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ANTARCTIC MARINE BENTHIC DIVERSITY

ANDREW CLARKE & NADINE M. JOHNSTON
British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK
e-mail: accl@bas.ac.uk

Abstract Species lists have been compiled for all the major groups of Southern Ocean benthic marine invertebrates, eliminating synonymies where possible and providing a subjective estimate of completeness and reliability for each group. Antarctic marine diversity (pelagic and benthic) is relatively high at the phylum and class level, with the gaps mostly comprising minor, meiofaunal or parasitic groups. Most benthic diversity data come from the continental shelves, with relatively few samples from deeper water. Even for the continental shelves, however, sampling is highly patchy with some areas hardly investigated at all. Over 4100 benthic species have been reported from the Southern Ocean, with the most speciose groups being polychaetes, gastropods and amphipods. Comparison with tropical and temperate regions suggest that decapods, bivalves and teleost fishes are poorly represented in the Southern Ocean benthic marine fauna, whereas pycnogonids, echinoderms and many suspension feeding groups are rich and diverse. Some groups that are currently low in diversity were previously well represented in the Antarctic shallow water marine fauna, notably decapods and many fishes. Other groups have undergone marked radiations in the Southern Ocean, including pycnogonids, amphipods, isopods and teleost fishes; in all cases, however, it is only some lineages that have diversified. This indicates that evolutionary questions concerning the origin, diversification or extinction of the Southern Ocean marine fauna will have no single answer; the evolutionary history of each group appears to reflect a different response to the tectonic, climatic and oceanographic changes to which they have been subject through history. The disposition of southern hemisphere continents makes it difficult to assess whether there is a latitudinal cline in shallow-water marine diversity to mirror that known from the northern hemisphere. Within Antarctica, many species appear to have circumpolar distributions, and the long established biogeographical division into continental Antarctic, Antarctic Peninsula and sub-Antarctic regions have not been challenged by recent sampling. For most groups the frequency distribution of species per genus ratios is typical, though none is well described by the predictions from current evolutionary or null models. Where data are available, size spectra indicate that many Southern Ocean taxa are small, a few spectacular examples of gigantism notwithstanding, and species abundance plots are normal. Knowledge of the Southern Ocean benthic marine fauna has reached a stage where we can now ask powerful evolutionary questions, and the development of new molecular techniques provides the mechanism for answering them.

Introduction

In the past two or three decades there has been an increasing recognition of the loss of species through the activities of man. This has lead to a resurgence of interest in biological diversity, both in its purely intellectual aspects and in terms of its relevance to conservation, management and environmental issues. Although there was considerable theoretical interest in the measurement of biological diversity in the 1960s and 1970s, such work then fell out of fashion. This was partly because an understanding of the underlying processes which produced the observed differences in diversity between habitats or areas had proved somewhat elusive. The theoretical framework provided by the work of MacArthur & Wilson (1963, 1967) on island biogeography did not translate easily to the more complex mainland, and no general theory of biological diversity emerged.

The present revival of interest in biological diversity can be traced back to a seminal conference, the National Forum on BioDiversity, held in Washington, DC, on 21–24 September 1986. This conference was the birthplace of the neologism *biodiversity* and resulted in a highly influential proceedings (Wilson & Peter 1988). There followed an almost exponential rise in the number of scientific papers and other literature concerned with biological diversity. Particularly influential amongst these was E.O. Wilson's lucid call to arms *The diversity of life* (Wilson 1992). In recent years interest in biological diversity has remained strong, with the appearance of a number of important text books and edited volumes (Magurran 1988, Huston 1994, Rosenzweig 1995, Hawksworth 1995, Gaston 1996) and compendious reviews of data (World Conservation Monitoring Centre 1992, Heywood 1995).

What is biological diversity?

There are currently well over a dozen formal definitions of biological diversity or biodiversity. The definition which has come to be most universally accepted is that enshrined within the Convention on Biological Diversity. This far-reaching treaty was signed by 156 nations on 5 June 1992 at the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro. The Convention on Biological Diversity was perhaps the most important outcome of UNCED, and it came into force approximately 18 months later. The UNCED definition of biodiversity is laid out in Article 2 of the Convention on Biological Diversity. It is:

> "Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

This definition provides a broad conceptual framework for any consideration of biological diversity. It also creates a problem in that it includes everything from the genome to the ecosystem. Although such all-encompassing definitions may have value in a political or management context, they tend not to help the development of science. More recent definitions have tended to be more focused, and a typical one is that of Hubbell (2001) who defines biological diversity as

> ...synonymous with species richness and relative species abundance in space and time. Species richness is simply the total number of species in a defined space at a given time, and relative species abundance refers to their commonness or rarity.

This definition, and many others like it, are far more useful in being more clearly expressed and restrictive. They also highlight a major concern of the early studies of biological diversity, which was the problem of how best to express the number of taxa (usually species) in an area or sample. The challenge was to devise a statistic which simultaneously expressed the number of species, and the distribution of individuals within those species. This proved both difficult and contentious, but these early theoretical studies did clarify the important distinction between local and regional taxonomic richness (MacArthur 1965, 1972, Whittaker 1972, 1977).

In attempting to develop a pragmatic approach to quantifying biological diversity, ecologists have recently developed three main themes. The first has stemmed from the recognition of the role of evolution and the intuitive feel that taxonomic distinctiveness is an important criterion in diversity: an assemblage of six grass species and an assemblage composed of a single grass, a moss, two species of shrub and two trees contain the same number of species but clearly differ greatly in some intuitive concept of diversity. Clarke & Warwick (1998, 1999, 2001) have developed a number of innovative new diversity indices which incorporate taxonomic distinctiveness or the evolutionary relatedness of component taxa, and a similar approach has been developed in parallel in terrestrial ecology (Webb 2000). Warwick & Clarke (2001) provide a recent review of this topic.

The second theme has been a move to studies of diversity at the molecular level. These have been important in emphasising the enormous taxonomic and functional diversity in organisms previously regarded as somewhat more uniform (particularly Archaea and Eubacteria). These approaches provide a valuable intellectual challenge to preconceived notions of metazoan importance, but they also emphasise both the limited value of a single measure of biological diversity and the danger of limiting studies of biological diversity to the well known macroscopic metazoans.

The third theme in recent work on biological diversity has been the return to simple taxon richness as a straightforward and informative quantitative measure of diversity. It had long been recognised that most intuitive concepts of diversity somehow merged the simple number of taxa present with the distribution of individuals amongst those taxa: a given number of equally common species form an assemblage that is in some way more diverse than one comprised of the same number of species but which vary in abundance. Unfortunately, attempts to incorporate both species number and species abundance into a single diversity index have resulted in no single agreed approach, and taxon richness has once again emerged as the most useful simple measure. Taxon richness does, of course, run the severe risk of sampling bias but when used with care it has the value of being quick, simple and informative, particularly when assessing diversity over large spatial scales where relative abundance data are rarely available. Furthermore, rare species can be as informative for evolutionary or biogeographic considerations as common ones.

Generally, species are regarded as the fundamental unit of diversity (Claridge et al. 1997). In some cases species level data are not available or are unreliable; here genus or family level richness can provide a good indication of underlying species richness. Examples are rapid assessments of the diversity of a previously unsurveyed area or, in palaeobiology, where sampling error is too great at the species level (Roy et al. 1996). A useful brief review of the use of higher taxonomic level richness measures is given by Lee (1997).

Marine diversity

The sea covers two-thirds of the earth's surface, making sea water the single largest habitat there is. Life originated in the sea and today marine metazoan diversity at higher taxonomic levels (class, phylum) significantly exceeds that on land (Table 1). The precise number of classes and phyla depends on the taxonomy used, as shown here by the contrast between the compilation by May (1994) and this study. Also listed in Table 1 are the number of major groups (classes and phyla) reported so far from the Southern Ocean; these numbers will almost certainly change as the Antarctic marine fauna becomes better known and taxonomies are revised.

At lower taxonomic levels the contrast between land and sea is very much reversed: the vast majority of described species are terrestrial. It is not at all straightforward to estimate the number of species described to date; Wilson (1988) provided a remarkably precise estimate of 1392485, May (1988) one of 1.8 million, and Stork (1988) a similar value of 1.82 million. Minelli (1993) has contributed an insightful review of the nature of the data on which such estimates are based, and provided his own estimate of 1.8 million described species. All authors recognise the many difficult problems inherent in making such estimates, notably the need to add together very different types of "species" but there is general agreement that at present about 1.8 million species have been described. Of this total, only about 200000 species are marine (Grassle 2001) whereas approximately 1 million are insects (an almost exclusively terrestrial group). This striking difference is driven in large part by the intense species richness of some insect groups (notably Hymenoptera, Diptera, Coleoptera, Lepidoptera and Homoptera), but it may also be a reflection of our ignorance of the sea.

In a highly influential paper, Grassle & Maciolek (1992) suggested that there may be a vast number of undescribed species in the deep sea. There followed an intense, and as yet unresolved, debate over the extent to which the deep sea contains a largely undescribed fauna (May 1993, 1994, Poore & Wilson 1993, Boucher & Lambshead 1995, Lambshead et al. 2000, Snelgrove & Smith 2002). Knowlton (1993) has drawn attention to the possibility that undescribed sibling species may harbour an immense amount of marine diversity, and Reaka-Kudla (1997) has estimated that coral reefs alone may contain over 600000 species (though perhaps only 35000 to 60000 have been described so far).

It is clear that we really have no idea how many species there may be in the sea. A series of recent estimates for individual higher taxa are shown in Table 2. It is striking how much variation there is even for apparently well known taxa such as molluscs.

Table 1 Two estimates of marine diversity at higher taxonomic levels. Data are restricted to metazoan animal phyla. Previous data are from Nicol (1971) as summarised by May (1994). Data for this study are based on taxonomy of Barnes (1998). The data for the Southern Ocean are based on all occurrences known to the authors; the number of marine phyla and classes reported for Antarctica will undoubtedly increase with further sampling and taxonomic work. nd = no data.

	May (1994)			This study		
	Total	Land	Sea	Total	Sea	Southern Ocean
Phylum	33	12	32	38	36	28
Class	nd	33	73	100	90	58

Table 2 A classification of metazoan animal phyla with the approximate number of described species. The taxonomy and sequence of phyla follows Barnes (1998), with species numbers taken from Margulis & Schwartz (1982), Wilson (1988), Minelli (1993), Nielsen (1995) and Barnes (1998).

Phylum	Approximate number of species					Comments
	Margulis	Wilson	Minelli	Nielsen	Barnes	
Porifera	10000	5000	6000	5000	10000	
Symplasma	–	–	–	–	500	Hexactinellids grouped with true sponges (Porifera) by all authors except Barnes
Placozoa			2	1	1	Enigmatic phylum comprising *Trichoplax adhaerans* and possibly one other species
Cnidaria	>9500	–	15000	8000	10000	
Ctenophora	90			80	100	Almost exclusively pelagic but a few benthic taxa known
Rhombozoa			50		75	Problematic obscure organisms, once classified as Mesozoa and sometimes treated as two phyla, Dicyemida and Heterocyemida, the latter with only two known species
Platyhelminthes	15000	–	–	20000	25000	Predominantly parasitic but includes free-living Turbellaria with planktonic and benthic species
Orthonecta	–	–	–	–	10	Obscure phylum of parasitic organisms, previously grouped with Rhombozoa in Mesozoa
Gnathostomula	80	–	–	–	100	Meiofaunal group of uncertain affinity; included with annelids by Nielsen
Gastrotricha	400	–	–	430	450	Meiofaunal; marine and freshwater
Priapula	8	–	9	17	17	A small group of infaunal worms with a fossil record extending back to the Cambrian in the Burgess Shale
Kinorhyncha	150	–	74	150	150	Meiofaunal; marine
Loricifera	10	–	–	100	>100	First described in 1983; meiofaunal; marine
Nematomorpha	240	–	230	325	325	Juveniles parasitic in arthropods; adult stages free-living but short-lived and non-feeding; mostly freshwater
Nematoda	80000	12000	20000	20000	20000	Many parasitic forms; a major component of the meiofauna and possibly harbouring an enormous number of undescribed marine species
Rotifera	2000	–	2000	1800	1800	Mostly freshwater
Acanthocephala	600	–	750	900	1000	Exclusively parasitic
Chaetognatha	–	–	110	200	200	Pelagic marine; higher level taxonomy (class, order) unresolved
Onychophora	80	–	–	80	70	Exclusively terrestrial
Tardigrada	–	–	531	600	600	Meiofaunal

Table 2 *continued*

Phylum	Approximate number of species					Comments
	Margulis	Wilson	Minelli	Nielsen	Barnes	
Pentastoma	70	–	–	–	100	A small phylum of uncertain affinities; parasitic
Crustacea	–	–	–	–	40 000	
Chelicerata	–	–	–	–	63 000	Includes pycnogonids (sometimes treated as a separate phylum)
Uniramia	–	–	–	–	1 000 000	Insects and allies; almost exclusively terrestrial
Crustacea, Chelicerata, Uniramia and sometimes Pentastoma often combined as a single phylum: Arthropoda						
"Arthropoda"	–	874 161	–	>1 000 000	–	
Nemertea	900	–	950	900	900	
Mollusca	110 000	50 000	130 000	100 000	100 000	
Sipuncula	300	–	–	320	350	
Echiura	140	–	140	–	150	Usually viewed as a separate phylum, but grouped by Nielsen with annelids
Annelida	>8800	12 000	18 600	15 000	15 000	
Pogonophora	100	–	100	–	150	Two classes (Perviata, Vestimentifera) sometimes regarded as separate phyla; grouped by Nielsen with annelids
Entoprocta	150	–	150	150	150	A small phylum of marine lophophorates (also known as Kamptozoa)
Cycliophora	–	–	–	–	1	First described 1995; only one species known, *Symbion pandora* (from mouthparts of *Nephrops*)
Phorona	–	–	10	12	<20	A small phylum of marine lophophorates
Brachiopoda	335	–	335	300	350	A once abundant group of sessile lophophorates
Bryozoa	5000	–	5000	4000	4300	The most diverse lophophorate phylum; also called Ectoprocta (Nielsen) or Polyzoa (defunct)
Hemichordata	–	–	<100	70	<100	Includes Pterobranchia and Enteropneusta, regarded as separate phyla by Nielsen
Echinodermata	6000	6100	6700	7000	7000	Most taxonomists regard the enigmatic *Xyloplax* (2 species) as an echinoderm
Chordata	–	>43 000	48 000	–	>43 000	A single phylum comprising Urochordata (=Tunicata), Cephalochordata and Vertebrata, sometimes each given individual status as phyla (e.g. by Nielsen)
Incertae sedis						
Senoturbella bocki						
Buddenbrockia plumatellae						
Lobatocerebrum (3 or 4 species) (Nielsen regards these as specialised annelids)						
Salinella salva (known only from a single report from saline lagoons in Argentina)						

The Southern Ocean

The Southern Ocean comprises all waters south of the Polar Front (referred to as the Antarctic Convergence in the earlier literature). This well-defined circum-Antarctic oceanographic feature marks the northernmost extent of cold surface water. The total area of the Southern Ocean is thus about 34.8 million km^2. Of this, up to 21 million km^{22} is covered by ice at the winter maximum but only about 7 million km^2 is covered at the summer minimum (Gloersen et al. 1992). Two influential schemes for subdividing this vast area of ocean are those of Tréguer & Jacques (1992) based predominantly on ice and nutrient dynamics, and Longhurst (1998) based on upper water column structure and remotely-sensed phytoplankton pigments. These schemes are based essentially on surface processes but they are relevant to the benthos in that almost all life on the sea bed depends on the flux of material from surface waters for its energy and nutrients. Patterns of surface production will therefore influence the diversity, abundance and ecology of benthic organisms, albeit modified by advective processes.

Much of the Southern Ocean overlies deep sea floor (Fig. 1). Relatively little of the Southern Ocean sea bed is continental shelf, and much of this shelf is unusually deep as a result of scouring from ice shelves and depression by the enormous mass of continental ice (Clarke 1996). Continental shelves elsewhere in the world are typically 100–200 m deep and 75 km wide (Walsh 1988); those around Antarctica average over 450 m deep, and in places they extend to over 1000 m depth. The deepest areas are trenches and basins, with the edge of the shelf usually being somewhat shallower. Although in some areas the continental shelves around Antarctica are narrow, and in many places are overlain extensively by ice shelves, their average width of 125 km is almost twice that of continental shelves elsewhere. This large average width is caused predominantly by the influence of the Ross Sea and the Weddell Sea. In both of these vast embayments much of the continental shelf is covered by floating ice shelf (Fig. 1). In other areas, for example, Dronning Maud Land between 0°E and 70°E, the continental shelf is relatively narrow. For the purpose of this review we have taken the 1000 m isobath to mark the edge of the continental shelf. The transition from the continental slope to the continental rise is less clear cut, and we have used the 3000 m isobath (Snelgrove 2001).

It is likely (but not known for certain) that there is little benthic life beneath the permanent ice shelves of the Ross and Weddell Seas, and other less extensive ice shelves (Lipps et al. 1977, 1979). The area of Antarctic continental shelf that is not beneath permanent ice totals about 3 million km^2 (Table 3). This is 8.5% of the Southern Ocean, and about 11.4% of the world's total continental shelf area, which is estimated to be 31.1 million km^2 (Walsh 1988).

The great depths of the Antarctic continental shelves means that the fauna living there may be expected to show physiological adaptations similar to (but perhaps not as marked as) those in the deep sea. Like that of the deep sea, the Antarctic continental shelf fauna must also be adapted to low temperatures and a marked seasonality of food (Clarke 1996).

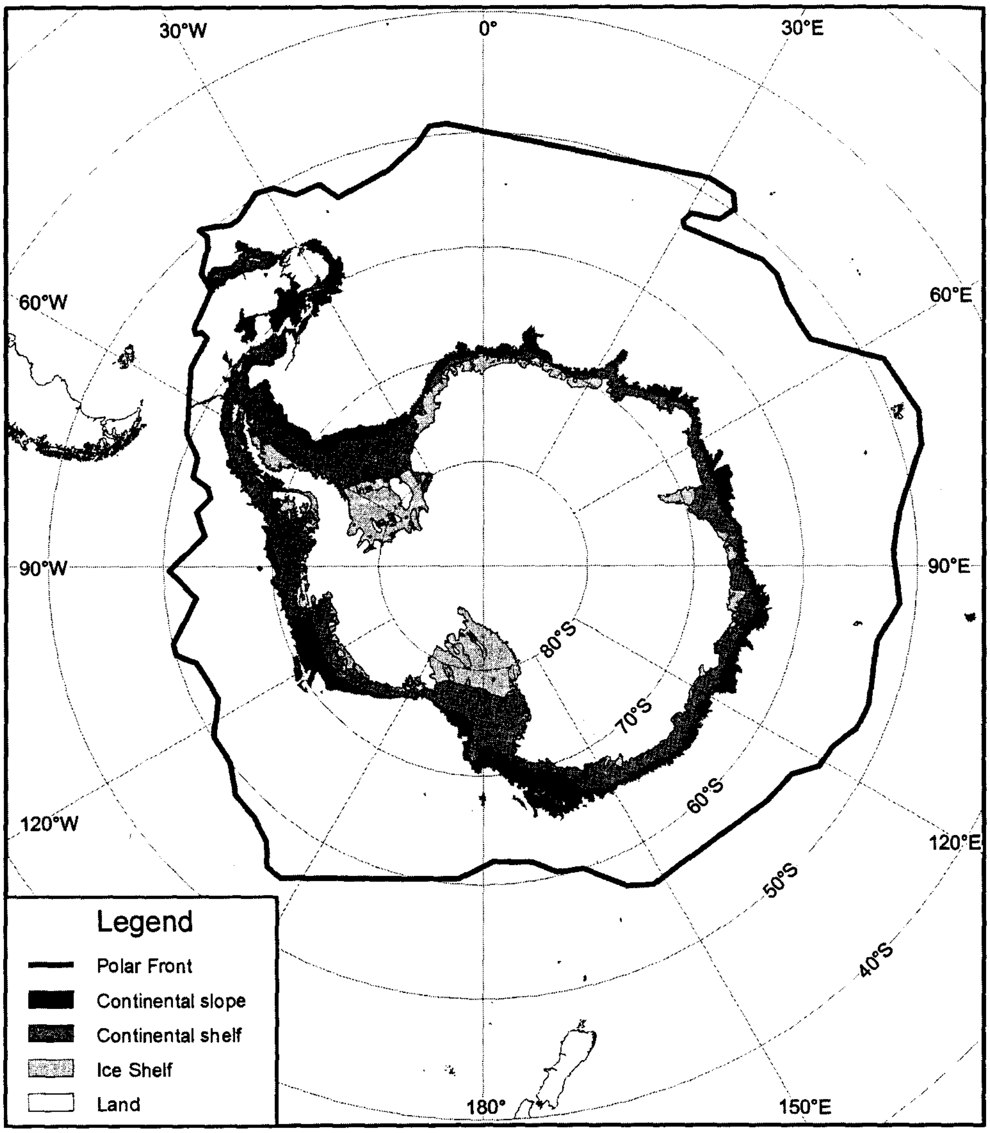

Figure 1 Map of the Southern Ocean showing the mean position of the Polar Front (the Antarctic Convergence in earlier literature) and broad scale bathymetry around the Antarctic continent. The 1000 m isobath marks the edge of the continental shelf around Antarctica, and the 3000 m isobath is taken to mark the transition from the continental slope to the deep sea. For reasons of clarity areas of depth <3000 m associated with mid-ocean ridges are not shown.

Table 3 Some characteristics of the Southern Ocean benthic environment. The fractal nature of coastlines and depth contours mean that all data depend on the length scale used. Deep-sea area calculated by subtraction, so ignores mid-ocean ridges. All data from latest edition of Antarctic Digital Database (ADD Consortium 2002), with mean position of the Polar Front from Trathan et al. (1997, 2000), Orsi et al. (1995).

Coastline	
Length (km × 10^3)	39.2
Ice coastline (%)	39.9
Ice front (%)	46.4
Rock coastline (%)	13.7
Continental shelf (<1000 m depth)	
Area not beneath ice shelves in 2002 (km^2 × 10^6)	2.97
Area beneath ice shelves in 2002 (km^2 × 10^6)	1.63
Total area (km^2 × 10^6)	4.59
Continental slope (area between 1000 m and 3000 m isobaths)	
Area (km^2 × 10^6)	2.35
Deep Sea (>3000 m depth)	
Area (km^2 × 10^6)	27.9
Total area of Southern Ocean (km^2 × 10^6)	34.8
Permanently open water	14
Seasonal ice cover (max)	21
Seasonal ice cover (min)	7

Aims of this study

The questions we have attempted to answer in this review were:

(1) How well do we know the Southern Ocean benthic marine fauna?
(2) Which groups of benthic marine organisms are well represented in the Southern Ocean, and which are not?
(3) To what extent does the Southern Ocean marine fauna match, or deviate from, established macroevolutionary patterns such as the latitudinal cline in diversity?

This required the compilation of validated species lists for all the major benthic taxa of the Southern Ocean. These data were then analysed for temporal trends in species description and the distribution of species amongst higher taxa (genus, family). Some preliminary macroecological analyses were also undertaken, and comparisons made with data from other geographical areas.

Methods

Data compilation

The initial task for this study was to assemble a species list for each of the major benthic taxa of the Southern Ocean. The approach taken was to combine a study of the most recent taxonomic review of a particular group with a thorough search of both the earlier literature and all of the literature published since that review that we could locate. Extensive searches of the modern literature were undertaken to locate newly described taxa, and the general reviews most important as a starting point were those of Dell (1972, 1990) and Arntz et al. (1994, 1997). Our definition of the Southern Ocean means that we have excluded taxa found only at Tristan da Cunha, Gough Island, Prince Edward and Marion Islands, Macquarie Island, Îles Crozet, Îles Kerguelen and the Magellan region of South America.

Data were stored in simple spreadsheet databases. For each major group these spreadsheets listed (where known), species, taxonomic authority and date, higher level taxonomy and references. The use of established numerical taxonomic codes was investigated but none proved suitable for use with the Southern Ocean fauna without extensive additional work. The higher level taxonomy (especially at the family level) of many phyla varies widely between different monographs. We have therefore generally utilised the higher level taxonomy given in the most recent taxonomic revision.

Where a particular group has been recently revised or reviewed in a monograph then synonymy is generally minimal. Where no recent revision is available we have not always been able to eliminate synonymies, and our compilation of the literature may thus overestimate species richness. In these groups we have also been unable to eliminate all inconsistencies in the taxonomic authorities (names, dates and requirement for parentheses). In a few cases we were unable to establish taxonomic authorities at all.

Distributional analyses

For plotting sampling data an established Geographic Information System (GIS) was used. The outline of the Antarctic continent was provided by Version 3.0 of the Antarctic Digital Database (ADD Consortium 2000), and the mean position of the Polar Frontal Zone digitised from previous work (Trathan et al. 1997, 2000, Orsi et al. 1995).

Bathymetric data proved far more problematical. Hydrographic maps of varying degrees of precision and accuracy exist for many areas of Antarctica but almost none of these is in digital form. Work by various nations has led to a small number of high resolution digital bathymetric datasets, but these generally cover only a small geographic area of the Southern Ocean. The best general bathymetric data for the Southern Ocean come from the General Bathymetric Chart for the Oceans (GEBCO) which is available in digital form on CD-ROM. It was decided to utilise this as the basis for plotting Southern Ocean marine diversity data, but unfortunately the GEBCO bathymetric contours contained many gaps where data were non-existent. In order to render such contours compatible with a GIS all these gaps were filled by interpolation.

It was originally planned to record sampling location data for all taxa but it was quickly realised that this would take several years of work. Instead we chose to concentrate on two well-studied taxa in the expectation that these would reveal general patterns for Antarctic marine benthos; the taxa chosen were gastropod and bivalve molluscs. For these we recorded the geographical co-ordinates (latitude, longitude) for every occurrence recorded in the literature. Much of the literature provides only a general sampling location (for example, South Georgia, or Weddell Sea) and for these no location data could be entered. This compilation has subsequently been extended and validated, forming the Southern Ocean Molluscan Database (SOMBASE: Crame, Griffiths & Linse, unpublished British Antarctic Survey data).

Historical and macroecological analyses

For each major group (phylum, class) the data were examined to establish the historical pattern of species description. The temporal trend in species description when coupled with knowledge of recent taxonomic monographs or revisions can provide an indication as to how well known the group is (Costello et al. 1996). A recent thorough revision of a well collected group, in which few new species have been described recently, indicates a well documented fauna. Conversely, a cumulative species description which is still climbing rapidly indicates an incompletely documented fauna.

We have also undertaken some preliminary evolutionary and macroecological analyses of the major groups. These have included a compilation of the number of species for each family, as a first order indication of which clades have radiated in the Southern Ocean, and an initial analysis of species to genus ratios within the major taxa.

Marine benthic diversity in the Southern Ocean: an inventory

The species lists compiled for this study total over 4000 and are therefore not reproduced here. Rather, for each major group we list all of the important taxonomic synopses, indicating whether these are complete or cover only a taxonomic or geographic subset. The most speciose families are listed, and for most taxa the historical pattern of species description is presented.

For most major groups of Antarctic benthic organisms we have been able to provide at least an estimate of known species richness in the Southern Ocean. It is not, however, possible to put a formal confidence estimate on these estimates, for we cannot judge how many species remain to be discovered. Instead we have assigned each group to one of three classes as an indication of how well that group is known. The criteria were:

(1) Well known: group relatively well sampled; taxonomy reasonably stable with recent monograph or review; relatively few species described in the past decade.
(2) Moderately well known: group fairly well sampled; taxonomic review or monograph published in past fifty years; species still being described regularly.
(3) Poorly known: group poorly sampled; no taxonomic revision since early in the century; group not currently receiving significant taxonomic attention in the Southern Ocean.

This is a purely subjective assessment based on the most recent taxonomic revision, the history of species description, and personal knowledge of taxonomic work underway. There may be, of course, active taxonomic work of which we are unaware, and these assessments cannot take into account the very large amount of work by scientists from the former Soviet Union which is currently unavailable to western scientists.

There is little agreement amongst systemacists or evolutionary biologists as to the higher level classification of living organisms, and even the number of phyla depends on the taxonomy in use (Table 1). As we are not taxonomists ourselves and cannot make meaningful judgements concerning higher level systematics, for this compilation and analysis of the inventory of the Southern Ocean benthic marine fauna we have therefore followed the classification scheme of Barnes (1998), noting where there are significant differences from older or competing arrangements. The sequence of phyla used here also follows Barnes (1998).

Macroalgae

Macroalgae (seaweeds) are a convenient grouping of three quite different taxa, Rhodophyta (red algae), Chlorophyta (green algae) and Phaeophyta (brown algae). These are generally treated as separate phyla within the Kingdom Protoctista (Margulis & Schwartz 1982, Barnes 1998). The Antarctic marine flora also contains a single macroscopic chrysophyte and Wiencke & Clayton (2002), in their review of Southern Ocean seaweeds, group the Chrysophyceae and the brown algae (Phaeophyceae) as subtaxa within the phylum Heterokontophyta. The Southern Ocean seaweed flora has a low species richness compared with temperate and tropical regions, with a total of only 119 species described to date (Clayton 1994, Clayton et al. 1997, Wiencke & Clayton 2002). Rhodophyta contribute 75 species to this total, Phaeophyta 26 and Chlorophyta 17, though Wiencke & Clayton (2002) comment that the rhodophytes are almost certainly underestimated. Endemism is high, ranging from 18% (Chlorophyta) to 42% (Phaeophyta).

Macroalgal species richness decreases markedly with increasing latitude along the Antarctic Peninsula (Moe & DeLaca 1976), and the seaweed flora of continental Antarctica is very sparse (Wiencke & Clayton 2002).

Phylum Porifera and Phylum Symplasma

Sponges are a very difficult group taxonomically. The four classes (Calcarea, Demospongiae, Sclerospongiae and Hexactinellida) are fairly well defined and have traditionally been grouped together in a single phylum (Porifera). It has now become clear that glass-sponges (Hexactinellida) differ from the others in important aspects of internal anatomy and cellular organisation, and are increasingly regarded as a separate phylum (Symplasma). The two phyla, Porifera and Symplasma, are then grouped in the superphylum Parazoa (Barnes 1998). We have followed this arrangement here.

The most important synopses for each class of the Antarctic sponge fauna are:

- Calcarea: Burton (1929), Brondsted (1931) and Koltun (1964, 1976) document particular material but none provides a complete revision of the entire class.
- Demospongiae: Sarà et al. (1992) provides a full revision.
- Sclersopongiae: Sclerosponges tend to occur in association with coral reefs or in caves and tunnels; they appear not to have been reported from the Southern Ocean.

- Hexactinellida: A very difficult group, some requiring microscopic examination of isolated spicules to confirm identification. Barthel & Tendal (1994) provide a full review for the Southern Ocean taxa.

Important systematic or faunal literature published since the above revisions include Gutt & Koltun (1995) for the Calcarea, Battershill (1989), Pansini et al. (1994), Gutt & Koltun (1995), Kunzmann (1996) and Thomas & Mathew (1986a) for the Demospongiae, and Battershill (1989), Gutt & Koltun (1995), Kunzmann (1996) and Barthel (1997) for the Hexactinellida.

The systematics of the Calcarea is unstable and there appears to be no accepted classification system at the level of family or order in the literature. The demosponges also have an uncertain systematics and Sarà et al. (1992) presented their species list down to order only. The systematics of the hexactinellids follows that adopted by Barthel & Tendal (1994), who themselves followed Ijima (1927), although somewhat simplified and with minor changes from Bergquist (1978), Burton (1929), Hartman (1982) and Lévi (1964a,b).

The time-course of species description (Fig. 2a) shows clearly how the groundwork for our current knowledge of the Antarctic sponge fauna was laid between the late 1880s and the early 1930s, with important contributions later from Koltun in the 1960s and 1970s. The pattern of species per genus values (Fig. 2b) shows a typical hollow curve distribution (Willis 1922). The most speciose orders are all demosponges: Poecilosclerida (132 species), Haplosclerida (36 species) and Hadromerida (22 species). The Calcarea have only 14 species recorded from Antarctica, and the Sclerospongiae appear to be absent. The glass-sponges (Hexactinellida) are a very important group ecologically, and there are 29 species reported from the Southern Ocean.

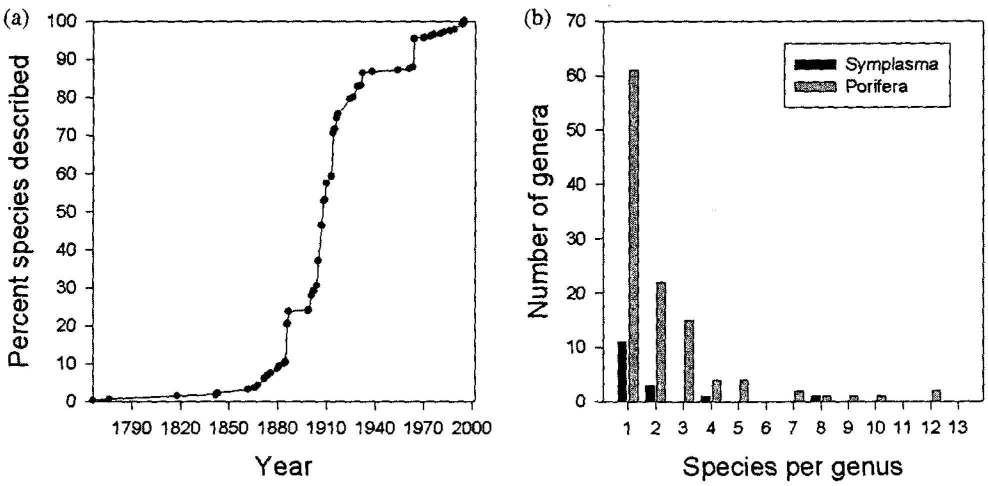

Figure 2 Sponges (true sponges, Porifera and glass sponges, Symplasma, combined). (a) Time course of description of Southern Ocean sponge taxa; data presented in percentage terms (total 279 species). (b) Distribution of species amongst genera for sponges. Data presented as a frequency distribution of species per genus values, with data for Porifera and Symplasma shown separately.

Phylum Cnidaria

Cnidarians comprise a varied collection of organisms united by their possession of nematocysts, and containing many difficult groups. The five classes are generally grouped into two subphyla, the Medusozoa containing the Hydrozoa, Scyphozoa and Cubozoa, and the Anthozoa containing the Alcyonaria and Zoantharia. The life cycle typically contains both a benthic and a pelagic phase. Whereas in anthozoans the larval phase is usually a simple planula larva and the medusa stage lost from the life cycle, in medusozoans the planktonic phase can be dominant (as in jellyfish). This can make the decision as to what constitutes a benthic taxon somewhat arbitrary. Within the Hydrozoa, the dominant stage in the hydroid life cycle is typically benthic; for hydromedusans or leptomedusans, the distinction between truly benthic or plankton taxa is more difficult. The Scyphozoa are predominantly pelagic and are not considered further here. The Cubozoa (box-jellyfish) are pelagic and exclusively tropical.

Within the Medusozoa, the most recent synopsis for Anthomedusae, Leptomedusae, Limnomedusae and Narcomedusae is O'Sullivan (1982) and for Stylasterina it is Cairns (1983). Subsequent references consulted were Browne (1902), Kramp (1957), Blanco & Bellusci de Miralles (1972), Blanco (1977, 1984), El Beshbeeshy (1991), Jarms & Tiemann (1996), Peña Cantero (1997a,b, 1998a,b,c), Peña Cantero & Garcia Carrascosa (1991), Peña Cantero & Vervoort (1995, 1998), Peña Cantero et al. (1995, 1996, 1997a,b,c). For Stylasterina there were no references after Cairns (1983) containing new species, or species not previously recorded from the Southern Ocean. As the hydromedusan groups were only reviewed in part by O'Sullivan (1982), a thorough literature search was undertaken. The systematics used here is that of O'Sullivan (1982) for all except the Stylasterina, for which we used Cairns (1983).

For Anthozoa the most recent synopses of the Antarctic fauna have been partial reviews of the gorgonians by Molander (1929), Thomson & Rennet (1931), Broch (1965), Dell (1972) and Bayer & Stefani (1987), a complete review of scleractinians by Cairns (1990), partial reviews of the actinarians by Dell (1972) and Dunn (1983, 1984), and a review of pennatularians by Broch (1959). References consulted in addition to these synopses were Pasternak (1961, 1975, 1993), Bayer (1980, 1996a,b), Williams (1981), Thomas & Mathew (1986a,b) and Keller (1990). The intermediate level systematics (order, family) of the Anthozoa used here follows that of the synopses listed above, with the addition of Pasternak (1975) for gorgonians. Cairns (1990) and Dunn (1983, 1984) have developed valuable keys for scleractinians and actinarians.

For both hydrozoans and anthozoans, the key period of taxonomic work was from the 1870s to the mid-1920s as the material collected during the early expeditions was worked up (Fig. 3a). Since then there has been a significant increase in taxonomic work in the 1990s, associated principally with the SCAR (Scientific Committee on Antarctic Research) programme on Ecology of the Antarctic Sea Ice Zone (EASIZ). The Southern Ocean cnidarian fauna is badly in need of a thorough taxonomic overhaul. This, coupled with investigation of cryptic species using modern molecular techniques, would almost certainly result in a drastic revision of Antarctic cnidarian diversity. The distribution of species to genus values is normal, though there is a notable outlier for the hydroid genus *Oswaldella* (Fig. 3b). Three hydrozoan and one alcyonarian anthozoan family contain more than ten species (Table 4).

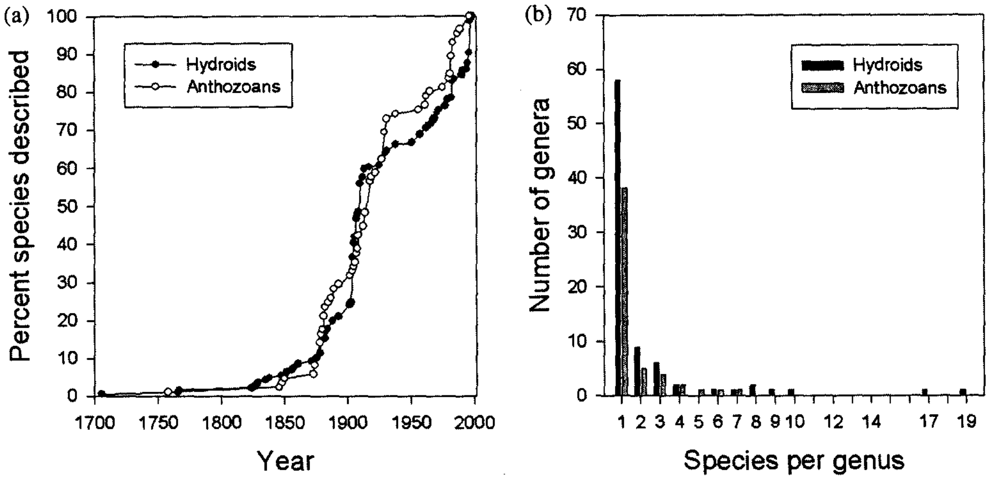

Figure 3 Cnidaria (Anthozoa and benthic Medusozoa). (a) Time course of description of Southern Ocean benthic cnidarian taxa; data presented in percentage terms (total 272 species). (b) Distribution of species amongst genera for benthic cnidarians. Data presented as a frequency distribution of species per genus values. In both plots data for Anthozoa and benthic Medusozoa are shown separately.

Table 4 The most speciose families of Southern Ocean cnidarians. The threshold for inclusion was ten species, and species numbers can only be approximate because of unresolved taxonomic difficulties and undiscovered species. The higher level taxonomy follows Barnes (1998) and within classes, families are listed in order of richness.

Subphylum	Class	Family	Approximate number of species
Medusozoa	Hydrozoa	Sertulariidae	42
		Plumulariidae	32
		Stylasteridae	13
		Haleciidae	10
Anthozoa	Alcyonaria	Primnoidae	28

Phylum Ctenophora

Although ctenophores are almost exclusively pelagic, a few species are benthic and one large benthic species, *Lyrocteis flavopallidus*, has been described from McMurdo Sound (Robilliard & Dayton 1972). These are delicate organisms, easily damaged by trawling and dredging, so any subsequent reports will likely come from photographic or direct SCUBA observation.

Phylum Priapula

This tiny phylum has only three representative in the Southern Ocean. The most recent synopsis is that of van der Land (1970), whose systematics we follow. Recent references consulted were Murina (1975) and Wu & Zhao (1986).

Phylum Crustacea

The arthropods have frequently been regarded as a single phylum comprising the insects and their close relatives, arachnids and crustaceans. Here we follow Barnes (1998) in regarding crustaceans, chelicerates (arachnids with pycnogonids) and uniramians (insects and relatives) as separate phyla, grouped with onychophorans and possibly tardigrades and pentastomans in the superphylum Panarthropoda.

The crustaceans are now one of the best-known marine invertebrate groups in Antarctica. We will therefore deal with the major orders individually.

Order Amphipoda (Class Malacostraca)

The peracarid crustaceans are among the most intensely studied marine taxa in the Southern Ocean. The amphipods have been thoroughly revised by De Broyer & Jazdzewski (1993). More recently De Broyer & Jazdzewski have collected new material from the Weddell Sea in particular, and this has added significantly to the previously published list. These studies have also shown that there are likely to be many more new species to be described from the very small elements of the fauna, previously under-sampled and poorly known.

The most recent estimate of benthic gammaridean species richness for waters south of the Subtropical Front is 692 (De Broyer & Jazdzewski 1996). This is not directly comparable with the data analysed here, since our compilation is for the Southern Ocean *sensu stricto*, as defined by the Polar Front. We have therefore excluded species found only at Tristan da Cunha, Gough Island, Prince Edward and Marion Islands, Îles Crozet, Îles Kerguelen, the Magellan region of South America and the sub-Antarctic islands of New Zealand. Recent literature we have included in our compilation is De Broyer (1985a,b), Rauschert & Andres (1993), Coleman (1994), Coleman et al. (1994), De Pina (1995), Jazdzewski et al. (1995), Wakabara et al. (1995) and Kunzmann (1996).

The systematics of the Amphipoda used here is generally that of De Broyer & Jazdzewski (1993). For the Gammarellidae we have followed Barnard (1969) and Barnard & Karaman (1991), for the Valettidae, Thurston (1989), for the iphimedid group, Coleman & Barnard (1991), and for the Carenioidae, retained in the Synopiidae, Jazdzewski & De Broyer (1990). For the *Orchomene* complex, still under revision, De Broyer (1984, 1985a) has been followed. For the Caprellidae, we have followed Laubitz (1993), and for the Clarenciidae, Zeidler (1994).

The time-course of species description (Fig. 4a) indicates an important phase of taxonomic work in the early decades of the last century, but also that ongoing work (most notably by Belgian and Polish taxonomists) is continuing to add new species. There is no indication that we have reached an asymptote in the description of new amphipod taxa for

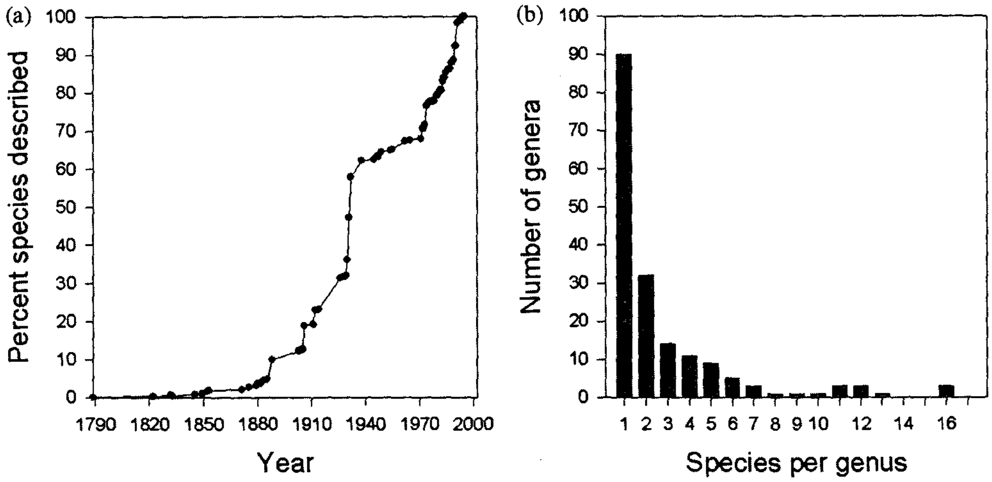

Figure 4 Amphipoda. (a) Time course of description of Southern Ocean amphipod taxa; data presented in percentage terms (total 496 species). (b) Distribution of species amongst genera for amphipods, presented as a frequency distribution of species per genus values.

the Southern Ocean and the true species richness is very likely significantly greater than the current figure. The frequency distribution of species per genus values (Fig. 4b) exhibits a normal pattern, and there are eight families with over 20 species (Table 5).

Table 5 The most speciose families of Southern Ocean crustaceans. The threshold for inclusion was 20 species, and species richness can only be approximate because of unresolved taxonomic difficulties and undiscovered species. The higher level taxonomy follows Barnes (1998) and, within orders, families are listed in order of richness.

Class	Subclass	Order	Family	Approximate number of species
Malacostraca				
	Peracarida			
		Amphipoda	Lysianassoidae	92
			Eusiridae	64
			Stenothoidae	50
			Iphimediidae	36
			Corophiidae	22
			Epimeriidae	21
			Isochyroceridae	20
			Phoxocephalidae	20
		Isopoda	Arcturidae	60
			Munnopsidae	40
			Serolidae	31
		Tanaidacea	Anarthruridae	39
Cirripedia		Thoracica	Scalpellidae	34

Order Isopoda (Class Malacostraca)

The isopod fauna of the Southern Ocean is now well known particularly through the extensive taxonomic work of Brandt (1988) and Wägele (1989). Key recent references are Brandt (1991b, 1992a,b, 1999), Brandt & Janssen (1994), Kunzman (1996), and Pirez & Sumida (1997). For systematics we have followed that used by Brandt (1991a) in her review of Southern Ocean isopods; this follows Wägele (1989), except where new genera have been erected.

The time-course of species description for isopods (Fig. 5a) shows the importance of descriptive work in the first two decades of the last century, based on material collected in the early expeditions, but also the continuing description of new taxa. As with amphipods there is no indication of an asymptote in species description for the Southern Ocean.

The frequency distribution of species per genus values shows a typical hollow curve shape (Fig. 5b). There are three speciose families (Table 5), two of which (Serolidae and Arcturidae) have clearly radiated within the Southern Ocean (Brandt 1991a).

Order Tanaidacea (Class Malacostraca)

The most recent synopses of the Southern Ocean tanaid fauna are those of Sieg (1983, 1984a,b, 1986a,b,c). Also consulted was Blazewicz & Jazdzewski (1996). The systematics followed Sieg (1986c, 1988). The influence of this recent attention is shown in the shape of the species accumulation curve (Fig. 5a). There are no unusual features in the frequency distribution of species per genus values (Fig. 5b), and only one family, Anarthruridae, contains more than 20 species (Table 5).

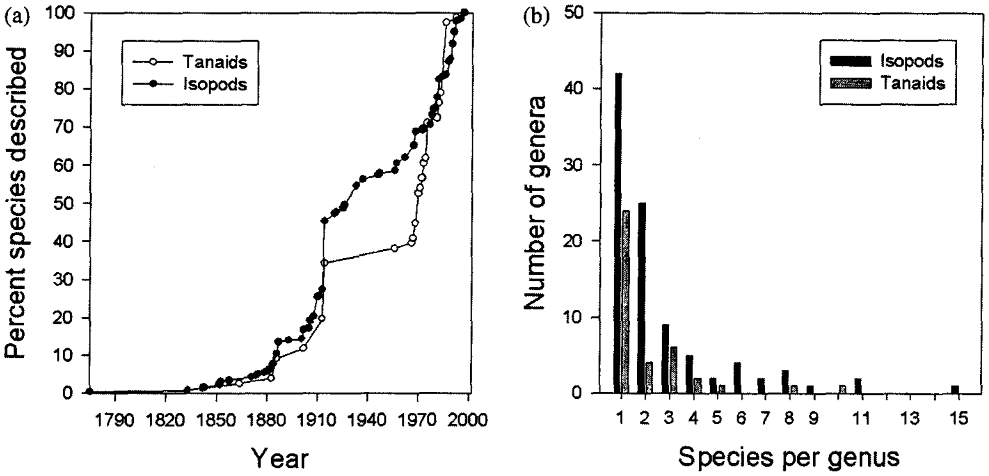

Figure 5 Isopoda and Tanaidacea. (a) Time course of description of Southern Ocean isopod taxa; data presented in percentage terms (total 257 species) with data for Isopoda and Tanaidacea shown separately. (b) Distribution of species amongst genera for isopods and tanaids. Data presented as a frequency distribution of species per genus values, with data for Isopoda and Tanaidacea shown separately.

Order Decapoda (Class Malacostraca)

The eucarid crustaceans are strikingly low in diversity in the Southern Ocean. The most recent review of the Southern Ocean decapod fauna is that by Kirkwood (1984). More recent references consulted were Tiefenbacher (1990) and Klages et al. (1995); the systematics follows Kirkwood (1984). The total fauna numbers only a dozen or so species, including six lithodid crabs from sub-Antarctic waters. Brachyuran crabs and lobsters are now completely absent from the Southern Ocean, although fossil evidence indicates a rich fauna which has since become extinct (Feldmann & Wilson 1988, Feldmann & Tshudy 1989, Feldmann & Quilty 1997, Feldmann & Crame 1998)

Class Cirripedia

For cirripedes the most recent synopsis is the partial review of Newman & Ross (1971). Since this latter review does not cover the complete fauna, the primary literature was searched as far back as possible. Key references were Hoek (1907), Gruvel (1907, 1910), Borradaile (1916), Nilsson-Cantell (1930a,b, 1939), Zevina (1964), Utinomi (1965), Zevina (1968), Grygier (1981, 1984, 1987), Kuznetsova & Neurova (1986), Ren & Huang (1989), Zevina (1990) and Young & Leta (1996). The systematics used here follows Newman & Ross (1971).

Ice-scour means that the intertidal barnacles so characteristic of temperate and tropical rocky shores are completely absent from the Southern Ocean. The total fauna is about 50 species, with only one family (Scalpellidae) containing more than 20 species (Table 5). It also includes the ascothoracians, parasitic in starfish.

Phylum Chelicerata

The chelicerates comprise the horseshoe crabs (merostomatans), the arachnids (spiders, mites, scorpions and allies) and the pycnogonids (also referred to as pantopods). There is no consistent view as to whether the pycnogonids should be included within the chelicerates, and they are sometimes regarded as a phylum in their own right (Minelli 1993). Here we follow Barnes (1998) in regarding them as a class within the chelicerates.

There are no horseshoe crabs in the Southern Ocean. Marine mites appear to occur widely, but we could locate no taxonomic review although Pugh (1993) lists 45 species of the family Rhagidiidae from a variety of Southern Ocean locations.

Class Pycnogonida

Although the phylogenetic status of this enigmatic group is not at all clear, they have most frequently been regarded as a relatively ancient lineage of marine chelicerates (Nielsen 1995).

The most recent taxonomic revision are those of Munilla León (2001a), Child (1994a,b, 1995a,b,c) and the partial review of Fry & Hedgpeth (1969). More recent references consulted were Arnaud (1972a,b), Turpaeva (1974), Pushkin (1976), Child (1987), Munilla León (1989, 2001b), Turpaeva (1990), Stiboy-Risch (1992), Jaya Sree et al. (1993), Bamber

(1995) and Kunzmann (1996). Unfortunately, Fry & Hedgpeth (1969) never completed their synopsis of the whole Antarctic pycnogonid fauna, and only one part was ever published. For systematics we follow Fry & Hedgpeth (1969), who commented that

> . . . the unsatisfactory state of the taxonomy of the higher taxa of the Pycnogonida has prevented us from attempting to devise keys to genera or families, which, in their layout reproduce the classification of the Pycnogonida, and throughout this work the keys are entirely artificial in their design.

Our compilation of the Southern Ocean pycnogonid fauna totals 175 species, in comparison with the 180 reported for the Antarctic plus sub-Antarctic by Munilla León (2001a). This discrepancy is related in part to a difference in the definition of the Southern Ocean, and partly to recent description of new taxa. The species accumulation curves devised from our data and the decadal summary provided by Munilla León (2001a) are broadly similar, though the recent description of new taxa is apparent in the different trajectories in the upper third of the two curves (Fig. 6a).

The shape of the frequency distribution of species per genus values is highly skewed and the data are unusually patchy (Fig. 6b). This, together with the striking outliers for *Nymphon* (55 species), *Colossendeis* (29), *Ammothea* (19) and *Pallenopsis* (17) suggests an immature taxonomy. The large number of species currently assigned to the genus *Nymphon* indicates either that this represents a clade in the process of active speciation, or that different taxonomic characters are required. This genus would seem to be a prime candidate for cladistic and/or molecular phylogenetics work.

Four families contain more than 20 species: Colossendeidae (33), Ammotheidae (39), Nymphonidae (58) and Callipallenidae (29).

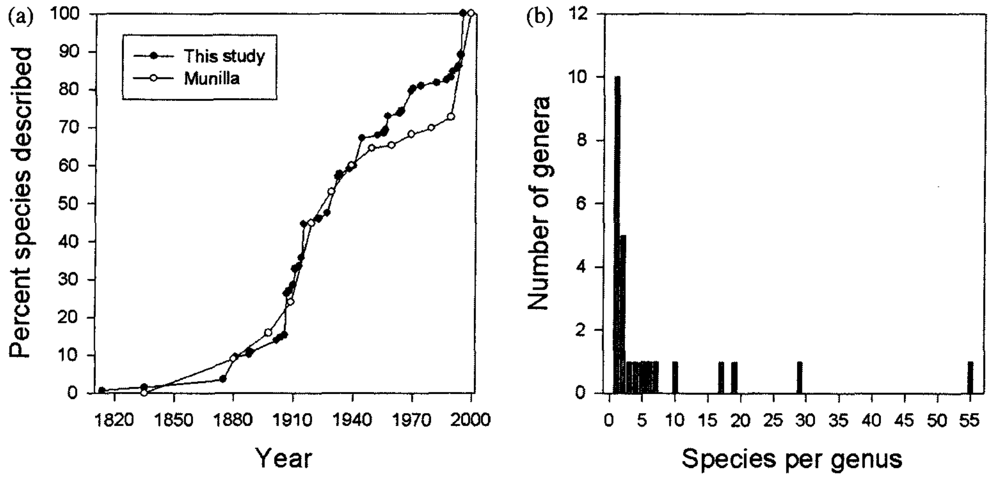

Figure 6 Pycnogonida. (a) Time course of description of Southern Ocean pycnogonid taxa; data presented in percentage terms (total 175 species). (b) Distribution of species amongst genera for pycnogonids, presented as a frequency distribution of species per genus values.

Phylum Nemertea

Benthic nemertean worms are relatively well known from the Southern Ocean, with the most recent taxonomic revisions being that of Gibson (1985) for the heteronemerteans and Dawson (1957) for the hoplonemerteans, both of whose systematics we follow here. We have been unable to locate any subsequent taxonomic or faunal work on Southern Ocean benthic nemerteans.

The overall diversity of nemertean is low at just over 30 species divided more or less evenly between the heteronemerteans (Class Anopla) and the hoplonemerteans (Class Enopla). The Southern Ocean is, however, unusual in that one very large species, *Parborlasia corrugatus*, is extremely common in shallow waters, where it is a major predator and scavenger (Gibson 1983).

Phylum Mollusca

The Mollusca are a well-described group in most seas of the world, and the Southern Ocean bivalve and gastropod fauna is fairly well known. Although the various molluscan classes differ strongly in species richness, many taxonomic monographs treat some or all of them together.

The major taxonomic synopses are those of Powell (1960) and Dell (1990), although the latter only covers species found in the Ross Sea. Taxonomic works since Powell's review are Nicol (1966a), Ponder (1971, 1983), Arnaud (1972a,b, 1974), Arnaud & van Mol (1979), Arnaud et al. (1986), Cantera & Arnaud (1984), Warén et al. (1986), Dell (1964a,b, 1972), Powell (1973), Egorova (1982), Oliver & Picken (1984), Mühlenhardt-Siegel (1989), Numanami et al. (1996), Hain (1990), Voss (1988), Numanami (1996) and Cattaneo-Vietti et al. (2000). We have also cross-checked our species list with that for the most recent comprehensive benthic sampling in the Weddell Sea (Gutt et al. 2000).

The systematics used here follows Dell (1990) and Numanami et al. (1996), with Hain (1990) for new species. Dell (1990) does not cite Hain (1990), and vice versa; as Dell (1990) is the larger and more complete work the allocation of genera to families generally follows Dell (1990). A few additions follow Numanami et al. (1996). The phylogeny of gastropod and bivalve molluscs is currently an area of active research and the results of molecular and cladistic analyses are leading to fundamental revisions of molluscan taxonomy (Ponder & Lindberg 1996, 1997). Changes to intermediate level taxonomy (orders, families) will have no immediate effect on diversity measures at the species level but they are important in generating evolutionary hypotheses. Continuing systematic work refining the composition of families and genera will, however, affect measures such as species to genus ratios or family richness. We can expect a period of continuing change in this area and the data presented here can be regarded only as an interim picture.

The time-course of species description for gastropods and bivalves is similar, with a major period of systematic work in the first two decades of the last century (Fig. 7a). There were significant additions to both the gastropod and bivalve faunas from systematic work in the final decade of the last century. Overall the bivalve and gastropod fauna of the Southern Ocean is probably described more completely than for any other major group of benthic marine invertebrates.

The frequency distribution of species per genus values was normal, although there were a number of outliers for gastropod genera containing very high numbers of species (Fig. 7b).

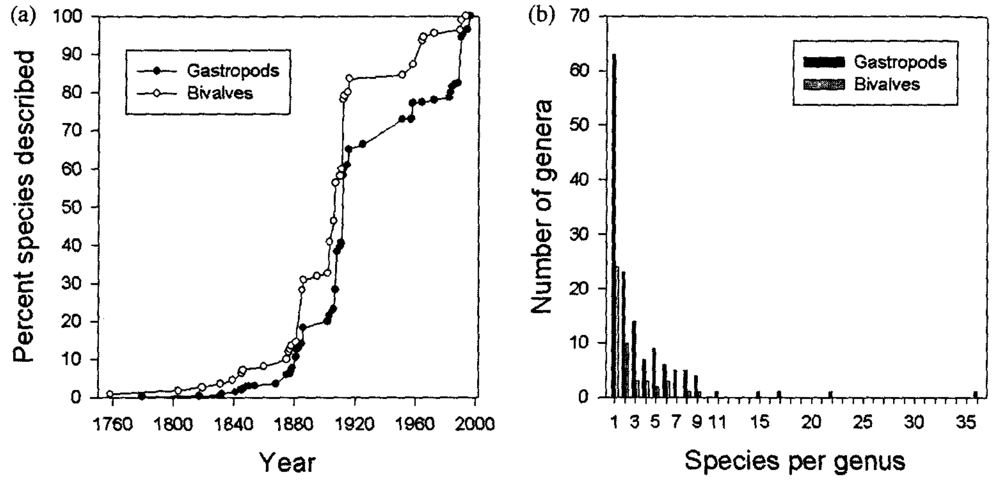

Figure 7 Gastropod and bivalve molluscs. (a) Time course of description of Southern Ocean gastropod and bivalve taxa; data presented in percentage terms (total 640 species) with data for gastropods and bivalves shown separately. (b) Distribution of species amongst genera for molluscs. Data presented as a frequency distribution of species per genus values, with data for gastropods and bivalves shown separately.

These included *Prosipho* (37 species), *Trophon* (22), *Onoba* (17) and *Eatoniella* (15). The most species-rich families of gastropods include the predatory and scavenging buccinids, naticids and muricids (Table 6), reflecting the radiation of these groups at high latitudes (Crame 1996).

Other molluscan groups are not well known in the Southern Ocean. The primitive Solenogastres are an obscure group often placed with other shell-less molluscs in the Aplacophora. The few Antarctic Solenogastres have been reviewed by von Salvini-Plawen (1979), with new species reported by García-Alvarez et al. (2000, 2001). Scaphopoda (tusk-shells) appear to be represented by fewer than ten species (Dell 1964b, Steiner & Linse 2000, Katrin Linse, pers. comm.); this is a fairly typical diversity for a group that is nowhere very speciose. Polyplacophora (chitons) appear to be similarly lacking in diversity in the Southern Ocean. A taxonomic review is badly needed but it is likely that the total fauna amounts to fewer than a dozen species.

The benthic octopods have recently been examined in detail by Allcock (1997), who reports 34 species from benthic samples taken in the Weddell Sea and the Antarctic Peninsula. Of these some 18 are new to science and await formal description. The most striking feature is the number of species of *Pareledone*, a genus which appears to have undergone a radiation in the Southern Ocean (Allcock et al. 2001).

Phylum Sipuncula

This is a small but relatively well-described phylum. The most recent Antarctic monograph is Saiz-Salinas (1995), but little work has been undertaken since. Currently, 16 species are

Table 6 The most speciose families of Southern Ocean gastropod and bivalve molluscs. The threshold for inclusion was ten species, and species richness can only be approximate because of unresolved taxonomic difficulties and undiscovered species. Gastropod taxonomy in particular is in a state of flux with families being renamed and subdivided. Families are listed within classes in order of richness.

Class	Family	Approximate number of species
Gastropoda	Buccinidae	84
	Turridae	45
	Trochidae	41
	Naticidae	29
	Rissoidae	24
	Muricidae	23
	Cerithidae	22
	Eatoniellidae	15
	Diaphanidae	15
	Cyclostrematidae	15
	Littorinidae	14
	Lamellaridae (Velutinidae)	12
	Philinidae	11
	Eulimidae	10
	Cancellaridae	10
Bivalvia	Nuculanidae	13
	Phylobryidae	13
	Pectinidae	11

recognised from three genera in two families: Golfingiidae (*Golfingia* and *Nephasoma*) and Phascolidae (*Phascolion*).

Phylum Echiura

This small phylum has largely been ignored in the Southern Ocean until the recent analysis of the extensive collections made by American research vessels (notably RV ELTANIN) between 1962 and 1986 and processed by the Smithsonian Oceanographic Sorting Centre (Saiz-Salinas et al. 2000). This collection of 855 individuals yielded nine species representing two families. The Echiuridae prefer sublittoral to shallow bathyal sediments, whereas the Bonellidae are more common at bathyal and abyssal depths.

Phylum Annelida

Although this phylum contains several groups known to occur in the Southern Ocean, including the oligochaetes and leeches (grouped together in the Class Clitellata by Barnes 1998), only the polychaetes have received sufficient attention for a preliminary species list to be assembled.

Class Polychaeta

The major taxonomic monographs for Antarctic polychaetes are those of Hartman (1964, 1966, 1967, 1978), although no single taxonomic revision for the whole group yet exists. More recent publications consulted in the compilation of the species lists were Benham (1921, 1927), Monro (1930, 1935, 1939), Levenstein (1964), Averintsev (1972), Sicinski (1986), Hopkins (1987), Hartmann-Schröder & Rosenfeldt (1988, 1989, 1990, 1992), Orensanz (1990), Vinogradova (1990), Ahn & Kang (1991), Gambi & Mazzella (1992), Cantone & Sanfillipo (1991), Castelli (1992), Gambi et al. (1994, 1997), Herman & Dahms (1992), Kudenov (1993), Sicinski & Janowska (1993), Cantone (1995), Stiller (1996), Kunzmann (1996), San Martin & Parapar (1997) and Cantone & Di Pietro (1998, 2001).

For polychaete higher level systematics we have followed Fauchald (1977). Fauchald & Rouse (1997) emphasise that all polychaete taxonomies in current use are unsatisfactory for a variety of reasons, although the major source of uncertainty is the lack of consistent morphological information. Many polychaetes are difficult to identify, and Knox & Lowry (1977) have suggested that the Southern Ocean polychaete fauna may exceed 800 species. Certainly the time-course of species description (Fig. 8a) gives us no indication of any slowing down and it is quite possible that the Southern Ocean may contain over 1000 polychaete taxa. Recent benthic sampling of soft sediments from the deeper waters of the continental shelf of the western Antarctic Peninsula has revealed many new undescribed taxa (Craig Smith, pers. comm.). A thorough taxonomic revision of the Southern Ocean polychate fauna is needed urgently, though this would be a major task.

The frequency distribution of species to genus values is classical in shape (Fig. 8b), with over 100 genera containing only single species and a notable outlier for *Harmathoe* (21 species). As with elsewhere in the world, syllids and polynoids are the most speciose families (Table 7).

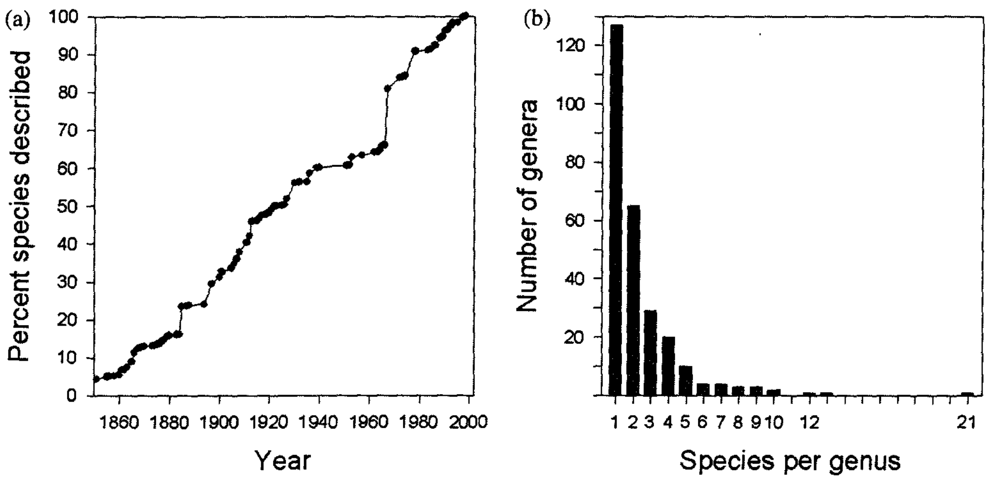

Figure 8 Polychaetes. (a) Time course of description of Southern Ocean polychaete taxa; data presented in percentage terms (total 645 species). (b) Distribution of species amongst genera for polychaetes, presented as a frequency distribution of species per genus values.

Table 7 The most speciose families of Southern Ocean polychaetes. The threshold for inclusion was 20 species, and species richness can only be approximate because of unresolved taxonomic difficulties and undiscovered species. Families are listed in order of richness.

Family	Approximate number of species
Syllidae	67
Polynoidae	66
Terebellidae	46
Phyllodocidae	37
Sabellidae	32
Onuphidae	29
Ampharetidae	27
Maldanidae	27
Flabelligeridae	26
Opheliidae	23
Serpulidae	21

Phylum Pogonophora

Although sometimes grouped with annelids (for example by Nielsen 1995), here we follow Barnes (1998) in assigning them to a separate phylum. To date only three species have been described from the Southern Ocean, all in the genus *Spirobrachia* (Smirnov 2000). It is possible that more taxa remain to be described from the extensive deep-sea collections made by scientists of the former Soviet Union.

Although no vestimentiferans have yet been described from the Southern Ocean, it is now known that hydrothermal vents and related features are present (Chin et al. 1996, German et al. 2000, Klinkhammer et al. 2001) and so they may remain to be discovered. If vent faunas are located, their biogeographic affinities will be of great interest because of their intermediate location between the very different vent faunas of the Atlantic and Pacific basins.

Phylum Brachiopoda

Brachiopods are a group of sessile suspension feeders which once dominated the seas. The rise of the bivalve molluscs has been associated with a decrease in the importance of brachiopods, which nowadays are confined largely to polar, deep-sea and cave habitats. The most recent taxonomic revisions of Southern Ocean brachiopods are those of Foster (1965, 1974). Recent references consulted were Foster (1989, 1997) and Sieg & Wägele (1990).

The systematics of brachiopods is in a state of flux, particularly with the current revision of the *Treatise of Invertebrate Palaeontology*. Specialists are revising each group, and the assignment of genera to families is likely to change radically (and indeed has already done so in comparison with the 1965 edition of the *Treatise*). We have followed Foster (1965), accepting that this is likely to change in the future.

The Southern Ocean brachiopod fauna is small, with 19 species described to date. Two are inarticulates (*Pelagodiscus* and *Crania*), with the most important articulate genus being *Liothyrella.*

Phylum Bryozoa

Bryozoans are now a relatively well-known group in the Southern Ocean, with a recent and very thorough taxonomic revision of the Cheilostomatida by Hayward (1995). The most recent synopses of the Cyclostomatida and Ctenostomatida were those of Androsova (1968). Recent references consulted are Androsova (1972), Moyano (1984), Rosso (1990), Winston (1994), Hayward (1996) and Ostrovskii & Taylor (1996).

For cheilostome systematics we have followed Hayward (1995). There appears to be no generally accepted higher level classification for ctenostome or cyclostome bryozoans. Hayward (pers. comm.) regards the current species list for Southern Ocean ctenostome bryozoans as a severe underestimate of the true species richness, and the cyclostome species richness may also be underestimated.

The ctenostomes are the most ancient bryozoan lineage. They are rare in the Southern Ocean and almost absent from shallow waters (Barnes & De Grave 2000). Only six species have been reported from Antarctic waters so far, although the taxonomy of *Alcyonidium* is particularly complex and difficult so this list may rise. The relatively low diversity of cyclostomes is not unusual for isolated areas (Barnes & De Grave 2000) and the bryozoan fauna overall is dominated by cheilostomes (Table 8).

The time-course of species description (Fig. 9a) shows two important periods of taxonomic work, in the first two decades of the last century, and in the past twenty years. The frequency distribution of species per genus values is normal (Fig. 9b), with the highest value being for *Cellarinella*. Over a dozen cheilostome families contain ten or more species, with the most diverse being Smittinidae (Table 8).

Table 8 The most speciose families of Southern Ocean bryozoans. The threshold for inclusion was ten species, and species richness can only be approximate because of unresolved taxonomic difficulties and undiscovered species. The absence of an agreed intermediate level taxonomy for cyclostomes and ctenostomes means that species richness can only be presented at the order level. Ctenostomes are not very diverse in the Southern Ocean, but are included for completeness. Higher level taxonomy follows Barnes (1998) and Hayward (1995).

Class	Order	Family	Approximate number of species
Stenolaemata	Cyclostomatida		67
	Ctenostomatida		6
Gymnolaemata	Cheilostomatida	Smittinidae	34
		Bugulidae	19
		Cabereidae	18
		Cellariidae	17
		Sclerodomidae	17
		Exochellidae	14
		Celleporidae	14
		Microporellidae	12
		Flustridae	11
		Calloporidae	11
		Chaperidae	10
		Arachnopusidae	10
		Phidoloporidae	10

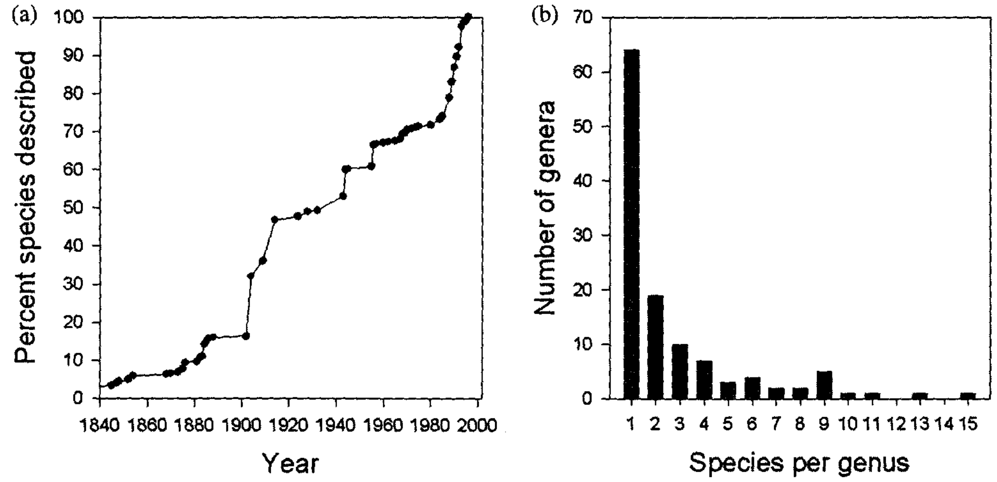

Figure 9 Bryozoa. (a) Time course of description of Southern Ocean bryozoan taxa; data presented in percentage terms (total 322 species). (b) Distribution of species amongst genera for Southern Ocean bryozoans, presented as a frequency distribution of species per genus values.

Phylum Echinodermata

Echinoderms have been collected by almost every biological expedition to the Southern Ocean, and typically being large and conspicuous are generally well described.

The major taxonomic synopses used for asteroids were Koehler (1920), Fisher (1940), Clark (1962) and McKnight (1976). For systematics we have followed Clark (1962). The key references and synopses for echinoids were Koehler (1926), Grieg (1929) and Mortensen (1936). Additional records came from Retamal et al. (1983), Larrain (1985), Voss (1988) and Mironov (1995). The key ophiuroid references were Koehler (1922), Madsen (1967), Alarcon-Castillo (1967) and Seno & Irimura (1968). Additional records came from Bernasconi & D'Agostino (1973a,b). The key references used in compiling the holothurian species list were Agatep (1967), Cherbonnier (1973), Pawson (1977) and Gutt (1988). For crinoids the key references used were Clark (1937), John (1938) and Speel & Dearborn (1983), with the latter references used for systematics. General echinoderm references consulted were Arnaud (1964), McKnight (1967), Cherbonnier & Guille (1974) and Piepenburg et al. (1997).

The time-course of species description (Fig. 10a) shows that over 80% of the known fauna had been described by the middle of the last century. This reflects the generally large and conspicuous nature of echinoderms, which together with molluscs and crustaceans tend to be among the first groups to be tackled by systematists.

The frequency distribution of species to genus values (Fig. 10b) is normal, with over 80 genera containing only a single described species, and two outliers with high species numbers (the ophiuroid genera *Amphiura* and *Ophiura*). The most speciose families are spread across all five echinoderm classes for which we have species lists in the Southern Ocean (Table 9).

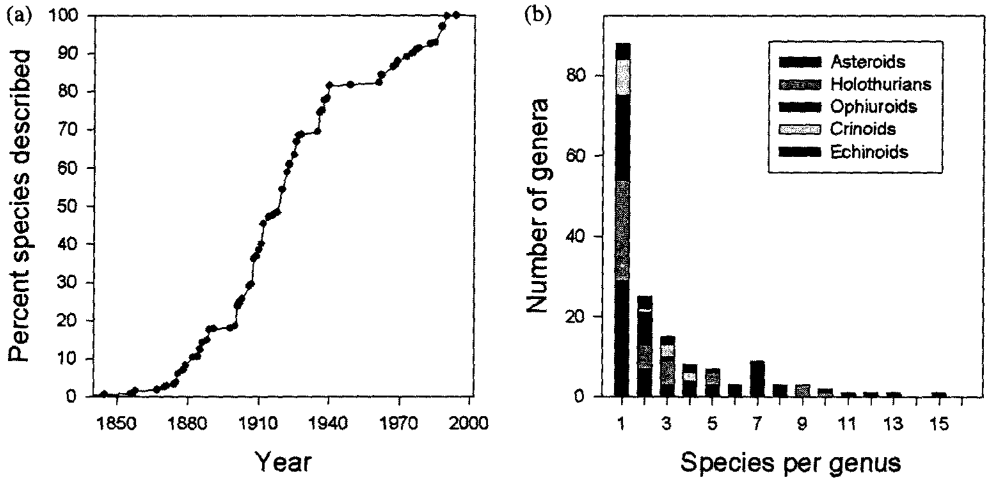

Figure 10 Echinoderms. (a) Time course of description of Southern Ocean echinoderm taxa; data presented in percentage terms (total 410 species). (b) Distribution of species amongst genera for all echinoderms combined, presented as a frequency distribution of species per genus values.

Table 9 The most speciose families of Southern Ocean echinoderms. The threshold for inclusion was ten species, and species richness can only be approximate because of unresolved taxonomic difficulties and undiscovered species. The higher level taxonomy follows Barnes (1998). Families are listed within classes in order of species richness.

Class	Family	Approximate number of species
Crinoidea	Antedonidae	22
	Asteriidae	37
Asteroidea	Odontasteridae	11
	Pterasteridae	10
Ophiuroidea	Ophiolepidae	69
	Ophiacanthidae	20
	Amphiuridae	20
Echinoidea	Schizasteridae	22
	Cidaridae	15
Holothuroidea	Psolidae	19
	Elpidiidae	17
	Cucumariidae	15
	Paracucumidae	15
	Synallactidae	13

Phylum Chordata

This phylum comprises three major groups which are sometimes elevated to phyla in themselves, the urochordates (ascidians, larvaceans and salps), cephalochordates (lancelets) and vertebrates. Here we follow Barnes (1998) in regarding them as subphyla. There are no cephalochordates known from the Southern Ocean, and amongst the urochordates only the ascidians are benthic.

Subphylum Urochordata, Class Ascidiacea

Ascidians are a conspicuous and ecologically important component of the continental shelf fauna. The most recent taxonomic revisions are those of Kott (1969) and Monniot & Monniot (1983, 1994). Recent references consulted were Monniot (1990) and Sreepada et al. (1995). For systematics we have followed Monniot & Monniot (1983), itself a modification of Kott (1969).

The time-course of species description (Fig. 11a) shows that over half the known Southern Ocean ascidians had been described by 1920. Since then new species have been described only slowly, with a small pulse in the latter part of the last century. The frequency distribution of species per genus values (Fig. 11b) is fairly typical apart from a single striking outlier caused by the genus *Aplidium* with 25 species. The four most speciose families are the Polyclinidae (37 species in 6 genera), Stylidae (19 species in 6 genera), Molgulidae (16 species in 4 genera) and Pyruidae (15 species in 6 genera).

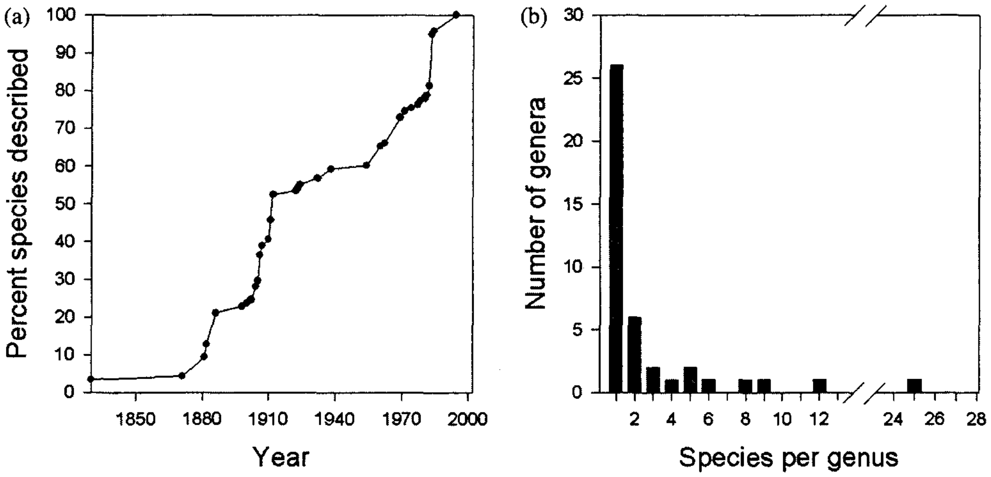

Figure 11 Ascidians. (a) Time course of description of Southern Ocean ascidian taxa; data presented in percentage terms (total 118 species). (b) Distribution of species amongst genera for Southern Ocean ascidians, presented as a frequency distribution of species per genus values.

Subphylum Vertebrata

The vertebrates are traditionally classified into seven major groups, here regarded as classes, of which three are referred to colloquially as fishes. These are the Agnatha (hagfishes and lampreys), Chondrichthyes (cartilaginous fishes, comprising sharks, rays, skates and their allies) and Osteichthyes (bony fishes, a group which includes the dominant fishes living today, the teleosts). All three fish classes are represented in the Southern Ocean though their mobility means that they are difficult to classify as truly benthic organisms. Of the other four classes, there are no amphibians or reptiles known from the Southern Ocean but both birds and mammals are important components of the oceanic food-web. Although some seabirds and marine mammals feed on or close to the sea bed, neither group can be regarded as benthic organisms.

Table 10 Dominant taxa (families) of benthic fishes inhabiting the continental shelf and upper continental slope of the Southern Ocean. The phylogenetic sequence is from Gon & Heemstra (1990). Table based on Eastman (1993) and Eastman & Clarke (1998). The liparids and six notothenioid families (*) together comprise >85% of all Southern Ocean species.

Class	Order	Family	Number of species
Agnatha			
	Myxiniformes		
		Myxinidae (hagfishes)	1
	Petromyzontiformes		
		Petromyzontidae (lampreys)	1
Chondrichthyes			
	Rajiformes		
		Rajidae (skates)	8
Osteichthyes			
	Ophidiiformes		
		Carapidae (pearlfishes)	1
	Gadiformes		
		Moridae (deepsea cods)	4
		Muraenolepididae (eel cods)	4
		Gadidae (true cods)	1
	Scorpaeniformes		
		Congiopodidae (horsefishes)	1
		Liparidae (snailfishes)	64
		Zoarcidae (eelpouts)	23
	Perciformes		
		Bovichtidae (thornfishes)*	1
		Nototheniidae (Antarctic cods or notothens)*	34
		Artedidraconidae (plunderfishes)*	24
		Harpagiferidae (spiny plunderfishes)*	6
		Bathydracondiae (dragonfishes)*	15
		Channichthyidae (icefishes)*	15
		Tripterygiidae (triplefins)	1
	Pleuronectiformes		
		Achiropsettidae (southern flounders)	4

The Southern Ocean fish fauna is well known. The most recent taxonomic monographs are by Gon & Heemstra (1990) and Miller (1993). Since the publication of these volumes, Russian ichthyologists have described several new species of nototheniids and many new liparids. For systematics we have followed Eastman (1993), as updated by Eastman & Clarke (1998); this is itself based on Gon & Heemstra (1990).

The Southern Ocean fish fauna is relatively low in diversity (Table 10). It is also unusual in containing by two striking radiations, the nototheniids on the continental shelf and the liparids on the continental slope (Eastman & Clarke 1998). The continental shelf fish fauna is dominated by nototheniids, not only in terms of diversity but more particularly in biomass: in a typical single haul over 95% of individuals can be nototheniids. This level of dominance by a single clade of fishes is unique in the sea, and the radiation of nototheniids exhibits many parallels with the species flocks of freshwater fishes in some lakes (Eastman & Clarke 1998). The radiation of liparid fishes on the continental slope is less well documented, partly because this is a very difficult group taxonomically but also because samples are fewer. Much of what we do know is the result of extensive work by Russian scientists.

Discussion

How many benthic species are there in Antarctica?

A long history of collection and taxonomic work in the Southern Ocean has meant that the benthic fauna is better known than might be thought. Some groups inevitably are in urgent need of taxonomic attention, but we are in a position to make some useful generalisations.

A summary diversity inventory for Southern Ocean benthos is shown in Table 11. Although most macrobenthic taxa are listed, this cannot be regarded as an all-taxon biodiversity inventory (ATBI) of the type widely promulgated following the publication of the Convention on Biological Diversity (Yoon 1993). This is because many important classes of fauna are excluded (notably the meiofauna and hyperbenthos), and no plants, protistans or viruses are listed. Because the benthos is linked intimately to the overlying water column, whereas the nekton are able to move freely into deeper water, it becomes very difficult to decide on a meaningful circumscription of an area or habitat within which to attempt to construct an ATBI. Recently a brave attempt has been made for Hawaii (Eldredge & Miller 1995, updated by Paulay 1997), including all plant and animal taxa, and encompassing marine, freshwater and terrestrial habitats.

The total species list for the Southern Ocean benthos currently exceeds 4100 (Table 11, see also Addendum, p. 114). The most species-rich group is the polychaete worms. This group is important in soft substrata, but most of the remaining taxa are important components of the epifauna. Of particular significance is the strong representation of suspension feeding taxa (bryozoans, sponges, hydrozoans, ascidians and anthozoans). Ranking by species richness thus emphasises the comments of many ecologists as to the predominance of suspension feeding communities in Antarctica. To some extent, however, this may represent under-sampling of soft substrata. The overall diversity of the Southern Ocean will also be influenced by the affect of ice scour on rocky intertidal and subtidal habitats, and the almost complete absence of rivers, estuaries and intertidal mud-flats; all of which habitats typically contain rich and diverse benthic communities elsewhere in the world.

Table 11 The best available estimates of higher taxon species richness for free-living Southern Ocean benthos. The tabulated data are from this study and from a review by Arntz et al. (1997). The reliability of the estimated richness for each taxon is classified on a subjective three point scale ranging from A (good) to C (poor) as defined in the text (see Methods section); also provided is the percentage

			Estimated species richness		Reliability	
Phylum	Subphylum or Class	Order	Arntz	This study	This study	Winston
Porifera			~300	250	B	50
Symplasma			–	29	A	
Cnidaria						
	Medusozoa		~200	186	C	90
	Anthozoa		85	86	C	50–95
Ctenophora			nd	nd	C	
Platyhelminthes	***Turbellaria***		nd	nd	C	
Gastrotricha						
Priapula			3	3	A	
Kinorhyncha			nd	nd	C	
Nematoda			nd	nd	C	
Tardigrada			nd	nd	C	
Arthropoda	Crustacea					
	Malacostraca	Amphipoda	520	496	B	
		Isopoda	346	257	A	
		Tanaidacea	50	80	B	
		Decapoda	(19)	13	A	
	Cirripedia		37	50	C	
	Ostracoda		nd	nd	C	
Chelicerata						
	Arachnida	Acarina	nd	45	C	
	Pycnogonida		>150	175	A	
Nemertea			nd	31	B	20
Mollusca						
	Polyplacophora			<10	C	
	Gastropoda		nd	530	A	40–50
	Bivalvia		nd	110		
	Scaphopoda			6	C	
	Cephalopoda			~34	B	
Sipuncula			~15	15	A	
Echiura			nd	9	A	
Annelida						
	Polychaeta		>650	645	C	
	Clitellata		nd	nd	C	
Pogonophora			nd	3	C	
Entoprocta			nd	nd	C	
Brachiopoda			16	19	B	
Bryozoa			310	322	A	40–50
Hemichordata			nd	nd	C	
Echinodermata						
	Crinoidea		22	28	B	
	Asteroidea		nd	108	B	
	Ophiuroidea		nd	119	B	70
	Echinoidea		44	49	B	80
	Holothuroidea		88	106	B	80
Chordata						
	Urochordata		>130	118	B	95
	Vertebrata	Agnatha	nd	2	A	
		Chondrichthyes	nd	8	A	
		Osteichthyes	nd	198	A	

of the shallow-water Southern Ocean fauna described, as estimated by Winston (1992). Higher level taxonomy follows Barnes (1998). nd = no data. Groups in bold italic are known to occur in the Southern Ocean, but for which no species lists appear to be available.

Comments
Arntz et al. include hexactinellids. Demosponges well reviewed; calcareous forms in need of revision
Benthic hydrozoan taxa only
Dunn (1983) estimates >90 actinarians alone for the Southern Ocean
One platyctenean ctenophore (*Lyrocteis flavopallidus*) reported from shallow benthos of McMurdo Sound
Free-living turbellarians known from intertidal sublittoral and sea-ice habitats
Larger forms well studied; many smaller species probably yet to be described (De Broyer, pers. comm.)
Recently well revised
Arntz et al. included some demersal and mid-water/pelagic taxa; total includes lithodid crab taxa reported recently from deeper water at South Georgia
Known from Southern Ocean; no recent taxonomic summary known to authors
Species list for marine mites only
Recently reviewed thoroughly by Munilla León (2001a)
Winston reliability estimate for opisthobranchs only
A small but relatively well known group
A small but relatively well known group
Knox & Lowry (1977) comment that the total Southern Ocean polychaete fauna probably exceeds 800 species; a thorough review is badly needed
Both oligochaetes and leeches known from Southern Ocean, but no species lists appear to be available
Vent faunas likely to increase known species; many deep-sea forms probably await description
Recent work has established new species; major recent review of cheilostomes; data for ctenostomes and cyclostomes probably underestimates
Pterobranchs known from the Southern Ocean
Data for ascidians only
Arntz et al. estimated 139 for all benthic fishes; definition of benthic/demersal taxa difficult

Before undertaking any further analyses, however, we need to ask how reliable these estimates of diversity are.

How good are our estimates of Southern Ocean marine benthic diversity?

For any meaningful interpretation of a biological diversity inventory, it is essential to understand the strengths and weaknesses of the information on which it is built. Thus only a knowledge of sampling coverage and intensity will allow a distinction to be made between a genuinely depauperate fauna (*there are very few species at this location*) and a poorly sampled fauna (*there may be many species here, but we have only collected a small fraction of them*). In this respect, Antarctica poses severe challenges for the benthic ecologist. Most of the Southern Ocean overlies the abyssal plain, the continental shelves are unusually deep, and access is impeded by floating ice shelves or vast areas of seasonal pack-ice. Despite these difficulties there is a long and proud history of benthic exploration in the Antarctic, and we now know a good deal about the fauna, at least for the major taxa of the continental shelves.

The early work on Southern Ocean benthos took place largely during expeditions concerned primarily with geographic exploration or important physical observations such as geomagnetism or meteorology (Headland 1989, Fogg 1992, Clarke et al. 2000). Nevertheless these early collectors were remarkably thorough and Dayton (1990) laments that these important pioneers will never gain the recognition they deserve. The importance of these early contributions can be seen in the history of the published descriptions of major benthic taxa: the time-course of species description for many taxa show the importance of the systematic work based on the extensive collections made by early exploratory expeditions. In the past decade there has been a significant increase in systematic work on Southern Ocean benthos, prompted largely by the SCAR programme on the ecology of the Antarctic sea ice zone (EASIZ).

An important factor in assessing completeness of sampling of the fauna is the geographic spread of collections. The strengths and weaknesses of Southern Ocean benthic sampling to date are well shown by molluscs. Data for gastropod molluscs (Fig. 12) suggest that samples from the continental shelf have a good geographical spread, if somewhat thin away from the Ross Sea, Weddell Sea and Antarctic Peninsula. There are, however, relatively few samples from deeper water (Table 12) and the deep-sea fauna of Antarctica appears to be known only very poorly (Clarke in press). Extensive collections were made in many areas of Antarctica by biologists of the former Soviet Union, but relatively few data are currently available to western scientists.

A broad scale analysis of the gastropod and bivalve data available for the Southern Ocean emphasises the patchy nature of the sampling. The number of samples taken in some areas is considerable (for example, Antarctic Peninsula, eastern Weddell Sea, Ross Sea and the islands of the Scotia arc): in other areas sampling is very thin (Table 12). To a large extent this pattern reflects ease of access; the Bellingshausen Sea is a very difficult area for a ship to visit because of ice. There is also an effect of proximity to research stations undertaking marine biological work. Both of these effects are, of course, well known from studies of biological diversity elsewhere, both on land and in the sea.

The number of samples taken in a given area is a key factor in the diversity recorded

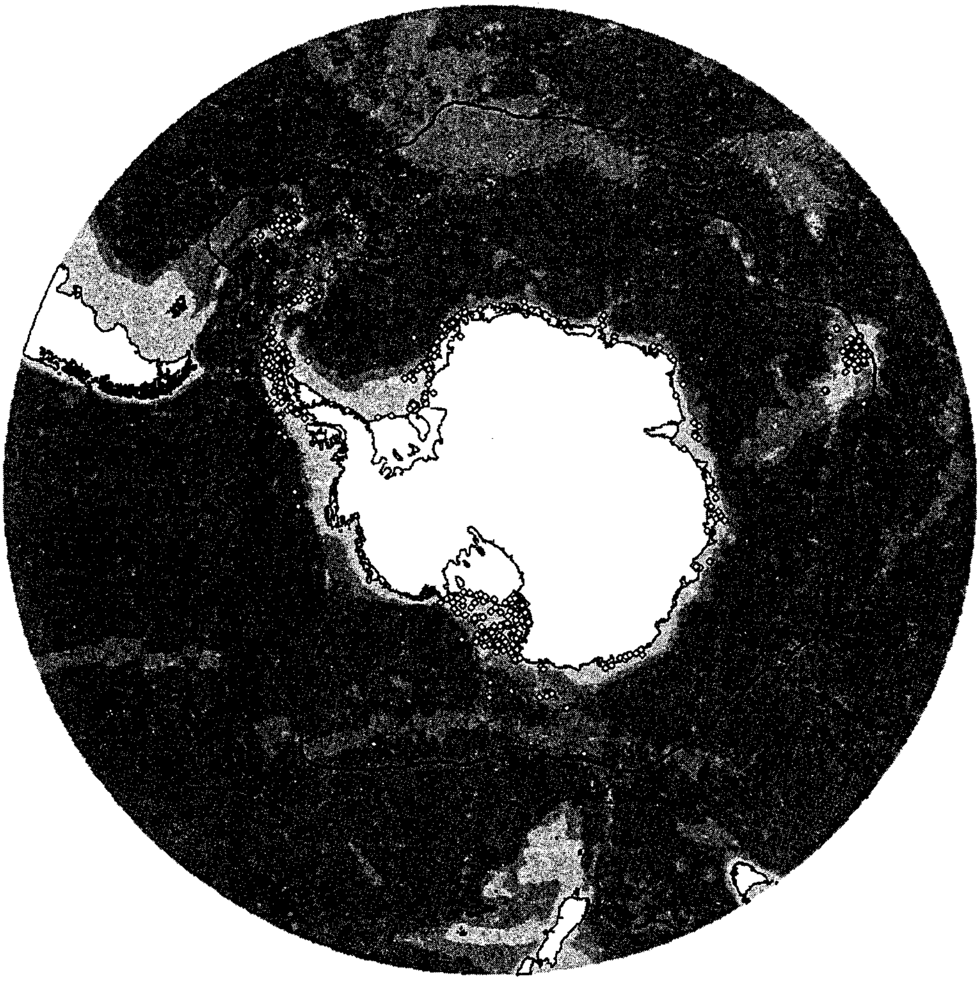

Figure 12 Distribution of gastropod samples in the Southern Ocean. Isobaths are shown to mark the edge of the continental shelf (1000m) and an arbitrary transition from continental slope to deep sea (3000m). Also shown is the Polar Front, which is the northern boundary to the Southern Ocean. The database contains >7000 records, so not all data can be distinguished on the plot because many samples overlap. Data kindly provided by Katrin Linse and Alistair Crame, and the map plotted by Huw Griffiths.

(Table 12). This is an almost universal feature of studies of diversity in the marine environment where few areas have been studied in sufficient detail for a high proportion of taxa to have been recorded. The exceptions are probably areas such as the northwest Atlantic, Mediterranean or Indo–West Pacific with a long history of sampling, and taxa which are well known such as fishes, echinoderms or molluscs. Even for a common and reasonably well known group such as bryozoans, patterns of recorded diversity in the north Atlantic are dominated by sampling effects (Clarke & Lidgard 2000).

Table 12 Spatial variability in sampling intensity and observed species richness for Southern Ocean gastropods and bivalves. Data from Southern Ocean Molluscan Database, courtesy of Alistair Crame, Katrin Linse and Huw Griffiths (British Antarctic Survey), updating previous compilation by authors. Data broken down by depth strata and broad geographical areas. The depth strata were continental shelf (0–1000 m), continental slope (1000–3000 m) and deep sea (>3000 m). Data shown are number of sites sampled (N), together with the number of species observed, in each depth/area bin: SRgas = number of gastropod species in that bin, SRbiv = number of bivalve species.

Area	Continental Shelf			Continental Slope			Deep Sea		
	N	SRgas	SRbiv	N	SRgas	SRbiv	N	SRgas	SRbiv
South Georgia, South Sandwich Islands and South Orkney Islands	209	148	44	24	17	8	16	9	4
Weddell Sea, east to 10°W	351	203	36	31	15	2	2	10	8
Dronning Maud Land, 10°W to 65°E	89	157	14	4	14	0	1	1	0
Prydz Bay, 65°E to 80°E	9	19	0	1	1	0	0	0	0
Wilkes Land, 80°E to 170°E	191	98	10	8	15	2	1	2	0
Ross Sea, 170°E to 150°W	408	147	40	18	18	9	5	4	3
Bellingshausen and Amundsen Seas, 80°W to 150°W	2	2	0	0	0	0	6	2	4
Western Antarctic Peninsula, 80°W to 50°W, including South Shetland Islands but excluding Weddell Sea	231	132	42	12	16	12	5	3	4

Which taxa are important in the Southern Ocean?

The Southern Ocean is geographically and environmentally extreme, in the sense that it has the highest southerly marine latitude and comprises water masses that are colder than anywhere else on earth. It is therefore of interest to ask whether the marine fauna shows any features which differ from those elsewhere.

A simple preliminary approach would be to determine which taxa are most speciose, and which are least, and compare this ranking with other marine areas. Those taxa for which >100 species have been described for the Southern Ocean are listed in Table 13. Of these perhaps the most noteworthy are the pycnogonids and ascidians, the remainder being taxa which are frequently speciose in seas elsewhere. Where taxa are low in species richness this could simply be an evolutionary characteristic of the taxa overall; examples for the Southern Ocean would be sipunculans, echiurans and priapulans. In other cases, however, a low species richness in the Southern Ocean might not be typical of that group in warmer waters; examples would include gastropods, decapod crustaceans and teleost fishes, all of which are highly speciose in many oceans but poorly represented in the Southern Ocean.

A simple comparison of the species richness of major groups in the Southern Ocean with recent taxonomic summaries for Hawaii (Eldredge & Miller 1995) and northwestern European seas around the UK (Hayward & Ryland 1995, Howson & Picton 1997) highlights the importance of ascidians, echinoderms, polychaetes, pycnogonids, bryozoans, amphipods, isopods and hydroids, all of which have more species in the Southern Ocean than in either Hawaii or northwest Europe (Fig. 13). Of these, the most striking contrast by far is for pycnogonids where the Southern Ocean fauna is an order of magnitude more diverse than in either Hawaii or northwest Europe; pycnogonids are genuinely diverse in the Southern Ocean. Echinoderms are generally a well-described group and we must conclude that these are also particularly diverse in the Southern Ocean (although not all lineages are equally

Table 13 Benthic invertebrate taxa showing the highest species richness in the Southern Ocean. Colloquial names are used as the groups represent different taxonomic levels (phylum, class or order). Taxa are ranked according to total species richness, with a threshold for inclusion in the table of 100. Also included are estimates of the percentage of the total world fauna for that taxonomic group, based on the range of data in Table 2.

	Species richness	Percentage of world species
Polychaetes	645	12.2
Gastropods	530	<1
Amphipods	496	8.3
Bryozoans	322	6.4–8.1
Isopods	257	2.6
True sponges	250	2.6–5.6
Hydrozoans (benthic forms only)	186	nd
Pycnogonids	175	17.5
Ophiuroids	119	6.0
Ascidians	118	5.9–9.4
Bivalves	110	5.5
Asteroids (sea-stars)	108	7.2
Holothurians (sea cucumbers)	106	9.2

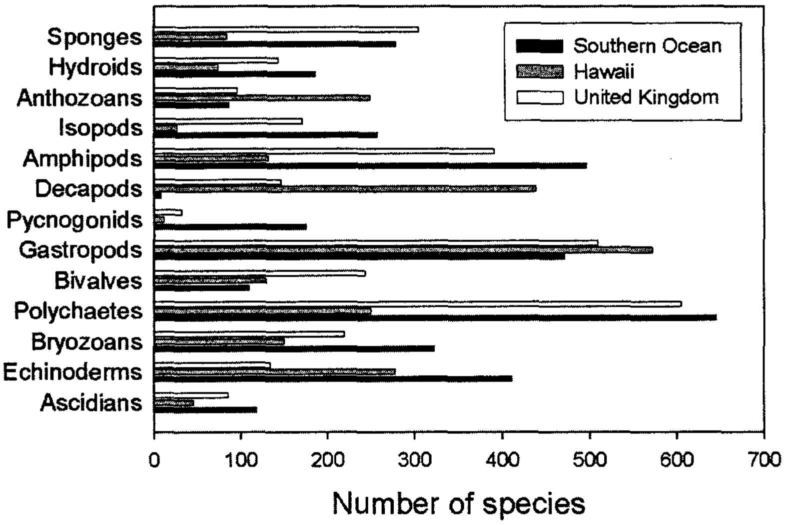

Figure 13 Comparison of species richness for selected benthic marine invertebrate groups in the Southern Ocean (this study), Hawaii (Eldredge & Miller 1995), and northwestern European waters around UK (Hayward & Ryland 1995, Howson & Picton 1997).

represented: Poulin & Féral 1996, Poulin et al. 2002). The data also suggest that bryozoans are notably diverse in the Southern Ocean.

For other groups (polychaetes, sponges, hydroids, amphipods, isopods and ascidians) species richness in the Southern Ocean significantly exceeds that in Hawaii but is broadly comparable with northwest Europe (Fig. 13). This may reflect any number of factors including isolation from continental shelves elsewhere, history of taxonomic work, and habitat (notably the balance between hard substrata and soft sediments). At present we can conclude that amphipods and isopods appear to be relatively well represented in the Southern Ocean, though not particularly diverse. Some amphipod and isopod lineages are, however, known to have radiated in the Southern Ocean (Watling & Thurston 1989, Brandt 1991a, 2000, Held 2000). The same may also be true of ascidians.

The comparison in Figure 13 also emphasises the genuinely low diversity of bivalves and decapods in the Southern Ocean. Gastropods are comparable in richness with both Hawaii and UK, but a global comparison emphasises the tendency for gastropods to be lower in diversity at high latitudes compared with tropical faunas (Crame 1996, 2001). This contrast is driven by the enormous richness of the gastropod fauna of the Indo–West Pacific region. To take a single example, intensive sampling of a single site in New Caledonia recovered 16 species of chiton, 16 scaphopods, 519 bivalves and 2187 gastropods (Bouchet et al. 2002). The data in Figure 13 also emphasise the diversity of anthozoans in tropical regions. Comparisons such as these are inevitably very crude, being beset with difficulties caused by differences in sampling intensity, taxonomic completeness, and area. Nevertheless when used with care, they can produce useful first-order conclusions and help to formulate more focused biogeographic or evolutionary questions.

An alternative approach to assessing which taxa are most important in the Southern

Ocean would be to calculate the fraction of the world's continental shelf fauna found in Antarctica for each group. Assuming that Antarctic contains 11% of the world's continental shelves (Table 3), then this might form a benchmark for a group of organisms whose representation in the Southern Ocean fauna is broadly proportionate to area. A large body of ecological work on terrestrial fauna, particularly of islands, has shown that the relationships between species richness and area is complex (and certainly not linear) (Rosenzweig 1995, Hubbell 2001). Nevertheless a benchmark of 11% might be taken as a first-order indication of *pro rata* representation in the fauna.

There are, however, numerous problems in the calculation of such data which must therefore be treated with great caution. The first is the wide range of estimates for the world species richness of many taxa (Table 2), the second is that the data for world species richness mixes species from a range of habitats in addition to continental shelves, and a third is that global data are not always easily available for lower taxonomic levels such as classes or orders. Even allowing for these difficulties, none of the Southern Ocean taxa achieves levels of representation greater than about 15%, and most are well below this (Table 13). The data do, however, reinforce the conclusion that polychaetes, bryozoans, sponges, pycnogonids, amphipods and ascidians are well represented in the Southern Ocean benthic fauna, whereas gastropod molluscs are not. Despite the inevitable difficulties inherent in such crude calculations, these do show that generalisations about the Southern Ocean marine fauna (and perhaps even generalisations about the marine fauna in general) based on data for molluscs alone, or any other single taxon, are unlikely to be valid. This contrasts with the terrestrial environment where it has long been assumed that broad-scale patterns exhibited by plants, birds or butterflies reflect general patterns for other terrestrial taxa (MacArthur 1972, but see Platnick 1992).

Both of the above comparisons are made problematic by difficulties of sampling intensity. One approach to correcting for sampling errors, which has been much used in diversity studies, has been to use rarefaction to estimate the number of species to be expected in a sample of a given number of individuals (Hurlbert 1971). Brey et al. (1994) used this technique for samples from Agassiz trawls in the Weddell Sea, and showed that data for bivalves, gastropods and isopods were distinctly higher than for northern polar waters (>70°N), and in the upper range of tropical values. This is a somewhat counter-intuitive result for the molluscan taxa, as the Southern Ocean contains less than 1% of world gastropod species (Table 13). Although rarefaction brings its own suite of statistical problems (discussed by Gotelli & Graves 1996) the differences between the results from these two approaches is probably related to differences in spatial turnover in species identity (beta diversity) between polar and tropical habitats. Thus Hubold (1992) has shown that whereas a given sample of demersal fishes from the Weddell Sea and the North Sea may contain similar number of species, the larger spatial variability in species identity in the North Sea leads to a larger overall species list (regional diversity). Abele (1974) documented a similar pattern for decapods, where within-habitat diversity was broadly similar across latitudes whereas regional diversity was much greater in the tropics because of larger differences in species composition between different habitats (turnover or beta diversity).

Overall, current data suggest that pycnogonids are the one group which is especially diverse in the Southern Ocean, with bivalves, decapods and teleost fishes notably under-represented. The most diverse group overall is the polychaetes, and a number of groups are well represented, including ascidians, echinoderms, bryozoans, sponges, amphipods and isopods.

Endemism

Many authors have commented on the high degree of endemism in the Southern Ocean fauna. The most recent compilation is that of Arntz et al. (1997) who showed a range of values from about 35% (scleractinian corals) to about 90% (pycnogonids). The recent compilation of amphipod species richness by De Broyer & Jazdzewski (1996) indicated a level of endemism of 80% at the species level, and 17% at the genus level for their Antarctic region.

These data indicate the length of time for which the Southern Ocean fauna has been isolated (Clarke & Crame 1997). The degree of endemism is also scale-dependent in that it is a strong function of the area over which it is calculated: endemism is 100% at the level of the whole globe, and 0% at the level of a small bay. The high level of endemism shown by the Antarctic benthic fauna is thus partly a function of the size of the Southern Ocean. Endemism remains high, however, on smaller spatial scales: De Broyer & Jazdzewski (1996) have shown that endemism at the species level in gammaridean amphipods is 38% in East Antarctica and 54% in West Antarctica. Overall we must conclude that a high level of endemism is a real feature of the Southern Ocean benthic fauna.

Spatial variation in species richness

Although the overall levels of species richness in the Southern Ocean are moderately high in some taxa, the Southern Ocean is a large place. Many Southern Ocean taxa appear to have a circum-Antarctic distribution, but not all species will be found in all places, even where apparently suitable habitat exists.

There are still relatively few places in the Southern Ocean for which comprehensive faunal lists exist. Two relatively well studied areas are the Weddell Sea and Admiralty Bay. Although a considerable amount of biological work has been undertaken in the Ross Sea sector, until recently relatively little of this work was taxonomic. A comparison, albeit crude, can, however, be made for the whole Southern Ocean with the fauna known for the Weddell Sea, the Ross Sea, and very preliminary data for the much smaller areas of Admiralty Bay, Arthur Harbour and Signy Island (Table 14). These data show that the general patterns of dominance by certain taxa are reflected at all scales.

Species/area relationships have been described for many areas of the globe, over a variety of spatial scales, and for many taxa (for a thorough review of this topic see Rosenzweig 1995). Few such relationships have been established for marine systems. The data collated in Table 14 indicate that there is a positive species/area relationship within the Southern Ocean, but with the spatial extent of sampling being known only poorly and with data not available for some taxa, we cannot even start to derive any meaningful quantitative relationships. The picture will also be confounded by latitudinal or other spatial variations in benthic species richness.

Latitudinal variations in Southern Ocean marine diversity

Although the Southern Ocean extends over a wide latitudinal band, from 54°S at South Georgia to 78°S at McMurdo Sound in the Ross Sea, there have been remarkably few

Table 14 A comparison of species richness in two regions and three smaller areas of the Southern Ocean with the total regional fauna. Data from Richardson (1976), Arnaud et al. (1986), De Broyer & Jazdzewski (1993), Siciñski & Janowska (1993), Jazdzewski et al. (1986), Arntz et al. (1997), Arnaud et al. (1998, 2001), Gutt et al. (2000) and unpublished British Antarctic Survey records. Further sampling will undoubtedly increase many of these richness figures. nd = no data.

	Southern Ocean	Regions		Areas		
		Weddell Sea	Ross Sea	Admiralty Bay	Signy Island	Arthur Harbour
Porifera + Symplasma	279	nd	57	nd	nd	nd
Cnidaria						nd
Hydrozoa	186	36	25	nd	nd	nd
Anthozoa	86	33	19	nd	nd	nd
Brachiopoda	19	nd	7	nd	nd	nd
Bryozoa						
Cheilostomatida	249	180	163	nd	87	nd
Mollusca						
Gastropoda	530	145	nd	35	82	8
Bivalvia	110	43	nd	27	nd	20
Echinodermata						
Asteroidea	108	50	28	15	nd	nd
Crinoidea	28	6	9	1	nd	nd
Echinoidea	49	nd	nd	4	nd	2
Ophiuroidea	119	43	nd	15	nd	6
Holothuroidea	106	35	nd	3	nd	2
Crustacea						
Decapoda	8	4	nd	2	nd	nd
Amphipoda	496	174	nd	99	nd	48
Isopoda	257	68	33	nd	nd	38
Pycnogonida	175	69	64	nd	nd	6
Annelida						
Polychaeta	645	225	97	~100	78	142
Urochordata	118	24	40	nd	nd	4

studies of latitudinal variation in marine species richness within Antarctica. It is generally accepted that, as on land, benthic species richness will be greatest around the sub-Antarctic islands such as South Georgia, and decline southwards through the maritime Antarctic to the high Antarctic regions of the Ross Sea and Weddell Sea. However, there have been almost no tests of this.

The clearest latitudinal cline reported so far in the marine realm of the Southern Ocean is for macroalgae along the Antarctic Peninsula (Moe & DeLaca 1976). Although the sampling was not comprehensive being limited to shallow depths, it was broadly comparable between sites and revealed a strong decrease in macroalgal species richness from north to south along the western Antarctic Peninsula (Fig. 14). Although this cline is likely to result in a similar cline of those epifauna reliant on macroalgae as a substratum, it is important to establish whether a latitudinal cline is a general feature of benthic diversity in the Southern Ocean.

Latitudinal diversity clines elsewhere in the marine system tend to be strongest where there are strong meridional clines in environmental and oceanographic variables (for

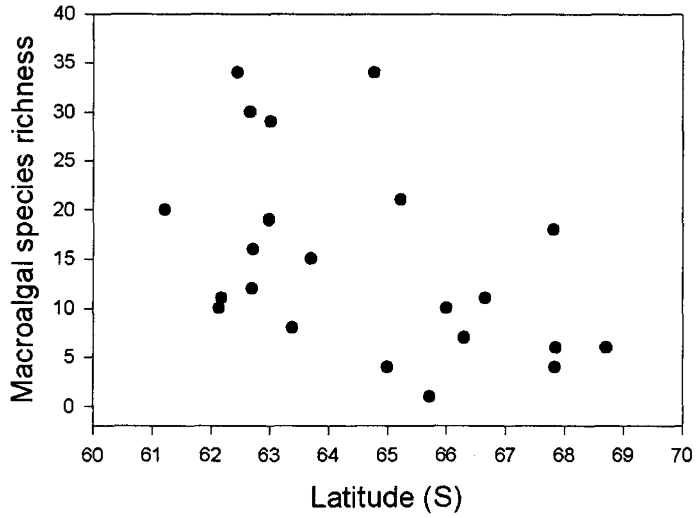

Figure 14 Latitudinal cline in macroalgal diversity along the Antarctic Peninsula. Data from Moe & DeLaca (1976).

example, along the Atlantic and Pacific coasts of North America), or where the imprint of glacial history is strong. Antarctica has relatively few places where the continental shelf has a strongly meridional orientation and the predominant features of the oceanography are circumpolar. This would suggest that latitudinal patterns will not be a major feature of the biogeography of Southern Ocean benthos, with the possible exception of the Antarctic Peninsula.

Apart from the sub-Antarctic islands such as South Georgia, benthic water temperatures are relatively homogeneous across the continental shelves of Antarctica. Winter minima are usually around −1.9°C, and annual variability typically less than 2°C; this annual range is small compared with annual ranges greater than 10 to 15°C typical of many lower latitude seas. The major differences within the Southern Ocean are in the timing and duration of the summer warming, and the peak temperatures reached (all of which are subject to significant variability between years). Coupled with variability in ice dynamics and latitudinal variations in photoperiod, these lead to strong spatial variation in the timing of the summer water column phytoplankton bloom. These factors are likely to influence much of the ecology of the benthos and together with the relatively small annual variation in temperature make the Antarctic benthic environment an ideal natural laboratory for distinguishing the ecological effects of temperature and food (Clarke 1991, 1998). It is not at all clear what effects, if any, these variations will have on the overall diversity of the fauna.

Biogeographic patterns in Southern Ocean marine benthos

There has long been an interest in the biogeography of Antarctica (Darlington 1965). In the terrestrial realm most attention has been directed at historical influences such as the break up of Gondwana and glaciation. In the marine realm the two major concerns have traditionally

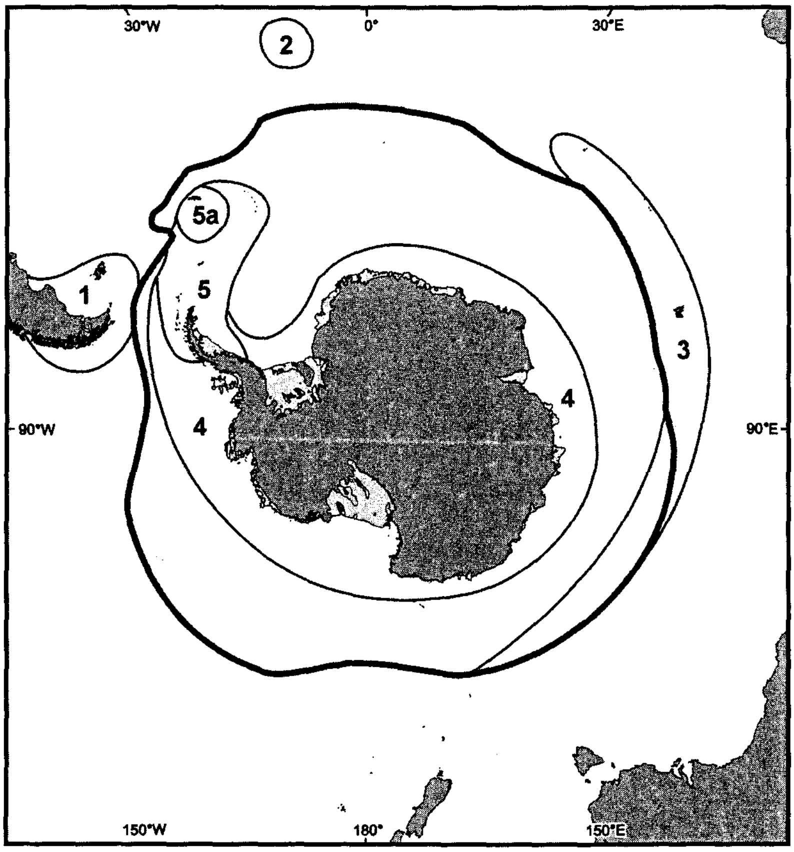

Figure 15 The basic biogeographical division of the Southern Ocean benthos as proposed by Hedgpeth (1970) and Dell (1972). This classification has stood the test of time, remaining valid in the context of considerable new sampling. The precise location of the boundaries between the Antarctic Peninsulas and continental Antarctic regions are, however, not well defined as they fall in areas where sampling intensity is especially low.

been the routes of faunal exchange, and the influence of the predominantly circumpolar oceanography.

By the early 1970s, knowledge of the Southern Ocean benthic fauna was sufficient for major biogeographic and taxonomic reviews to be written (Hedgpeth 1969, 1970, 1971, Dell 1972). These resulted in a biogeographic scheme for Southern Ocean benthos that has remained the working paradigm ever since (Fig. 15). More recent analyses for amphipods (De Broyer & Jazdzewski 1996) and bryozoans (Barnes & De Grave 2000) have largely confirmed the previously established patterns, though adding the extra dimension of differences between the faunas of East and West Antarctica. The basic biogeographic subdivisions of the Southern Ocean benthic fauna are thus South Georgia, the Antarctic Peninsula (including the South Orkney Islands) and high Antarctica, comprising the fauna of the continental shelf at highest latitudes although with significant differences between East and

West Antarctica. The intermediate latitudes of the Antarctic Peninsula and the South Orkney Islands are sometimes referred to as the maritime Antarctic.

These patterns are usually interpreted in terms of history (Clarke & Crame 1997, in press, Crame & Clarke 1997, Crame & Rosen 2002). The fauna of the Antarctic Peninsula shows many features of exchange with South America along the Scotia arc, and the differences between East and West Antarctica will reflect the different evolutionary histories of these areas during the break up of Gondwana (especially in relation to the influence of Tethys). The continental shelves around Antarctica have been both more and less extensive in the past as the size and extent of the continental ice sheet has waxed and waned, and at times the Ross and Weddell Sea embayments would have represented extensive shallow seas (Clarke & Crame 1989). Brey et al. (1996) have shown that many Antarctic benthic taxa have a wider bathymetric range than relatives elsewhere, and this would appear to reflect previous extensions of the continental ice sheet reducing the area of available shelf habitat and forcing many benthic taxa into deeper water refugia.

It is possible that frequent fluctuations in the extent to which the continental ice sheet covered and exposed the continental shelf would have driven speciation in the Southern Ocean benthos (Clarke & Crame 1997, in press). Such variations in habitat, together with the effects of the long-term cooling of sea water, may have been a key factor in the very low species richness of some taxa (such as bivalves or decapod crustaceans), or in the complete absence of others (for example, brachyuran crabs and many families of teleost fishes). The difficulty faced by ecologists concerned with the evolutionary history of the Antarctic marine fauna is moving from *post hoc* explanations to testable ideas. The fossil record would be the obvious source of data, but unfortunately the fossil record of Antarctic marine invertebrates is patchy with gaps in many key periods (Crame 1992, Clarke & Crame 1989).

Some preliminary macroecological analyses

The main aim of this review has been to derive the best inventory for Southern Ocean benthic diversity from the available data. Although these data suffer from severe sampling problems, they do permit a number of preliminary analyses which throw light on current problems of macroecological interest.

The latitudinal cline in marine diversity

The latitudinal cline in diversity is a distinctive, well described feature of both flora and fauna on land. Although it had long been assumed that a similar cline would be found in the sea, evidence for this has proved to be more equivocal (Clarke 1992, Clarke & Crame 1997). A clear cline has been described for continental shelf molluscs on the Atlantic and Pacific coasts of North America (Roy et al. 1994, 1998), bryozoans in the North Atlantic (Clarke & Lidgard 2000) and some taxa in the deep sea (Rex et al. 1993, but see Gray 1994). In other areas, notably in the southern hemisphere, there is little evidence for a strong latitudinal cline in diversity (Poore & Wilson 1993, Brey et al. 1994, Clarke & Crame 1997).

The Southern Ocean fauna is critical to the existence of any cline in marine diversity in the southern hemisphere. Given the high diversity of many tropical marine habitats, a low

Southern Ocean diversity would essentially create a latitudinal gradient by itself, whereas high polar diversity would significantly decrease the intensity of any such gradient. The problem in determining the existence of a diversity cline in southern hemisphere shallow-water marine benthos is the current disposition of continental land masses. In strong contrast to the northern hemisphere there are relatively few continental shelves with extensive meridional (north–south) alignment. Comparison of marine diversity between Antarctica and either southern Africa or Australasia would be interesting, but the only sites where the existence of latitudinal gradients in shallow water benthos is likely to be demonstrated unequivocally are the Pacific and Atlantic coasts of South America, the Scotia arc and the Antarctic Peninsula.

The low diversity of gastropod and bivalve molluscs in the Southern Ocean is striking in comparison with the richness of both groups in some tropical regions. This suggests that in these two groups, at least, diversity broadly declines from a tropical high towards both poles (Crame 2000a,b, 2001). These diversity clines are steepest for the youngest clades, suggesting a pattern dominated by tropical diversification and subsequent migration polewards (Crame 2001). It is, however, important to recognise that some molluscan taxa have undoubtedly radiated at high southern latitudes. An example here would be the predatory buccinid and muricid gastropods (Crame 1996), and molecular phylogenetic work will undoubtedly uncover other high latitude molluscan radiations.

Two other groups with notably low diversity in the Southern Ocean are decapod crustaceans and teleost fishes. The reasons for this are unclear, as both groups are well represented in the fossil record and the demise of the decapod fauna appears to have been relatively recent (Feldmann & Tshudy 1989). Among fishes the notothenioid radiation is now fairly well understood, and it has been argued that this shows many of the features of a species flock analogous to the cichlid fishes of African rift lakes or the cottids of Lake Baikal (Eastman & Clarke 1998). In the case of both fishes and decapod crustaceans the earlier Southern Ocean fauna appears to have been almost eradicated by a historical event. It is not clear what this event might have been, although the best estimate for the date of the basal radiation of the notothenioids suggests that a critical event was the initial cooling of Antarctica and the onset of glaciation (Clarke & Johnston 1996). The reason for the extinction of many decapods is still obscure.

In contrast to the decapods and fishes, some groups appear to be strikingly diverse in the Southern Ocean. These include sponges, ascidians, amphipods, isopods and pycnogonids (Fig. 13). These data are not easy to interpret in terms of latitudinal clines, however, because there are few comparative data available. One exception to this are bryozoans, for which there has been recent extensive work in South America (Moyano 1984, López Gappa 2000). These studies have shown that whereas there is a cline in diversity along the South American coasts, the Southern Ocean fauna is both rich and quite distinct. Moreover, for cheilostomes there is a strong relationship between the age of a bryozoan family and the likelihood of having representatives in the Southern Ocean (Barnes & De Grave 2000).

These examples show clearly that the diversity and composition of the Southern Ocean benthic marine fauna can be understood only in terms of historical processes (Lipps & Hickman 1982). The origins of the present fauna are with the coastal fauna of Gondwana prior to break up. The fragmentation of Gondwana influenced the fauna particularly by the introduction of a Tethyan element through the Weddell province (Clarke & Crame 1989). Subsequent development of the fauna was influenced particularly by exchange (in both directions) along the Scotia arc and with the deep sea, but the dominant feature was evolution *in situ*. The relative representation of the different major taxa would appear to reflect accidents of history rather than the nature of the Antarctic marine environment. Climatic change and glaciation resulted in the extinction of some groups, and provided evolutionary opportunities for others.

This is not to say that ecological factors have had no role to play; there is, for example, strong evidence that reproductive ecology has had an important role to play in determining which echinoderm taxa are present in the modern Antarctic benthic fauna (Poulin & Féral 1996, Poulin et al. 2002). Overall, however, we should look to historical processes as the first order explanation of why the fauna has the diversity and composition it does.

Distribution of species amongst genera

It has been known since the pioneering work of Willis & Yule (1922) that the distribution of species amongst genera tends to follow a characteristic shape. Monotypic genera are typically the most frequent, genera with two species somewhat less common, and so on through a tail of fewer genera containing increasingly large numbers of species. Willis & Yule (1922) named this the *hollow curve* distribution, and noted that the relationship was often linear after logarithmic transformation of both variables. This frequency distribution appeared to apply both within taxonomic groups (for example many plant families) and also for local floras (where all taxa are pooled). Willis (1922) provided a conceptual basis for these observations through his age and area hypothesis, with younger taxa being less speciose and also less widely distributed geographically than older ones. This simple and intuitively appealing explanation has not stood the test of time (see, for example, Cronk 1989), but there remains a feeling that this more or less universal distribution must be telling us something about evolutionary processes.

More recent analyses have been built around a series of theoretical frequency distributions or evolutionary null models. Dial & Marzluff (1989) explored a series of null models of evolutionary diversification and Minelli et al. (1991) examined the fractal nature of diversity within the taxonomic hierarchy. Such analyses depend on particular models of evolutionary diversification, and also assume that taxonomy reflects evolutionary history in some meaningful way. Walters (1986) takes the extreme view that the patterns are entirely artefactual being driven exclusively by taxonomic biases.

The long period over which the Southern Ocean benthic marine fauna has evolved in isolation (Clarke & Crame 1989) suggests that the distribution of species per genus would be worth examining in that it might reveal the patterns to be expected for a radiation in the relative absence of dilution by immigrant taxa. Many of those taxa which are well represented in the Southern Ocean exhibit hollow curve distributions (Figs 2–11). Few of these are, however, convincingly linear on a double logarithmic plot (Fig. 16), suggesting that null models predicting a power law relationship do not reflect the underlying evolutionary processes accurately.

Size and abundance in Southern Ocean benthos

In general, studies of Antarctic benthos have relied on remote sampling techniques that are essentially destructive (for example, grabs, dredges and bottom trawls). Trawls and dredges

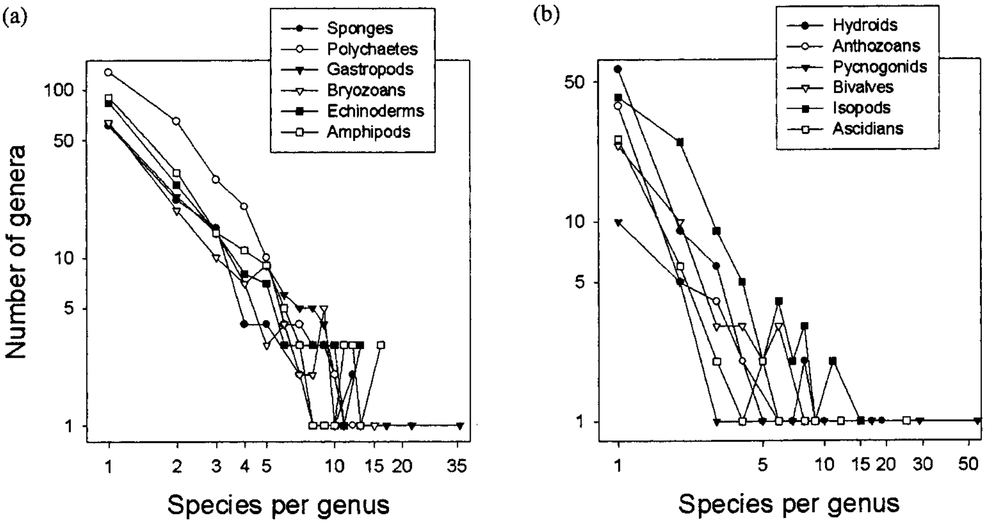

Figure 16 The distribution of species amongst genera for Southern Ocean benthos. Note logarithmic axes. For clarity of presentation, taxa have been divided into those with high species richness in the Southern Ocean (a, left) and low species richness there (b, right).

in particular suffer from the disadvantages of damaging many specimens, destroying any structure in the community (such as tiering or ecological associations) and mixing samples from many different habitats, thereby masking any heterogeneity in the distribution of different assemblages. In shallow waters these difficulties can be overcome by the use of SCUBA techniques, but safety considerations restrict both the depth and the amount of time available underwater and thereby limit the types of study that can be undertaken. Remote photographic techniques were used in deeper waters for some of the earliest studies of Antarctic benthos (Bullivant & Dearborn 1967) but were then largely ignored. Recently, however, German biologists have made extensive use of modern photographic techniques in the Weddell Sea, and these new studies have demonstrated clearly the value of such techniques to marine ecology (Barthel et al. 1991, Ekau & Gutt 1991, Gutt et al. 1991, 1994, Gutt & Piepenburg 1991, Barthel & Gutt 1992, Gutt & Schickan 1998, Gutt & Starmans 1998).

One of the primary considerations for any ecologist faced with making the choice of sampling gear is that of size selectivity. Photographic techniques are by their very nature limited almost exclusively to epifaunal macroinvertebrates above a certain size. Sampling techniques based on nets will also miss all organisms below a size set by the mesh of net being used, and the mesh size of sieves used for sorting will also influence the size distribution or organisms finally collected. These considerations are of particular relevance to Antarctic benthic communities, for although the small number of Antarctic taxa which are unusually large have long attracted attention (Arnaud 1974) it is now recognised that many Southern Ocean benthic organisms are very small.

Brey & Clarke (1993) collated all the data on the population dynamics of Antarctic marine benthos available up to 1992. Comparison of the polar species with species from temperate and tropical waters indicated no significant difference in mean adult size. This result, however, reflects the tendency of ecologists to choose larger organisms for study rather than the actual size distribution of polar marine invertebrates. Antarctic bivalves and gastropods, for example, have long been known to be typically small (Nicol 1964, 1966a,b, 1978, Arnaud 1974). In the case of gastropods many Antarctic species are so small as to be missed by some conventional types of sampling or sorting gear.

The most thorough investigation of size in Antarctic benthos has been for amphipods. Chapelle & Peck (1999) examined size spectra for amphipod assemblages from a range of marine regions and showed clearly that while minimum size was effectively invariant, maximum size was inversely related to water temperature. The explanation for the existence of larger taxa in colder water was a combination of absolute oxygen content and the architecture of the vascular system. This explanation was confirmed by examining amphipod assemblages from freshwater lakes (where oxygen solubility is different from sea water) and at high altitude (Chapelle & Peck 1999).

Whereas maximum size in amphipods appears to be determined by a combination of an environmental factor and internal *bauplan*, the constraint on minimum size is less clear. It may be related to constraints on egg size but this is by no means certain (Chapelle & Peck 1999). The minimum size for Antarctic amphipods, however, does suggest that there may be many undescribed small taxa waiting to be discovered (De Broyer & Jazdzewski 1996).

The importance of *bauplan* (specifically vascular system architecture) in determining maximum body size in amphipods suggests that the environmental factors setting size constraints will vary between groups of organisms. It has been suggested that an important factor in determining the size and shell morphology of molluscs is the cost of calcification (Graus 1974), and this might explain the generally small size of polar molluscs (Nicol 1964, Clarke 1983). Some Antarctic molluscs do achieve a large size, however, and although in some cases this is achieved through a poorly calcified or very thin shell, this is not universal. It is quite possible that the absence of crushing predators (notably crabs, lobsters and fishes specialising in molluscs) may also be an important factor. If water temperature does play a role in determining body size and/or skeletal construction through its effect on calcification costs, then this influence should be apparent in echinoderms, brachiopods and solitary corals. To date these groups have not been examined in this context.

A second feature of importance in describing patterns in animal communities is the distribution of individuals amongst species. Typically species/abundance plots will exhibit a log-normal distribution, and the conventional graphical representation is that proposed by Preston (1962). Construction of Preston plots requires careful attention to sampling techniques: the sampling must be quantitative to ensure all individuals are taken, cover the entire size range, and be sufficiently thorough to ensure that most of the rare species are sampled. Two Antarctic samples where these criteria have been fulfilled, at least approximately, are shown in Figure 17. These two plots derive from very different types of sample. The gastropod data were obtained by pooling a series of repeated monthly samples obtained by suction sampling of standard sized quadrants (0.25 m^2) in an area of shallow water (2–12 m-depth) with a mixed substratum (Picken 1980). These data therefore represent a fully quantitative sample for all animals above about 2 mm in size. The amphipod data are from a semi-quantitative study which covered a range of different habitats using a variety of sampling techniques. The full collection was then analysed by Thurston (1972). The Preston plot for the gastropod data (Fig. 17a) shows a roughly normal shape, whereas that for amphipods (Fig. 17b) suggests the influence of sampling error (no data in octaves 3 to 5, and three species represented by two or fewer individuals).

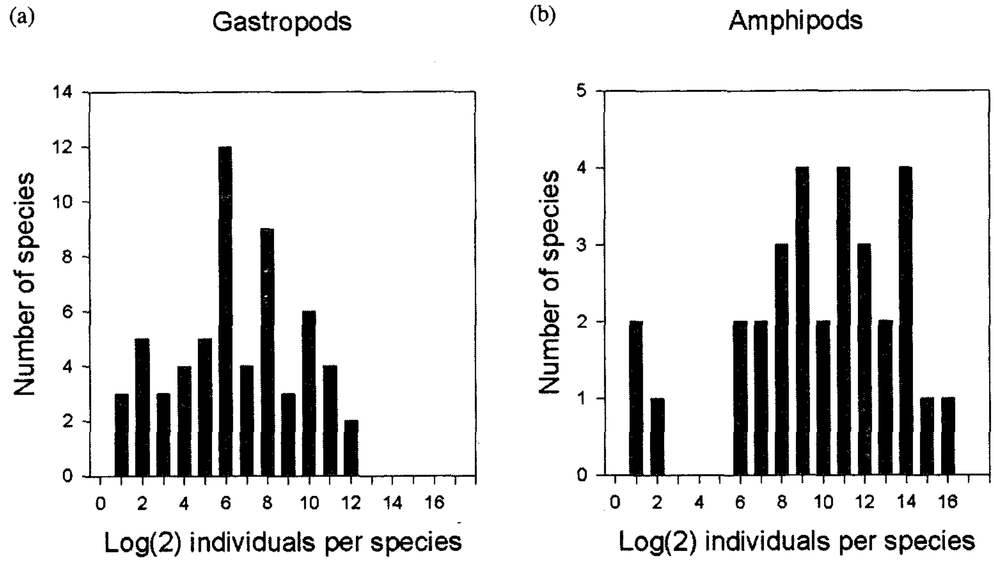

Figure 17 Preston plots for two groups of Southern Ocean benthos. Note that the abscissa is in the conventional units of log2(n) where n is the number of individuals per species. (a) Gastropod molluscs from Signy Island (Picken, 1980). (b) Amphipod crustaceans from Signy Island (Thurston 1972).

Ecologists have long debated the significance of the shape of Preston species/abundance plots. A typical plot of logarithmically transformed data where a large number of individuals have been sampled often looks as though it would be well described by a normal distribution truncated to the left. This truncation (the so-called veil line) is inevitable because those species which are so rare that the expected number of individuals in the sample being plotted is less than one, would be unlikely to be recorded (Pielou 1969). The position of the veil line would be expected to move to the left as sample size increases (Magurran 1988).

The underlying process (or processes) leading to the frequently (but by no means universally) observed log-normal distribution of species' abundances has remained elusive. Although some theoretical models have proved successful under some circumstances, no single model has been found to provide a general description of species/abundance data. In fact the log-normal distribution would be expected as a result of a large number of interacting influences, and hence its general applicability as a descriptor may simply be telling us that the abundance of species in the wild is dictated by many factors and not a single process.

Figure 17 shows the only species/abundance data for Antarctic marine benthos known to the authors where a quantitative collection has been accompanied by a thorough taxonomic study. These data indicate that although many species are small, species/abundance distributions are not discernibly different from those found in marine habitats elsewhere (Magurran 1988, Gaston 1994, Gray 1997).

Concluding remarks

The benthic fauna of the Southern Ocean continental shelves is now reasonably well known. Although detailed knowledge probably lags behind that of the fauna of the North Atlantic, the Caribbean or parts of the Indo–West Pacific, it is by no means as poor as might be envisaged from the isolation of the Antarctic continent.

The long period of evolutionary history *in situ* around Gondwana has resulted in a generally diverse fauna, though some taxa are absent or poorly represented. Notable amongst the latter are decapod crustaceans and teleost fishes apart from the notothenioids. Neither bivalve nor gastropod molluscs are diverse in the Southern Ocean when compared with many tropical regions, whereas, in contrast, amphipod and isopod crustaceans, pycnogonids and many suspension feeding taxa, especially bryozoans, sponges and ascidians, are well represented. In all cases it is only some lineages which have diversified, indicating that evolutionary questions concerning the origin, diversification or extinction of the Southern Ocean marine fauna will have no single answer. The evolutionary history of each group appears to reflect a different response to the tectonic, climatic and oceanographic changes to which they have been subject through history.

Endemism is high, mainly because of the large area of the Antarctic continental shelf, and the oceanographic isolation of the fauna. Although most of the Southern Ocean is deep water, the fauna of the continental slope and the abyssal plain of Antarctica are known only poorly. It is only in recent years that the spectacular radiation of liparid fishes on the continental slope of Antarctica has become recognised, largely through the work of biologists of the former Soviet Union. There is much we have still to learn of the marine fauna of this unique and important area.

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Addendum

Recently, Julian Gutt and colleagues (pers. comm., manuscript under review) have used data from quantitative bottom samples taken in the Weddell Sea to estimate how many species might exist on the entire continental shelf of Antarctica. A variety of species-accumulation, jack knife and incidence-based average techniques led to estimates in the range 11000 to 17000. Gutt and colleagues propose that the entire Southern Ocean macrobenthic fauna of the continental shelves probably exceeds 17000 taxa.