living in marine shelf habitats in their dominance by diversity, abundance and biomass. Furthermore, the radiation in some notothenioid clades includes ecological and morphological diversification, sometimes with respect to buoyancy as well. Finally, to bring research on the nature of the notothenioid radiation into a more analytical phase, we will need more completely resolved cladograms, especially for phyletically basal species, as an essential framework for testing hypotheses about this radiation.

As a scientist and a citizen valuing preservation of the world's biodiversity, I conclude by admitting to limited foresight as to what the future might hold for Antarctic fishes. I first stood on the sea ice of McMurdo Sound in 1971 and remember thinking that these obscure fish would unlikely ever attract the attention of anyone but scientists. After 33 years, commercial vessels are fishing within a few hundred kilometres of McMurdo Sound, almost as far south as a ship can sail. Nor could I have imagined that the creamy white axial muscle of the *Dissostichus* swimming beneath my feet, muscle I thought was too oily for human consumption, would be bringing $19.99 per pound as "Chilean sea bass" in upscale fish markets near my current home in the beef-dominated heartland of America. That I could write a paper on the present topic shows that evolution has no geographic or thermal bounds and, unfortunately, neither does commerce.

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