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# I Biodiversity and evolution

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## INTRODUCTION

Biodiversity and its assessment is a field undergoing unexpected developments (Wilson 1988). This feature of all communities has assumed considerable political importance since the meeting in Rio de Janeiro. Unfortunately, before deciding 'what should be preserved' it is necessary to know what there is to preserve. Even in Antarctica, viewed nowadays as an immense natural reserve to be protected from human impact, biodiversity must be assessed. The traditional taxonomic approach is necessary but not sufficient to answer all the questions. Whilst the species concept remains at the centre of any classification, to understand better the processes and mechanisms which have led to the evolution of biodiversity in time and space, the problems need to be tackled at various levels of organisation, from communities or multispecies assemblages to the intraspecific levels.

The evaluation of intraspecific biodiversity, for instance at the levels of Mendelian populations, or of genes and their molecular constituents, may help in solving various problems of species taxonomy. This approach may also help with aspects of the functional role of biodiversity, provide criteria for the identification of 'key' species and reveal new mechanisms of adaptation and evolution (e.g. DeLong *et al.* 1994). Moreover, changes in biodiversity may also provide an effective tool for monitoring the effects of environmental impact, even those of global change (Solbrig *et al.* 1992).

Antarctic biodiversity, both at the species and community levels, varies from place to place and from group to group. Whilst in some cases we now have a positive indication of the factors causing this, in most cases a convincing picture is still lacking. New sampling methods, new analytical techniques and, above all, the adoption of conceptually and methodologically more advanced criteria to face new as well as old problems, are already taking us down new pathways. For many of those problems a multidisciplinary approach is absolutely essential. Understanding the evolutionary processes which have led to the present diversity relies upon the cooperative efforts of taxonomists, ecologists, geneticists, physiologists and molecular biologists. The contributions to this section of the Symposium can be divided into two groups – both having in common an evolutionary viewpoint. The first group deals with community and species

diversity. Arntz *et al.* (Chapter 1), in their paper on biodiversity in the Antarctic marine ecosystem, stress the lack of agreement between various authors in estimates of species numbers. This may be due to insufficient taxonomic knowledge, to the multiplicity of techniques adopted for assessing biodiversity at the species level, to lack of standardized sampling, or to the misleading effect of older records on delimiting endemisms. Benthic biodiversity is clearly very considerable but many groups are still inadequately described, especially in the deep sea (Grassle 1991). There are continuing problems in providing accurate comparisons of community diversity from different areas.

On land there is also taxonomic confusion. The species status of the Antarctic lichen flora has been thoroughly revisited in the contribution of Castello and Nimis (Chapter 2), who consider valid only a few of the species previously described by Dodge (1973). In their view the known lichen flora is thus reduced from 415 to 260 species, with the percentage of endemic species falling from 91% to 38%, but the percentage of bipolar and cosmopolitan species increases greatly. Partly on the grounds of a high endemic component, previous workers have always concluded that the lichen flora is ancient but the present authors now suggest that the lichen flora is a young one, possibly due to long distance dispersal in the Quaternary.

An interesting example of taxonomic and bionomic bipolarity is provided in a study conducted by Svoboda *et al.* (Chapter 3) on a symbiotic relationship between a Hydractinia and a brittlestar. The Arctic and Antarctic counterparts of both symbionts are closely related, and the morphological features of this commensal symbiosis are remarkably similar. It appears that these unique relationships must have developed independently in both polar seas.

The first group of papers concludes with the contribution of Zimmerman *et al.* (Chapter 4) on the composition and community structure in the demersal fish fauna of the Lazarev Sea. In this area, abundance and biomass exhibit great variability and species diversity is higher than in any other region of the Southern Ocean. These results indicate distribution patterns characterised by pronounced small-scale heterogeneities.

The second group of papers deals with problems of variation at the gene level. It is at this level that studies on population characterization and microevolution need to be pursued. A very

good example is provided by Adam *et al.* (Chapter 5) who studied the geographic and microgeographic patterns of genetic variation in the morphologically variable moss *Bryum argenteum*. Both isozyme and DNA (RAPD) analyses were employed, the latter revealing levels of variation much higher than the former. From these results the authors draw interesting inferences about the patterns of colonisation by this moss in Antarctica.

A stimulating ecogenetic study of fish and seal anisakid endoparasites in both polar regions by Bullini *et al.* (Chapter 6) used isozymes. As well as providing a description of colonisation patterns they also draw conclusions about the host–parasite mechanisms of mutual adaptation and co-evolution. These anisakids exhibit a genetic variability which is higher in the Antarctic species than in the Boreal ones, a difference which is attributed to the lower habitat disturbance of the Antarctic area.

Molecular tools have also proved very useful for establishing phylogenetic relationships. The study by Bargelloni *et al.* (Chapter 7) on nineteen species of notothenioids used mitochondrial DNA genetic analysis, and allows them to infer phylogenetic relationships among and within five families of these fishes. This provides the first example of the use of molecular techniques to address phylogenetic issues in notothenioids, and offers new ways for determining the tempo and mode of their evolution.

These tools can also be effectively applied to the inheritance of specific gene sequences that may have significant evolutionary

advantages. The disputed issue of whether myoglobin is expressed in any of the channichthyid fishes seems to be solved by the demonstration by Vayda *et al.* (Chapter 9) of the expression and accumulation of this protein in two icefish species. The problem is discussed in the light of the genetic events occurring during radiation of channichthyid species.

The use of molecular techniques has greatly increased our knowledge of prokaryotes diversity (Franzmann & Dobson 1993). The contribution of Franzmann *et al.* (Chapter 8) to the problem of adaptive speciation and evolution of this group is of considerable importance. Analysis of the 16 S RNA gene as a molecular clock shows that the Antarctic species diverged long before Antarctica established as a permanent cold environment. The problem is: are there any Antarctic prokaryotes? Whether or not individual species are unique to Antarctica remains an open question, which will perhaps find an answer with the development of adequate new methods.

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# 1 Antarctic marine biodiversity: an overview

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## ABSTRACT

*The unique Antarctic marine environment, its evolutionary history, its biotic peculiarities and its (hitherto) comparatively low degree of human impact make a biodiversity approach and a comparison with other areas particularly worth while. Current knowledge seems to indicate that there is no common pattern for species richness in the various Antarctic subsystems (e.g. pelagic/benthic, shallow/deep) or for different taxonomic groups. Some assemblages appear to be fairly rich in species, others consist of only a few, and the same pattern applies to the various taxa at a higher taxonomic level. The Antarctic marine ecosystem as a whole seems to have a lower percentage of species known to date in most higher taxa than would be expected from its share of the area of the world's oceans. However, comparison with other marine ecosystems is difficult because of differences in area, environment, sampling and processing, and taxonomic knowledge. Comparison with the Arctic Ocean indicates that species numbers of most groups are much higher in Antarctic waters, but many more comparable data are needed to judge whether this also holds generally true for diversity, and whether large-scale latitudinal gradients exist for more than a few groups. Few authors have calculated diversity and evenness indices, and these, too, are often of very limited comparability. High species numbers do not necessarily imply high values of diversity and evenness.*

**Key words:** biodiversity, Antarctica, species richness, evenness, benthos, plankton.

## INTRODUCTION

The term 'biodiversity' is often used in a rather broad sense, which may sometimes lead to a confusion of terms. Many people believe, rather intuitively, that the 'richness' of a community is not only reflected by the numbers of species present and in the distribution of individuals among these species, but also by the total number of individuals, total biomass, and possibly also by a variety of trophic or other ecological functions. Furthermore, there is growing evidence that biological diversity may play a key role in protecting the global biosphere, which is increasingly affected by human influences. We need to measure biological diversity to identify those factors which govern it, and to arrive at a better understanding of the consequences of high or low biodiversity for different ecosystems. In this context, studies on Antarctic biodiversity are of special interest, since the Southern Ocean is still a rather pristine, and presumably a very sensitive, ecosystem.

An earlier paper (Arntz *et al.* 1994) looked at the Antarctic zoobenthos in general and it is useful to begin by considering some of the findings:

- Like other marine ecosystems, the South Polar Sea reveals distinct differences between its various subsystems in shallow water (<30 m), on the deeper shelf and slope, and in the deep sea, although these subsystems share a surprisingly high number of eurybathic species. The intertidal and upper sublittoral levels are heavily impacted by ice. The richest communities, mostly dominated by sessile suspension feeders, are found on the deeper shelf and the upper slope. Seemingly, the deep sea does not reveal great differences from other deep-sea areas of the world ocean; however, sampling in that area has been very limited to date, and further sampling may provide new evidence.
- Densities in most benthic communities, excluding those of

shallow water, are of the same order of magnitude as in similar marine communities in other areas, and are usually much below the numbers that are reached in temperate soft bottoms (see e.g. Linke 1939, Ziegelmeier 1970). Only in one single case (an infaunal community in McMurdo Sound; Dayton & Oliver 1977) have exceptionally high values been found.

- Biomass appears high at first glance in the epifaunal suspension-feeding communities (however, with an important share of silici- and calcimass), although it does not reach the peak values that can be found elsewhere, e.g. in temperate mussel banks (Thamdrup 1935) or intertidal clam beds of upwelling regions (Arntz *et al.* 1987). It seems comparatively low in most infaunal communities of the high Antarctic (Gerdes *et al.* 1992). However, according to Brey & Clarke (1993), average benthic biomass in the Antarctic is higher than that of temperate and subtropical communities. The distribution of both biomass and abundance values is highly patchy.
- Various kinds of life history strategies in the zoobenthos have been found in the Antarctic, from close coupling to the primary production cycle in the pelagic (which is considered to be the main ecological factor in the South Polar Sea, in terms of seasonal food limitation, rather than the low temperature; see Clarke 1988) to total uncoupling. However, meroplanktonic larvae seem to be scarce, despite the fact that a certain number of such larvae has been found recently, mostly belonging to larger organisms living in shallow water (Pearse *et al.* 1991).

This paper will be restricted to the narrower meaning of biodiversity, i.e. to species numbers and the distribution of individuals among the species. We will not be discussing the usefulness of different diversity indices (see, e.g. Hurlbert 1971, Margelef 1977). We think that with respect to the Southern Ocean the real problem is that technical progress has hampered comparative studies of biodiversity. People have been ingenious in inventing ever more perfect grabs, corers, plankton nets and trawls. There have also been major developments in sampling methods and treatment of samples. However, not even the most refined techniques can reduce data to a common denominator if some basic requirements of comparable sampling and processing of samples are neglected. If Antarctic researchers do manage to agree on a limited range of standardized equipment and procedures in the future, they should then be able to answer the basic questions of interest to them:

- Is biodiversity high or low in the Southern Ocean?
- What degree of variability in biodiversity is there among different Antarctic subsystems and assemblages?
- Which ecological factors (physical, biological) shape and characterize areas or assemblages of high and low diversity?
- How do Antarctic communities compare with those in other parts of the world ocean? In particular, is there any such thing as a general latitudinal gradient?

Despite the fact that the Southern Ocean, in terms of physical environmental factors, is a relatively homogenous ecosystem of enormous dimensions compared with the seas around other continents, a closer look reveals distinct differences among the different subsystems. This is true not only for the various zones or belts surrounding the continent, from the high Antarctic across the pack-ice belt, through the sub-Antarctic including parts of the Antarctic Peninsula, to the 'maritime' groups of islands (e.g. Hempel 1985). It is valid also in a vertical sense, from the barren Antarctic shores scoured by ice across the much richer sublittoral communities on the shelf and slope to the virtually unstudied vast areas of deep sea surrounding the continent. Talking about marine biodiversity in 'the Antarctic' we have to refer to a multitude of different sites and species assemblages. Life in the pelagial and a great part of life in the benthic has been described as being essentially circumpolar (Hedgpeth 1971), but in some benthic groups such as the asteroids (Voß 1988), molluscs (Hain 1990) and holothurians (Gutt 1991a), distinct differences have been observed in species composition between the subregions of the Southern Ocean.

Taxonomic knowledge of the Antarctic fauna may be better than one would suspect (see table 10.2 in Winston 1992); knowledge of the fauna of the pack-ice zone has improved considerably in recent time (Arntz *et al.* 1994), but much of the deep-sea fauna and the meio- and microfauna in general are almost unknown (Arnaud 1992, Dahms 1992). Unfortunately, many taxonomists work on timescales which are not particularly helpful to the ecologist who is in need of rapid species identification now, in order to be able to calculate species numbers and diversity indices. In this respect, limitations for Antarctic research resemble very much those for scientists working in the deep sea.

Finally, if we want to compare conditions in 'the Antarctic' with those in other marine areas (e.g. species numbers) what other area would make a valid comparison? All other continents have a wide range of climatic zones, and the extensions of most other relatively homogenous marine regions are much smaller than those of the Southern Ocean. The deep sea is an exception, and a comparison certainly is worth while, as was shown over a decade ago by Lipps & Hickmann (1982). Comparisons also appear reasonable with the Arctic Ocean, taking into account the great differences between the two systems (Dayton 1990, Dayton *et al.* 1994).

Thus, finding an answer to the questions as to what Antarctic marine biodiversity is like and how it compares to that of other areas is not simple. On the other hand, it is worth while making the attempt because Antarctica is unique, it has a number of abiotic and biotic peculiarities (Dayton 1990, Dayton *et al.* 1994, Arntz *et al.* 1994), it has a long evolutionary history (Clarke & Crame 1989, 1992), and, despite a growing human impact, it is still much less anthropogenically disturbed than any other marine ecosystem. We will have to consider these peculiarities, and also the difficulties outlined above, when looking at the available data. The focus will be on benthic species as the most

numerous group, but other groups will be considered where data are available.

## BIODIVERSITY

### Species numbers

There have been several estimates of species worldwide (e.g. Wilson 1992), which also include terrestrial and limnic organisms. The recent estimate of species numbers in the major groups of marine organisms in the world's oceans by Winston (1992, table 10.1) is quite detailed, but may turn out to be an underestimate for many groups, in the light of a recent discussion on the subject (Grassle & Maciolek 1992, May 1992, Poore & Wilson 1993 and reply by May in that paper). Using estimates of species along spatial gradients, Grassle & Maciolek (1992) arrived at a few hundreds of millions of benthic invertebrates in the world ocean, which they scaled back to 10 million because they believed that species numbers should be lower on the floor of ocean basins than on continental shelves or slopes. May (1992) doubted their estimate, mainly because he thought that there is no linear increase of species numbers along global gradients, and he proposed an upper limit of half a million species. Poore & Wilson (1993) used isopod data to demonstrate that Grassle & Maciolek's final estimate might be rather on the low side since the ratio between known and unknown species (31% known) in their samples was unusually favourable. While May used a factor of two for the ratio of unknown to known deep-sea species, Poore & Wilson suggested a factor of 20. Furthermore, whereas Grassle & Maciolek assumed that shallow marine infaunal communities outside the tropics have generally lower species numbers, using as an example 200 species from comprehensive sampling on Georges Bank, Poore & Wilson mention values of 700 and 800 invertebrates from two SE Australian communities.

Without further information, the estimates in table 10.1 from Winston (1992) have to stand. We have added 'true' seabirds from Tuck & Heinzel (1980) and Harrison (1983), seals from Deimer (1987, based on the 'Marine Mammal Protection Act' of 1972) and Bonner (1989), and cetaceans from Gaskin (1982) to complete the list.

Probably the first person to call the attention to the fact that some groups in the Antarctic are 'rich' in species and others are 'poor' was Dearborn (1968). With improved taxonomic data, species numbers of Antarctic marine fauna were compiled by Dell (1972, table I) and White (1984, table III). The former author also provided figures on the percentage of endemic species, and the latter compared Antarctic species numbers with those in the Arctic, revealing in all cases higher species richness in the Southern Ocean. White's figures have been reused by Grebmeier & Barry (1991), so the Arctic species catalogue may not have changed much recently. Decapods do not fit the general picture in that they have higher species numbers in the Arctic (Dearborn 1968).

The Antarctic species numbers provided by White were in

each individual case substantially higher than those given by Dell, which apparently again reflects taxonomic progress. White (1984, table VII) also cited endemism values on the species and genus levels from various sources, which in some cases compared well with Dell's figures but differed substantially in others. Based on extensive isopod material, White (1984, table VIII) showed that species and genera numbers differ considerably at different Antarctic localities, as do the percentages of endemism both on the species and genus level. This is a very important point in that it indicates that, as with the species numbers, most endemism figures found in the literature cannot simply be compared; they must be referred to specific regions of the Southern Ocean. Unfortunately, by no means all authors who have compiled the data of particular groups have indicated clearly whether and to what extent they include the area north of the Polar Front (in some cases even the Magellan Region is included). Obviously, both the species number and endemism values have to be lower than for the total Southern Ocean if they refer to subregions, but see Brandt (1991, table 2) for a different way of presentation. It is not surprising, considering the 7 years between the publication dates, that Brandt's (1991) data include more isopod species than those of White (1984), but the data (where they are comparable by regions) bear very little resemblance. This reflects the problems a reviewer has to face with Antarctic data.

Our recent compilation (Fig. 1.1A) suffers from the uncertainties just indicated. As can be seen from this illustration, there is a variety of species-rich and species-poor taxa. For example, stomatopods are totally absent, and reptant decapods are almost absent from the Antarctic fauna, natant decapod species are few, whereas groups such as sponges, bryozoans, mollusks, polychaetes, amphipods and isopods have a high number of species. Since White's (1984) compilation many new species of Antarctic amphipods, isopods, bryozoans and pycnogonids have been added to the list, which would increase the difference from the Arctic provided the figures there actually remained the same. Interestingly, those groups that are rich in species belong to quite different trophic guilds and also differ substantially in terms of motility. Some currently poor groups, such as the decapods and fish, used to be quite rich around the fragments of Gondwana in Cretaceous and Early Tertiary times, but may have been eliminated by glacial advances (Clarke 1990).

What do 'high' and 'low' species numbers mean, and how do they compare with other marine areas? Again, there is the problem of scales and depths, even if we agree to compare different latitudes and (thus) climatic zones. Clearly, we cannot compare species numbers from the total Southern Ocean with those from a single transect in another area, or compare data from a box corer with Agassiz trawl data. Gutt (1991b) has discussed these problems in detail. In some cases – e.g. most of the peracarids – the Southern Ocean will outcompete many marine areas in the world whereas in others, such as the decapods, it is obvious that they are under-represented under the present conditions. Interestingly, some of the taxa with few species in

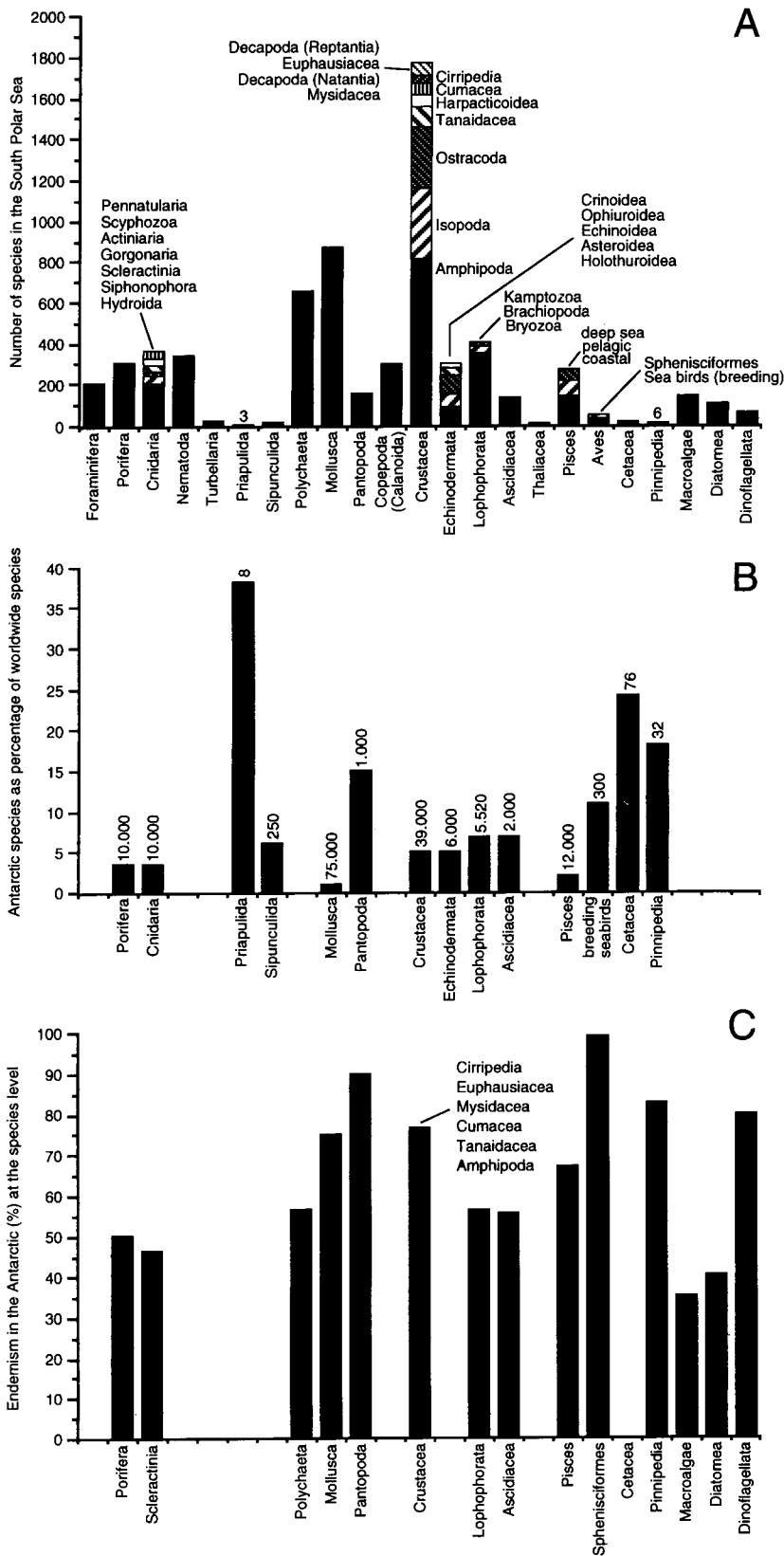


Fig. 1.1. A. Species numbers of different taxa in the Southern Ocean, present estimates. Data sources: Sieg & Wägele (1990); additional information: Porifera, Tendal (pers. commun.), Sarè *et al.* (1992); Hydroida, Svoboda (pers. commun.); Siphonophora & Scyphozoa, Pagès (pers. commun.), Larson (1986); Scleractinia, Cairns (1990); other Cnidaria, Turbellaria and Nematoda, Dell (1972); Copepoda (pelagic), Razouls (1992); Decapoda, Arntz & Gorny (1991); Euphausiacea, Kirkwood (1982); Cirripedia, Newman & Ross (1971); Cumacea, Ledoyer (1993); Isopoda, Brandt (1991); Amphipoda, de Broyer & Jazdzewski (1993); Asteroidea, Voß (1988); Ophiuroidea, Dahm (pers. commun.); Echinoidea, Pawson (1969); Holothuroidea, Gutt (1988); Kamptozoa, Emschermann (1993); Thaliacea, Lohmann & Hentschel (1933); Pisces, Kock (1992); Aves, Odening (1984), Laws (1989); Pinnipedia, Bonner (1989); Cetacea, Gaskin (1982); Macroalgae, Wiencke (pers. commun.); Diatomea & Dinoflagellata, Balech (1970), Heywood & Whitaker (1984). B. Antarctic species numbers (as in A) as a percentage of species numbers in the world ocean (worldwide estimates derived from Winston 1992, table 10.1; see numbers above columns). C. Endemism at the species level of various taxa in the Southern Ocean (only south of Antarctic Convergence). Data sources as in A; in addition: Porifera, Koltun (1970); Polychaeta, Knox (1970); Pantopoda, Frey (1964); Ascidacea, Kott (1969).

Antarctica, such as the euphausiids, natant decapods and brachiopods, include species with a high numerical or biomass dominance rank in their communities.

In terms of total species numbers within assemblages, the rich epifaunal suspension feeder communities of the Antarctic can be compared with tropical or subtropical seagrass (Ros *et al.* 1984, Gambi *et al.* 1992, Mazella *et al.* 1993) or even with coral communities (see Gutt 1991b), both of which are also three-dimensional. On the other hand, Antarctic intertidal assemblages have an extremely low species richness, much lower even than temperate or upwelling assemblages suffering from severe oxygen deficiency (Arntz 1981, Tarazona *et al.* 1988). Another example of very low species richness in the Antarctic is provided by the warm-blooded animal assemblages on sea ice; e.g. emperor penguin colonies host at most a handful of other species.

The total numbers of invertebrate species from the Southern Ocean, the overwhelming majority of which are benthic, are quite similar to those presented by Fredj & Laubier (1985, table 1) for the Mediterranean benthos. The echinoderm figure (144 species) is twice as high in the Antarctic, but in all other cases more species are known from the Mediterranean, which has been studied in more detail but has a much smaller extension. The 'total crustaceans' group has about the same number of species in both ecosystems, but decapods are quite rich in the Mediterranean and extremely poor in species in Antarctic waters.

Using our present best estimates for the Southern Ocean again and comparing these with the estimated marine species numbers in the world's oceans from Winston (1992, table 10.1), most of the Antarctic higher taxa provide between 3 and 7% of the worldwide marine species number of their respective group (Fig. 1.1B). Only pycnogonids and priapulids have much higher values, as have the warm-blooded animals, the majority of which, however, are migrant species. Three to seven per cent is clearly less than the share of the Southern Ocean in the world ocean; the area covered by pack ice in winter alone exceeds 10% of the world ocean surface (Laws 1989). However, the data presented by Winston (1992) have been derived from actual knowledge on shelf species, whereas shelf areas of the same depths are relatively scarce in the Antarctic under present geological conditions. The figures may change in either direction in the future depending on how many new species are detected in the deep sea and whether Grassle & Maciolek's (1992) estimate holds true.

For those species that live in Antarctic waters, our data confirm a high level of endemism in most groups (Fig. 1.1C). The problems that arise in calculating valid figures have been referred to above. Endemicity values of taxa may reflect environmental changes in the past and both duration and degree of isolation from other biogeographic zones. If marked environmental changes such as the advance and retreat of ice shelves coincide with isolation, as is suggested for the Antarctic, allopatric speciation may be favoured, leading to adaptive radiation into groups with many endemic species. Levels of endemism are thus

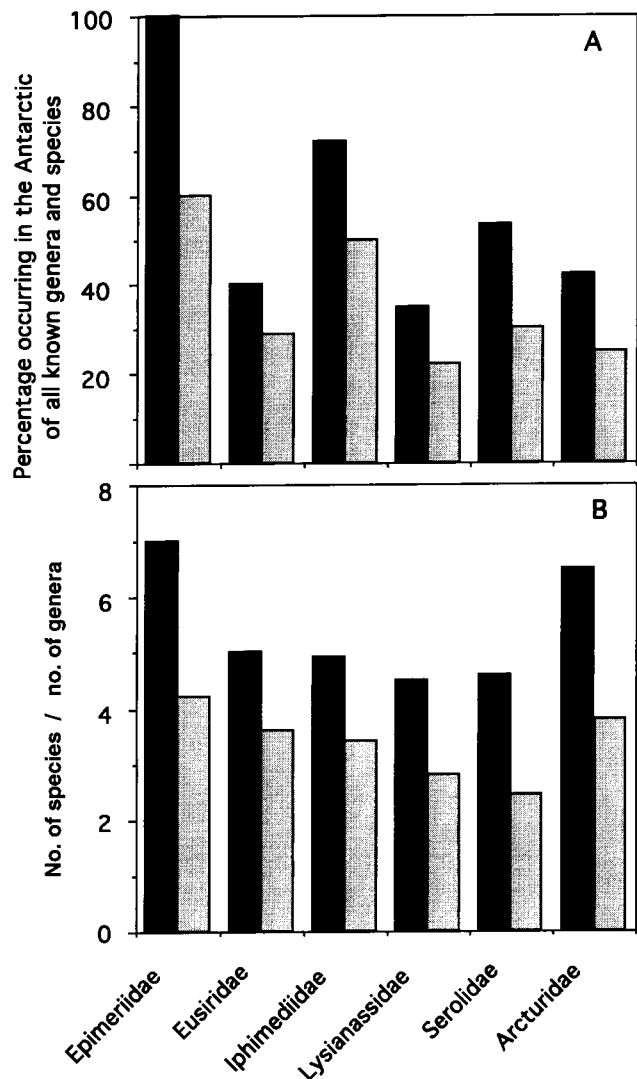


Fig. 1.2. A. Numbers of Antarctic genera (black columns) and species (shaded columns) of four amphipod and two isopod families as a percentage of the numbers of genera and species of these groups known worldwide. B. Taxonomic diversity. Ratio of species:genera numbers in four amphipod and two isopod families. Black: worldwide ratios, shaded: Antarctic ratios. Data are derived from de Broyer & Jazdzewski (1993), Klages (1991 and unpublished data), Brandt (1991) and Wägele (1994).

helpful in explaining the great differences in species richness found among Antarctic taxa.

On the other hand, the ice shelf processes which favour species formation must have caused extinctions of many species as well. This may be the reason why taxonomic diversity is not higher in most cases. For example, four common gammaridean amphipod and two common isopod families contribute a high share of their genera (35–100%) and species (22–60%) known in the world's oceans to the Antarctic ecosystem (Fig. 1.2A), but the species:genus number ratios, ranging between 2.8 and 4.2, are lower than on a worldwide level (Fig. 1.2 B). In the other groups referred to in Fig. 1.1 A this ratio always ranged between 1 and 4. However, a general trend (e.g. an increase from old to young groups), or the presence of any distinct taxonomic subgroups, were not recognizable. Another reason for the low ratios encountered (i.e. the high taxonomic diversity), which adds to

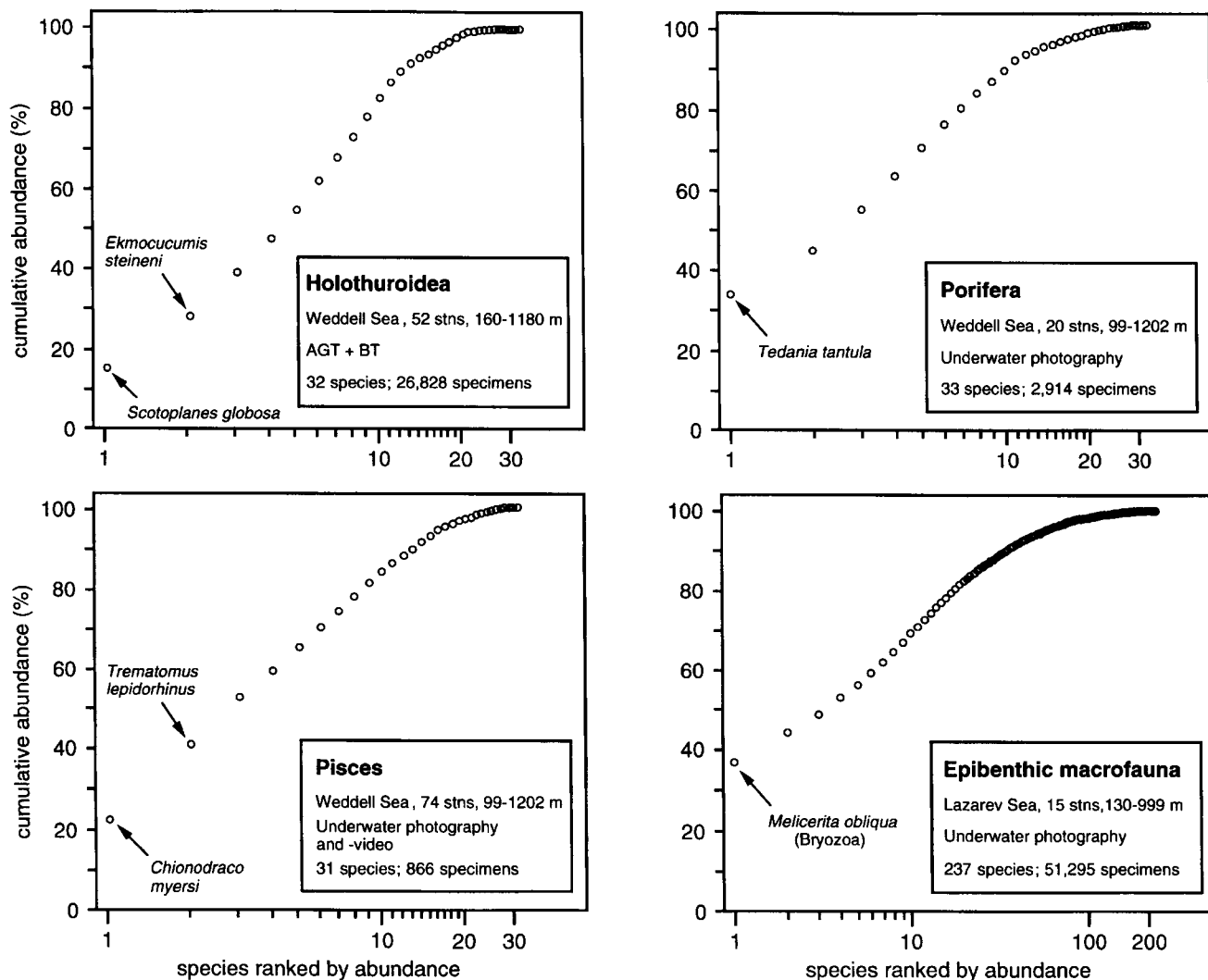


Fig. 1.3. Cumulative dominance plots of three benthic/demersal taxa in the Weddell Sea and total epibenthic macrofauna in the Lazarev Sea. Data derived from Gutt (1991), Barthel & Gutt (1992), Ekau & Gutt (1991), Gutt *et al.* (1994) and Gutt & Starmans in press AGT=Agassiz trawl, BT=bottom trawl.

the one discussed above, may be that within some families only a few genera have split up into numerous species, whereas many of the others are monospecific; an average then is of little use. For example, shelled gastropods and bivalves in the Weddell Sea reveal a remarkably high taxonomic diversity: the 145 gastropod species belong to at least 26 families and 69 genera, while the 43 bivalve species belong to 17 families and 25 genera. Many genera and some families are monospecific. High species numbers only occur in three families (Buccinidae, Turridae, Philobryidae). Some, elsewhere very successful, groups are missing in the Southern Ocean altogether: Cardoidea, Veneroidea, Tellinoidea, Mactroidea (Hain 1990). Holothurians (Gutt 1991a) also have a high taxonomic diversity in the Weddell Sea. All eight species of caridean shrimp in that area belong to different genera (Arntz & Gorny 1991).

#### Dominance curves: epibenthic macrofauna

If data are at hand that allow for a breakdown into species and include counts of individuals, cumulative dominance plots are

the most illustrative way to demonstrate differences between assemblages and to show whether there is a certain balance (evenness) between the numbers of individuals of different species. Data, both for total epifaunal communities and for higher taxa such as holothurioids, most of which stem from surveys with imaging methods (UW camera and ROV) are available for the Weddell Sea and the Lazarev Sea (Fig. 1.3). From 1085 UW photos taken at 15 stations in the Lazarev Sea between 130 m and 1000 m depth (981 m<sup>2</sup> area), Gutt & Starmans (in press) counted 51 295 individuals of epibenthic macrofauna which could be assigned, on different taxonomic levels, to 237 taxa. Within-site species numbers as found by this method varied substantially (between 39 and 182) but were higher than those of epifaunal communities in temperate areas such as the Baltic (Arntz *et al.*, unpublished observations). Visual methods have proven to be very useful for the quantitative study of the epifaunal macrofauna and megafauna component, which is difficult to sample with grabs and cores (Hamada *et al.* 1986), or for comparison with trawl catch data (Brey & Gutt 1991, Ekau



& Gutt 1991, Gutt *et al.* 1991, 1994, Barthel & Gutt 1992, Gorny *et al.* 1993).

The resultant dominance curves are by no means flat; there are always a few dominant species, particularly in the three groups (holothurians, sponges and fish) presented in Fig. 1.3. On the whole, however, dominance appears to be lower than in boreal temperate communities (Arntz & Rumohr 1982). This is particularly true for the 'epibenthic macrofauna' curve (lower right in Fig. 1.3) where only the dominant bryozoan *Melicerita obliqua* reduces an otherwise very high evenness (Gutt & Starmans *in press*). A surprisingly high evenness – 11 species with populations > 2000 ind. m<sup>-2</sup> – was also registered by Dayton & Oliver (1977), in a dense community in McMurdo Sound, which was, however, infaunal.

#### Diversity (Shannon–Wiener) and other indices

##### Macrobenthos

Almost all studies where diversity or evenness indices have been calculated in the Antarctic cannot be compared due to the use of different equipments and procedures (Clarke 1992). Even where the same persons worked at different localities, changes were made in the gear used (Gallardo 1992). In many other cases, either higher taxa only were presented due to taxonomic difficulties, or the breakdown to species was restricted to a few groups.

Using *H'* diversity and Margalef's species richness index SR, Richardson (1976) made an attempt to compare the soft-bottom macrofauna data from Arthur Harbor (Anvers Island) with data from similar environments elsewhere in the world's oceans. He concluded that the Arthur Harbor indices were quite high. However, Richardson & Hedgpeth (1977) noted the apparent lack of comparability of the then existing Antarctic macrofaunal data (Gallardo & Castillo 1968, 1969: Deception and Greenwich Islands, respectively; Lowry 1975: Arthur Harbor; Hardy 1972: Signy Island) and found only Boesch's (1972) investigations on the Virginia and N Carolina shelf to be comparable with their own data. The *H'* values did not differ between the two localities, and species richness (SR according to Margalef) was much higher and evenness much lower at Arthur Harbor – the latter probably due to recruitment of dominant species at the time of sampling. Independently, the other investigators mostly claimed that their diversity values from Antarctic sites were high; only Gallardo & Castillo (1969) reported lower values from Deception Island due to frequent volcanic activity.

There does not seem to have been much advance in the question of calculating diversity indices of infaunal macrobenthos communities in the Antarctic since Richardson & Hedgpeth (1977). Future, comparable, studies are necessary to reveal whether Antarctic macrobenthos – with the exception of the intertidal and upper sublittoral – is really more diverse than the benthic macrofauna in other areas.

##### Meiobenthos

To our knowledge, there has been only one diversity investigation of an Antarctic meiobenthos community to date. Herman

& Dahms (*pers. commun.*) collected benthic meiofauna along a transect off Halley Bay (SE Weddell Sea) during the 'European Polarstern Study' in 1989. They could not distinguish the individual species but calculated different diversity indices for 13 major taxa. Consequently, their *H'* values were 'monotonously low' (Dahms 1992) due to the overwhelming dominance of nematodes. Much more, and more detailed, work on the meiofauna is needed to arrive at definite conclusions.

##### Fish

Hubold (1992) calculated diversity from trawl (bottom trawl and Agassiz trawl) catches taken by various investigators in different Antarctic regions and compared them with data from the North Sea and Arctic waters (S Greenland). Hubold himself admits that comparability is limited due to the use of different trawls and somewhat variable trawling duration and speed. However, it seems noteworthy that *H'* diversity and evenness values were consistently highest in the high Antarctic (Weddell Sea, Prydz Bay, and Ross Sea) compared with the Scotia Arc region, whereas the values for the latter were mostly in the same range as the northern hemisphere data. Within the Atlantic sector of the Southern Ocean the data indicate a steady latitudinal increase of *H'* diversity towards the high Antarctic (Hubold 1992, fig. 11). Towards the benthopelagial and the true pelagial, diversity and evenness of the respective fish communities seem to decrease (again, the values are not strictly comparable since different trawls were used).

Hubold (1992) stresses that the within-site species richness and diversity of Antarctic demersal fish communities is surprisingly high, despite a very low taxonomic diversity on the levels of orders and families (Kock & Kellermann 1991) and generally lower species numbers compared, for example, with the north-west Atlantic. He argues that the Antarctic shelf has been colonized by a mostly endemic (strongly eurybathic?) demersal fish fauna which has occupied many niches, whereas the development of species with a pelagic life cycle has been restricted by the advance of the ice shelves and distinct changes in hydrography during glacial periods.

##### Zooplankton

Boysen-Ennen (1987) and Boysen-Ennen & Piatkowski (1988) studied meso- and macrozooplankton communities in the southeastern Weddell Sea. Based on rectangular midwater trawl (RMT) catches, they distinguished three communities (with a number of regularly occurring species): the Southern Shelf (55), the Northeastern Shelf (64), and the Oceanic Community (61). They calculated mean *H'* diversity and evenness for each of the three communities. The Oceanic Community had the highest values followed by the Southern Shelf community; all values differed significantly. All three communities were much poorer at the surface (0–50 m) than at depths between 51 and 300 m.

Piatkowski (1987) also calculated mean *H'* diversity and evenness for four macrozooplankton communities in the Antarctic Peninsula area. As would be expected, species

numbers for the macroplankton were generally lower because the mesoplankton was not considered. Again the oceanic community revealed the highest values. However, all figures were very low in this area and varied greatly with the consequence that no significant differences were detected. Piatkowski (1987) compares these data with macrozooplankton data from the three southeastern Weddell Sea communities mentioned above, taken by the same method, and shows the southeastern Weddell Sea values to be consistently higher. In this case the Northeast Shelf Community (which combines elements of the other two communities) was most diverse and had the most even distribution of individuals over species.

Using the same equipment again, Siegel *et al.* (1992, table 5) measured diversity of macro- and mesozooplankton in the open north Weddell Sea. The values were fairly high at the sea surface and increased to 200–300 m depth.

So, as with the fish communities, the available zooplankton diversity data seem to indicate highest diversity in the high Antarctic. There are, however, distinct differences, particularly between the oceanic communities of the two regions: whereas in the southeast Weddell Sea copepods contribute up to 85% of individuals, euphausiids may provide over 90% dominance off the Antarctic Peninsula and in the Scotia Sea and north Weddell Sea (Mujica & Torres 1982, Siegel *et al.* 1992), and at stations with a great preponderance of one group the other is almost excluded (Boysen-Ennen 1987).

#### *Latitudinal clines*

Within the Antarctic, regional differences in within-site diversity have already been discussed in the cases where data from different sites were comparable. This is clearly not the case for macrobenthos. However, a breakdown into species and their numbers of individuals is available for part of our material from the Weddell Sea, which may give an indication of what we might expect if we had comparable data.

The issue of latitudinal clines was first put forward by Thorson (1952), who showed that the average species number of three epifaunal groups (amphipods, nudibranchs and brachyuran crabs) increased strongly from the high Arctic towards the tropics, whereas there was no such change in the mean numbers of infaunal species. Surprisingly, this finding has been generalized by many scientists and extended in a way that would yield a bell-shaped curve for the world's oceans, with highest faunal species numbers on the equator and lowest numbers in the Arctic and Antarctic (note that the seaweed flora does not show highest species richness in the tropics, cf. Lüning 1990).

Clarke (1992) has shown that at this time the evidence for an overall latitudinal gradient in marine species richness is not convincing, although there are three cases where a bell-shaped curve does indeed apply: for gastropods (Fischer 1960), bivalves (Stehli *et al.* 1967) and planktonic foraminiferans (Stehli *et al.* 1972). As Clarke (1992) points out, these groups have in common a calcareous skeleton, and the metabolic cost of calcification is higher at low temperatures. However, even for these groups the database from the Southern Ocean is much

smaller than from other latitudes. The evidence for a latitudinal cline in coastal waters remains weak (Gage & May 1993).

In the deep sea, latitudinal gradients seemed less likely than in coastal waters due to the large distance of the communities in this area from environmental impacts at the surface and the 'endless sameness of the deep-sea bed' (Gage & May 1993), although there has been much discussion on plankton aggregates reaching the seafloor at great velocity (Graf 1989). However, Rex *et al.* (1993) presented evidence from epibenthic sled data that shows continuous poleward declines in the Atlantic Ocean to be existent for deep-sea bivalves and gastropods, and also in the northern hemisphere for abyssal isopods. Again, the database is much weaker for the South Atlantic deep sea, and the authors lacked data south of 40° S. Rex *et al.* (1993) presented their data as 'normalized expected number of species',  $E(S_n)$ , which is Hurlbert's (1971) modification of Sanders' rarefaction method. It normalizes species numbers to a common number of individuals and measures evenness, not species richness, although large values of this index will often indicate that more species are present (May 1992).

Brey *et al.* (1994, table 1) responded by providing  $E(S_n)$  values from the southeastern Weddell Sea which were normalized to  $E(S_{100})$  for inter-taxon comparison, and the three groups that had been presented by Rex *et al.* (1993) were adapted to the normalized sample sizes used by these authors. The resultant values for the three groups in question were much higher than the Arctic values presented by Rex *et al.* and rather in the upper range of their values from the tropics, indicating that the trend of the bell-shaped curve may be reversed in the Antarctic in these cases. However, other benthic groups clearly have much lower  $E(S_{100})$  values whereas amphipods had the highest value at all (same table).

Brey *et al.*'s (1994) paper certainly contributes to the discussion, but again there is a distinct question mark as to the comparability of the data. Agassiz trawls and epibenthic sleds have very different catch characteristics, the mesh size in the codend differed markedly, and the SE Weddell Sea data were clearly taken (on the average) from lower depths. There are also arguments in favour of a comparability of the datasets – the meshes are mostly clogged by sponge spicules or bryozoan debris which prevent smaller individuals from being washed out, and eurybathy is a characteristic property of Weddell Sea benthos. Whether increased numbers of species as taken by an epibenthic sled would increase or decrease the  $E(S_n)$  values would finally depend on the numbers of individuals. At any rate, the issue of latitudinal gradients has to be treated with great caution until better samples are available. At this time we cannot even be sure that the paradigm of exceptionally high diversity in the deep sea is true (Gray 1994).

## DISCUSSION

The belief that Antarctic communities are rich and diverse, as has often been suggested in the literature, receives some support from our study but at the same time it has become obvious that