Zoogeographic and richness patterns in Southern Ocean benthos

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Doctor of Philosophy

By

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ABSTRACT

This thesis describes the large scale biogeographic patterns found in the Southern Ocean benthos. Using SOMBASE and SCAR-MarBIN, the two most comprehensive, georeferenced databases of Antarctic marine biodiversity ever compiled, a range of taxa were investigated but focusing on the Mollusca, Bryozoa and Pycnogonida. Over 8,000 species of marine invertebrates from over 5,000 sites constituting ~34,000 records were used in the analyses.

The strong faunal links between the Antarctic and South America were confirmed but I found little evidence for a biogeographical relationship between the Antarctic or South America and New Zealand or Tasmania. Regional levels of Southern Ocean endemism proved the influence of the Antarctic Circumpolar Current upon the distribution of Southern Ocean benthos. My study shows the Southern Ocean as a ‘single functional unit’ with no evidence for an earlier proposed biogeographical split between East and West Antarctica. Some general rules on Antarctic benthic biogeography are viable, including species endemism rates of around 50% and a definite distinction between the sub-Antarctic islands influenced by either South America or by New Zealand.

In the context of potential shifts in species distribution with climate change I investigated the current ranges of selected Southern Ocean taxa (Mollusca, Amphipoda, Ophiuroidea and Hexacorala), and looked for hotspots of coinciding northern and southern geographic range limits. Southern Patagonia, South Georgia and Kerguelen had the greatest range-limit hotspots. Monitoring range shifts in these key places and taxa will enable us to track the influence and effects of climate change on benthic species distributions in the Southern Ocean.

ACKNOWLEDGEMENTS

It was whilst bobbing about in the JCR somewhere on the Scotia Sea in 2006 that Dave Barnes offered to supervise me for a PhD, all I had to do was find a second supervisor. I was lucky enough to find two willing volunteers in the shape of Katrin Linse and Lloyd Peck. Three supervisors meant that at least one of them would be in the same country as me at any one time!

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Finally, thanks to my family and friends who have put up with me jetting off all over the world and especially to Steve for his patience.

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GENERAL INTRODUCTION

Biogeography

Biogeography is a branch of science which encompasses a wide range of other scientific disciplines. Biogeographers can be ecologists, palaeontologists, taxonomists, evolutionary biologists and more recently phylogeneticists (Ebach & Humphries, 2003). Augustin Pyramus de Candolle (1820) divided biogeography into two parts; historical and ecological. In his review of plant biogeography, de Candolle defined historical biogeography as the "country where the plant is native" and refers to the geographical and geological explanations of the distribution of organisms. Ecological biogeography was seen as the "special nature of the locality in which each species customarily grows" and included the climate and terrain of the study area.

The history of biogeography since de Candolle has been one of defining regions and explaining distribution patterns (Ebach & Humphries, 2003). During the early twentieth century many biogeographers searched for the centres of origin for taxa taking their lead from the evolutionary works of Charles Darwin and Alfred Russell Wallace (Nelson, 1978). The main works on dispersal biogeography Willis (1922), Cain (1944), Wulff (1950), Matthew (1915), and Darlington (1957) culminated in the work by MacArthur & Wilson (1967) on island biogeography. Most of these early works concentrated on the biogeography of plants and terrestrial animals.

Early marine biogeographic works included those of Ekman (1953), Forbes (1856) and Hedgpeth (1957). Later works by Briggs (1974), Hayden et al. (1984), Bailey

(1998) and Longhurst (1998 were based upon biological classifications with the exception of Longhurst (1998) which was entirely pelagic and based upon physical oceanography. The widely adopted scheme of Briggs (1974) defined coastal and shelf regions based upon a >10% degree of endemism.

The development of the theories of plate tectonics in the mid twentieth century altered the way in which biogeographers worked. The theories of dispersal biogeography were pushed aside in favour of one of a dynamic Earth (Croizat, 1964). This theory that life and Earth evolved together sees continental drift and other geological processes as the main drivers of biogeography. Although dispersal biogeography has largely fallen out of fashion it does still have a place in helping to understand the effects of climate change and other factors which happen on a far shorter timescale than plate tectonics (Wilkinson, 2001).

Assessing biodiversity and biogeography

Many early studies of biogeography were done using hand drawn range maps or species lists for large geographic areas. In recent years relational databases have started to displace faunal lists in biogeographical and diversity studies (Budd et al., 2001; Rosenberg 1993; Hill et al., 2000; Zhang et al., 2000). The advantages of relational biogeographic databases over simple faunal lists are many: including the ability to examine the data at a range of scales, ability to investigate abundance and to include ecological and environmental information (Grassle & Stocks, 1999). When such relational databases are connected to a Geographic Information System (GIS) the full potential of the underlying data can be explored. A GIS based approach enables biogeographers to investigate quantitatively large-scale biogeographic patterns and to link them to physical and historic factors (Markwick, 2002; Markwick & Lupia, 2002).

The advances in internet based technology have enabled online databasing and mapping of biodiversity (Bisby, 2000), including global initiatives such as the Global Biodiversity Information Facility (GBIF) (www.gbif.org) (Edwards, 2004) and the Ocean Biogeographic Information System (OBIS) (www.iobis.org) (Grassle & Stocks, 1999; Zhang & Grassle, 2002). These global databases are themselves formed from individual data contributions and a network of regional nodes e.g. for the Antarctic the regional node of OBIS is the Scientific Committee on Antarctic Research - Marine Biodiversity Information Network (SCAR-MarBIN). The Southern Ocean Mollusc Database (SOMBASE) (Griffiths et al., 2003), which forms the basis of much of the work, in this thesis is a major contributor to SCAR-MarBIN and all of the data used are freely available through the web-portal.

Global biogeographic patterns

Wallace (1876) stated “nothing like a perfect zoological division of the Earth is possible. The causes that have led to the present distribution of animal life are so varied, their action and reaction have been so complex, that anomalies and irregularities are sure to exist which will mar the symmetry of any rigid system”. However with our increased understanding of plate tectonics and phylogenetics coupled with vast biogeographic databases it is possible to comment on the origins of global scale patterns and trends.

One of the great paradigms of global biogeography is that of the East Indies/Indo-West Pacific diversity hotspot (Briggs, 1999). The Indo West Pacific has been a centre of evolutionary radiation and species diversity decreases with distance from the region in every direction (Bellwood and Hughes, 2001; Bellwood and Wainwright, 2002; Connolly et al., 2003). Many authors have discussed latitudinal gradients in species richness (Rohde, 1992; Gaston, 2000) but cannot, in isolation, explain global biodiversity patterns.

The Southern Ocean

The biogeography of the Southern Ocean has been the subject of several major works over the last century. Even the earliest work by Ekman (1935, 1953), Powell (1951, 1955 and 1960), Hedgpeth (1969) and Dell (1972) identified the fauna of the region as highly independent from its neighbours. All of these authors cited a lack of continuous circumpolar data as a potential source of error within their proposed biogeographic schemes. Nevertheless, Hedgpeth's (1969) regions in particular have been widely adopted over the last four decades in comparative studies of the distribution patterns of Antarctic benthos, but usually without including the doubts of the original author about the validity of the observed differences between East and West Antarctica. Following these initial biogeographic studies a second wave of research emerged after a period of intensified sampling in the Weddell and Ross Seas in the 1980s, e.g. Voss (1988), Brandt (1991), De Broyer & Jazdewski (1996), Linse (2002).

This work aims to re-examine the large-scale biogeographic patterns in the Southern Ocean by using SOMBASE and SCAR-MarBIN, the two most comprehensive, georeferenced databases of Antarctic biodiversity ever compiled.

CHAPTER 1 - ANTARCTIC MARINE BIODIVERSITY – WHAT DO WE KNOW ABOUT THE DISTRIBUTION OF LIFE IN THE SOUTHERN OCEAN?

[The data in this chapter are also presented in: Griffiths, H.J. (in press) Antarctic Marine Biodiversity – What do we know about the distribution of life in the Southern Ocean? PLoSOne.]

Chapter 1 - ANTARCTIC MARINE BIODIVERSITY – WHAT DO WE KNOW ABOUT THE DISTRIBUTION OF LIFE IN THE SOUTHERN OCEAN?

Introduction to the region

For the purposes of this study, the definition of the Antarctic region is the same as that used by the Census of Antarctic Marine Life (CAML) (www.caml.aq) and the Scientific Committee on Antarctic Research Marine Biodiversity Information Network (SCAR-MarBIN) (www.scarmarbin.be). The CAML/SCAR-MarBIN "area of interest" is the Southern Ocean in its widest sense, as used by oceanographers (Deacon, 1984; Tréguer & Jacques, 1992; Longhurst, 1998; Rintoul 2007). The priority, however, is the Antarctic region (Southern Ocean or "Antarctic Ocean"), that is, the water masses extending south of the Polar Front (formerly known as the Antarctic Convergence) to the coasts of the Antarctic continent (Figure 1.1). The total area of the Antarctic region is ~34.8 million km^2. The sub-Antarctic region, here defined as the expanses of water extending from the Polar Front in the south to the Subtropical Front in the north (Figure 1.1), will be covered by SCAR-MarBIN in a second step of research spanning beyond 2010.

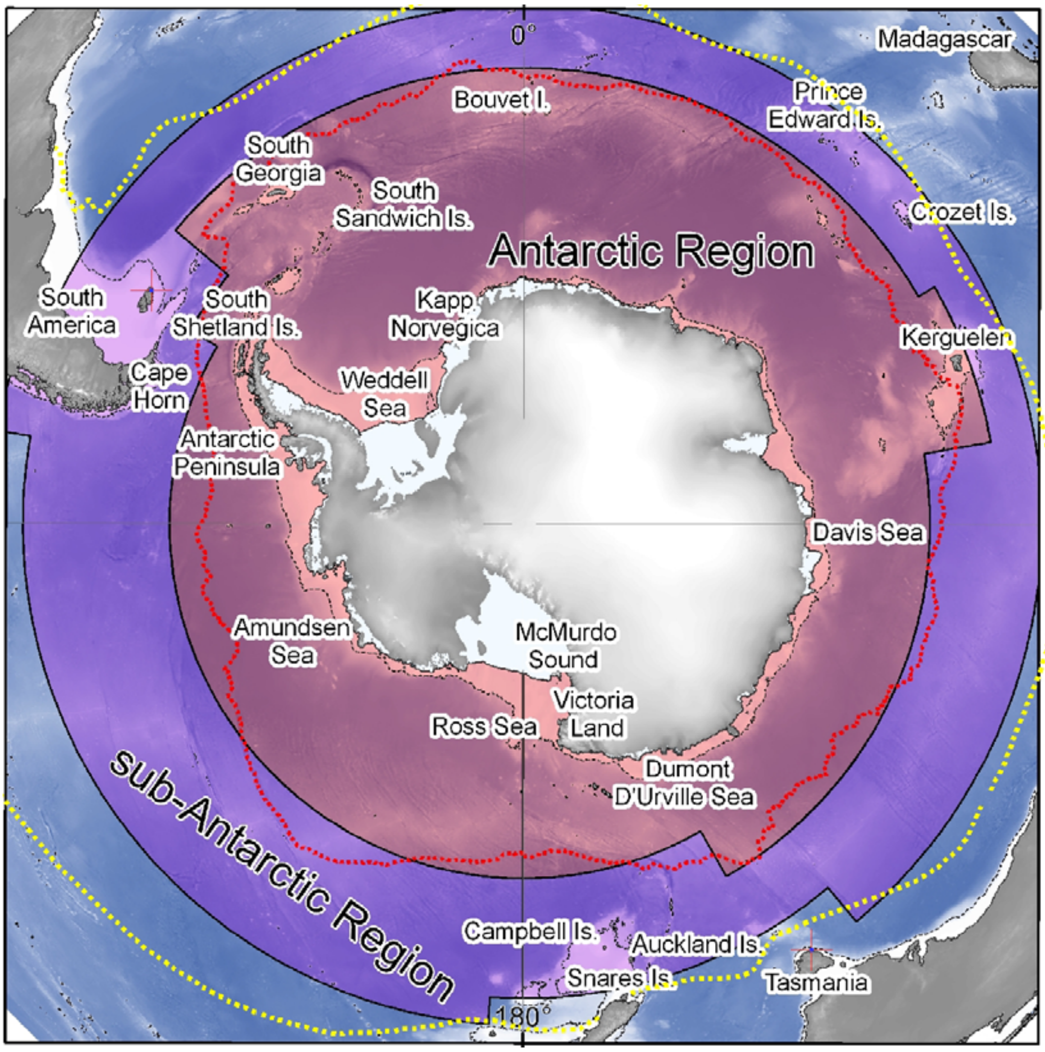

Figure 1.1. The SCAR-MarBIN/CAML areas of interest. Red dashed line = mean position of the Polar Front, yellow dashed line = mean position of the Subtropical Front.

The Southern Ocean has a vital role in the global ocean circulation system, as it interacts with the deep water circulation in each of the Pacific, Atlantic, and Indian oceans. The fastest ocean current in the world, the Antarctic Circumpolar Current, continuously circles the continent, driven by strong westerly winds that are unimpeded by land. Closer to the continent, easterly winds form a series of clockwise gyres (most notably in the Ross and Weddell seas) that form the westward-flowing

Antarctic Coastal Current (Deacon, 1984; Tréguer & Jacques, 1992; Longhurst, 1998; Rintoul 2007).

The majority of Antarctic Circumpolar Current water is transported by jets in the Sub-Antarctic Front and the Polar Front. The Polar Front marks the northern extent of very cold fresh (low salinity, <34), Antarctic surface water (Orsi et al., 1995). North of the Polar Front, the moderately fresh, cool sub-Antarctic surface waters are separated from the more saline subtropical waters by the Subtropical Front, marking the northernmost extent of the Antarctic Circumpolar Current (Orsi et al., 1995).

The extreme seasonality of Antarctica is most obvious in light levels, weather, and temperature, but best illustrated by the formation and extent of sea ice. The area covered by sea ice increases from around 3-4 x 106 km^2 in the summer to 18-20 x 106 km^2 in winter, essentially doubling the continental surface area of Antarctica each winter (Gloersen et al., 1992). At its maximum extent, the sea ice reaches far beyond the continental shelf and covers large areas of deep ocean. The most productive regions of the Southern Ocean are generally found within this sea ice zone. Extremely cold (katabatic) winds blowing off the Antarctic Ice Sheet, push water and sea ice offshore, contributing to high rates of sea ice formation. This sea ice formation creates cold, dense, salty water that sinks to the seafloor and forms very dense Antarctic bottom water. This in turn pushes the global ocean's nutrient-rich, deep water closer to the surface, helping to create areas of high primary productivity in Antarctic waters, similar to areas of upwelling elsewhere in the world.

The Southern Ocean is predominantly made up of three deep ocean basins (Pacific, Indian, and Atlantic basins) separated by submarine ridges and the island chain of the Scotia arc. The majority of the seafloor around the continent is composed of siliceous ooze formed over thousands of years from dead phytoplankton deposits. More than 75% of all oceanic silica accumulates on the seafloor between the Polar Front and the Antarctic continental shelf. The continental slope is predominantly made up of glacial sediments.

The continental shelf is unusually deep in Antarctica (an average of 450 m, and in places over 1,000 m deep) (Clarke & Johnston, 2003). The shelf sediments are a combination of glacial deposits and diatomaceous muds. As well as being deeper than other continental shelves, some unique features of the Antarctic Shelf are the glacially excavated over-deepened inner basins. These basins can be over 1,500 m deep and give the shelf in some areas the unusual profile of being deeper near to the continent and shallower toward the shelf break. This is amplified by the weight of the ice cap compressing the land, a process known as isostatic loading. Antarctica has some narrow shelf areas, but is characterized by glacial embayments that support floating ice shelves, the largest of which are the Ross and Weddell seas and to a lesser extent the Amundsen and Bellingshausen seas (Clarke & Johnston, 2003). Despite having large regions with narrow shelves, the average width of the shelf off Antarctica is almost twice that of shelves elsewhere in the world (~125km), mainly due to these wide shelf seas. This large, deep shelf constitutes about 11.4% of the world’s continental shelf area.

The waters south of the Polar Front have a distinct chemical signature (Orsi & Whitworth, 2004). The upper and surface waters have low salinity (less than 34.0), except in the Weddell and Ross seas, where sea ice formation removes freshwater, increasing the overall salt content. At the seafloor the Antarctic bottom water is highly saline, as it is also created during sea ice formation. In general oxygen levels are significantly higher than most other regions of the world (>320 µmol/kg at 50 m depth) (Orsi & Whitworth, 2004).

Nutrients such as nitrates (>16 µmol/kg at 50 m depth) and phosphates (>1.55 µmol/kg at 50 m depth) are found in high concentrations, as is silicate (>10 µmol/kg at 50 m depth). Nutrient levels are often highest in areas close to the continent and in the Weddell Sea, where silicate values can exceed 60 µmol/kg (Orsi & Whitworth, 2004). In general, the Southern Ocean is considered high in nutrients but low in chlorophyll. One of the most important factors controlling primary production in the Southern Ocean is iron. Iron availability is limited and phytoplankton blooms occur near natural sources of mineral iron, such as islands (Korb et al., 2004).

The carbonate compensation depth (CCD) is the depth in the oceans below which the rate of supply of calcium carbonate (in the form of calcite and aragonite) is exceeded by the rate of dissolution, such that no calcium carbonate is preserved. Globally the CCD sits between 4,500 m and 5,000 m, while in the Southern Ocean the CCD is multibathyal and shallower than elsewhere. For example, in the Eastern Pacific region (Bellingshausen and Amundsen seas) there is a relatively shallow CCD (~300 m) on the inner shelf (possibly due to high local primary productivity) and a far deeper CCD on the outer slope and rise (~2,100 - ~2,800 m) (Hillenbrand et al., 2003).

Sea surface temperatures in the Southern Ocean have been well studied using both traditional and satellite-based methods (Orsi et al., 1995). The different temperature regimes of the upper waters are separated by marked gradients across various fronts (Orsi et al., 1995). There is a change of around 4-5 °C across the Subtropical Front from subtropical waters of >11.5 °C to sub-Antarctic waters of 5-7.5 °C (Orsi & Whitworth, 2004). Across the Polar Front there is a sharp temperature gradient of 1-2 °C (Moore et al., 1999), with temperatures south of the Polar Front increasing from < -1.5 °C close to the continent to ~4 °C south of the front.

Benthic temperatures are largely very cold (<1 °C) with a few exceptions, such as shallow areas in the summer, around South Georgia, and on the Kerguelen Plateau (Clarke et al., 2009). Around the continent marked spatial variations in shelf seabed temperature have been recorded. The mean annual temperature of the Western Antarctic Peninsula at around 1-2 °C is significantly warmer than shelves around East Antarctica or the Weddell Sea, <0 °C. The cold waters of the shelf and deep of the Weddell Sea and East Antarctica are made up of Antarctic bottom water, whereas the warmer waters of Western Antarctic Peninsula are explained by incursions of circumpolar deep water onto the shelf. There is also distinct latitudinal variation in the difference between bottom temperatures on the shelf, slope, and deep sea, of which the deep sea is warmer by up to ~2 °C at high latitudes and colder by ~2 °C around sub-Antarctic islands.

The unusually deep shelf and large areas of deep ocean basins mean that more than 90% of the Antarctic region is deeper than 1,000 m (Figure 1.2). Within this expanse of deep water there are a large number of small shallow features, including seamounts, archipelagos, and isolated islands (Figure 1.3). The depth of habitats on the shelf can have a profound effect on the level of disturbance from anchor ice (0-30 m) and icebergs; regions below 500 m tend to be less disturbed (Smale et al., 2008).

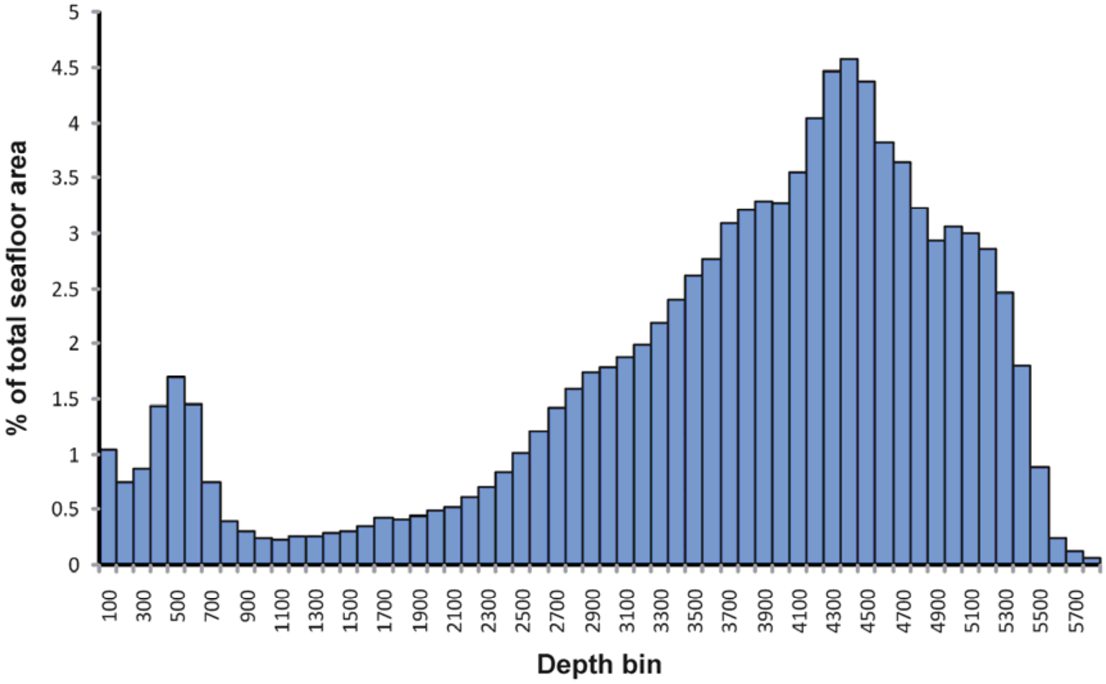

Figure 1.2. Percentage of Antarctic seafloor area found within 100-m interval depth bins.

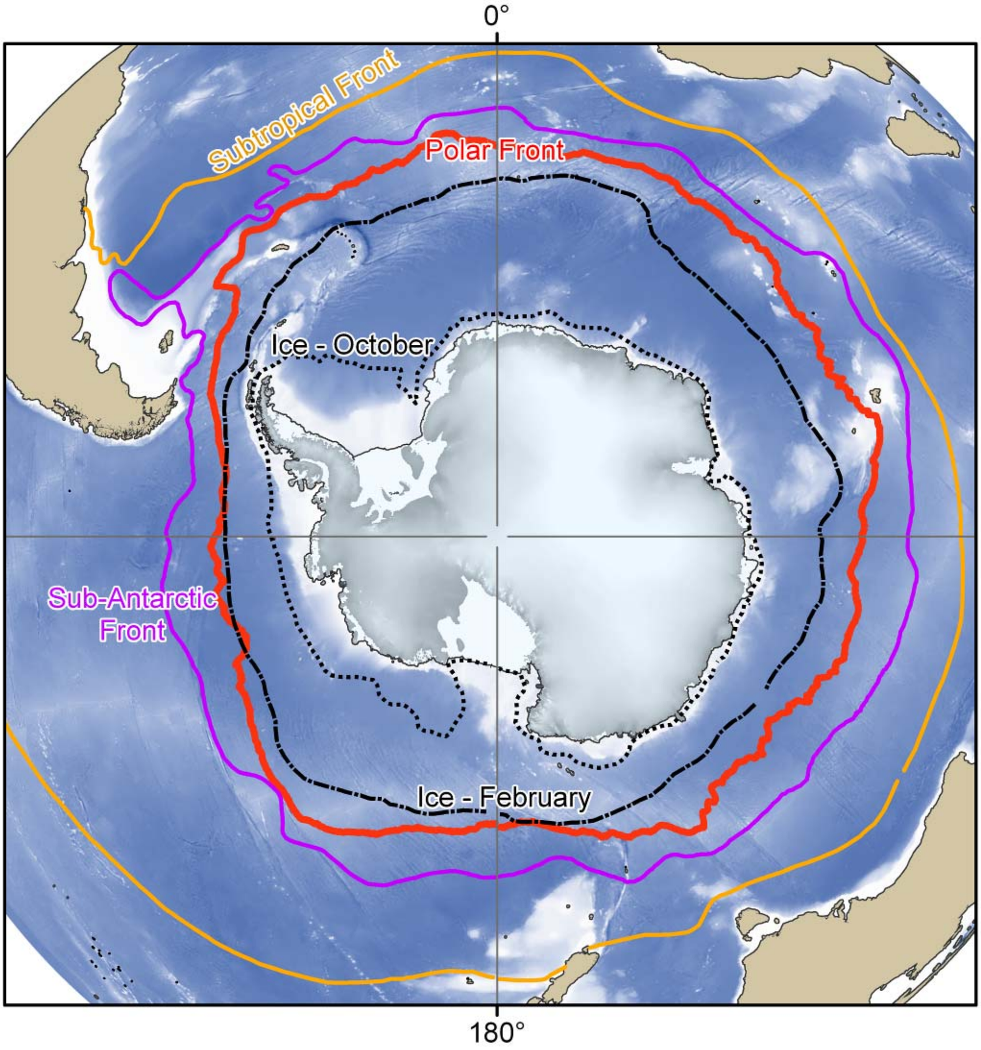

Figure 1.3. Major oceanographic features of the Southern Ocean. Mean positions of the major oceanographic fronts and summer and winter ice extents for the Southern Ocean (Orsi & Whitworth, 2004; Moore et al., 1999). Bathymetry: Shallow = light blue, Deep = dark blue. Orange = Subtropical Front; purple = sub-Antarctic Front; red = Polar Front; thick dashed line = ice extent in February; thin dashed line = ice extent in October.

Biological structure of the Southern Ocean

The dominant flow of energy through the Southern Ocean is production at the surface by phytoplankton, followed by sinking and breakdown in the benthic microbial loop. Several food webs available for the Antarctic marine ecosystem focus on animal consumers of phytoplankton in the water column (Hempel, 1985). They offer a relatively simple model of phytoplanktonic primary production and zooplankton primary consumers, followed by a series of predators, including fish, whales, and seabirds and benthic detritivores. Although food webs such as this provide a useful simplified model of the flow of energy through the system, they tend to ignore the complicated relationships within some of these categories and often disregard the important and complex role of microbial communities in nutrient cycling (El-Sayed, 1988). The benthos are the richest element of the food web in terms of numbers of macrospecies, but their roles and interactions are poorly known and thought to be dominated by suspension feeders in the shallows and deposit feeders in deeper waters.

Both benthic and pelagic communities tend to show a high degree of patchiness in both diversity and abundance. The benthic communities show, as in most oceans, a decrease in biomass from shallow to deep water (Arntz et al., 1994), with notable differences in areas of disturbance due to anchor ice and icebergs in the shallows (Smale et al., 2008). Hard and soft sediments from the region are known to be capable of supporting both extremes of diversity and biomass, in some cases levels of biomass far higher than those in equivalent habitat in temperate or tropical regions. Little evidence exists for strong latitudinal diversity gradients in the benthos of the Southern Ocean.

Early studies of biodiversity in the region found, contrary to previous expectations, a rich and varied fauna. This level of richness does not extend to all taxa, with some groups radiating extensively and others relatively underrepresented or completely absent. The taxa that have high species richness include bryozoans, sponges, and amphipods (Arntz et al., 1994). The gastropod and bivalve molluscs and isopods show lower species richness in the Southern Ocean than in equivalent areas of shelf elsewhere, and some groups of fish and decapod crustaceans are completely absent, despite being known from the Antarctic fossil record until the Eocene (Clarke, 1990).

The types of ecosystem found in the Antarctic region depend on a complex combination of factors and are not easily defined. The range of ecosystems found in each of the marine realms (benthic and pelagic) can vary greatly within a small geographic area, or in other cases remain relatively constant across vast areas of ocean. The interaction of different physical and biological factors can be found in a wide range of combinations, leading to a complex tapestry of different ecosystems, the distribution and extent of which are poorly understood. These physical factors include sea ice, substratum, light, iceberg scour, oceanographic fronts, depth, temperature, isolation, geomorphology, seasonality, and currents. Biological factors include primary production, biological substrata, dispersal ability, and community type. The region also contains many completely unsampled areas for which nothing is known (Figure 1.4); these areas include the majority of the intertidal zone, areas under the floating ice shelves, and the greater benthic part of the deep sea.

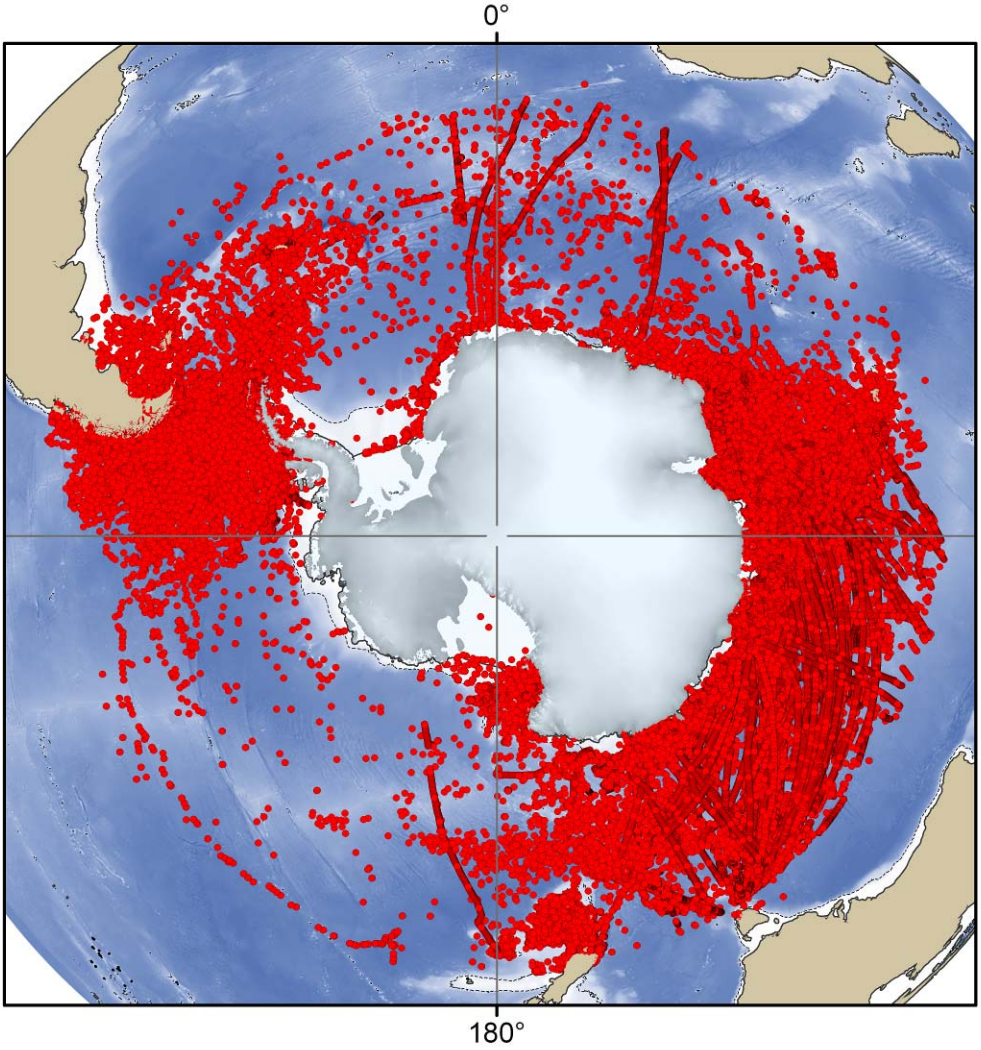

Figure 1.4. The distribution of the more than 1 million SCAR-MarBIN sample locations in the Southern Ocean.

Research and species discovery in Antarctica

The economic exploitation of Antarctica's marine resources dates back to the eighteenth century (Hempel, 2007). However, scientific research into the marine ecosystem only began in the mid-nineteenth century. Expeditions such as Challenger, Belgica, and the Discovery (Figure 1.5) were among the first to catalogue the benthos and plankton and became the foundation of modern taxonomy in the region. Recent advances in technology, such as scuba diving, underwater video footage, ice-capable research vessels, and remotely operated vehicles, have increased the rate of new species discovery (Figure 1.5). Molecular genetic techniques are revealing many established species to be, rather, groups of morphologically similar, but genetically distinct, cryptic species (Grant & Linse, 2009). The age of marine biological exploration in Antarctica continues, as dedicated cruises sample its remotest and deepest areas for the first time under the auspices of the recent International Polar Year (IPY) in 2007-08 and CAML.

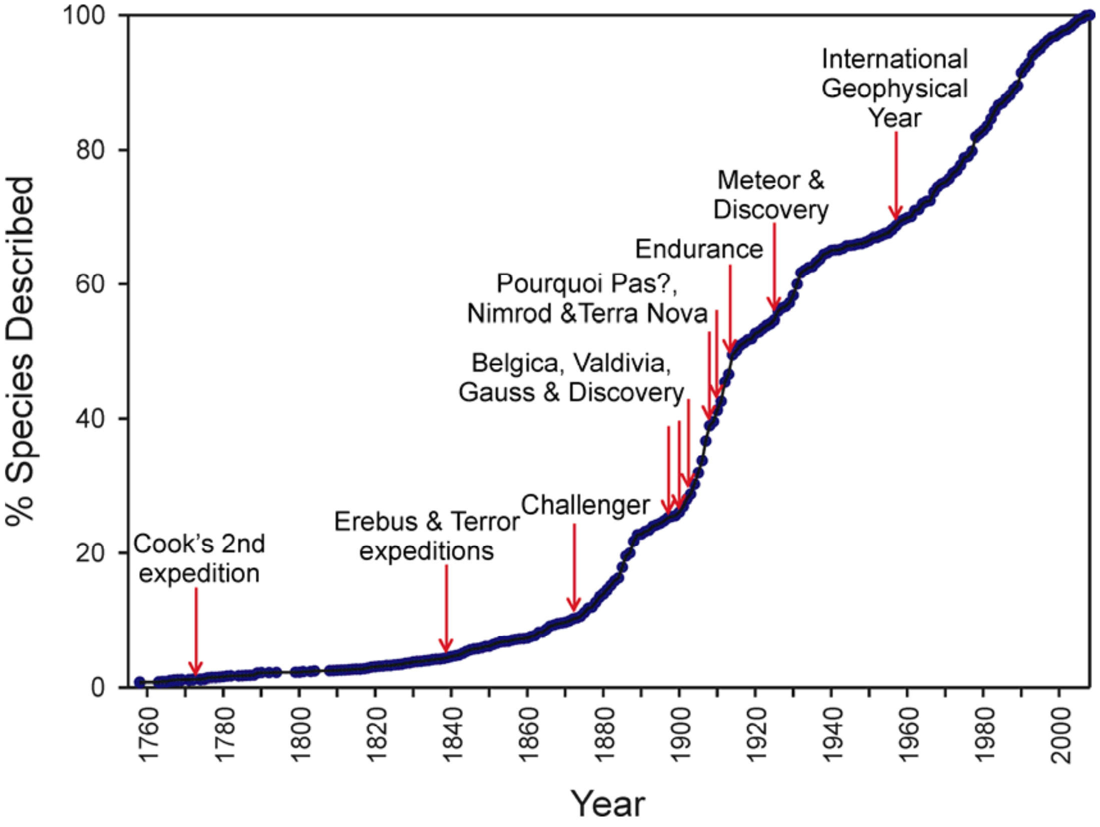

Figure 1.5. The rate of species description and main scientific expeditions conducting biological research in the Southern Ocean through time. The history of Antarctic

marine biological research (red arrows) plotted with the increase of new species descriptions for the region over time.

The recent IPY and CAML cruises (2007-2009) comprised an estimated 34 nationalities, 18 vessels, and 321 scientists. Besides work done at sea, a considerable amount of research is conducted at the various international bases. There are 64 bases in the Antarctic, of which 27 are seasonal and 37 are open year-round. The earliest of these bases opened in 1904: Orcadas Base is one of six permanent research stations established by Argentina in Antarctica and managed through the Council of Managers of National Antarctic Programs (www.comnap.aq).

Sources of data for analysis

All taxa occurring south of the Polar Front will be included in the Register of Antarctic Marine Species (RAMS) (www.scarmarbin.be), as well as having georeferenced records in SCAR-MarBIN (De Broyer & Danis, 2010). This work is in progress and relies on the data provided by scientific community and taxonomic editors. SCAR-MarBIN establishes and supports a distributed system of interoperable databases, forming the Antarctic Regional Node of OBIS (Ocean Biogeographic Information System), under the aegis of SCAR. There are currently over 1 million distribution records, representing over 5,200 species (validated by taxonomic experts), in SCAR-MarBIN (Figure 1.4). This forms the largest repository of Antarctic marine georeferenced biodiversity information compiled to date. This database is made up of over 100 contributing databases which cover a range of taxa and sample collection methods. These data are based upon published and unpublished records dating back as far as the early scientific expeditions of the nineteenth century, through to the latest results from the CAML/IPY expeditions.

The objective of RAMS is to compile and manage an authoritative taxonomic list of species occurring in the Antarctic marine environment and to establish a standard reference for marine biodiversity research, conservation, and sustainable management. The taxonomic scope of RAMS covers Antarctic species from the three realms of the Southern Ocean: the seafloor (meio-, macro- and megazoobenthos; micro- and macrophytobenthos), the water column (phytoplankton, zooplankton, nekton), and the sea ice. The register currently lists over 8,800 species from more than 1,300 families of Antarctic marine organisms (Table 1.1).

Table 1.1. Taxonomic expertise within the Antarctic study area and estimated numbers of described species per taxon[1]. State of Knowledge 5 = very well-known (>80% described, ID guides <20 years old, and current taxonomic expertise); 4 = well-known (>70% described, ID guides <50 years old, some taxonomic expertise), 3 = poorly known (< 50% species described, ID guides old or incomplete, no present expertise within region), 2= very poorly known (only few species recorded, no ID guides, no expertise), 1 = unknown (no species recorded, no ID guides, no expertise)..

Taxonomic group	**No. Species**[a]	**State of knowledge**	**No. experts**
Domain Archaea	0	1	1
Domain Bacteria (including Cyanobacteria)	0	1	2
Domain Eukarya			
Kingdom Chromista	256	1	1
Phaeophyta	0	1	
Kingdom Plantae			
Chlorophyta	24	4	1
Rhodophyta	70	4	1
Angiospermae	0	5	
Kingdom Protoctista (Protozoa)			
Dinomastigota (Dinoflagellata)	75	3	1
Foraminifera	179	5	2
Kingdom Animalia			
Porifera	267	4	1
Cnidaria	459	3	2
Platyhelminthes	125	5	1
Mollusca	740	3	6
Annelida	536	4	3
Crustacea	2,900	4	15
Bryozoa	316	3	1
Echinodermata	565	5	6
Urochordata (Tunicata)	114	2	1
Other invertebrates	586	3	
Vertebrata (Pisces)	314	4	6
Other vertebrates	284	3	6
SUB-TOTAL	7,810		
TOTAL REGIONAL DIVERSITY[b]	>8,200		

[a]From the Register of Antarctic Marine Species. [b]Total regional diversity including all taxonomic groups as reported in the Register of Antarctic Marine Species.

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[1] Numbers correct for time of accessing the database and can differ from other numbers used in later tables where data was accessed at different times.

Only records of validated species were used in analyses. The validated species names from RAMS were used to remove synonymies from the georeferenced data. The data includes records collected from trawling, scuba diving, tagging and video transects. The wide range of methods used in sampling makes anything more than broad scale comparisons across the entire dataset difficult.

Sampling intensity

Sampling intensity varies considerably with geographic location. Key elements in the distribution of sampling intensity are the locations of the various national bases. First, much of the sampling, tagging, and observing of animals is done either from, or in the immediate vicinity of, the bases. Second, due to the high cost both in resources such as fuel and in scientist's time spent at sea, much of the more open water sampling has been done along the transit routes of the vessels that regularly visit these bases from neighboring continents.

Historically, South American and European nations have concentrated their efforts around the West Antarctic and the Scotia and Weddell seas, whereas Australia, New Zealand, and Asian nations have worked mainly in East Antarctica. Russia and the United States operate in both areas. The remote Amundsen Sea has no neighboring continent, making it the least accessible region due to the vast distances involved (Figure 1.4). Other poorly sampled areas include the Western Weddell Sea and the Eastern Ross Sea, which are hostile to marine sampling methods because of sea ice cover and vast numbers of icebergs.

The logistical efforts and time-consuming nature of sampling the deep sea mean that the vast majority of benthic samples come from depths of less than 500 m (Figure 1.6). The distribution of benthic samples with depth thus contrasts sharply with the depth distribution of the seafloor (Figure 1.2), most of which is far deeper than 500 m.

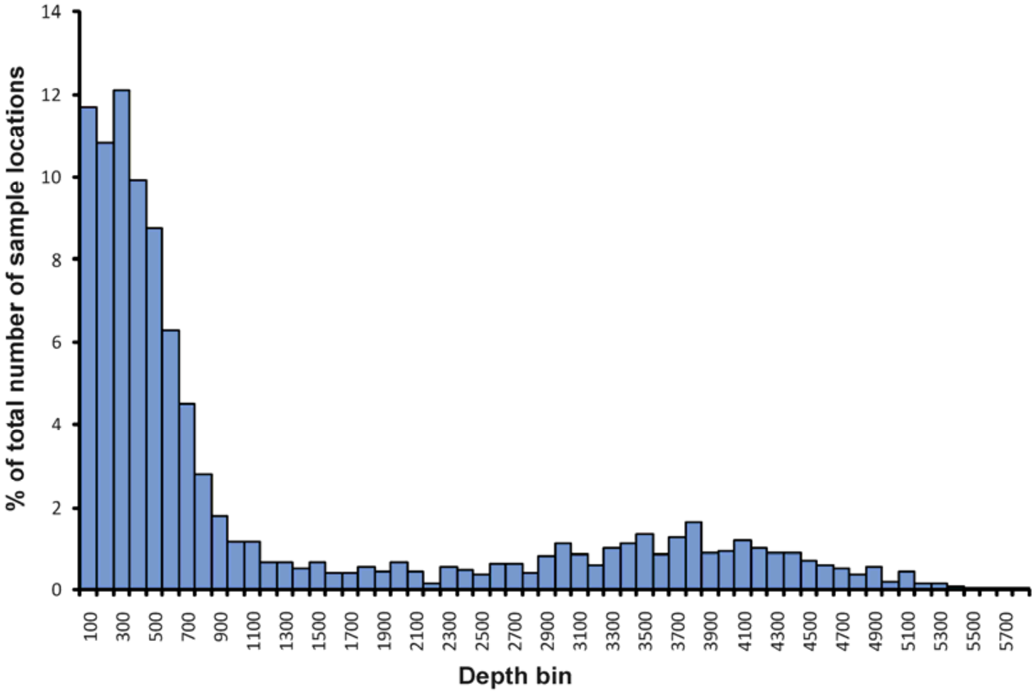


Figure 1.6. Depth distributions of Southern Ocean benthic samples. The percentage of benthic sample depths from SCAR-MarBIN found at 100-m interval depth bins.

Which taxa have been adequately sampled and which have not?

It is difficult to say whether any particular taxa in the Southern Ocean have been adequately sampled and databased in SCAR-MarBIN, but it is clear that some are considerably better studied than others. For some taxa, such as the chordates, a large number of samples have been taken of a limited number of large, charismatic megafaunal species, such as penguins, seals, and albatrosses, while fish and ascidians are underrepresented. For the arthropods, an extremely speciose group, the majority of records come from the Southern Ocean Continuous Plankton Recorder (Hosie et al., 2003). However, planktonic arthropods represent only a minority of the total species numbers in this group, the vast majority of which are benthic. Of the groups that are mainly benthic, molluscs and echinoderms are best represented. Both have relatively high numbers of georeferenced records representing, respectively, ~93% and ~79% of known species (Table 1.2). Previous works have examined the extent of our knowledge of benthic groups (Clarke et al., 2007a) and the biogeographic patterns in their distributions e.g. molluscs (Linse et al., 2006), amphipods (De Broyer & Jazdzewski, 1993), ascidians (Primo & Vázquez, 2007), or a combination of taxa 9~ (Hedgpeth, 1969; Griffiths et al., 2008).

Table 1.2. The numbers of various taxa represented in the Register of Antarctic Marine Species and SCAR-MarBIN.

Taxon	Number of valid species	Number in MarBIN	Percentage with location	Number of stations
Annelida	487	45	9.24	445
Arthropoda	2,309	1,014	43.92	132,585
Brachiopoda	68	10	14.71	17
Chaetognatha	5	4	80.00	1,588
Chordata	718	395	55.01	359,968
Cnidaria	372	65	17.47	1,112
Echinodermata	550	434	78.91	5,314
Mollusca	684	633	92.54	13,121
Nematoda	1,909	301	15.77	702
Nemertina	77	74	96.10	2
Porifera	268	12	4.48	39

Groups that are clearly underrepresented in existing databases include the species-rich nematodes, of which only ~700 records represent a taxon with more than 1,900 known species from the region. Important and abundant habitat-forming organisms, such as the sponges, are also largely missing from SCAR-MarBIN, limiting our ability to comment on the distribution of these diverse habitats and communities. It may be that several of these groups, for which we have limited or no data, have been adequately sampled but that these records have not been combined into a digital database.

The state of knowledge and number of validated species vary widely among taxa (Table 1.1). Some phyla, such as molluscs and crustaceans, are historically well known and have a relatively large community of taxonomic experts. Others, such as nematodes and marine tardigrades, are known to be little studied and are probably vastly underrepresented. Since 1993, numbers of known marine species from the region have more than doubled from over 4,000 (Clarke & Johnston, 2003) to over 8,200, thanks to an international team of taxonomic editors working on the RAMS database.

The Antarctic is known for having a high level of endemic species (Arntz et al., 1994). Our understanding of how isolated the Antarctic really is has changed recently with our increased understanding of its relationship to the sub-Antarctic and the deep sea. Although previous estimates of over 80% endemic species for many benthic groups have been reduced by recent studies (Griffiths et al., 2009), rates of around 50% or more within a class are common (Bryozoa: Cyclostoma 47%, Cheilostoma 56%; Mollusca: Cephalopoda 54%, Bivalvia 43%, Gastropoda 74%, Pycnogona 55%, Ascidiacea 44%). These numbers may rise again in future as the use of molecular techniques identifies cryptic species in the region.

The huge area covered by the Antarctic and the previous lack of good baseline knowledge have made it difficult to assess the true human impact on the region. As with other regions, most species in the Southern Ocean are rare, with over half of the known benthic species having only been found once or twice (Clarke et al., 2007a). Because the status and numbers of the majority of marine species in the region are unknown, it is impossible to comment on how many of them are threatened or endangered. It is known that at least 4 species of cetacean and 18 species of birds found in the Southern Ocean are currently classified as threatened or endangered on the International Union for the Conservation of Nature Red List. There have been no recorded extinctions in the Antarctic since research began, but considering that many species are known from a single specimen or scientific cruise, our ability to comment is greatly restricted (Clarke et al., 2007a). Recent efforts by CAML, IPY, and SCAR-MarBIN aim to produce a robust baseline of knowledge against which future change in the region can be measured.

The distribution of known species richness tends to be a reflection of sampling effort (Figure 1.7) (Clarke et al., 2007a). Regions with fewer than 100 species per 3° by 3° grid square tend to be either those with few sample points (Figure 1.4) or those well sampled but only for the relatively species-poor plankton, birds, and mammals. The areas with the highest numbers of species are those in which the benthos is well sampled, such as areas around the South Shetland Islands. The regions with the longest history of scientific exploration and manned bases, such as the islands of the Scotia Sea, the West Antarctic Peninsula, the Eastern Weddell Sea, the Ross Sea, and Prydz Bay, show the highest levels of benthic sampling and the highest numbers of species.

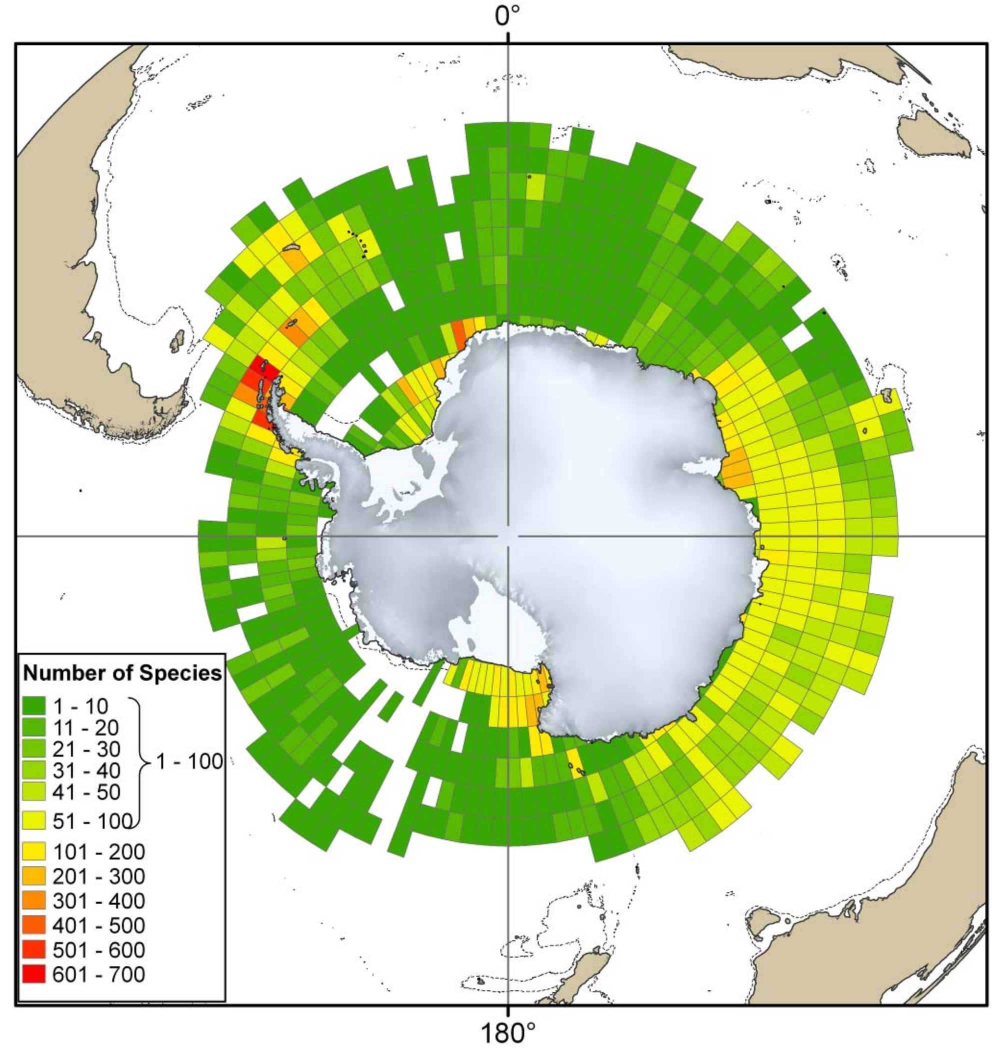


Figure 1.7. Counts of recorded species within the Southern Ocean. The total numbers of all marine species from distribution records in SCAR-MarBIN found within each 3° of latitude by 3° of longitude grid square.

Known and Unknown

There are currently 8,806 described species listed in the Register of Antarctic Marine Species. Gutt et al. (2004) predicted that, on the shelf alone, there could be as many as 17,000 species, implying that there are still a great many species yet to be described. While many of these new records will come from undersurveyed regions of Antarctica, many other new species may in fact come from areas that have already been investigated. Modern molecular techniques have found cryptic species and species complexes in almost every Antarctic group that has been studied, including bivalves, isopods, and pycnogonids, but interestingly not in the truly circumpolar krill (Grant & Linse, 2009).

Major geographic unknowns include the Amundsen Sea, the Western Weddell Sea, and the continental shelves underneath floating ice shelves, which because of ice conditions and inaccessibility are poorly sampled. The recent BAS/CAML cruise, BIOPEARL II, became the first to sample the benthos of the Amundsen Sea shelf in March 2008, including the overdeepened shelf basins of Pine Island Bay. Preliminary assessments showed high phylum richness, including up to 13 phyla present in a single Agassiz trawl and up to 19 phyla in an epibenthic sledge sample. These results are comparable with those shown for the well studied (Griffiths et al., 2008). The taxa identified to date show high biodiversity and a large number of previously undescribed species (Kaiser et al., 2009).

With over 90% of the region being greater than 1,000 m deep, but only 30% of benthic sample locations found from below this depth, it is clear that sampling is biased toward shallower areas. The relatively few investigations of the Antarctic deep sea have shown the presence of different habitats, including hydrothermal vents, seeps, and mud volcanoes. Other than the ANDEEP (Antarctic benthic deep-sea biodiversity) cruises, little work has been done in the deep sea (Brandt et al., 2004; Brandt et al., 2007). This series of cruises is largely limited to the Scotia and Weddell Seas, and the full geographic extent of the sample locations covers less than 11% of the total area of deep sea. The ANDEEP cruises reported 585 previously undescribed species of isopod crustaceans, potentially adding another 20% to the number of known arthropods from the region. Even with our restricted data on the deep, it is clear that there are far more species waiting to be described.

At the opposite bathymetric extreme is the intertidal zone. Until recently this region of Antarctica was considered to be virtually devoid of life. Work (Waller et al., 2006) has shown that, even with few sample locations on the Antarctic Peninsula and islands of the Scotia arc, the intertidal zone is host to a diverse and rich community of organisms that can survive the huge variations in environmental conditions.

Major threats to biodiversity

The major industry in Antarctic waters is fishing, and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is the main regulatory body for Southern Ocean fisheries. The Commission was set up as part of the Convention on the Conservation of Antarctic Marine Living Resources in 1982 (part of the Antarctic Treaty System). It was established because of concerns that any increase in krill catches could have a serious effect, not only on krill stocks, but also on a whole food web that is dependent on krill. The primary aim of the commission is conservation, but not at the exclusion of rationally conducted harvesting.

There are four main target species: krill (*Euphausia superba*), Antarctic toothfish (*Dissostichus mawsoni*), Patagonian toothfish (*D. eleginoides*), and the mackerel icefish (*Champsocephalus gunnari*) (Figure 1.8). Hundreds of thousands of tonnes are landed each year, with a total value of about US$25 million. Despite krill being the biggest catch, the toothfish have the highest economic value.

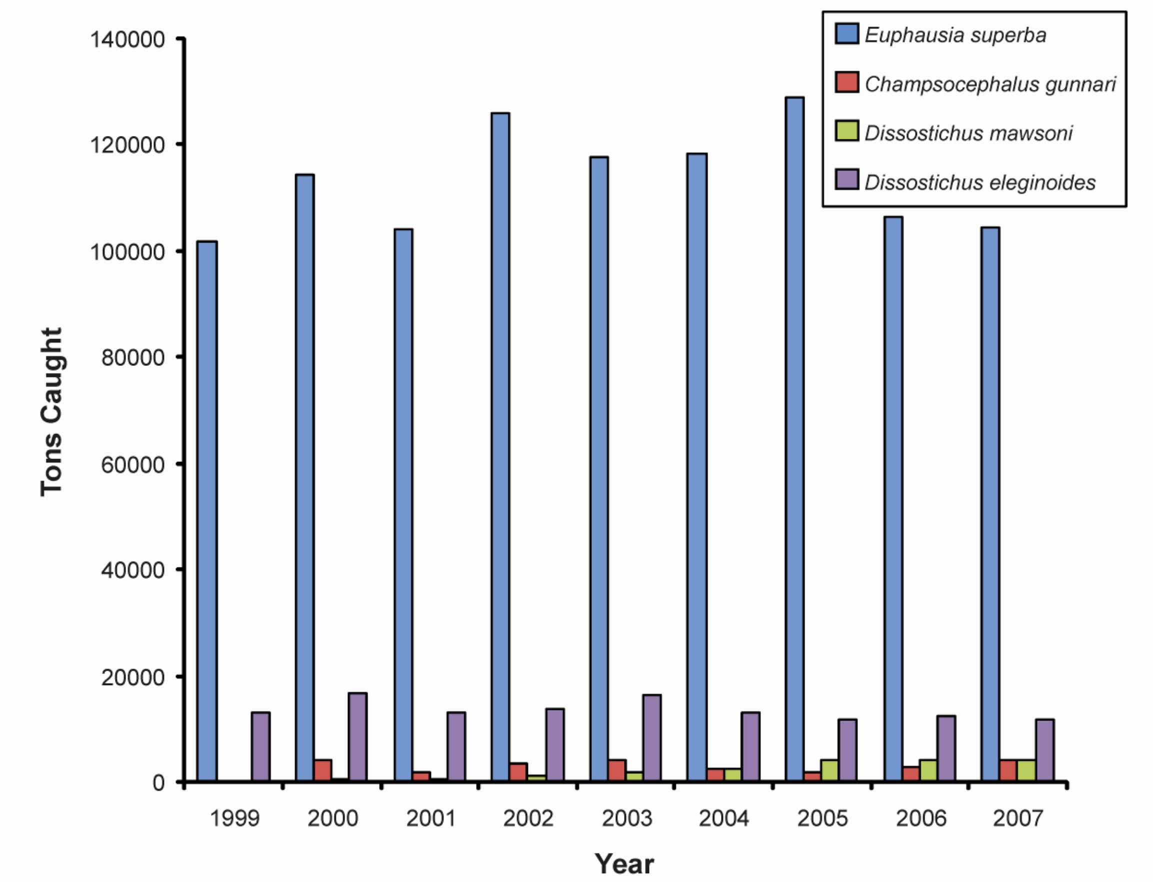


Figure 1.8. Southern Ocean fisheries catch data. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) catch statistics (in tonnes) for the major commercially caught species in the Southern Ocean from 1999 to 2007 (www.ccamlr.org).

Overexploitation of living resources, such as krill, fish, and their associated bycatch, is a major threat to the pelagic ecosystem (Trathan & Reid, 2009). Benthic trawling in the South Georgia region was banned because of overfishing in the 1980s, but longline fishing still continues. There is currently only one small benthic commercial toothfish fishery off Heard Island. Although commercial fishing in Antarctica is heavily legislated, one of the biggest problems faced by fishery managers CCAMLR is illegal, unlicensed vessels. Historically the region has been overexploited for certain target groups, most notably whales and seals. Commercial sealing ended in the 1950s and all but scientific whaling ending in the mid-1980s. The International Whaling Commission (iwcoffice.org) established its Southern Ocean Whale Sanctuary, in which commercial whaling is prohibited, in 1994.

There are currently no records of successfully established invasive marine animal species within the Southern Ocean. There have been several reports of either adults or larvae of alien animals at Antarctic coastal localities (e.g., South Georgia and King George Island), but none were found again or in more than one stage of their life cycle (Thatje & Fuentes, 2003; Tavares & De Melo, 2004). It is thought that the only evidence of successfully established marine invaders is benthic macroalgae found off the South Shetland Islands and the northern Antarctic Peninsula (Clayton et al., 1997). The rate of discovery of new species at deep shelf, slope, and abyssal depths is high, such that even recognizing whether species are native or alien may prove challenging.

Tourism in Antarctica is a growing and lucrative industry, much of which is based on the wildlife of the region, and recent visitor numbers have increased year on year from less than 7,000 per year in 1992 to around 35,000 in 2007. Antarctic tourism is regulated by the International Association of Antarctic Tour Operators, a voluntary organization made up of private-sector tour operators. Although tourist levels are increasing, they do not seem to pose a major threat to the region at current levels, other than localized incidents of pollution (Liggett et al., in press).

The impact of scientific research is harder to measure. The Protocol on Environmental Protection was adopted by all Antarctic Treaty nations in January 1998 and includes mandatory regulations for environmental impact assessment, waste disposal, conservation of flora and fauna, preventing marine pollution, protection of special areas, and liability for environmental damage (http://www.antarctica.ac.uk/about_antarctica/geopolitical/treaty/update_1991.php). Marine pollution does occur in the Antarctic, mostly as a result of localized oil and sewage spills, but also with global pollutants from outside the Southern Ocean (Bargagli, 2005).

Climate change is a significant potential threat to the long-term survival of Antarctic marine communities. The vulnerability of Antarctic marine species to the many facets of climate change is hard to gauge and much debated (Clarke et al., 2007b; Barnes & Peck, 2008). The seas to the northeast and the west of the Antarctic Peninsula are some of the fastest warming areas on Earth (Meredith & King, 2005; Whitehouse et al., 2009). The marine environment is also changing rapidly. The collapse of several floating ice shelves has dramatically altered coastal and shelf habitat on the Peninsula. Sea ice formation in the Amundsen and Bellingshausen seas has decreased by 10% per decade and has also shortened in seasonal length (Stammerjohn et al., 2008). Because the frequency of ice scour on the shelf seabed is closely linked to sea ice duration, the catastrophic disturbance of shallow biodiversity is likely to significantly increase (Smale et al., 2008). There has been an overall warming of surface waters (in the Bellingshausen and Scotia seas) by ~1 °C in the last 50 years, but so far there is no evidence of any biologically meaningful temperature change in waters below about 100 m deep.

The surface waters of the Southern Ocean are saturated with calcium carbonate. The anthropogenic increase in atmospheric carbon dioxide concentration is reducing the pH of the oceans. Experimental evidence suggests that this decreasing pH will reduce the calcium carbonate concentration, compromising the calcification of the skeletons of marine organisms, such as corals and planktonic molluscs (pteropods) (Hall-Spencer et al., 2008). The Southern Ocean is predicted to be the first place where this acidification will reduce aragonite concentrations to below saturation point, by the year 2100 (Orr et al., 2005). As pteropod skeletons are aragonite based, it is unlikely that pteropods will be able to adapt quickly enough to survive in the Southern Ocean.

Under the Antarctic Treaty System, several international agreements are in place to protect Antarctic wildlife and vegetation. Antarctica is protected by the Protocol on Environmental Protection, which came into force in January 1998 (http://www.antarctica.ac.uk/about_antarctica/geopolitical/treaty/update_1991.php). There are currently 67 Antarctic Specially Protected Areas (ASPAs) and 7 Antarctic Specially Managed Areas (ASMAs), of which 6 are dedicated marine ASPAs, while 11 ASPAs and 4 ASMAs contain both marine and terrestrial habitat (Figure 1.9). More recently, CCAMLR adopted a proposal by Australia to declare two areas in the Southern Ocean as Vulnerable Marine Ecosystems (VMEs) and to prohibit fishing in

CCAMLR waters shallower than 550 m to protect benthic habitats. Fishing is currently prohibited in these VMEs until an appropriate management system for these areas is decided upon.

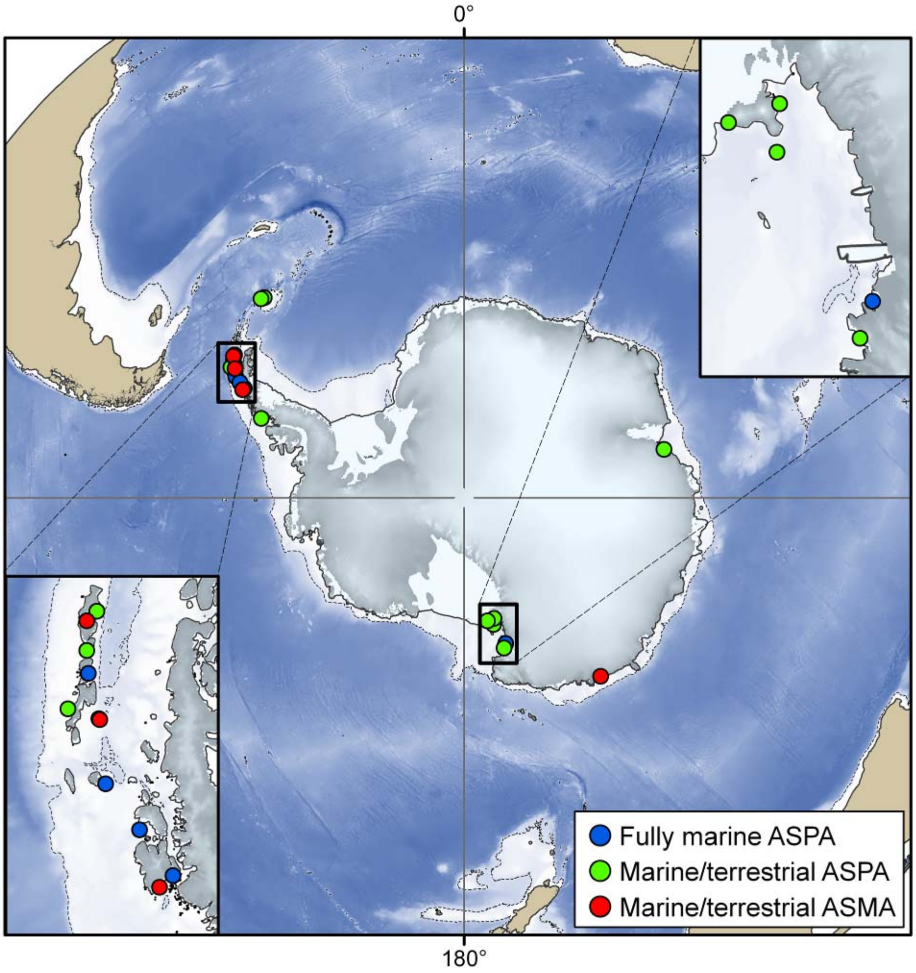


Figure 1.9. Marine conservation areas in the Antarctic. The locations of the marine and partly marine Antarctic Specially Protected Areas (ASPAs) and Antarctic Specially Managed Areas (ASMAs). (Courtesy of Susie Grant of the British Antarctic Survey, using data extracted from the Antarctic Treaty Secretariat Protected Areas Database) (www.ats.aq).

Potential and priorities for future discovery and research in region

The key scientific challenges for research on the Antarctic marine environment are improved estimates of Antarctic marine biodiversity and better understanding of ecology and physiology, as well as the potential faunal response to climate change. Only then can the biological information be used in conjunction with models of predicted change in the region to enable any consequences for biodiversity to be predicted. The completion of the RAMS inventory will be key to establishing a baseline against which future changes can be judged.

Very little is known about the behaviour of Southern Ocean animals during the winter months or those found in the deep sea or under ice shelves. The technological challenges involved with sampling the deep, more remote, or ice-covered regions, as well as obtaining good winter data, require year-round access to field sites with specialist research vessels. The use of autonomous underwater vehicles and remotely operated vehicles is increasing our knowledge of how communities appear in their natural environment, but will need new methods of interpretation and analysis. For the pelagic communities, the use of new acoustic technologies and continuously observing systems placed on moorings will give a new understanding of temporal changes beyond the snapshots available through point-sampling methods.

The proposed Southern Ocean Observing System (Rintoul et al., 2009), with its goal to provide the sustained, multi-disciplinary observations needed to detect, interpret, and respond to changes in the Southern Ocean, aims to include a biological component. This would require the establishment of long-term biological monitoring stations distributed around the Antarctic as well as regularly monitored deep water and pelagic stations or areas. Such long-term efforts will require long-term commitments of funding and international cooperation.

Although molecular techniques, such as DNA barcoding, are commonplace for some taxa and regions of the world, the Antarctic scientific community has only recently embraced such methods on a broad scale (Grant & Linse, 2009). These techniques are revealing more and more cryptic species while increasing our understanding of speciation and gene flow in the region (Grant & Linse, 2009).

The use of Internet-based data portals such as SCAR-MarBIN has enabled the scientific community to build a living resource that will serve as a tool for assessing future impacts on the region. Computer based ecological modeling techniques and habitat suitability predictions based upon the known distributions of animals will enable scientist to infer community compositions and diversity levels for regions that are too remote or costly to sample. Initiatives to digitize all remaining records of marine species from the region, in particularly for ecologically important groups such as the corals and sponges, will allow scientists to advise policy makers regarding conservation planning.

Given the rapid climatic changes affecting the region, the identification of taxa and geographic areas in the Southern Ocean that are likely to be the most affected by climate and oceanographic changes should, therefore, be a major priority to enable the best use of limited funds and resources and to highlight the early signs of any changes.

CHAPTER 2 - DISTRIBUTION OF MACROBENTHIC TAXA ACROSS THE SCOTIA ARC, SOUTHERN OCEAN.

[The data in this chapter are also presented in: Griffiths, H.J., Linse, K., Barnes, D.K.A. (2008) Distribution of macrobenthic taxa across the Scotia arc, Southern Ocean. Antarctic Science, 20: 213-226.]

Chapter 2 - DISTRIBUTION OF MACROBENTHIC TAXA ACROSS THE SCOTIA ARC, SOUTHERN OCEAN.

INTRODUCTION

The Scotia arc is a very geologically and oceanographically dynamic region of archipelagos linking South America and the Antarctic Peninsula. It encompass islands with a wide range of isolation levels, size and age, some of which have been well sampled whilst others are poorly known. It is the only Southern Ocean area with 'staging posts' between any southern continent and Antarctica, reports of marine non-indigenous species (Ralph et al. 1976, Clayton et al. 1997) and is the meeting point of a number of proposed biogeographic provinces (Dell 1972). Some of its islands are rapidly warming (Quayle et al. 2002) and others, the youngest in Antarctica, are currently active volcanoes. Over the last ten million years the Scotia arc has been the most rapidly changing area around the Southern Ocean as it expanded out to create the Scotia Sea, new sea floor and archipelagos (Livermore et al. 2007). Further back in time the Drake Passage opened in this area, about 34 million years ago, leading to the circulation of deep water, the Antarctic Circumpolar Current (ACC) and the subsequent oceanographic isolation of Antarctic marine benthos (Lawver & Gahagan 2003). Thus the Scotia arc now comprises islands as disparate as large ancient continental fragments such as South Georgia with many marine endemics (Barnes & De Grave 2000, Linse et al. 2006) and very small young volcanoes, like Montague Island, which was erupting at the time of the current study.

Although some large areas have been barely sampled at all, the data available suggest that the Southern Ocean is clearly rich in benthos (Clarke & Johnston 2003), especially on the shelf (Brey et al. 1994). Most of Antarctica's richness occurs on its seabed and understanding the nature of this should be considered a scientific priority for a number of reasons. The Southern Ocean seabed has very low anthropogenic impact, high endemism (Arntz et al. 1997), an arguably sensitive fauna (Peck et al. 2004) and is already showing signals of the predicted regional warming (Meredith & King 2005). Past studies on the benthos of the region have generally concentrated on the uppermost shelf (Arntz & Rios 1999, Arntz & Brey 2003, Arntz et al. 2006), especially with respect to disturbance such as ice scour (Barnes & Conlan 2007). Most of these Southern Ocean benthos studies have assessed benthos by broad-scale distribution patterns at high taxonomic levels (e.g. Ramos 1999). More detailed studies have focused on specific sites, such as the South Shetland Islands (Saiz-Salinas et al. 1997, Arnaud et al. 1998, San Martin et al. 2000) or particular taxa (Manjón-Cabeza & Ramos 2003, San Vicente et al. 2007). In the past many datasets have relied on estimating percentages of total catch by eye or by semi-quantitative abundance scales due to large catch sizes and time limitations (e.g. Ramos 1999). In the current study I attempt to semi-quantitatively sample richness at four depths, 200–1500 m at all the major archipelagos of the Scotia arc. In doing so I aim to provide a powerful and novel baseline data set on how rich and abundant benthos is in this dynamic region and how it changes with depth, archipelago, environment and latitude.

METHODS

Study area

Eight study areas were selected within the Scotia arc, in the Southern and South Atlantic oceans (Figure 2.1). Although all of these areas are in the same region, similar latitudes, influenced by the Antarctic Circumpolar Current (ACC) and broadly similar in terms of low temperatures and high salinities, they also differ in many respects. Most importantly the study areas vary in age, geological history, isolation, ice interaction, primary productivity, substrata (e.g. sediment accumulation) and position relative to the Polar Front. Two of the areas are relatively young volcanic calderas, Deception Island and Southern Thule, and both have erupted in recent time. Southern Thule is thought to have experienced possible 20th century eruptions (Baker 1968) and Deception Island last erupted in 1967–70 (Cranmer et al. 2003). Our samples were taken from within the caldera at Deception and outside the caldera, on the slopes of the volcano, at Southern Thule. Most of the study areas are crustal fragments, which have true shelf and slope areas, except for Southern Thule, which is a volcano that rises steeply from the sea floor (Smellie et al. 1998). Those areas closest to the Antarctic Peninsula or under the influence of the Weddell Gyre (South Shetland Islands, South Orkney Islands and South Sandwich Islands) are within the extent of the winter sea ice zone (Simmonds & Jacka 1995) and also tend to experience greater numbers of icebergs and therefore greater iceberg scouring than those further north (Barnes & Conlan 2007).

Sample collection

Sampling of benthos was undertaken using a 2 m wide Agassiz trawl (AGT). This was deployed at one area in the South Atlantic (Falklands Trough - FT) and seven areas in the Southern Ocean (Deception Island - DI, Livingston Island - LI, Elephant Island - EI, Powell Basin/South Orkney Islands - PB, Southern Thule - ST, South Georgia - SG and Shag Rocks - SR) (Figure 2.1, Table 2.1) during the JR144 (BIOPEARL) cruise with RRS James Clark Ross from February–April 2006. Sampling was carried out at four sites/depths over a depth gradient from 200 m to 1500 m at each area (with the exception of just one site within the volcanic caldera of Deception Island at 150 m). CTD readings were taken at each location and depth to acquire temperature and salinity readings.

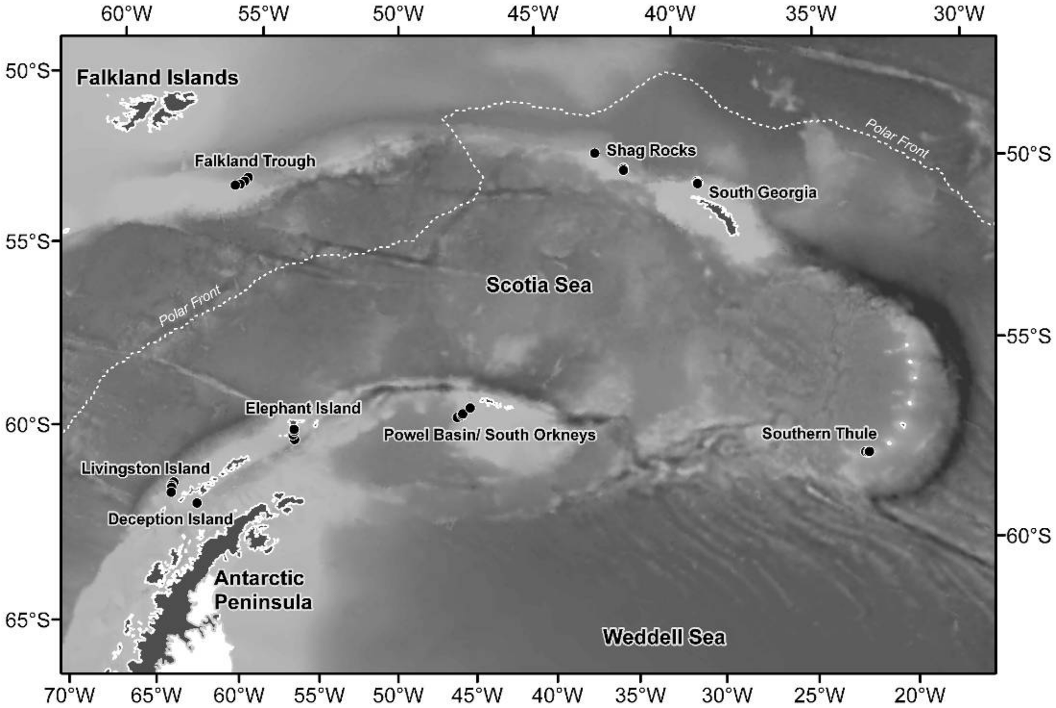


Figure 2.1. The position of the Scotia arc in the Southern Ocean and the study sites where the Agassiz trawl (AGT) was deployed during the cruise JR144 (dark circles)

Table 2.1. Geographic, bathymetric and environmental details of Agassiz trawl (AGT) stations of the Southern Ocean cruise JR144.

Station	Date	Start Lat	End Lat	Start Long	End Long	Depth (m)	Length (m)	Sediment in catch	Temp (°C)	Salinity
DI-AGT-1	6-Mar-2006	62' 56.8542 S	62' 5.6964 S	60' 37.6572 W	60' 38.0028 W	150	388	Clean	-0.38	34.0
LI-AGT-4	4-Mar-2006	62' 31.5006 S	62' 31.503 S	61' 49.6488 W	61' 50.1276 W	200	427	Soft sediment	0.77	34.3
LI-AGT-3	4-Mar-2006	62' 23.7798 S	62' 23.7378 S	61' 45.759 W	61' 46.2858 W	500	507	Soft sediment	0.88	34.6
LI-AGT-2	3-Mar-2006	62' 20.0796 S	62' 19.8912 S	61' 39.2142 W	61' 39.5616 W	1000	665	Soft sediment & pebbles	1.14	34.7
LI-AGT-1	3-Mar-2006	62' 16.5714 S	62' 16.3482 S	61' 3.5754 W	61' 36.1236 W	1500	720	Soft sediment & pebbles	0.77	34.7
EI-AGT-4	11-Mar-2006	61' 20.0322 S	61' 20.0958 S	55' 11.6838 W	55' 12.0492 W	200	526	Some soft sediment	0.62	34.3
EI-AGT-3	11-Mar-2006	61' 23.1564 S	61' 23.2482 S	55' 1.1598 W	55' 11.9982 W	500	606	Some soft sediment	-0.03	34.5
EI-AGT-2	12-Mar-2006	61' 34.5264 S	61' 3.4656 S	55' 15.381 W	55' 16.0884 W	1000	958	Some soft sediment	-0.85	34.5
EI-AGT-1	6-Mar-2006	61' 36.8616 S	61' 36.6756 S	55' 13.2756 W	55' 12.8832 W	1500	546	Some soft sediment	-0.81	34.5
PB-AGT-4	13-Mar-2006	60' 4.9074 S	60' 49.2438 S	46' 29.3832 W	46' 29.1828 W	200	408	Clean	-0.73	34.4
PB-AGT-3	13-Mar-2006	60' 59.6658 S	60' 59.4168 S	46' 49.9086 W	46' 49.9062 W	500	566	Pebbles	0.20	34.6
PB-AGT-2	17-Mar-2006	61' 2.1336 S	61' 1.7634 S	46' 51.9174 W	46' 51.9162 W	1000	760	Few pebbles	0.07	34.6
PB-AGT-1	12-Mar-2006	61' 0.5754 S	61' 0.543 S	47' 5.3082 W	47' 5.1396 W	1500	859	Large drop stones	-0.28	34.6
ST-AGT-4	18-Mar-2006	59' 28.2132 S	59' 28.3128 S	27' 16.6596 W	27' 16.9998 W	200	427	Clean	-0.08	34.5
ST-AGT-3	17-Mar-2006	59' 28.8798 S	59' 28.8798 S	27' 16.7208 W	27' 17.1774 W	500	586	Some pumice	0.28	34.6
ST-AGT-2	18-Mar-2006	59' 30.4554 S	59' 30.363 S	27' 18.2802 W	27' 18.987 W	1000	958	Clean	0.17	34.7
ST-AGT-1	18-Mar-2006	59' 31.071 S	59' 3.1254 S	27' 26.1738 W	27' 27.1614 W	1500	938	Clean	0.06	34.7
SG-AGT-4	24-Mar-2006	53' 36.6666 S	53' 3.6666 S	37' 52.6476 W	37' 5.2968 W	200	408	Pebbles	1.50	34.2
SG-AGT-3	23-Mar-2006	53' 35.847 S	53' 35.8482 S	37' 53.4708 W	37' 53.8878 W	500	566	Clean	2.11	34.5
SG-AGT-2	27-Mar-2006	53' 34.5912 S	53' 34.5918 S	37' 52.0188 W	37' 52.6212 W	1000	879	Coarse gravel	1.69	34.7
SG-AGT-1	24-Mar-2006	53' 33.0642 S	53' 33.0678 S	37' 54.207 W	37' 5.4792 W	1500	899	Clean	1.29	34.7
SR-AGT-4	5-Apr-2006	53' 37.7886 S	53' 37.7016 S	40' 54.1476 W	40' 54.4032 W	200	408	Small pebbles	1.76	34.2
SR-AGT-3	5-Apr-2006	53' 35.1036 S	53' 35.1246 S	40' 55.3674 W	40' 55.2504 W	500	606	Rocks	2.20	34.5
SR-AGT-6	6-Apr-2006	53' 1.5186 S	53' 15.1842 S	42' 8.3934 W	42' 0.8916 W	1000	958	Clean	1.93	34.7
SR-AGT-1	28-Mar-2006	53' 34.0902 S	53' 3.3942 S	40' 54.5214 W	40' 54.9474 W	1500	859	Pebbles	1.52	34.7
FT-AGT-1B	27-Feb-2006	54' 18.8712 S	54' 18.8034 S	56' 40.7508 W	56' 41.0664 W	200	399	Clean	5.36	34.1
FT-AGT-2	28-Feb-2006	54' 18.0744 S	54' 17.9898 S	56' 29.4318 W	56' 29.8224 W	500	542	Few pebbles	4.71	34.1
FT-AGT-3	28-Feb-2006	54' 13.4784 S	54' 13.3128 S	56' 17.361 W	56' 17.6874 W	1000	795	Few pebbles	3.51	34.2
FT-AGT-4B	28-Feb-2006	54' 7.6842 S	54' 7.7178 S	56' 6.7398 W	56' 7.0914 W	1500	723	Clean	2.70	34.5

Stations: DI=Deception Island, LI=Livingston Island, EI=Elephant Island, PB=Powell Basin/South Orkney Islands, ST=Southern Thule, SG=South Georgia, SR=Shag Rocks and FT=Falkland Trough.

At most areas and sites the seabed topography was examined prior to trawl deployment using multibeam sonar (SWATH). The deployment protocol was standardized as described in Allcock et al. (2003). The position of the AGT's arrival on and leaving of the seafloor was recorded using the vessel's cable tension meter. The mesh size of the AGT net was 10 mm and on board the catch was sieved, finishing with 0.5 mm mesh. The mouth of the trawl was 2 m wide. Once on board the entire samples were hand-sorted and identified into taxonomic groups (mainly class level). The systematic assignment to higher taxonomic groups followed Barnes (1998). The wet mass of the different taxa was measured using calibrated scales (0.001 kg). Numbers and wet masses for each taxon were recorded in a digital database, which also contained all information on each trawl. To enable comparisons between trawls all numbers and masses were standardized to per areas of 1000 m^2. The relationship between wet mass and the number of classes per catch and the resulting geographic trends were examined using ANOVA.

Comparisons of community compositions between stations were measured using Bray-Curtis similarities (Bray & Curtis 1957). The relative abundances and wet masses (standardized per 1000 $m^{2)}$ to were used to compensate for the semi-quantitative nature of the AGT data using a 4th root transformation. The class level richness data are compared with data from LAMPOS (Arntz & Brey 2003) and South Georgia groundfish survey 2005 (unpublished report South Georgia Government). Results were displayed using MDS in PRIMER (Clarke & Warwick, 2001).

RESULTS

The benthic communities around the Scotia arc were rich at higher taxonomic levels. The macro- and megafauna comprised a total of 15 phyla and 29 classes from the 29 trawls (Table 2.2). The total number of individual (counting colonies as one individual) animals was 10 483 with a total wet mass of 130.341 kg. The maximum numbers of phyla and classes found in one site/trawl (one depth of one study area) were 12 and 19 respectively.

Table 2.2. Abundances of phyla and classes (standardized per 1000 m^2) by study area and site (depth) around the Scotia arc in the samples of JR144. The area abbreviations are as in Table 2.1.

		DI	LI				EI				PB				ST				SG				SR				FT			
		150m	200m	500m	1000m	1500m	200m	500m	1000m	1500m	200m	500m	1000m	1500m	200m	500m	1000m	1500m	200m	500m	1000m	1500m	200m	500m	1000m	1500m	200m	500m	1000m	1500m
Porifera	Calcarea																						5						2	
	Demospongiae	1		3	4				1		2	1		3		1	1		18	1	1		32	12	2	2	35	32	131	2
	Hexactinellida						38	4				19							1					1			1		1	
Cnidaria	Hydrozoa	1	4	4			1					4		3		2					7		37	1	3	6	91	71	7	
	Anthozoa		1	1	1	5	8	4	40		5	13	7	10	6	2	1		13	1	12		127	3	1	27	98	6	102	
Priapula	Priapulida			1	1											2														
Chelicerata	Pycnogona		68	9	1		2	2	9		4	25	89	2	121	1	6	1	2				11				23	2	4	
Crustacea	Malacostraca	5	25	10	1		239	9	10	2	86	13	19	3	49	2	11	49	232	5	12	3	25	2	3	5	41	7	9	1
	Cirripedia		2						6														1				11			
Mollusca	Polyplacophora						1																							
	Gastropoda	8		3	5		15	7	3		45	7	4		11	1		2		1			12	2	1		79	3	2	
	Bivalvia	113	1				24	4	54	1	42	1			2		2		1				1				11			
	Scaphopoda							4	1		13																			
	Cephalopoda		4				11	2	3		1	4		1	2		1		5				1						1	
Sipuncula	Sipunculida			5	3			3					2				1													
Echiura	Echiurida				1				1				1								1									
Annelida	Polychaeta	124	55	55	420	3	16	27	14	2	88	2	9	47	32	8	3	1	15	1	199	2	232	7	2	55	694	2	1	
Nemertea	Anopla	4														2														
	Nemertea		1	7			3								4		1										5			
Brachiopoda	Inarticulata													1												2				
	Articulata								1			1											11	1			1			1
Bryozoa	Gymnolaemata			1			10	1	1	1	21	9		83	12		1		6		40		588	1	1	48	147	6	28	
	Stenolaemata													26							5		98			19	15			
Echinodermata	Crinoidea			1	1						11		2		7	2	1						5	2			25	1	4	
	Stelleroidea	323	22	16	5	4	634	34	14	1	21	108	18	13	36	28	9	28	69				227	21			772	5	6	
	Echinoidea	21		1	1		67	1	2		55	11	5	2			2		51	158			82	2			99			
	Holothuroidea					1	11	2	25		1	11	26	3	6	1	36	33	1				1	1			31		2	
Chordata	Ascidiacea	103	15	1			41		1		1			1	93	23	1		82	28			11		2		203	1	3	

The abundance of macro- and megafauna varied by more than two orders of magnitude, sometimes even within classes and within study areas (Table 2.2). Just a single individual represented many taxa at some or many sites. The occurrence of taxa could be broadly categorized into a few basic patterns. Some were well represented across areas and depths in either high (e.g. malacostracans) or low (e.g. anthozoans) numbers. A second category of classes was well represented at certain depths (e.g. Stelleroidea at the 200 m sites of DI, EI, PB, SR and FT), though not so in certain areas (at the 200 m sites of LI, SG and ST). The stenolaemate bryozoans (cyclostomes) showed a third type of occurrence, in being found at only few sites but were often abundant where they occurred (200 m site at SR). Fourthly, there were classes, such as the calcarean sponges or polyplacophoran molluscs, which were rare by site and depth and never abundant. Finally some taxa were very patchy or showed no obvious pattern (e.g. bivalves). I also found two single occurrences of Chaetognatha (not listed in Table 2.2) at 1000 m at Southern Thule and at 1500 m at Elephant Island.

The total abundance and wet mass of zoobenthos per 1000 m^2 (Figure 2.2a & b) varied considerably between regions and between depths. The Falkland Trough region had the largest combined total for all four trawls (2825 ind. 1000 m^{-2}) whilst the lowest overall abundance was at Southern Thule (637 ind. 1000 m^{-2}). However, variability in abundance was more obvious with bathymetry. The shallow shelf (160–200 m) trawls showed the highest values (except for Livingston Island) and the most variability ranging from 379 at ST to 2383 at FT (ind 1000 m^{-2}) (Figure 2.2a). For the majority of regions (but see Southern Thule and Shag Rocks) the deepest trawls, 1500 m, yielded the least abundance. At deep shelf/shallow slope depths (500 m and 1000 m) there was greater similarity in values and no distinct pattern or depth gradient.

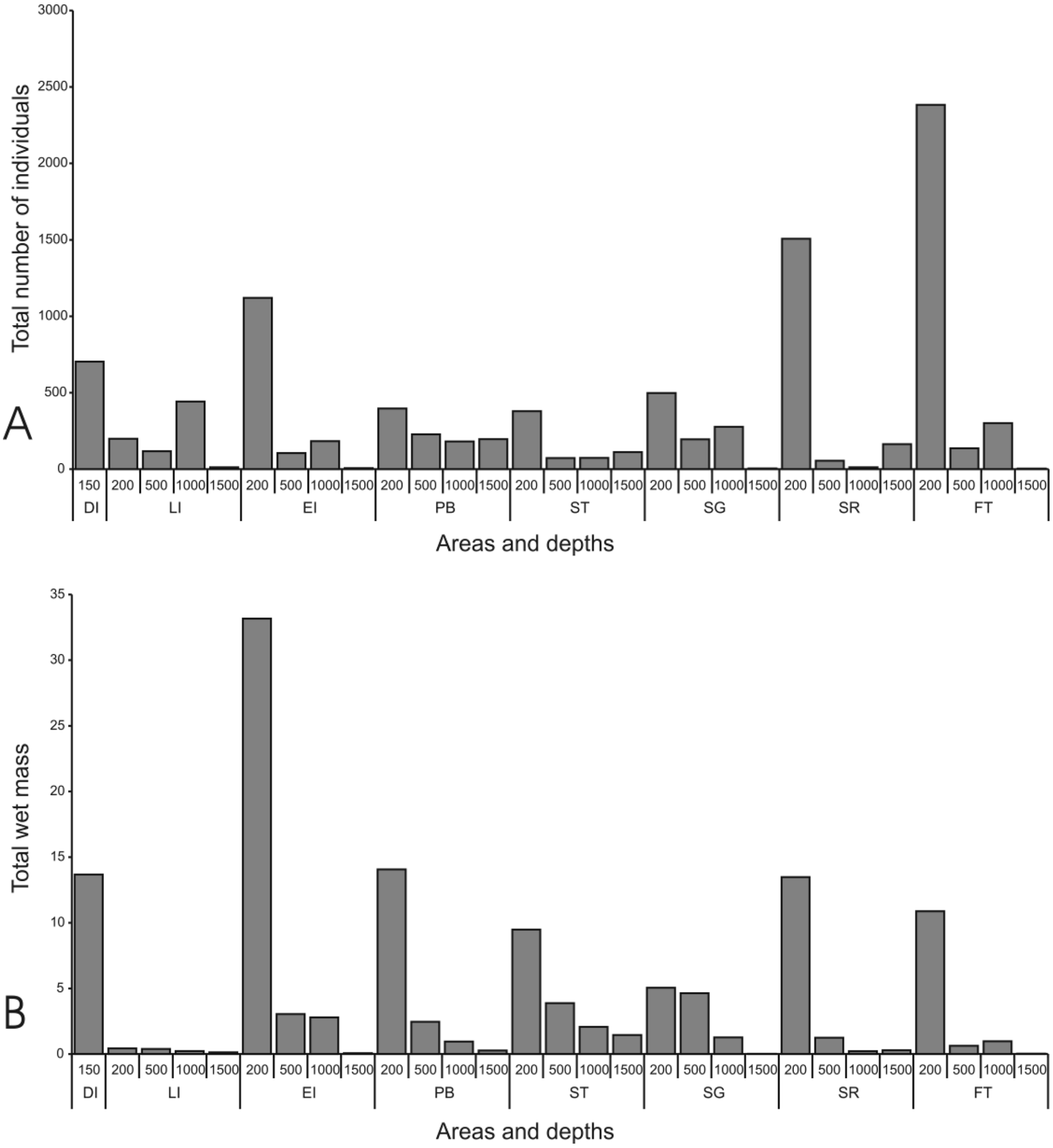


Figure 2.2. Abundance and wet mass of zoobenthos with sites and depth. a. Abundance of pooled zoobenthos standardized to per 1000 m^2 trawl area. b. Total wet mass (kg) of zoobenthos standardized to per 1000 m^2 trawl area. The area abbreviations are as in Table 2.1.

The wet mass of animals, standardized to 1000 m^2 trawls, recorded from each trawl also varied between geographical areas and with depth (Figure 2.2b). The highest total regional mass was found at Elephant Island (39.07 kg) and the lowest at Livingston Island (1.19 kg). As with the numbers of individuals, the shallowest stations had the greatest mass of macro- and megabenthos. Amongst the study areas only Livingston Island did not show considerably higher mass at its 200 m station. Generally wet mass decreased with increasing depth. Notably the site/depth trawls that contained the highest abundance were not the same as those with the highest wet mass (Figure 2.2).

The relative abundances of each phylum (Figure 2.3a) showed great variation both between regions and depths. Some trawls were dominated by representatives of a single phylum e.g. the Livingston Island 1000 m sample comprised over 95% annelid worms. Shallow water sites were less dominated by any single phylum and tended to have a wider range of taxa that were also more evenly spread. The deeper water sites were dominated by fewer, typically two to four, different phyla. Some phyla were consistently present, usually as a large proportion of most trawls e.g. Annelida, Mollusca, Echinodermata and Crustacea. Other phyla tend to show a patchy distribution of dominance despite being found in many trawls e.g. Bryozoa, Chelicerata, Cnidaria, Chordata and Porifera.

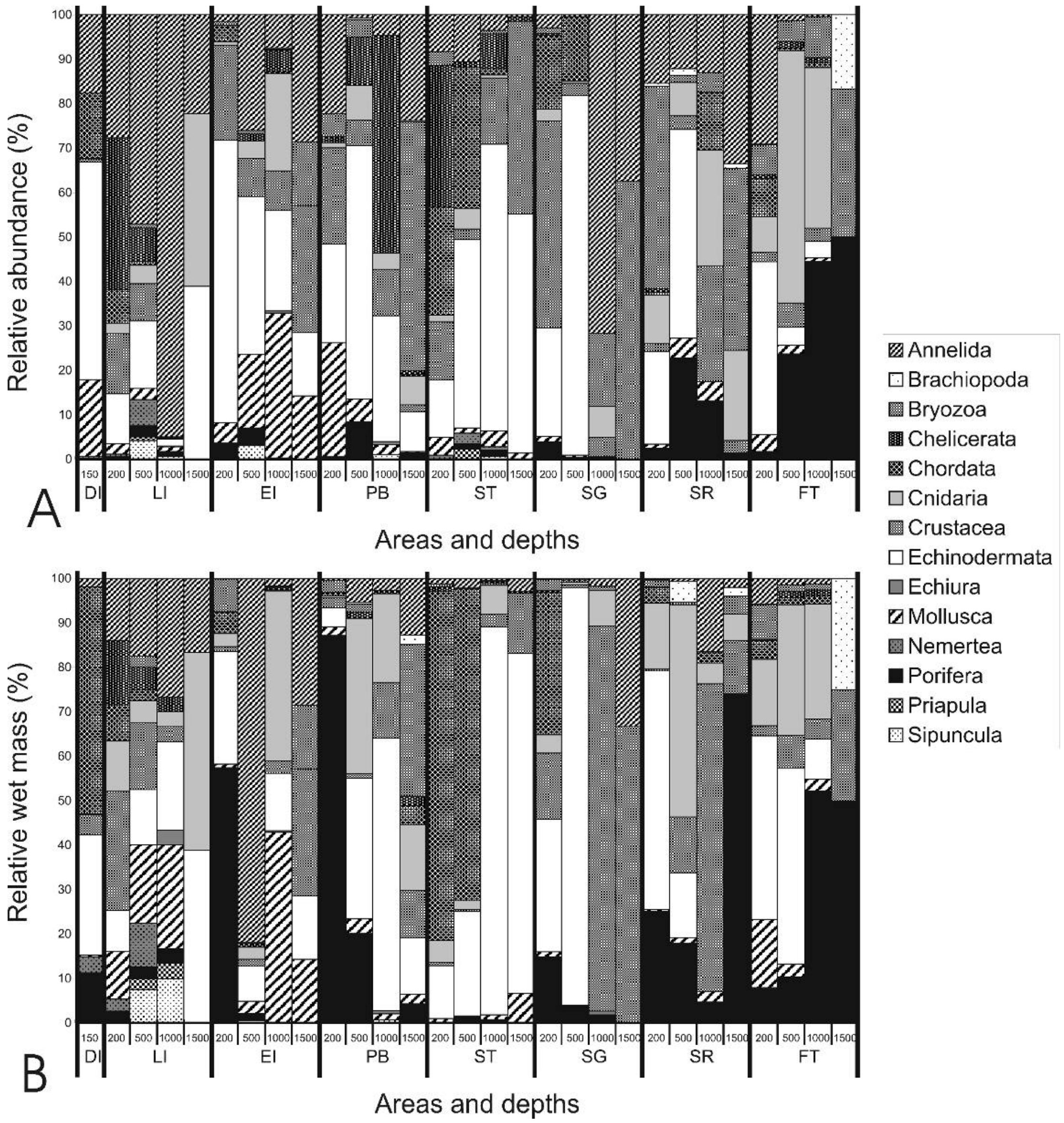


Figure 2.3. The relative composition of benthos a. by abundance, and b. wet mass of each phylum per trawl sample. The area codes are as in Table 2.1 and the key to the taxa is shown.

The dominance of phyla by site by wet mass (Figure 2.3b) was often quite different to that shown in terms of relative abundance. Many phyla present in small numbers can dominate the relative mass due to a few very heavy individuals e.g. the sponges of the family Rosellidae. Conversely some phyla can be represented by hundreds of individuals but make up a very small percentage of the wet mass due to very low individual masses e.g. most bryozoans. As with relative abundance, the relative wet mass of phyla varied considerably between taxa, regions and depths.

The two volcanic study areas, Deception Island and Southern Thule, showed very similar patterns of relative mass of phyla. Chordata and Echinodermata dominated both. Crustacea were present in most trawls but only seem to dominate in the deeper trawls, especially those from South Georgia and Shag Rocks.

The relative abundance and wet mass patterns of those phyla represented by a single class (Priapula, Chelicerata, Sipuncula, Echiura, Annelida and Chordata - see Figures 2.4a & b) obviously had identical class and phylum level patterns. Other phyla (Bryozoa, Crustacea and Porifera) represented by two or more classes, often had one class widespread and commonly found and the other classes being more patchy in distribution, wet mass and abundance. These more patchy classes could be regionally important, such as the hexactinellid sponges, which were only found in seven out of 29 samples but constituted 57% of the wet mass of a single trawl at Elephant Island. In contrast, classes such as the Gastropoda were present in 19 samples but did not form a large proportion of the relative abundance in any samples and only formed a substantial proportion of the relative wet mass in three samples.

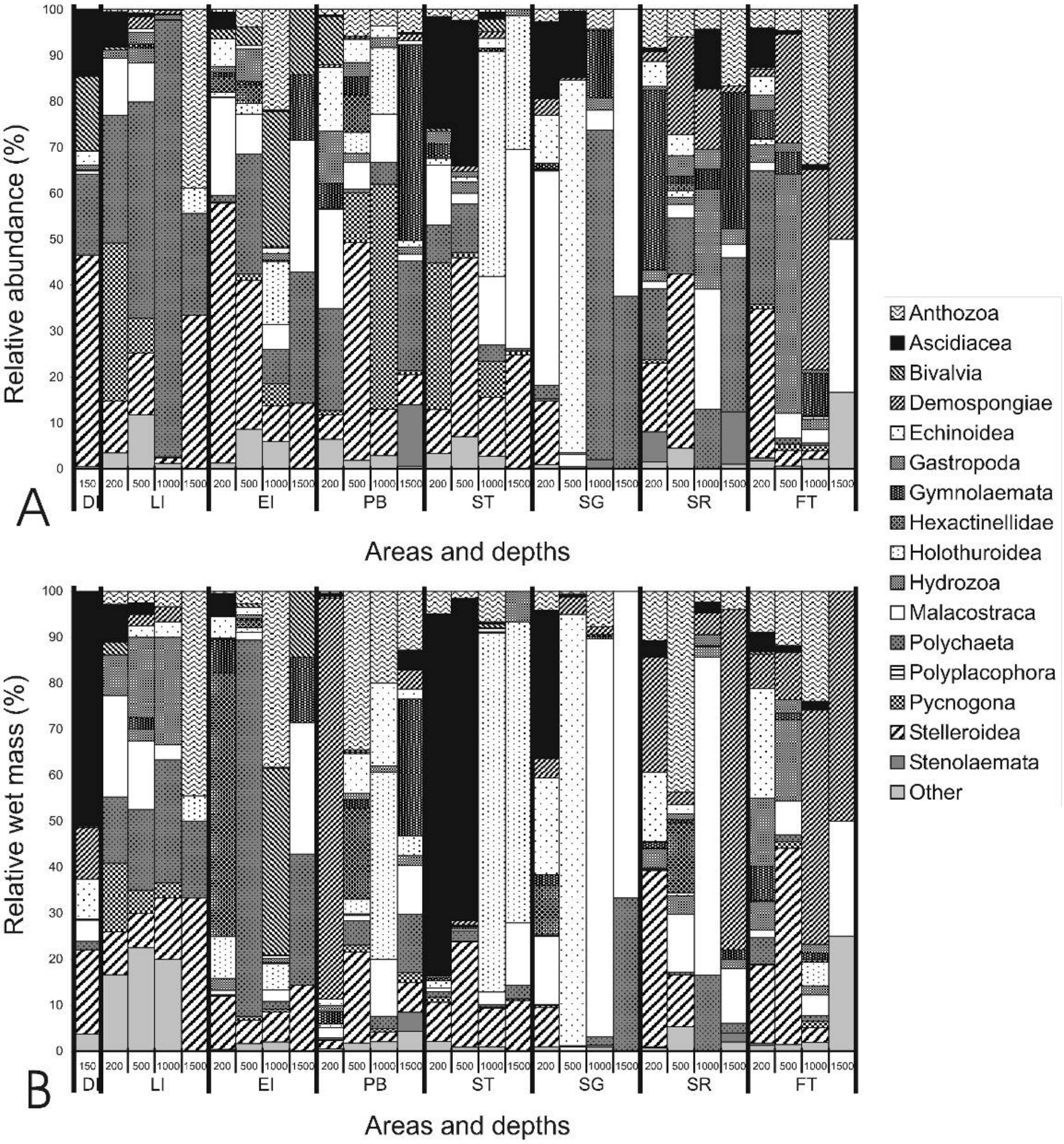


Figure 2.4. Proportional abundance and wet mass of classes in trawl samples around the Scotia arc. The plots shown are a. relative (%) abundances, and b. wet mass of each class per trawl (A) minor classes (Anopla, Articulata, Calcarea, Cephalopoda, Cirripedia, Crinoidea, Echiurida, Inarticulata, Nemertea, Priapulida, Scaphapoda and Sipunculida) were combined to form “other”. The area abbreviations are as in Table 2.1.

With the exception of the class Crinoidea, the Echinodermata formed a major component of both the relative abundance and relative wet mass in most trawls (constituting over > 10% of 20 trawls). The relative importance of each class of echinoderm varied with region and depth. Echinoidea were not abundant in most trawls, with the notable exception of 500 m at South Georgia where they accounted for 80% of the individuals and >90% of the wet mass. Holothuroidea were widely distributed and made up a large proportion of abundance and wet mass in several deeper trawls, most significantly at Southern Thule. The fifth class of Echinodermata, Stelleroidea, which formed a significant proportion of abundance and wet mass of most samples (found in 23 out of 29 trawls), were only absent from deeper water samples in the three regions furthest to the north.

The absence/presence of phyla and classes at sites and areas was analysed to study biogeographic and bathymetric trends in the occurrence of the taxonomic group (Figure 2.5). Seven (Porifera, Mollusca, Echinodermata, Crustacea, Cnidaria, Chordata and Annelida) out of the 14 phyla were found in all study areas, a further two (Chelicerata and Bryozoa) were only absent at Deception Island, where only one trawl was taken. The same seven dominant phyla were found at all depths (160 m, 200 m, 500 m, 1000 m and 1500 m). Brachiopoda, Chelicerata and Bryozoa were all present at every depth except for the 160 m Deception Island sample. Nine of the twenty-nine classes were found in all areas and a further five groups were only missing from the Deception Island sample. The same nine classes were also found to occur at every depth and another six classes were only absent from the single Deception Island sample.

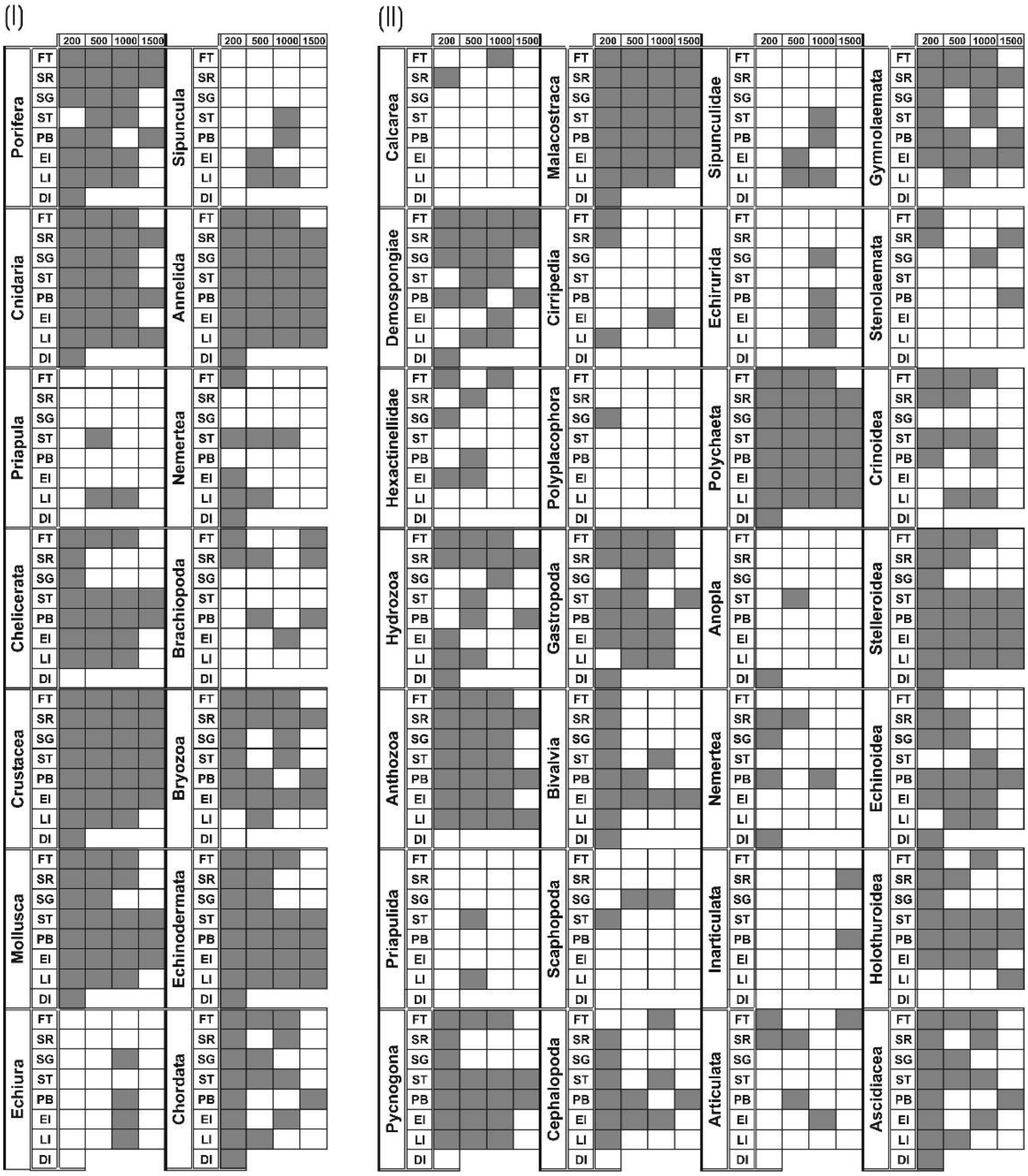


Figure 2.5. Higher taxa with depth and site around the Scotia arc. Presence/absence matrix for both (l) Phylum and (ll) Class levels for all samples. Grey squares show the presence of a taxon. The 200 m Deception Island sample = 160 m depth). For area name abbreviations see Table 2.1.

Levels of faunal similarity between trawl samples (nMDS plots, Figure 2.6a & b) showed strong depth and site patterns. Overall samples were typically more similar (clustered) by depth rather than site, but levels of similarity changed with depth. Shallow shelf (160–200 m) trawls were most similar to each other. Deeper shelf and shallow slope samples were indispersed whilst deeper (slope - 1500 m) trawls were least similar to each other (i.e. showed most dispersion). Some Shag Rocks samples showed close similarity to those of their nearest geographical neighbour, South Georgia. Patterns of similarity were clearer with abundance data (Figure 2.6a) than with wet mass data (Figure 2.6b) but showed similar trends. The nMDS analyses were also characterized by relatively high, but acceptable stress (> 0.13).

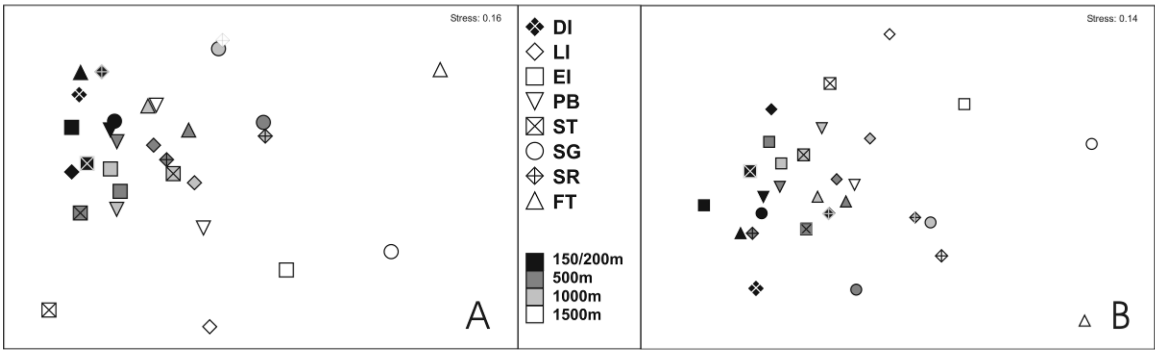


Figure 2.6. Similarity of Scotia arc samples with site and depth. The plots are two-dimensional ordination (MDS) of class level data using a 4th root transformed abundance, and b. wet mass data from Bray-Curtis similarity. For area name abbreviations see Table 2.1.

Generally the number of classes found increased with wet mass in Scotia arc samples but relationships differed with site. There was no significant trend in the increases at

Powell Basin and Southern Thule samples (R^2 values were 0.235 and 0.202 respectively) and only one sample was taken at Deception Island (Figure 2.7a). The increase of class level richness with mass was steepest at Livingston Island ($P = 0.11$) but, as at Elephant Island ($P = 0.111$) and South Georgia ($P = 0.154$), increases had high R^2 values but were not significant. In two regions, Shag Rocks and the Falkland Trough, there were significant and similar trends of increasing richness with increasing wet mass ($R^2 = 0.993$ and 0.964 respectively). The relationship with pooled data of these two sites (Figure 2.7b, $R^2 = 0.962$, $P = <0.0001$) showed that the number of classes approximately doubles with order of magnitude increases in wet mass. The overall trend when all data are pooled was an increase in richness with increasing wet mass ($R^2 = 0.4971$, $P = <0.0001$). Repeating these analyses using phyla as the measure of richness gave similar increasing patterns with wet mass as at class level, and with the only significant relationships being for the Shag Rocks and Falkland Trough sites.

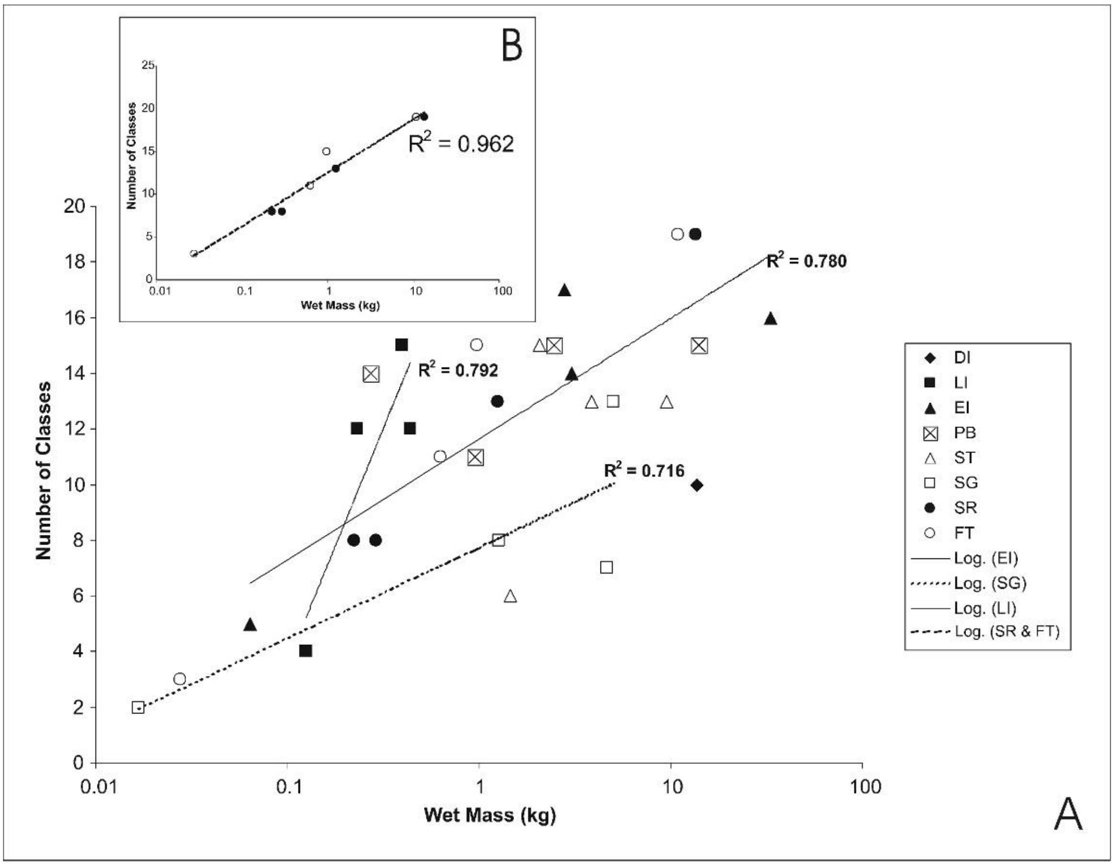


Figure 2.7. Class level richness with wet mass of shelf and slope benthic samples, standardized to 1000 m^2 trawl area, around the Scotia arc. The plots are class level richness with wet mass for a. all samples, and b. specifically for Shag Rocks and Falkland Trough samples. Regression lines shown are all significant ($P < 0.05$). The key to sites is shown (for area name abbreviations see Table 2.1) and on the insert (b) Shag Rocks samples are shown as open circles and the Falkland Trough are shown as solid circles.

DISCUSSION

Richness

The current study showed Scotia arc continental shelf samples to be remarkably rich at higher taxonomic levels, even at remote and geologically young sites. I found 15 phyla (major types of animals) in total across the Scotia arc as has a previous study in the South Shetland Islands (but using grabs and corers, see Saiz-Salinas et al. 1997), but such richness needs context to be meaningful. Representatives of 21 phyla, (more than half the world's phyla) could potentially be found by coarse sampling, e.g. by Agassiz trawl, the seabed (the remainder are either microscopic, parasitic or terrestrial). Of these phyla, Ctenophora, with the exception of a few, not very abundant benthic species, would be unusual as they are typically pelagic. Of the remaining 20 phyla, I could find no Southern Ocean record of the Phorona in the published literature. The Phorona and another phylum of small (<1 cm long, 1 mm wide) animals, the Entoprocta occur attached to hard surfaces so would not be readily sampled using an Agassiz trawl (but see Gallardo & Castillo 1969) and would be difficult to see on removal from water. Thus the 15 phyla found in the current study represent all but three phyla of the total I could realistically expect and, furthermore, I found up to 12 different phyla within some single trawls. Class level richness found by the current study, 29, was also very high. Other studies, using a variety of apparatus have supported these findings of both high local-scale richness and this being widespread in the region. Even on the shelf of the world's most remote island, Bouvetøya, Arntz et al. (2006) found a total of 11 phyla and 20 classes. Intensive sampling has been undertaken at a few locations, such as around the South Shetland

Islands. Of the 15 phyla found at the South Shetland Islands, rarely were more than 50% found in any one sample (Gallardo & Castillo 1969, Saiz-Salinas et al. 1997, Lovell & Trego 2003). Previous sampling at Shag Rocks and South Georgia, two of our study locations, did so using benthic trawls enabling more robust comparisons between our and other studies. Trawls reported by previous studies found approximately similar levels of class richness (Figure 2.8). The higher number of classes found by the current study at these sites, compared to most previous sampling, probably reflects differences in apparatus (Agassiz vs. bottom trawl). Like the current study, previous sampling around Shag Rocks and South Georgia found a non-linear decrease in richness with increasing depth (see Figure 2.8).

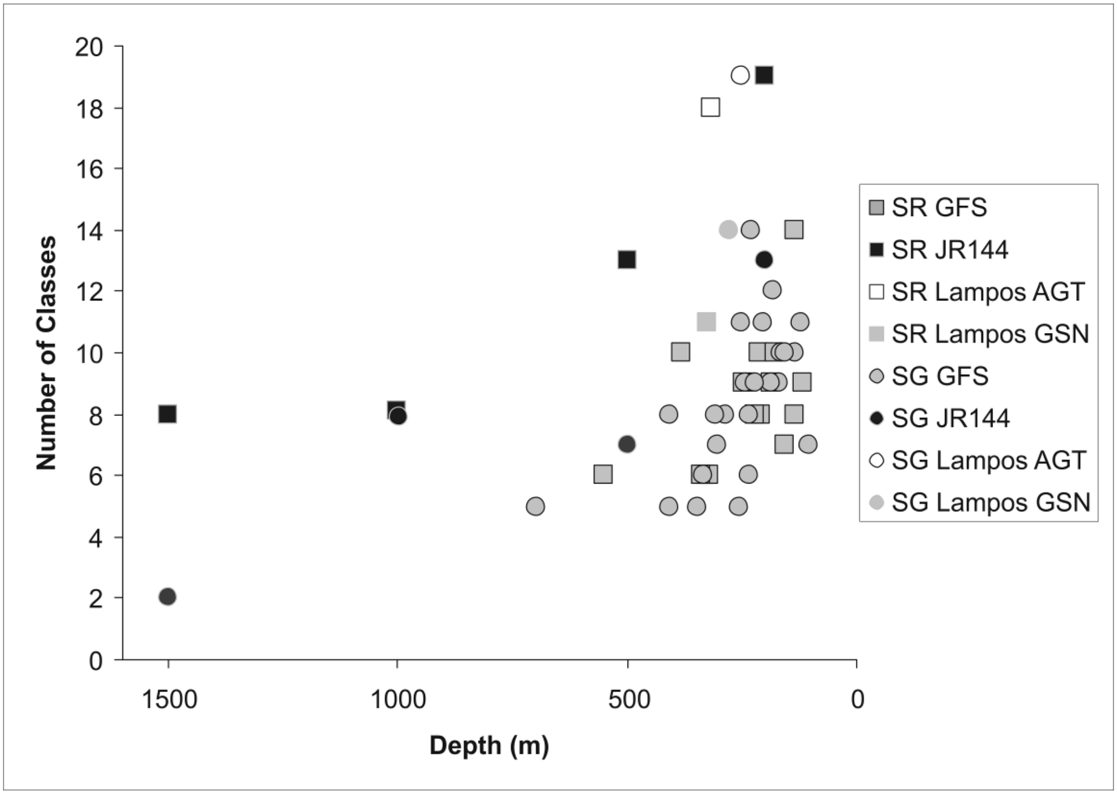


Figure 2.8. Class level richness with depth at Shag Rocks (SR) and South Georgia (SG). The scientific cruises collecting the data were; the current study (JR144), a 2005 South Georgia Groundfish Survey (GFS) (unpublished) and in 2002 LAMPOS. The apparatus used were Agassiz (AGT) and bottom (GSN) trawls.

Abundance and biomass

Faunal abundance showed no relationship (regression not shown) with latitude but decreased with increasing depth as has been found at a number of localities in the region (e.g. Piepenburg et al. 2002 but see Saiz-Salinas et al. 1998). Total wet mass also showed no latitudinal or regional pattern and similarly decreased with increasing depth (Saiz-Salinas et al. 1998). Food quantity and quality (Cadée 1992, Saiz Salinas et al. 1998) as well as decreasing availability of hard substratum type (see Barnes 2008) seem likely to be major influences. The lowest values of wet mass in the current study were found at Livingston Island as was the least difference between shallow and deep samples. These samples were predominantly muds (Table 2.1). The apparently low abundance and wet mass at Livingston Island could be due to sampling bias. The Agassiz trawl samples epifauna well but infauna poorly (Arnaud et al. 1998) but Saiz-Salinas et al. (1998) also found decreased biomass with depth using a grab well suited to sampling infauna.

Dominance of taxa by abundance or wet mass did not show such clear relationships to depth, as for example found by Saiz Salinas et al. (1998). I, like Arnaud et al. (1998), found a strong dominance of single taxa in some areas such as the Annelida at Livingston Island. Typically though, at shallow shelf depths (160–200 m) a number of phyla were abundant and this varied considerably between sites. Some to much variability for shallow assemblages can be linked to patchiness in recovery time and seabed topography due to ice-scour and, to a lesser extent, other disturbance (Gutt & Piepenburg 2003, Barnes & Conlan 2007). Much lower food levels, a more homogenous seabed, fewer hard surfaces and other factors contribute to a depth pattern but it was perhaps surprising that no regional pattern was evident considering the study encompassed sites each side of the Polar Front, of very different ages and levels of isolation. With small number of samples (such as at 1500 m), chance catches of a patch of one type of animal lead to an increased chance of samples appearing to be dominated by a single group.

The most striking site similarity was between the shallow shelf in the two active volcanoes, Southern Thule and Deception Island. There have been recent eruptions in both areas, the 1967–1970 events at Deception Island destroying virtually all of its local fauna before gradual recovery (Gallardo et al. 1977). The rapidly colonizing and growing ascidians (Rauschert 1991) dominated the wet mass of fauna at both locations as seems to be the case in the shallows newly exposed by the collapse of the Larsen B iceshelf (J. Gutt personal communication 2007). Future work drying and ashing these samples will undoubtedly reveal them to constitute a much lower proportion of the dry mass or organic (ash-free dry) mass, because of the high proportion of water in an ascidian body. Several phyla and classes are characteristically absent from impoverished Deception Island and the composition of our trawl was mainly typical of this most well sampled site (see Barnes et al. 2008). The other young volcano, Southern Thule, is much more isolated and surrounded by deep sea. It is unsurprising, therefore that the Holothurioidea, which are particularly important in deep-sea communities (Gutt 1988, Billett et al. 2001), dominated the deeper samples of Southern Thule.

Half of the phyla, and nine of the classes, found in the current study occurred at all study regions and depths. Many others were only absent from a few locations.

Considering only one sample was taken at each site-depth combination, it seems likely most higher taxa are ubiquitous in this area at shelf and slope depths. This is supported by the collecting of the few taxa I did not record from several Scotia arc localities and depths by previous benthic surveys (e.g. Ramos 1999, Lovell & Trego 2003, Figure 2.8). Conversely other studies (e.g. Ramos 1999) have not found certain taxa at some sites (e.g. Crinoidea at Shag Rocks or Southern Thule).

Generally representatives of the classes Inarticulata (brachiopods) and Stenolaemata (bryozoans) were only found in samples which contained rocks (Table 2.1). Samples which included boulders could have a very high richness of cryptofauna, even at 1500 m (Barnes 2008). Such boulders can be associated with any type of substrata as many are ‘dropstones’ which have been released from melting icebergs (Oskierski 1988, Thomson 2003). As large icebergs have been recorded throughout the Scotia arc it is probable that most regions have some dropstones. The lower densities of hard substrata for cryptofauna, and generally of animals, at deeper slope depths (Rex et al. 2006) would require a much greater trawling effort to sample taxa to the same extent as on the shallow shelf.

Despite most higher taxa probably being fairly ubiquitous in the Scotia arc and present in most site-depth samples my (Bray-Curtis) data showed little similarity to that by Ramos (1999). For example, in contrast to the current study, Ramos (1999) found definite groupings between South Georgia and the South Orkney Islands, with Shag Rocks and the South Sandwich Islands as relative outliers. In common was the South Shetland Islands and Elephant Island similarity, however this was dependent on use of ‘abundance’ rather than ‘wet mass’. I found only one pattern that was reflected in both relative abundance and wet mass, the grouping of Shag Rocks and the Falkland Trough. This is of particular interest given that these areas are south and north of the Polar Front respectively. However, both areas are in regions of strong currents, eddies and turbulence (Clarke et al. 2005) and perhaps have similar overlying productivity. The highest levels of assemblage similarity across sites were between those in the shallows probably as a result of the higher abundances, masses and richness of these samples. The relatively high stress levels of the nMDS plots are probably due to the high dispersion (dissimilarity) of the deeper sites from each and all others.

The shelf around Antarctica is known to be richer in benthos than average for its area (Clarke & Johnston 2003) but this study convincingly shows that this high taxonomic level richness can be seen at most sites throughout the Scotia arc, and even in single samples. I found abundance and richness to be strongly linked to depth as other workers have suggested (Saiz-Salinas et al. 1998) whilst I observed no distinct latitudinal gradient in benthic abundance and biomass in the Southern Ocean (Piepenburg et al. 2002). I found considerable variability within regions and habitat types - soft sediments at nearby Livingston and Elephant islands showed the lowest and highest wet masses of fauna, perhaps due to primary productivity (Holm-Hansen et al. 1997). This study provides an important first insight into how shelf and slope fauna are distributed across the entire Scotia arc from shelf to slope at higher taxonomic levels. However, Antarctic endemism rarely exceeds genus level and thus these data should prove of most value as a source of comparison when the same samples are identified to genus and species level.

CHAPTER 3 - QUANTIFYING ANTARCTIC MARINE BIODIVERSITY: THE SCAR-MARBIN DATA PORTAL.

[The data in this chapter are also presented in: Griffiths, H.J., Danis, B. and Clarke, A. (in press) Quantifying Antarctic marine biodiversity: the SCAR-MarBIN data portal. Deep-Sea Research Part II.]

Chapter 3 - QUANTIFYING ANTARCTIC MARINE BIODIVERSITY: THE SCAR-MARBIN DATA PORTAL.

INTRODUCTION

Polar regions are changing fast. The most marked changes are in air temperature around the Antarctic Peninsula over the last 50 years, and these have been associated with the widespread retreat of glaciers (Cook et al., 2005) and collapse of ice shelves (Peck *et al*., 2009b). However increases in surface seawater temperatures have also been detected to the west of the Antarctic Peninsula (Meredith & King, 2005). Although these temperature increases are small, they are possibly of physiological significance: the Antarctic marine fauna appears to be unusually sensitive to small increases in water temperature (Peck , 2005b; Peck *et al*., 2008, 2009b; Morley *et al*., 2009a), and hence may be vulnerable to even slight shifts in marine climate (Barnes & Peck, 2008). If we are to track changes to the Antarctic marine fauna as its environment changes, we need to establish current patterns of abundance and diversity; for this a modern database is an essential tool.

Antarctic biological diversity: what we know so far

Whilst the economic exploitation of Antarctica's marine resources dates back to the 18th century, scientific research into the marine ecosystem only began in the mid 19th century. Expeditions such as those of HMS *Challenger*, *Belgica* and the *Discovery* Investigations were amongst the first to undertake systematic sampling of the benthos and plankton. The taxonomic work that resulted from these early expeditions was frequently undertaken by museum specialists and the resultant monographs provide the foundations of modern taxonomy in the region (Gordon, 1932; Gordon, 1944; Powell, 1960; Hoek, 1881 etc.). Advances in technology such as SCUBA diving, ice-capable research vessels and underwater imagery from remotely operated vehicles, have revitalised marine ecological work in polar regions and, together with the recognition by SCAR and some national agencies of the importance of fundamental taxonomy, have increased significantly the rate of discovery and description of new species in the Southern Ocean (Clarke & Johnston, 2003). In Table 3.1 I compare the number of species reported for selected groups of marine invertebrates, with the current value in RAMS. This gives a feel for the current state of knowledge, and an indication of the importance of recent support for exploratory biology and primary taxonomy.

It is certain that further taxonomic work will revise many of these totals. Also the recent upsurge in the use of molecular genetic techniques has shown many established species to be groups of morphologically similar but genetically distinct cryptic species (Held 2003; Held & Wägele, 2005; Raupach et al. 2006, 2007; Linse et al. 2007). Furthermore, the age of marine biological exploration in Antarctica is far from over, with dedicated cruises continuing to sample its remotest and deepest areas for the first time under the auspices of both the recent International Polar Year (IPY) and the Census of Antarctic Marine Life (CAML). These are certain to add to our knowledge, and to build on this continuing investment in primary research it is essential that there is a mechanism in place to update and validate a definitive set of data on the diversity, abundance and biogeography of southern Ocean marine biota.

Table 3.1. The total numbers of marine species per taxonomic group as reported by Clarke & Johnston (2003) and by the Register of Antarctic Marine Species (RAMS) (2010). Taxonomy presented as phylum (**bold**), class (*italic*) or order (roman). Asterisk indicates that the RAMS total includes some pelagic taxa not included in the Clarke & Johnston (2003) total.

Taxon	Clarke & Johnston, 2003	RAMS	Notes
Porifera	250	276	
Cnidaria			
Hydrozoa	186	311*	
Bryozoa	322	323	
Annelida			
Polychaeta	645	589*	Removal of synonyms
Mollusca			
Gastropoda	530	431	Removal of synonyms
Bivalvia	110	131	
Crustacea			
Amphipoda	496	945*	460 benthic taxa
Isopoda	257	444*	Includes new deep-sea taxa (more to be described)
Pycnogonida	175	183	Extensively revised
Echinodermata			
Ophiuroidea	119	132	
Asteroidea	108	247	Includes Subantarctic taxa not inlcuded in C&J
Holothuroidea	106	105	
Chordata			
Ascidiacea	118	154	

The creation of SCAR-MarBIN

The political context for the development of a web-based system for managing biological diversity data in the Southern Ocean is provided by the Antarctic Treaty, Article 3.1.c of which states:

> *In order to promote international cooperation in scientific investigation in Antarctica, as provided for in Article III (1c) of the Treaty, the Contracting Parties agree that, to the greatest extent feasible and practicable: […] Scientific observations and results from Antarctica shall be exchanged and made freely available*.

The simplest way to ensure that this aim is met, at least for data on diversity and biogeography, is to have a well-maintained database of validated data available to all. Not only would such a database be a stimulus to research, but it would also contribute to the fundamental understanding of the impact of environmental processes on Antarctic marine biodiversity necessary to design adequate conservation measures. Since 2005, the Marine Biodiversity Information Network of the Scientific Committee on Antarctic Research (SCAR-MarBIN) (De Broyer & Danis, 2009) has compiled and managed information on Antarctic marine biodiversity (www.scarmarbin.be). It is home to the first complete Register of Antarctic Marine Species, a searchable online species list maintained by a board of expert taxonomic editors. SCAR-MarBIN is supported by the Belgian Science Policy (BELSPO), the Alfred P. Sloan Foundation (SLOAN) through the Census of Marine Life (CoML) and the Scientific Committee on Antarctic Research (SCAR). Although it is focused primarily on biogeographic data, SCAR-MarBIN is developing tools to improve its usefulness for conservation and sustainable management. Data can be processed and presented in a variety of ways, allowing the integration of biogeographic data into the development of policy for Antarctic conservation. Furthermore current data can be used to construct a panel of indicators to detect changes in biodiversity and hence adapt conservation strategies.

In this chapter I describe the SCAR-MarBIN data portal, and present some preliminary analyses to show its capability and illustrate its potential for future analyses of Southern Ocean biological diversity or biogeography. The main aim of the study was to give an overall picture of the state of our current level of knowledge of the distribution and richness of the marine fauna of the Southern Ocean, based on the data which are freely available through SCAR-MarBIN.

METHODS

SCAR-MarBIN and the RAMS provide access to information on more than 15,000 taxa, and contribute to both the World Register of Marine Species (www.marinespecies.org) and to the Catalogue of Life (www.catalogueoflife.org). These data are also made available through larger initiatives, such as the Ocean Biogeographic Information System (www.iobis.org) or the Global Biodiversity Information Facility (www.gbif.org). Through an online mapping system, SCAR-MarBIN allows data on marine organisms to be visualized and downloaded. This offers, for the first time, a way to quantify the diversity and distribution of Antarctic marine life and to document how, when and where it has been studied.

Selection and handling of data

SCAR-MarBIN accepts and publishes data at a range of taxonomic levels; a critical task is therefore to select only those distribution records for animals which have a valid species name. This is done by using the most up to date species lists and taxonomy validated by the RAMS taxonomic editors. The validated species names list is then used to determine which data points are used in all further analyses.

For the analyses presented here I define a station as a unique combination of latitude and longitude irrespective of sampling date. To avoid the potential problem of duplicate records in such a large dataset only the first occurrence of a species at a station is included in my working data set. I also confined my analyses to stations within the mean position of the Polar Front as the Southern Ocean is the primary area of interest for SCAR-MarBIN and the area for which most data has been assembled (currently 368,970 records from >271,000 stations). For biogeographical analysis each station was assigned to a unique cell in a a 3° of latitude by 3° of longitude grid.

Depth is an optional field in the SCAR-MarBIN data scheme (http://www.scarmarbin.be/obisschema.php) and hence many of the records are not associated with a depth. For these records I extracted a depth from the ETOPO2 global bathymetry data set. Depths were extracted in bins at 100m intervals as the two minute resolution of the bathymetry dataset was coarser than that of the sampling locations. As every station and species record had been assigned to a 3° grid cell it was possible to determine the number of distinct species and the number of distinct stations per cell using simple queries run in Microsoft Access©. These counts were then linked to ArcGIS to produce maps of species and site numbers per grid cell.

This approach allowed us to undertake analyses and plot maps at a range of taxonomic and functional scales. These included an analysis of all species combined (that is, the entire data set), analyses of individual phyla (Nematoda, Annelida, Cnideria, Echinodermata, Mollusca, Arthropoda and Chordata), and analyses of broad functional groups (benthic, planktonic, fish and endothermic higher predators). Marine invertebrate taxa were assigned to either benthos or plankton on the basis of literature or, for the more difficult groups, information from the taxonomic editors. Where a given phylum is essentially entirely benthic, then assignment is straightforward; for example Echinodermata. Other taxonomic groups, such as amphipods (phylum Arthopoda), Cnidaria or Mollusca are comprised of a mixture of pelagic and benthic species; these required detailed advice from the relevant RAMS taxonomic editor to ensure a species was assigned to the correct functional group. These groups can be analysed at a lower taxonomic level so that the group contains only a single life-style, but for analysis at the phylum level, these life-styles are inevitably pooled.

RESULTS

There are 814 grid cells (3^{o} latitude by 3^{o} longitude) in the Southern Ocean, defined as water south of the mean position of the Antarctic Polar Front. Of these, 678 cells (83%) contained at least one data record (Figure 3.1). However the distribution of these records is far from even, with 149 cells containing fewer than 5 stations and, at the other extreme, 10 cells containing over 5,000 stations. There is a similar pattern to the distribution of species numbers with 187 cells containing fewer than 5 species and 19 with more than 200. Areas of combined intense sampling and high species richness fall in two broad areas: the West Antarctic Peninsula (WAP) plus the South Shetland Islands (SSI), and the Australian (50°E to 165° E) section of East Antarctica (EA). In contrast two areas of high species richness, in the Eastern Weddell Sea (EWS) and the Ross Sea (RS), are not associated with high numbers of samples. All four areas of high species richness (diversity hotspots), however, are in areas with a long history of biological work. This suggests that they may not be particularly rich in comparison with other less studied areas of the Southern Ocean continental shelf, but merely areas that have been well sampled and studied. This simple mapping exercise also points to important areas with particularly poor sample coverage, and notable examples include the Amundsen Sea (AS) and the Western Weddell Sea (WWS) (Figure 3.1).

These broad patterns, however, mask important differences in the distribution of benthic and pelagic (planktonic) samples. Benthic samples have been mostly taken on the continental shelf, whereas pelagic samples have been taken over both shallow and deep water, and this shows up clearly in the apparent distribution of richness (Figure 3.2). With the present level of available data and the differences in sampling intensity and strategy between the two realms, I thus cannot make any meaningful comparisons between the benthic and pelagic realms in terms of diversity (species richness), or point to any areas that might be particularly important for pelagic/benthic coupling.

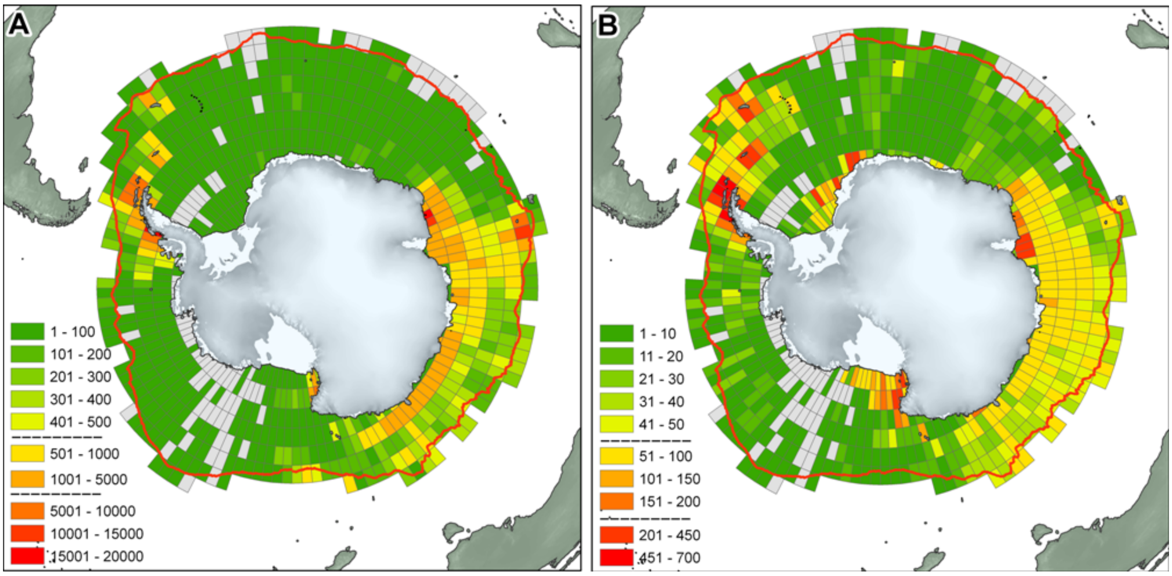


Figure 3.1. The total numbers of all marine sample sites and species found within each cell of a 3° of latitude by 3° of longitude grid, from distribution records in SCAR-MarBIN (grey cells = no records). The red line indicates the mean position of the Antarctic Polar Front, which defines the maximum northern extent of this study. A. Sample sites. B. Species richness (total number of all marine species recorded in that cell).

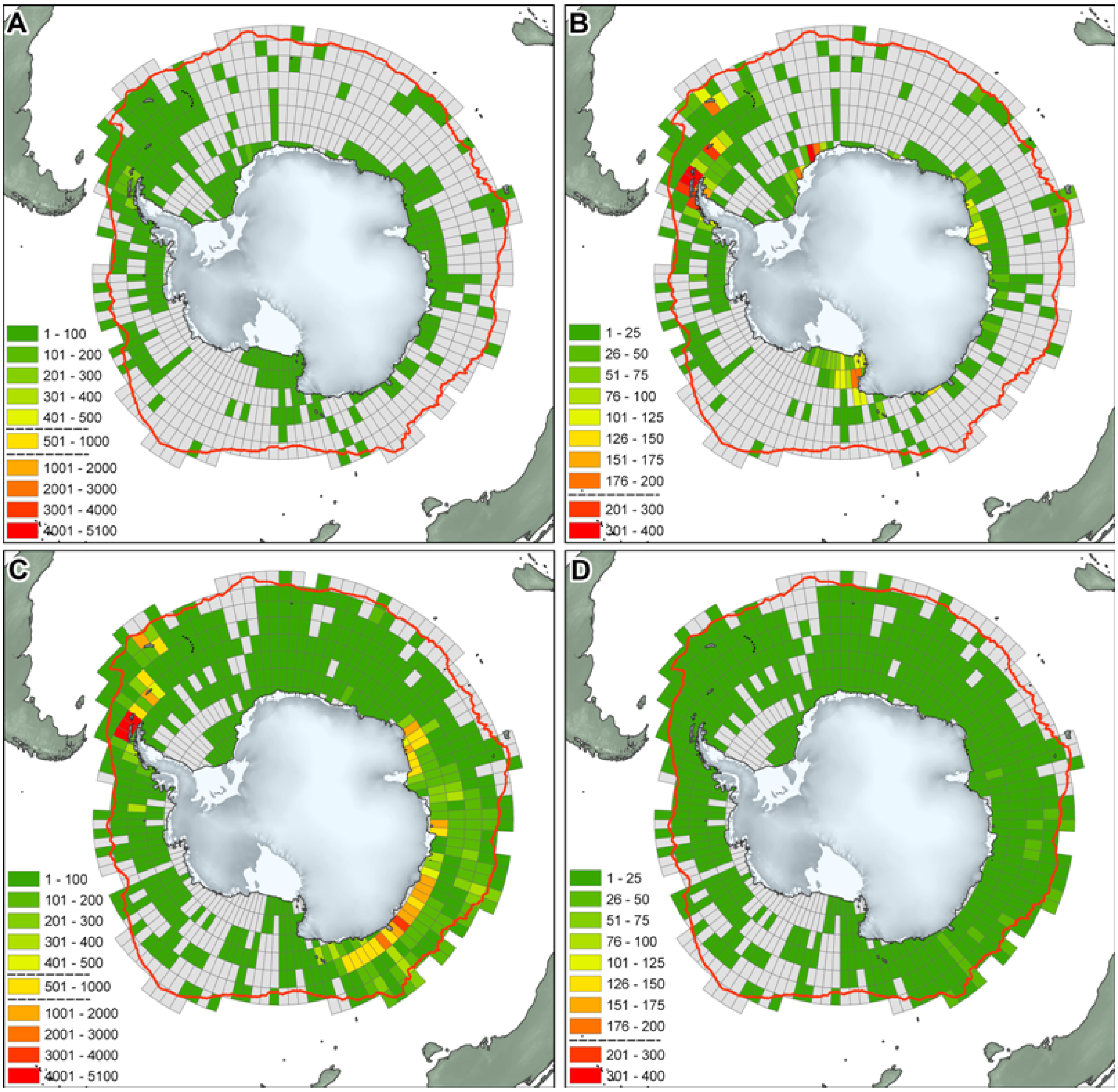


Figure 3.2. The total number of sample sites and marine species for each 3^{o} x 3^{o} grid cell, with data for benthic and planktonic samples plotted separately to show very different pattern of sampling in the two marine realms. Presentation as for Figure 3.1. A. Number of benthic samples per grid cell. B. Total number of benthic species recorded per grid cell. C. Number of planktonic samples per grid cell. D. Total number of planktonic species per grid cell.

Patterns within individual phyla

Two phyla which comprise both benthic and pelagic species, though in different proportions, are Annelida and Cnidaria. The phylum Annelida is well represented in the Southern Ocean benthic fauna (Dell, 1972; Knox & Lowry, 1977). The pattern of sampling (Figure 3.3a) revealed for the Annelida shows a relatively wide distribution of thinly scattered stations, with one notable hotspot off the north-west Antarctic Peninsula with 71 stations. This high concentration of samples is in the cell surrounding Elephant Island (EI) at the northern tip of the WAP. This cell is also relatively high in richness (58 species), with other hotspots in the southern Weddell Sea, the South Shetland Islands (SSI) and the South Orkney Islands (SOI) (Figure 3.3b). The majority of East Antarctica (EA) is represented by low numbers of species, and these are mostly pelagic polychaetes from plankton trawls. The Southern Ocean polychaete fauna is over 640 species (Clarke & Johnston, 2003), so the pattern of richness observed to date is dominated clearly by those few areas where taxonomic specialists have examined benthic samples.

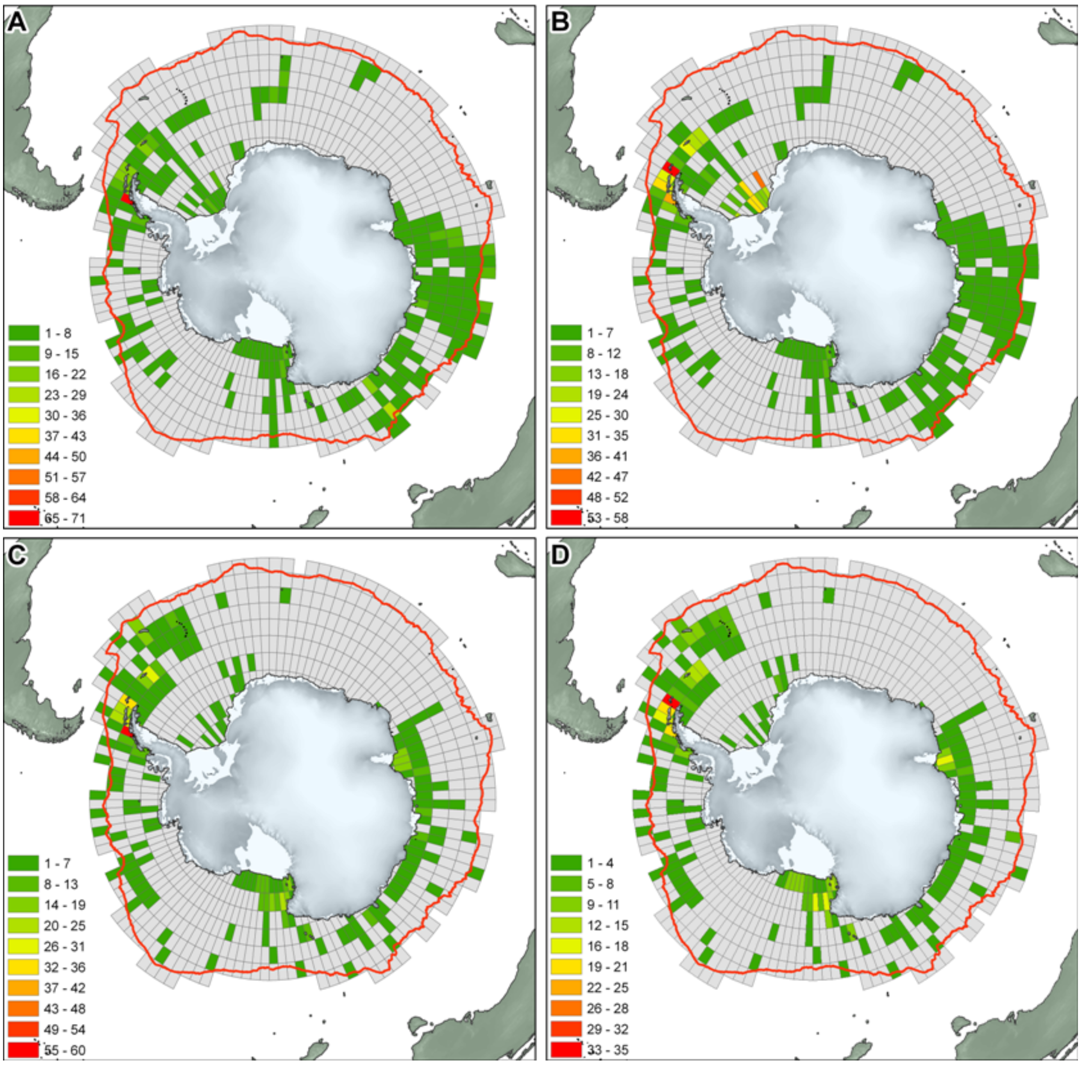


Figure 3.3. The total number of sample sites and species for each $3^{o} \times 3^{o}$ grid cell, for two phyla containing both benthic and pelagic taxa. Presentation as for Figure 3.1, though note the differing scales for the two phyla. A. Total number of stations recording Annelida per grid cell. B. Total number of Annelid species recorded per grid cell. C. Total number of stations recording Cnidaria per grid cell. D. Total number of Cnidaria species recorded per grid cell.

A similar pattern to that for annelids is shown by the Cnidaria, both for stations and species (Figures 3.3c, d). One notable difference between the patterns for the two phyla being a lack of deep/open water samples in the Cnidaria, together with no obvious peak of richness in the Weddell Sea . As with the Annelida, the scattering of open ocean cells with a small number of stations and species reflects records for pelagic forms (medusa). The three areas of marked species richness (in the Ross Sea, East Antarctica and northern WAP) reflect work by taxonomic specialists on benthic cnidarians.

These patterns can be compared with those for two phyla that are exclusively benthic (Echinodermata) or for where data are only available for benthic taxa (Nematoda). Most sampling for Echinodermata has been undertaken in the northern WAP (154 stations) and the Eastern Weddell Sea (Figure 3.4a). The species richness hotspots (Figure 3.4b) reflect this sampling trend, with notable exceptions in the SOI and the Prydz Bay (PB) area, both having high species numbers despite the relatively low numbers of stations (Figure 3.4a & b). There is also a relatively large number of echinoderm species recorded from the Ross Sea.

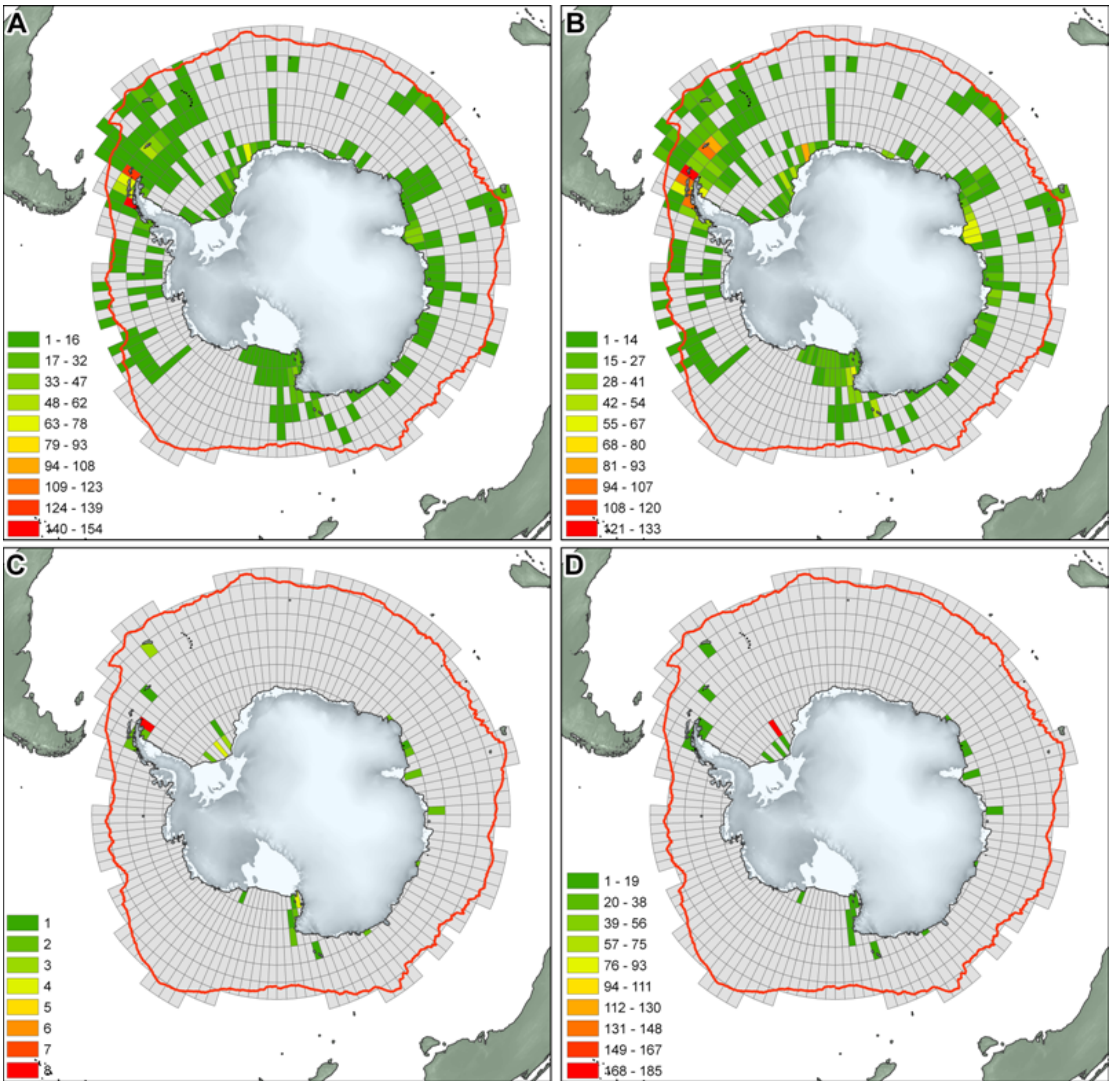


Figure 3.4.The total numbers of sample sites and species for each 3° x 3° grid cell for two exclusively benthic phyla. Presentation as for Figure 3.1, though note the differing scales for the two phyla. A. Total number of stations recording Echinodermata per grid cell. B. Total number of echinoderm species recorded per grid cell. C. Total number of stations recording Nematoda per grid cell. D. Total number of nematode species recorded per grid cell.

The Nematoda had the smallest geographical coverage of all the taxa examined in this study. The low numbers of reported stations (Figure 3.4c) were also very patchily distributed; they included the northern WAP, the Ross and Weddell Seas and South Georgia (SG). The pattern of reported nematode species numbers (Figure 3.4d) largely reflects the low number of stations. However, for one grid cell in the Weddell Sea 185 species have been recorded from a single station, indicating the diversity of nematodes to be found in at least one high latitude site when samples are worked up taxonomic experts. Clearly the marine nematode fauna of the Southern Ocean is very poorly known at present.

Two phyla which are generally among the better known from almost any marine area are the Mollusca and the Arthropoda. Both phyla contain a number of disparately-sized classes, not all of which have received equal attention from ecologists or taxonomists. Here I present data for bivalve, gastropod, pteropod and cephalopod molluscs, and malacostracan, maxillopod, ostracod and pycnogonid arthropods. Mollusca are one of the most well-sampled taxa in the Southern Ocean, and there are stations from roughly half of all Southern Ocean grid cells. These are relatively well distributed though there are notable gaps in the Amundsen Sea and western Weddell Sea (Figure 3.5a). Although most species are benthic, the concentration of stations near the Polar Front (PF) off East Antarctica (200 stations in a single cell) reflect records for the two pelagic groups, cephalopods and pteropods. Species richness hotpots (Figure 3.5b) for the Mollusca reflect the sampling intensity only partially. As well as hotspots in the South Shetland Islands and at South Georgia, there are high numbers of species reported from both the Weddell Sea (198 species in a cell) and Ross Sea, and relatively few species reported from open water.

Arthropods show a widespread distribution of stations (Figure 3.5c), with high numbers in a cluster in the Scotia Sea area (SSI, SOI and SG) and in the coastal part of the Australian sector of East Antarctica (up to 5,000 stations in a cell). By far the highest numbers of arthropod species (204) are reported from the SSI region (Figure 3.5d). In general higher numbers of arthropod species have been recorded from shallow coastal regions (South Georgia, WAP, Weddell Sea and Prydz Bay) with low numbers in the open ocean. The marked band of high station numbers off East Antarctica reflects intensive sampling of the pelagic realm with the continuous plankton recorder (CPR).

By far the greatest number of stations recorded in any grid cells are for the vertebrates, which here combine fish, with the endothermic marine mammal and seabird higher predators. The two major sampling hotspots for vertebrates occur in coastal areas to the west of the Antarctic Peninsula (predominantly seals) and off the Mawson Coast (predominantly seabirds) (~17000 stations in each) (Figure 3.6a, b). Vertebrates overall have their highest numbers of species recorded off Elephant Island (113 species), reflecting the use of this area for scientific investigations of fish, and relatively low numbers of species from the areas of high station numbers (Figure 3.6c, d). The widely spread stations and relatively high number of species recorded for the whole of the Australian sector of East Antarctica between the continent and the APF reflects the intense at-sea recording of marine mammals and seabirds undertaken from research vessels traversing this region.

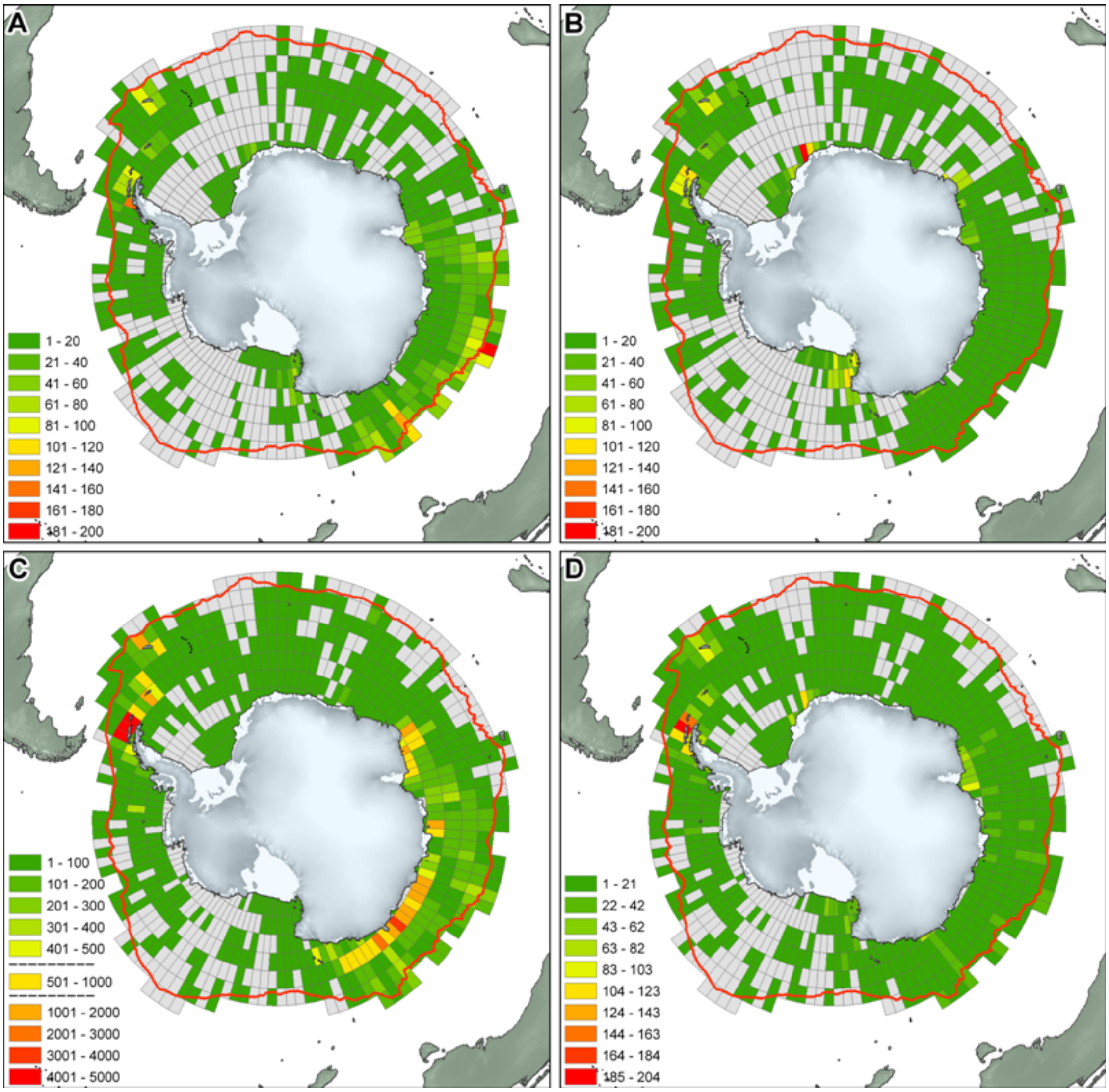


Figure 3.5. The total number of sample sites and species for each 3° x 3° grid cell, for two well-studied phyla containing both benthic and pelagic taxa. Presentation as for Figure 3.1, though note the differing scales for the two phyla. A. Total number of stations recording Mollusca per grid cell. B. Total number of molluscan species recorded per grid cell. C. Total number of stations recording Arthropoda per grid cell. D. Total number of arthropod species recorded per grid cell.

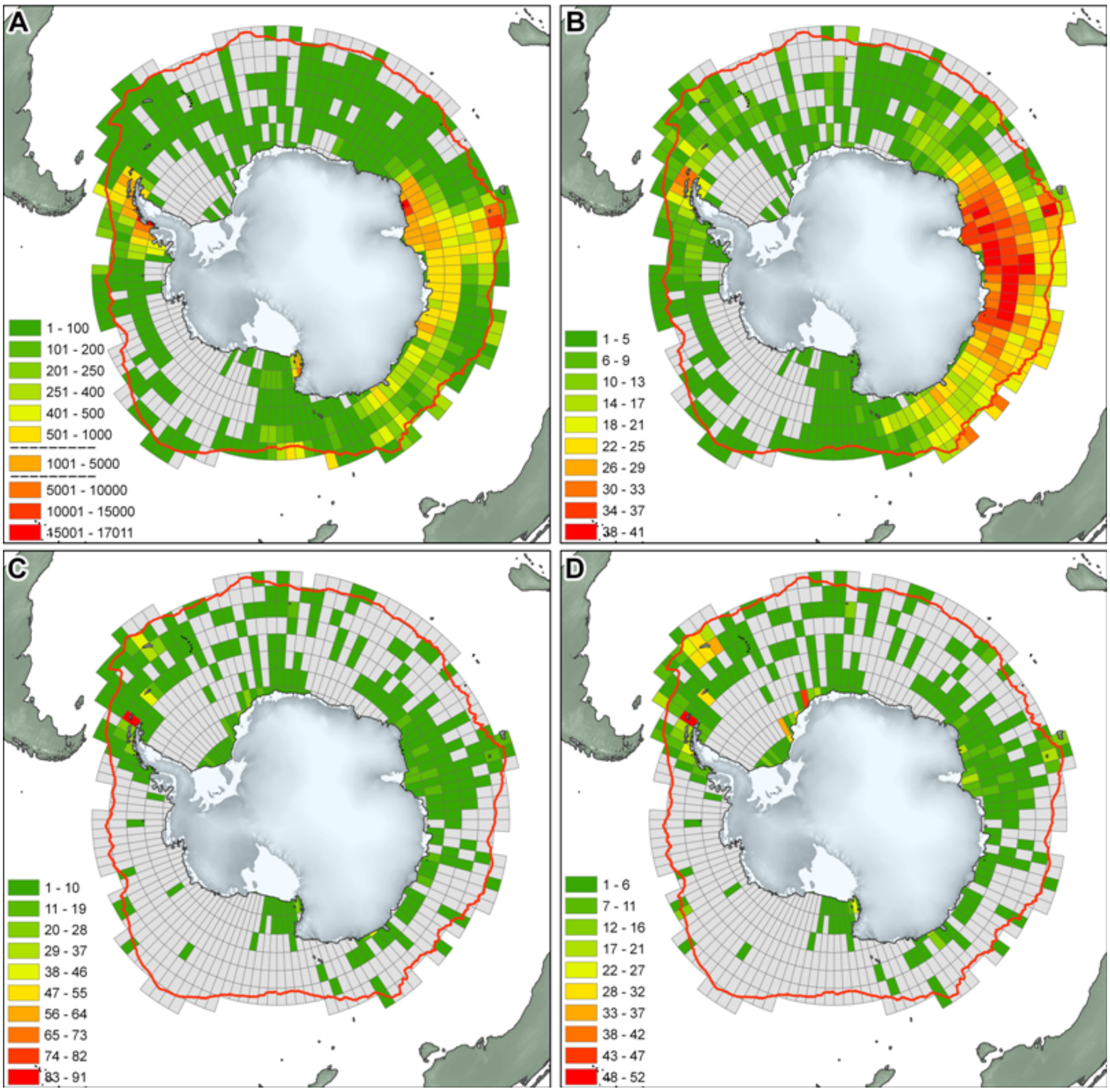


Figure 3.6. The total number of sample sites and species for each $3^{\circ} \times 3^{\circ}$ grid cell, for two groups of primarily pelagic vertebrates. Presentation as for Figure 3.1. A. Total number of stations recording endothermic higher predators (seabirds and marine mammals) per grid cell. B. Total number of bird and mammal species recorded per grid cell. C. Total number of stations recording fish per grid cell. D. Total number of fish species recorded per grid cell.

DISCUSSION

Before I can proceed to analyse and interpret any large scale patterns or biogeographic trends I first need to ascertain how robust the dataset I am using is, and where I have sufficient data to draw meaningful conclusions. Understanding the limitations to the data is critical to the identification of patterns and richness, and a knowledge of the gaps and peculiarities in the sampling data will also help to identify areas for future investigation as well as those suitable for more detailed analyses.

Geographical distribution of sample stations

The logistical challenges inherent in biological sampling within the Southern Ocean have resulted in a number of biases in the distribution of sampling locations. The benthic stations are typically concentrated in the areas of continental shelf and around islands (Figure 3.2a). The highest numbers of stations are found in the South Shetland Islands (~280 stations per cell) , with relatively high sampling also around South Georgia, the eastern Weddell Sea, the Ross Sea and Prydz Bay. These are all areas that offer relatively easy access, and are often close to the routes taken by logistical supply vessels travelling to national research stations. Thus benthic sampling stations are largely concentrated within relatively short distances of onshore research bases: a quarter of all benthic stations lie within 50 km of a base and half are within 150 km (Figure 3.7). Notable gaps in sampling include the majority of the deep sea, the perennially ice-covered western Weddell Sea and the geographically remote Amundsen Sea.

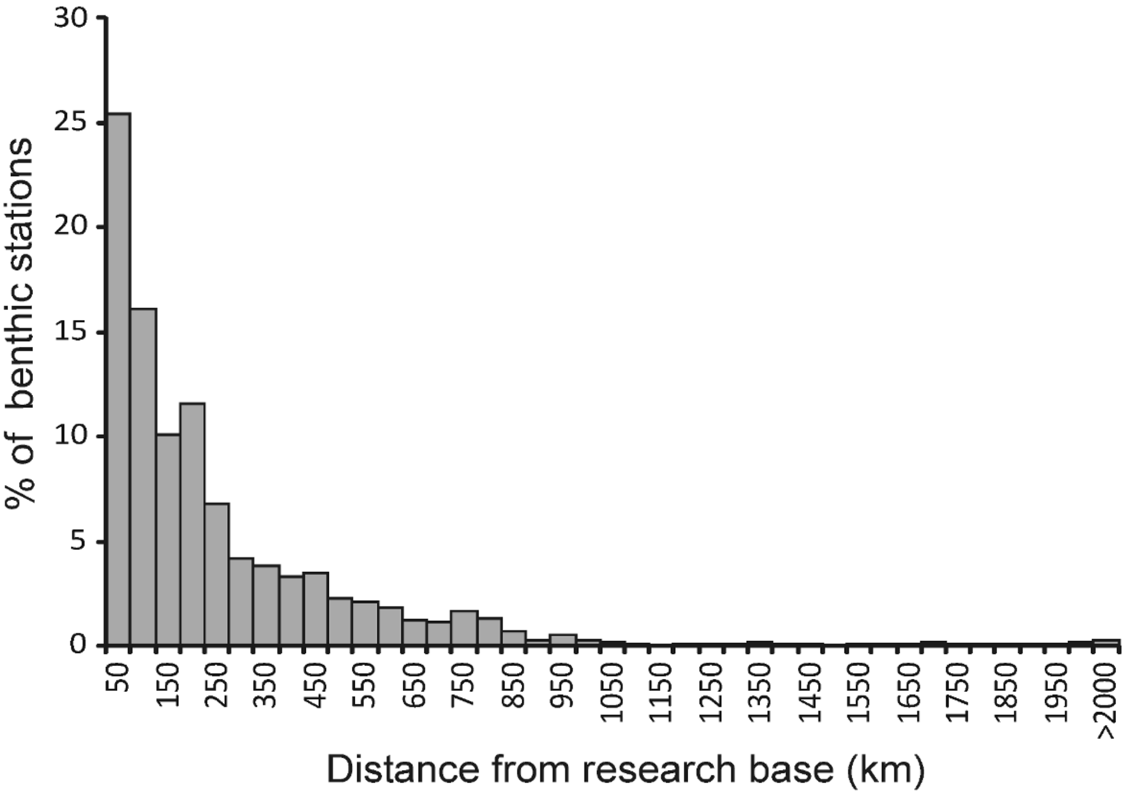


Figure 3.7. Frequency distribution of the distance of all stations where a benthic sample has been taken, to the nearest national research base.

The depth distributions of benthic stations in the Southern Ocean (Figure 3.8a) shows that the majority of samples (>50%) have been taken in water of <400 m depth. A similar trend is shown for the depth distribution of recorded benthic species, with a sharp drop off in species numbers at depths deeper than 700 m (Figure 3.8b). The depth distribution for the area of Southern Ocean sea floor (Figure 3.8c) is very different; it exhibits a small peak (8%) at shelf depths (100-800 m) reflecting the broad continental shelf centered on these depths. The shelf-break around Antarctica typically lies between 800 m and 1000 m, depending on the impact of glacial processes on the seabed, and the transition to the abyssal plain is often ascribed to the relatively sharp change in gradient at about 3000 m. These two isobaths thus define the continental slope (conventionally 1000 – 3000 m in the Southern Ocean), which comprises a relatively small proportion of the seabed.

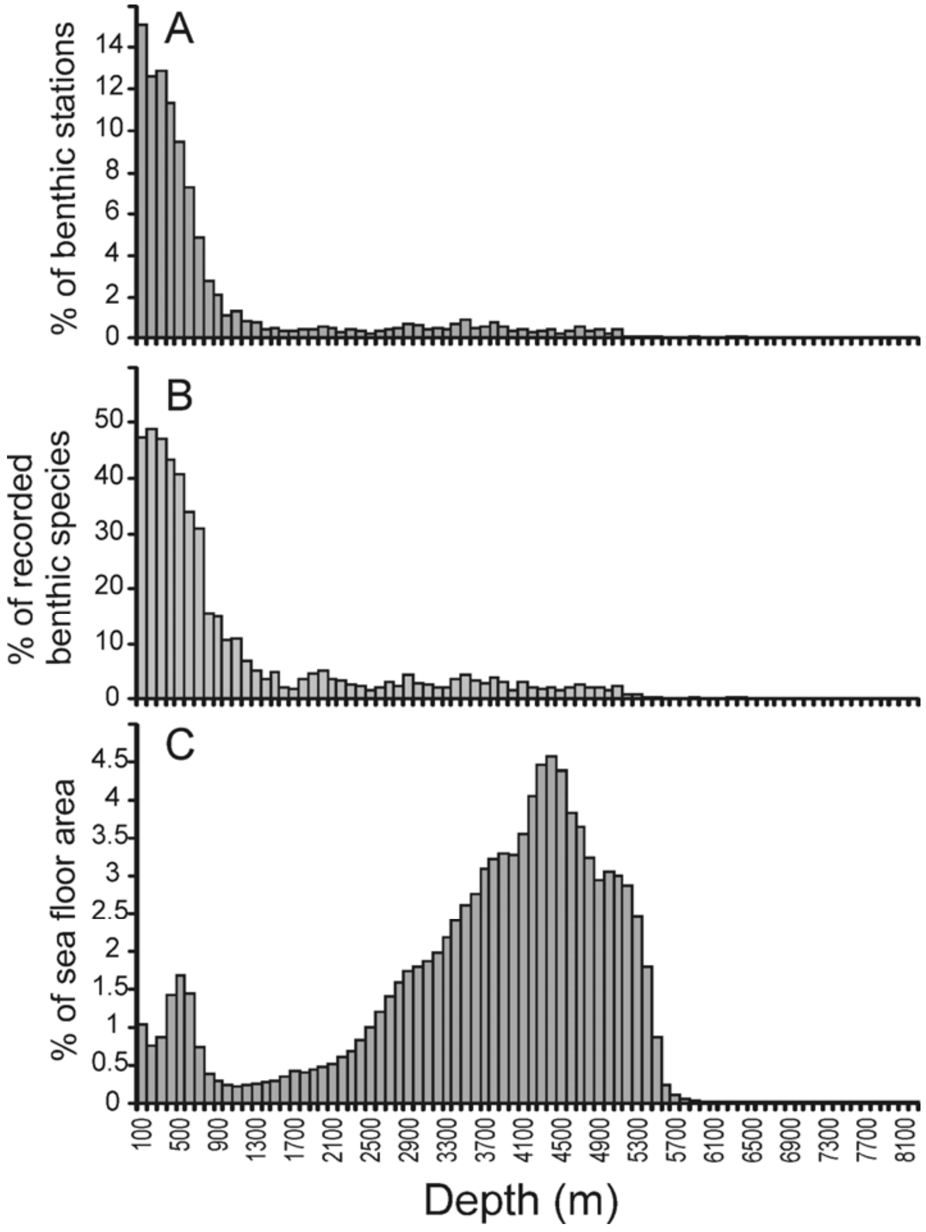


Figure 3.8. Frequency distribution of depth (m) of benthic sampling in the Southern Ocean, and of the available habitat. All data plotted in depth bins of 100m. A.

Benthic stations. B. Benthic species. C. Total sea floor area in the Southern Ocean south of the mean position of the Antarctic Polar Front.

The majority of the Southern Ocean seabed is abyssal, but this area contains relatively few samples and only a small proportion of the recorded benthic species. Although recent cruises have specifically targeted the deep sea (for example the ANDEEP cruises: Brandt & Hilbig, 2004; Brandt et al. 2007), the deep sea remains a major unexplored area in the Southern Ocean, and further sampling from this region is bound to have a significant impact on our understanding of Southern Ocean biological diversity and of the evolution of the Southern Ocean marine fauna.

The effect of sampling intensity

The extent to which observed species richness is dictated by sampling intensity can be assessed by examining the species richness in each grid cell as a function of the number of samples taken in that cell (Clarke & Lidgard, 2000; Clarke et al., 2007a). I have examined the relationship between sampling intensity and observed species richness for data available through SCAR-MarBIN. Because there are a large number of grid cells with very low numbers of samples, the data were log-transformed. The plot for all data shows a strong positive relationship (Figure 3.9a), though there are grid cells with only one sample with between 1 and 11 species recorded, and one cell with over 450 samples but only a single species recorded. The latter situation reflects intensive sampling when only the target species is recorded; a typical example would be directed sampling for Antarctic krill, *Euphausia superba*.

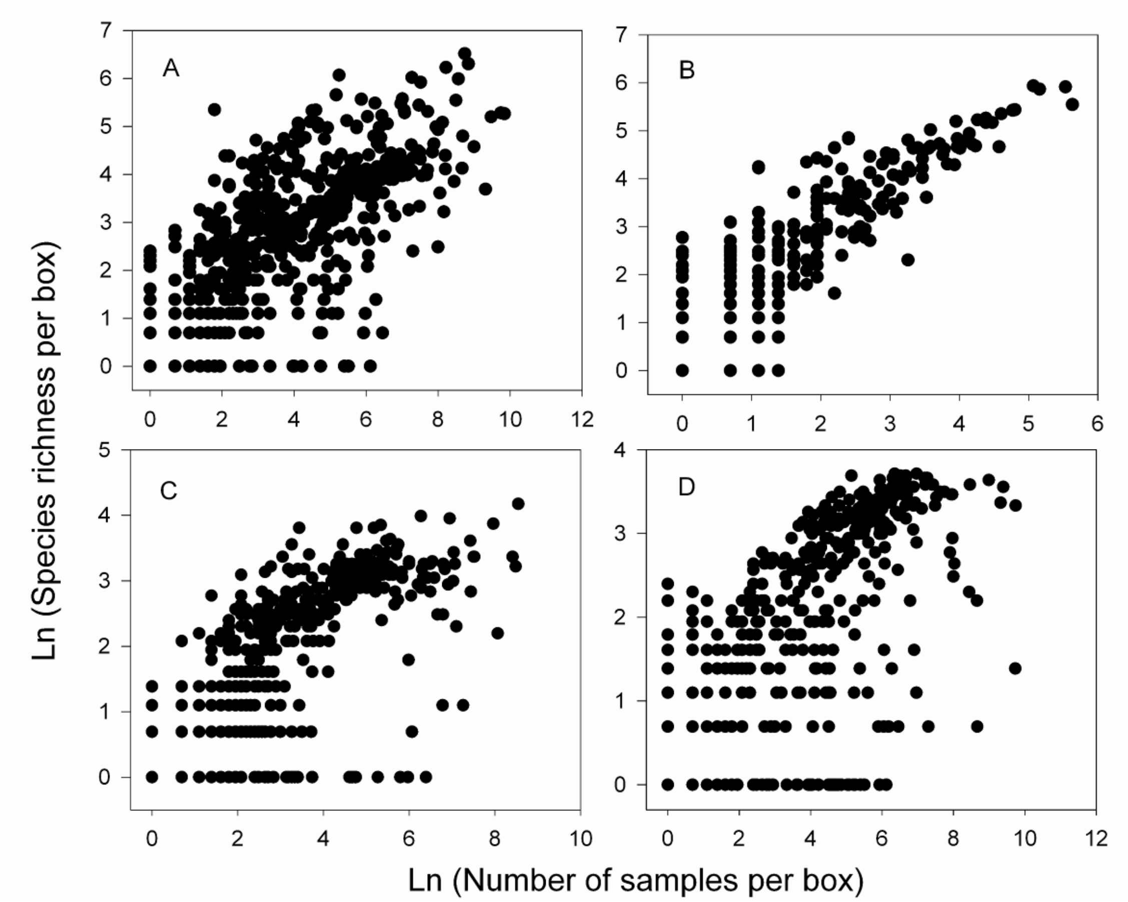


Figure 3.9. The relationship between sampling intensity (number of sample stations per grid cell) and species richness (number of species recorded for that grid cell), both variables natural log-transformed. A. All taxa. B. Benthic taxa only. C. Pelagic (planktonic) taxa only. D. Seabirds and marine mammals.

Marine ecologists sampling benthos generally attempt to record all the species collected, and this results in a much tighter relationship between the number of samples and the species richness (Figure 3.9b). Whilst there are grid cells with up to 16 species recorded from only a single sample station, there are also cells with four stations but only a single species recorded. The influence of large numbers of stations recording only a single species of interest is shown most clearly in the data for plankton (Figure 3.9c); this plot clearly mixes stations where only the target species was recorded (typically *Euphausia superba*), with stations where a complete inventory of the sampled fauna was attempted. The data for birds and mammals (Figure 3.9d) show evidence of a similar mix of sampling strategies, together with an indication that species richness reaches an asymptote of around 41 species.

These plots indicate that although some grid cells have been well sampled and a high species richness recorded, many other boxes have been subject to a very different sampling strategy, and the preliminary maps of richness shown here (Figures 3.2 to 3.6) are thus heavily influenced by the spatial pattern of the different sampling strategies. The overall pattern reveals a small number of areas where high species numbers do not appear to be coupled directly to high sampling intensity, particularly for benthos; these include South Georgia, the South Orkney Islands, the South Shetland Islands, the Eastern Weddell Sea, Prydz Bay and the Ross Sea. Of these, whilst the high benthic species richness for the Weddell Sea and South Shetland Islands does correspond with above average sampling intensity, those at South Georgia, the South Orkney Islands, East Antarctica and the Ross Sea correspond with far lower levels of sampling. These latter areas thus show the effect of intense taxonomic work coupled with good sample coverage, rather than sampling intensity alone. Where intense sampling is matched with strong taxonomic expertise an individual cruise to a new area can detect high levels of benthic diversity, for example 15 phyla representing 29 classes of animals in just 29 trawls (Griffiths et al., 2008). It is also striking that many of the grid cells with high benthic species richness are close to research bases with a long history of benthic expertise.

These biases have not, however, prevented the construction of biogeographic schemes, either for well-studied individual groups such as Mollusca (Linse et al. 2006) or Amphipoda (De Broyer & Jazdzewski, 1993), or based on a combination of taxa (Hedgpeth, 1969; Griffiths, 2009). An improved understanding of the real patterns of species richness in the Southern Ocean requires both a more even spread of sampling effort, and the development of improved statistical methods for removing the effects of sampling bias.

Patterns for individual taxonomic or ecological groups

Each of the major functional groups examined showed different patterns of station distributions and species richness hotspots, and there was relatively little correspondence between them apart from a general tendency for more intense sampling in the northern AP, the Weddell Sea, Ross Sea and off East Antarctica. The distribution of planktonic station numbers (Figure 3.2c) is almost identical to that of the Arthropoda, and this is because the data are dominated by records from the Continuous Plankton Recorder (CPR) data in East Antarctica and more localized sampling in the Scotia Sea. The pattern for planktonic species numbers (Figure 3.2d) differs notably from that of the Arthropoda, with no single overriding hotspot and, instead, more of a pattern that tends to reflect sampling effort. The highest numbers of species are reported from the Australian section of East Antarctica with even hotspots representing relatively low numbers of species (~36).

Higher predator data (birds and mammals) clearly shows two regions of high sampling intensity (Figure 3.6a). The number of samples is reflected in the number of observed species for many areas. Once again the South Shetland Islands and the Australian section of East Antarctica contain high numbers of both stations and species. (Figure 3.6a, b). Fish data are largely concentrated in the Scotia Sea, with patchy data from EA (Figure 3.6c, d). Elephant Island is a hotspot for both fish stations (91) and species (52). Other fish species hotspots include the eastern Weddell Sea, South Georgia, South Shetland Islands and the Victoria Land coast of the Ross Sea.

Linking the pelagic and benthic realms

One major conceptual problem in amalgamating large volumes of marine diversity data into a single dataset is the very different ways in which benthic, pelagic and free-flying organisms are sampled and recorded. The benthos has traditionally been studied using remote sampling gear such as bottom trawls and dredges, box corers or grabs, remote imagery from remotely operated vehicles or submersibles, or in shallow waters by SCUBA divers; plankton are sampled using towed nets, and the Continuous Plankton Recorder (CPR); seabirds and marine mammals are recorded from observation data or their location determined remotely from electronic geolocator tags.

Sampling for plankton is largely concentrated around the continental shelf regions and islands. The majority of the open ocean sampling has been undertaken in the Australian section of East Antarctica, an area regularly surveyed by the Southern

Ocean CPR, which is deployed opportunistically behind vessels in transit to research stations, particularly those vessels from Australia travelling to and from the Casey, Davis and Mawson Stations. These CPR transects are approximately 450 nautical miles long and are processed and recorded in 5 nautical mile sections, giving ~90 stations per tow. Localized sampling around the South Shetland Islands is related to the high numbers of national bases and research stations (16) in the region enabling both work in transit and more localized small boat based research.

Station data for seabirds and marine mammals comprise a combination of observation based data (from ships, small boats and shore) and data from individuals carrying electronic geolocator tags. In the case of the major station hotspots (grid cells to the west of the Antarctic Peninsula and off the Mawson Coast) the high numbers of stations can be explained by tracking data collected for tagged crabeater seals (*Lobodon carcinophagus)* and Adélie penguins (*Pygoscelis adeliae*) respectively. Geolocator data from electronic tags provides a great deal of information for a small number of individual animals and can give the impression of high sampling effort. In reality the high number of stations represents a small number of tracks divided up into time intervals. Ecologists working with such data use a variety of geostatistical techniques to retrieve meaningful distribution data from large volumes of geolocator records (Williams et al., 2002), and a challenge for databases such as SCAR-MarBIN is to incorporate such interpreted data so that vertebrate geolocator data can be used alongside catch or observation data without biassing the results.

The data for fish sampling effort is concentrated around the historically fished areas of South Georgia, the South Orkney Islands and Elephant Island (Kock, 1992). Of these historic fishing grounds, South Georgia is the only currently active fin-fishery. Other active fisheries include the Heard Island region and the Ross Sea (Williams *et al*., 2002; Horn, 2002) which appear to be under-represented in SCAR-MarBIN in terms of both commercial and scientific fisheries data. The absence of the majority of recorded commercial catch data (held by the Convention for the Conservation of Antarctic Marine Living Resources, CCAMLR) from the database means that the numbers of fish stations and species per grid cell are significantly underestimated within this study.

At present these data are thus not helpful in identifying ecological patterns, such as for example areas where bentho-pelagic coupling is particularly important, or where zooplankton abundance might be linked to vertebrate predator feeding. Plankton species numbers are typically far lower than those of the benthos, despite having a far higher average number of samples per grid cell. The well sampled South Shetland Islands appear to be less diverse than some neighboring areas. This could be the result of the different types of sampling and research carried out in the Scotia Sea. The Scotia Sea is an area fished commercially for krill and therefore the majority of records for the area will be from targeted krill research and catches that may not have reported or sampled for non-target species. The opposite is true for the Australian section of EA, with the majority of data provided by the CPR, which is a non-targeted study aimed at recording all species present (although it does not record the majority of gelatinous organisms as they tend not to be well preserved using this method).

FUTURE PERSPECTIVES

The approach taken by SCAR-MarBIN, combining a collection of both large and small datasets adds value to all of the individual contributions and enables the scientific community to see a wider picture of the state of marine biological research and biodiversity in the Southern Ocean. The critical importance of the development and continuation of taxonomic expertise is illustrated clearly by the RAMS which forms a cornerstone of this database and removes any potential confusion due to synonymies. SCAR-MarBIN has thus already proved to be an invaluable resource for marine ecologists interested in the marine diversity and biogeographic patterns in the Southern Ocean. A major limitation, however, is that not all extant data are yet available through the SCAR-MarBIN portal, and this restricts the value of any analyses. In particular cetacean and marine vertebrate tracking data are only poorly represented, and regions known for large colonies of birds and mammals, are therefore currently significantly under-represented in SCAR-MarBIN. A notable exception is the large dataset for East Antarctica, which shows a relatively uniform distribution of species numbers from the continent out to the Antarctic Polar Front.

In addition many taxa that are known to be ecologically significant or speciose in the region are absent or only represented by a handful of data points, notable examples here are the phyla Porifera and Nemertea. Furthermore several classes of arthropods known to have a wealth of existing records for the Southern Ocean in the literature are currently not well represented in the database; notable examples here are pycnogonids and isopods. Current efforts within the Antarctic scientific community to assemble databases on these groups together with the Annelida and Bryozoa will, in coming years, increase the size, geographic range and taxonomic scope of SCAR-MarBIN. The best represented invertebrate phyla (Mollusca, Cnidaria, Echinodermata and Arthropoda) are those which have had one or more dedicated databases created to study their biogeography: these include SOMBASE for molluscs (Griffiths et al., 2003), databases for hexacorallians of the world (http://hercules.kgs.ku.edu/hexacoral/anemone2/index.cfm), Antarctic Echinoids (David et al., 2003) and amphipods (http://www.scarmarbin.be/ramsamphipoda.php), and the Southern Ocean CPR database (http://data.aad.gov.au/aadc/cpr/). Detailed databases such as these, with strong taxonomic control and including biogeographic information will be important in our attempts to understand large scale patterns in Antarctic biogeography. They do, however, rely on accurate identifications from expert taxonomists and distribution data assembled from international sources.

One technical advance which promises to revolutionise work on the diversity and biogeography of the Antarctic marine biota is the development of molecular techniques (Grant & Linse, 2009). In particular such work is starting to uncover a wealth of cryptic species within what were once regarded as single widely-distributed species (Mahon et al., 2008; Held & Wägele, 2005); not only does this work increase the known species richness of the Southern Ocean, but it also influences biogeographic patterns (typically reducing the range size or depth range) and hence affects our interpretation of the evolutionary history of the fauna. SCAR-MarBIN and the RAMS will be important tools in providing the repository of the latest data for the scientific community, both within and outside Antarctic.

The preliminary study reported here gives a snapshot of a constantly evolving database, showing what can be achieved currently and demonstrating the enormous potential for the future. The addition of data for currently under-represented taxa, data sets not yet available, coupled with the extensive new data arising from the recent CAML cruises, should give us a strong benchmark against which future changes in the region can be measured.

CHAPTER 4 - TOWARDS A GENERALIZED BIOGEOGRAPHY OF THE SOUTHERN OCEAN BENTHOS.

[The data in this chapter are also presented in: Griffiths, H.J., Barnes, D.K.A. & Linse, K. (2009) Towards a generalized biogeography of the Southern Ocean benthos. Journal of Biogeography, 36: 162-177.]

Chapter 4 - TOWARDS A GENERALIZED BIOGEOGRAPHY OF THE SOUTHERN OCEAN BENTHOS.

INTRODUCTION

The distribution of organisms on the Southern Ocean (SO) seabed largely reflects the complex interaction of geological, oceanographic and biological elements through space and time. The interpretation of such distributions can lead to a greatly increased understanding of the role of the SO in shaping ecological processes in the Southern Hemisphere. The early Antarctic expeditions such as *R.R.S. Discovery* (1925–27) and *H.M.S. Challenger* (1872–76) concentrated their efforts on the collection and identification of fauna, but it was not until later that scientists began to investigate how they were spatially distributed – Antarctic biogeography. Based on only a tiny proportion of the number of species we know now, Ekman (1935, 1953) suggested that the Antarctic shelf fauna was highly independent and could be divided into subregions. He defined these as South Georgia, West Antarctica (Weddell Sea, Graham Land and its surrounding islands) and East Antarctica. Ekman (1935, 1953) also suggested that the source of the apparent split could be due to gaps in knowledge; for example, a lack of samples from the East Antarctic Peninsula or the Amundsen Sea. Similarly, Powell (1951, 1955, 1960) subdivided the sub-Antarctic into three regions, Magellan, Kerguelenian and Antipodean, and eventually concluded that it was 'not desirable at this stage of our knowledge of southern high-latitude molluscs to formulate a comprehensive scheme of proposed biogeographic provinces' (Powell, 1965). Only 4 years later, however, Hedgpeth (1969) proposed his biogeographical zones of the Antarctic and sub-Antarctic, which have remained the cornerstone of much of modern Antarctic benthic biogeography. Referencing Ekman, he too shows a South Georgia province and an East Antarctica–West Antarctica split, although he also questions the validity of such a split and suggests that increased knowledge would diminish support for this pattern (Hedgpeth, 1971). Hedgpeth (1969) also defined the sub-Antarctic as Magellanic, Tristan da Cunha and Kergeulenian (including the New Zealand sub-Antarctic islands), which was later adapted by Dell (1972) to combine East and West Antarctica into a single Antarctic region including a South Georgia district, once again citing the state of current knowledge.

In the last 35 years there has been a proliferation of work examining SO biogeography referencing previous studies as the definitive patterns in Antarctic biogeography. Arnaud (1974), White (1984), De Broyer & Jazdzewski (1996), Barnes & De Grave (2000), Clarke & Johnston (2003), Rodriguez et al. (2007) and many others define their biogeographical regions or categories based upon those of Hedgpeth (1969). The more recent works range in taxonomic scale from discussing the SO benthos as a whole to individual groups of taxa, for example sea anemones (Rodriguez et al., 2007), bryozoans (Barnes & De Grave, 2000) and amphipods (De Broyer & Jazdzewski, 1996), while most recently, Linse et al. (2006) and Clarke et al. (2007) concentrated on biogeographical patterns of the molluscs within the Polar Front (PF), without including any initial assumptions based on previous studies. The resulting patterns tended to agree with those of Hedgpeth (1969) but went on to define finer-scale divisions within East Antarctica and splitting West Antarctica into the Antarctic Peninsula and Weddell Sea components.

Many publications have now used, or slightly adapted, Hedgpeth's (1969) regions but tend not to include the doubts of the original author about the validity of the observed differences between East and West Antarctica. Subsequently, this inherited assumption of a divided Antarctic fauna has been used as the basis of most biogeographical analyses. The sampling locations for molluscs shown by Clarke et al. (2007) are a good illustration of the large gaps in our knowledge of the Antarctic benthos and demonstrate that a complete lack of sampling in the Amundsen Sea coupled with poor sampling of the Bellingshausen Sea coincide directly with the border between East and West Antarctica in Hedgpeth's (1969) regionalization. Furthermore, Hedgpeth's original distribution maps show large gaps in sampling in the Weddell Sea and Dronning Maud Land, which correspond exactly with the other boundary of this split. Further areas of paucity of sampling include the western Weddell Sea (East Antarctic Peninsula) and parts of Wilkes Land. Recent advances in publicly available Antarctic species distribution data such as SCAR-MarBIN (http://www.scarmarbin.be/) have shown these sampling gaps to be true across all benthic taxa. Our knowledge across faunal taxa in other Antarctic regions has, however, greatly increased over the last 30 years (reviewed in Clarke & Johnston, 2003).

In the current study I investigate whether the biogeographical regions proposed by Hedgpeth (1969) and widely adopted by other authors hold true, are an oversimplification or would show a unified Antarctic province with further data as suggested in his key paper. To accomplish this, the current work uses several model taxa to test for biogeographical patterns around the SO and examine any commonality. I attempt to answer the key question of whether it is possible to draw up general rules or trends for the SO benthos as a whole or on a group-by-group basis. My study goes beyond the scope of previous work to include comparisons with the SO's nearest geographical neighbours from South America, South Africa, Tasmania and New Zealand, allowing the Antarctic fauna to be placed into a Southern Hemisphere context. This is crucial given the historic relationships and links between the (Gondwanan origin) fauna from the time when their shelf areas were closely connected. The approach I take is to analyse some of the best-studied taxa and start without a pre-conceived notion of how these regional components interact. Once identified, potential causes for any patterns will be considered, including oceanographic, geological and biological factors.

MATERIALS AND METHODS

Biogeographical regions and data

The 29 regions used for my analyses combine those previously used for the Mollusca (Linse et al., 2006; Clarke et al., 2007a) and for the Bryozoa (Barnes & Griffiths, 2008) in recent biogeographical studies. The data within these regions include the most recent record updates to SOMBASE (the Southern Ocean Mollusc Database, Griffiths et al., 2003). For this comparative study new regions were added for the molluscs, including South Africa (Costello et al., 2007), Tasmania (Grove et al., 2006) and the Kermadec Islands (Spencer et al., 2002), while the lists for New Zealand (Spencer et al., 2002) and Southern Argentina (Rosenberg, 2005) were updated (Figure 4.1).

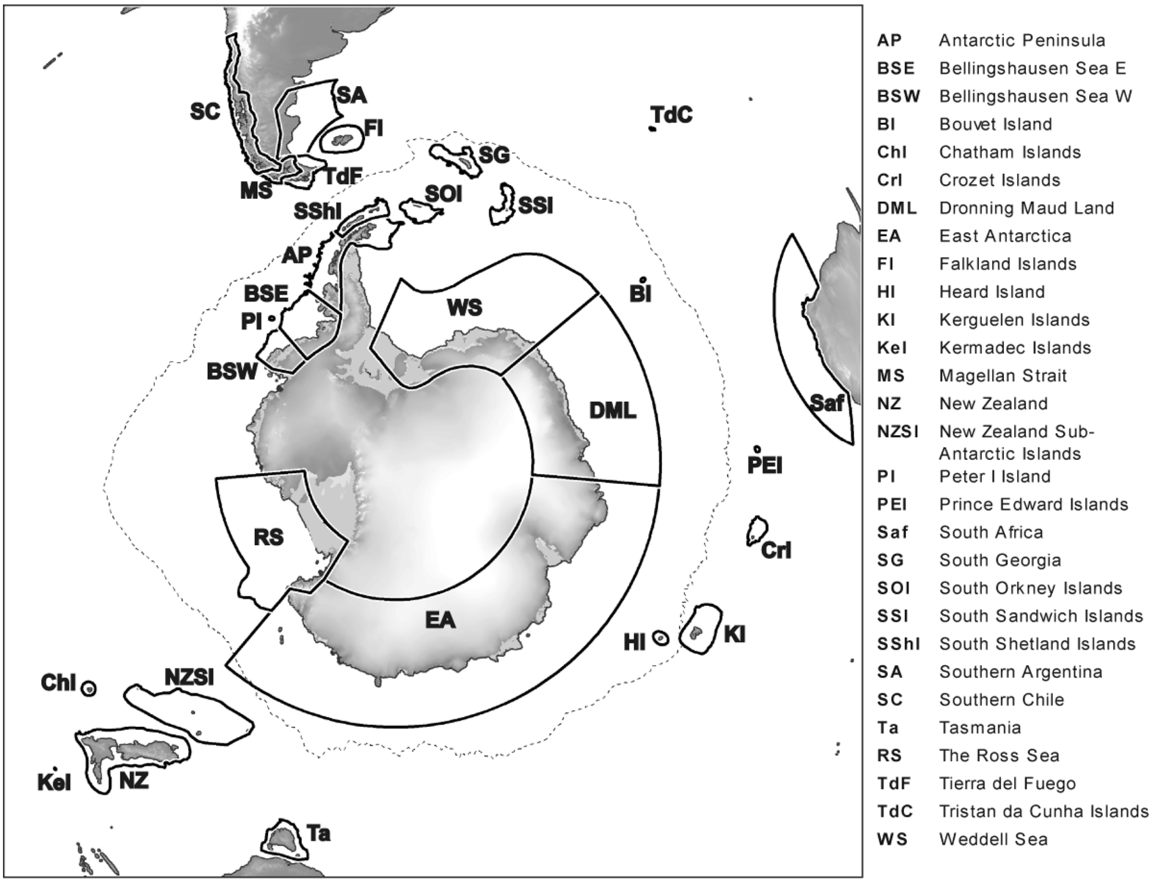


Figure 4.1. The 29 study regions in the Southern Hemisphere. A key to study regions is included in the figure. Grey dotted line = mean position of Antarctic Polar Front (from Moore et al., 1999).

The bathymetric range of the species occurrence records in the regions has been modified to cover depths of 0–3000 m. Some regions used in Linse et al. (2006), Clarke et al. (2007) and Barnes & Griffiths (2008) were merged to allow for comparison between the molluscan and bryozoan data sets due to differing regional boundaries between the data sets. The two subregions of New Zealand used in Barnes & Griffiths (2008) have become a single region. Data from the Bounty, Auckland, Campbell and Macquarie islands were combined to form the New Zealand sub-Antarctic Island region. The areas around Antarctica between 45° and 170° E (Linse et al., 2006) were combined to form a single East Antarctic region. I refer to all regions within the PF (Figure 4.1) as Antarctic. The term Southern Ocean is used when referring to the Antarctic and the sub-Antarctic islands, outside, but close to and influenced by, the PF, e.g. the Prince Edward Islands, Crozet Islands and Kerguelen Islands. For each of my designated regions, the area of seafloor shallower than 3000 m was calculated to analyse the effect of regional size on the species richness (Table 4.1).

Table 4.1. The area (km^2) of sea floor, between 0 and 3000 m depth, and number of species and genera within each region.

		Bryozoa				Mollusca			
		Cyclostomata		Cheilostomata		Bivalvia		Gastropoda	
Region	Area (km^2)	Species	Genera	Species	Genera	Species	Genera	Species	Genera
Antarctic Peninsula	353773	34	14	147	70	55	31	107	65
Bellingshausen Sea E	247251	22	12	127	68	15	12	8	8
Bellingshausen Sea W	86753	23	12	125	69	8	6	2	2
Bouvet Island	2626	2	1	20	17	14	11	22	20
Chatham Islands	30045	2	1	120	69	146	106	309	190
Crozet Islands	68450			10	9	11	10	75	44
East Antarctica	2113684	26	12	105	51	54	29	150	77
Dronning Maud Land	407434	29	12	97	50	11	11	94	52
Falkland Islands	158879	32	15	116	60	49	40	77	42
Heard Island	27332	10	7	37	25	3	3	12	9
Kerguelen Islands	252265	14	9	54	34	31	24	101	54
Kermadec Islands	722			203	112	77	59	296	188
Magellan Strait	25293	29	18	132	74	56	48	60	41
New Zealand	550220	32	18	423	161	380	195	1376	486
NZ Sub-Antarctic Islands	627604	12	8	114	69	105	63	293	145
Peter I Island	2007			12	11	9	8	17	13
Prince Edward Islands	3894	6	5	45	27	20	17	32	27
South Africa	581063	20	13	326	132	221	115	1050	325
South Georgia	122672	21	12	105	58	53	32	146	75
South Orkney Islands	91170	12	8	100	57	32	26	84	51
South Sandwich Islands	80294	7	6	43	32	30	22	30	26
South Shetland Islands	104180	28	14	139	67	62	33	99	59
Southern Argentina	488073	17	12	128	68	89	71	295	146
Southern Chile	147186	28	17	126	67	64	55	61	41
Tasmania	175120	7	5	237	110	232	146	879	385
The Ross Sea	679693	24	14	176	81	47	32	150	83
Tierra del Fuego	96920	41	21	156	81	67	43	111	64
Tristan da Cunha Islands	2293	16	11	42	31	5	5	7	4
Weddell Sea	639681	25	11	76	39	67	36	214	86
Antarctic	4958549	66	24	320	111	141	53	543	170
Southern Ocean	5283158	70	25	356	115	162	57	611	175

Taxon counts and endemism

The overall data set included occurrence data on species of two molluscan classes, Bivalvia and Gastropoda, and two bryozoan classes, Cyclostomata and Cheilostomata. When referring to the gastropod molluscs only shelled species have been considered. The data set was queried to produce a list of species per class per region, where each species was accounted for only once regardless of how many times it was found within a region; the same was done at the genus level for each of the classes. The regional species and genera lists were used to produce regional counts of taxa per class (Table 4.1) and the regional species lists were also used to calculate regional endemism rates. For the purposes of my investigation, endemic species were those found only within a single region (analysis included occurrences within the data base which fell outside my defined regions, e.g. deeper than 3000 m). It is appreciated that data have not been comprehensively included for sites to the north of the South African and Kermadec Islands regions (for all classes) and for Southern Argentina, Southern Chile and Tasmania (for the Gastropoda and Bivalvia). For these regions, therefore, species may have ranges that extend beyond these study areas and may not be truly endemic, but are not shared between my study regions. From the numbers of endemic species I produced a percentage of the total number of species per region that were endemic (Table 4.2) and this process was repeated twice, first combining the Antarctic regions and second the SO regions.

Table 4.2. The percentage of endemic species per study class and region. Pycnogonid data from Munilla & Soler (2009) and Cephalopoda data from Collins & Rodhouse (2006). The regions for which numbers may not reflect the true endemism levels as more northerly distributions are not accounted for are South Africa and the Kermadec Islands (for all classes) and Southern Argentina, Southern Chile and Tasmania (for the Gastropoda and Bivalvia).

	Cyclostomata	Cheilostomata	Bivalvia	Gastropoda	Pycnogona	Cephalopoda
Antarctic Peninsula	0.00	3.40	1.82	10.28		
Bellingshausen Sea E	0.00	0.00	6.67	37.50		
Bellingshausen Sea W	0.00	0.00	12.50	0.00		
Bouvet Island	0.00	5.00	14.29	50.00		
Chatham Islands	0.00	9.17	8.90	14.24		
Crozet Islands	0.00	10.00	18.18	5.33		
Dronning Maud Land	0.00	0.00	0.00	21.28		
East Antarctica	0.00	2.86	11.11	13.33		
Falkland Islands	12.50	4.31	10.20	22.08		
Heard Island	0.00	8.11	0.00	0.00		
Kerguelen Islands	0.00	3.70	22.58	15.84		
Kermadec Islands	0.00	30.54	68.83	70.95		
Magellan Strait	3.45	6.06	23.21	8.33		
New Zealand	59.38	37.83	52.37	65.55		
NZ Sub-Antarctic Islands	8.33	2.63	23.81	28.67		
Peter I Island	0.00	0.00	0.00	11.76		
Prince Edward Islands	16.67	11.11	25.00	12.50		
South Africa	20.00	21.78	93.67	97.05		
South Georgia	4.76	15.24	13.21	36.30		
South Orkney Islands	0.00	2.00	0.00	25.00		
South Sandwich Islands	0.00	0.00	6.67	26.67		
South Shetland Islands	7.14	5.04	3.23	4.04		
Southern Argentina	0.00	7.03	65.17	68.47		
Southern Chile	10.71	19.84	32.81	29.51		
Tasmania	0.00	2.11	93.10	93.29		
The Ross Sea	4.17	5.11	0.00	16.00		
Tierra del Fuego	9.76	12.18	28.36	18.02		
Tristan da Cunha Islands	25.00	16.67	60.00	100.00		
Weddell Sea	4.00	5.26	5.97	26.17		
Antarctic	46.97	55.63	42.55	73.66	54.70	53.45
Southern Ocean	47.14	53.93	49.38	78.89	56.90	60.00

I used the list of endemic species produced during the previous analyses and counted how many of those species occurred in each of the regions to measure the regional input to the overall number of SO endemic species. This was repeated for all four classes in the study. The proportion of SO endemic species in each region was measured as a percentage of the total number of species in the corresponding region. Trends in percentages of each region made up of SO endemic species with geography were tested using the Spearman rank correlation coefficient (rs), calculated by ranking taxon data for each region in terms of percentages and distance from South America and then conducting a Pearson correlation between the ranks.

Biogeographical patterns

Centres of radiation

The relative importance of each region to each genus was measured and standardized to make genera of different sizes (low vs. high number of species) comparable by calculating the maximum number of species from that genus found in any region. Only genera with three or more species in total were selected in order to avoid genera with low numbers of species appearing to be at their maximum in a wide range of locations. The total number of species from each genus per region was calculated as a percentage of this maximum. Regions showing the maximum number of species per genus then all had a value of 100%.

PRIMER analysis

The multivariate statistical software primer 5 (Clarke & Warwick, 2001) was used to analyse faunal similarities between regions by implementing the Bray–Curtis measure performed on non-transformed, species presence/absence data. The similarity matrix was then used for cluster analysis, non-metric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM) tests. Three major groupings were used for the ANOSIM test: Antarctica (BI, PI, SG, SSI, SOI, SShI, AP, WS, RS, BSE, & BSW); South America (SC, MS, SA, FI, HI, PEI, CrI & KI) and New Zealand (NZSI, ChI, NZ, KeI, TA & Saf)

Percentage similarity

A matrix was created showing the number of shared species between each of the regions, and was subsequently used to produce a further matrix, giving the percentage of the total species from each region shared with each of the other regions. The resulting percentage matrix shows the relationship between the regions and the weighting of that relationship. For example, regions A and B may share 20 species, constituting 80% of region A but only 40% of region B, thus implying that the species in region A are a subset of the species found in region B. Reading the table as vertical columns shows the percentage shared from that region's total with each of the regions in the horizontal rows. Any relationships showing a shared composition of 50% or more were drawn on a map as directional arrows pointing from the region being compared with (rows) towards the region being considered (columns). Grouping these arrows allows the identification of large-scale patterns of shared fauna and areas of community overlap.

Cyclostomata

	Southern Chile	Magellan Strait	Tierra del Fuego	Southern Argentina	Falkland Islands	Prince Edward Islands	Crozet Islands	Kerguelen Islands	Heard Island	Bouvet Island	Peter I Island	South Georgia	South Sandwich Islands	South Orkney Islands	South Shetland Islands	Antarctic Peninsula	Weddell Sea	Dronning Maud Land	East Ant	The Ross Sea	Bellingshausen Sea E	Bellingshausen Sea W	NZ Sub-Antarctic Islands	Chatham Islands	New Zealand	Kermadec Islands	Tasmania	South Africa	Tristan da Cunha Islands
Southern Chile	☒	62	44	53	47	17		50	60	0		48	43	50	29	29	20	21	23	33	23	26	33	0	6		29	15	25
Magellan Strait	64	☒	54	53	53	17		50	50	0		48	57	67	36	32	28	31	35	38	36	39	33	0	6		29	15	25
Tierra del Fuego	64	76	☒	76	72	67		79	70	0		48	57	58	39	32	16	17	19	29	27	26	25	0	9		43	15	44
Southern Argentina	32	31	32	☒	34	17		43	30	0		29	43	50	32	21	12	14	15	25	9	9	25	0	13		43	15	25
Falkland Islands	54	59	56	65	☒	17		57	50	0		57	57	67	39	32	24	24	27	42	27	26	17	0	9		43	10	25
Prince Edward Islands	4	3	10	6	3	☒		29	20	0		5	14	8	4	3	0	0	0	0	5	4	0	0	0		0	0	0
Crozet Islands							☒																						
Kerguelen Islands	25	24	27	35	25	67		☒	90	0		33	57	58	29	24	24	21	23	33	27	26	17	0	6		29	10	13
Heard Island	21	17	17	18	16	33		64	☒	0		24	43	42	21	21	16	17	19	29	18	17	17	0	3		14	5	13
Bouvet Island	0	0	0	0	0	0		0	0	☒		0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	10	6
Peter I Island											☒																		
South Georgia	36	34	24	35	38	17		50	50	0		☒	71	75	39	38	28	28	31	38	32	30	17	0	9		29	5	6
South Sandwich Islands	11	14	10	18	13	17		29	30	0		24	☒	58	25	15	4	7	8	13	5	4	8	0	6		14	10	6
South Orkney Islands	21	28	17	35	25	17		50	50	0		43	100	☒	39	26	20	21	23	29	18	17	17	0	9		29	10	13
South Shetland Islands	29	34	27	53	34	17		57	60	0		52	100	92	☒	71	48	34	35	42	36	35	25	0	9		29	10	19
Antarctic Peninsula	36	38	27	41	34	17		57	70	0		62	71	75	86	☒	80	62	65	75	73	74	33	0	6		14	10	25
Weddell Sea	18	24	10	18	19	0		43	40	0		33	14	42	43	59	☒	66	65	58	59	61	8	0	3		14	10	13
Dronning Maud Land	21	31	12	24	22	0		43	50	0		38	29	50	36	53	76	☒	100	75	59	61	17	0	3		14	15	13
East Ant	21	31	12	24	22	0		43	50	0		38	29	50	32	50	68	90	☒	71	59	61	17	0	3		14	15	13
The Ross Sea	29	31	17	35	31	0		57	70	0		43	43	58	36	53	56	62	65	☒	55	57	17	0	3		14	15	19
Bellingshausen Sea E	18	28	15	12	19	17		43	40	0		33	14	33	29	47	52	45	50	50	☒	96	25	0	3		14	5	19
Bellingshausen Sea W	21	31	15	12	19	17		43	40	0		33	14	33	29	50	56	48	54	54	100	☒	25	0	3		14	10	19
NZ Sub-Antarctic Islands	14	14	7	18	6	0		14	20	0		10	14	17	11	12	4	7	8	8	14	13	☒	50	16		71	5	13
Chatham Islands	0	0	0	0	0	0		0	0	0		0	0	0	0	0	0	0	0	0	0	0	8	☒	6		0	5	0
New Zealand	7	7	7	24	9	0		14	10	0		14	29	25	11	6	4	3	4	4	5	4	42	100	☒		57	25	6
Kermadec Islands																										☒			
Tasmania	7	7	7	18	9	0		14	10	0		10	14	17	7	3	4	3	4	4	5	4	42	0	13		☒	5	13
South Africa	11	10	7	18	6	0		14	10	100		5	29	17	7	6	8	10	12	13	5	9	8	50	16		14	☒	19
Tristan da Cunha Islands	14	14	17	24	13	0		14	20	50		5	14	17	11	12	8	7	8	13	14	13	17	0	3		29	15	☒

Cheilostomata

	Southern Chile	Magellan Strait	Tierra del Fuego	Southern Argentina	Falkland Islands	Prince Edward Islands	Crozet Islands	Kerguelen Islands	Heard Island	Bouvet Island	Peter I Island	South Georgia	South Sandwich Islands	South Orkney Islands	South Shetland Islands	Antarctic Peninsula	Weddell Sea	Dronning Maud Land	East Ant	The Ross Sea	Bellingshausen Sea E	Bellingshausen Sea W	NZ Sub-Antarctic Islands	Chatham Islands	New Zealand	Kermadec Islands	Tasmania	South Africa	Tristan da Cunha Islands
Southern Chile	☒	56	49	47	49	36	50	50	27	25	0	19	21	14	11	8	1	2	2	5	5	4	18	9	6	5	5	3	29
Magellan Strait	59	☒	56	53	62	38	50	48	32	20	0	26	21	17	14	10	1	4	4	6	7	7	18	13	6	6	4	2	21
Tierra del Fuego	60	67	☒	65	65	42	50	59	38	25	0	24	19	17	14	9	3	4	4	5	6	6	20	10	6	6	4	3	31
Southern Argentina	48	52	53	☒	66	31	60	48	35	30	0	21	19	16	12	7	4	4	4	5	6	6	21	8	7	7	5	4	31
Falkland Islands	45	55	48	59	☒	33	50	50	35	20	0	26	21	16	13	10	0	6	6	7	8	8	18	8	5	6	3	2	29
Prince Edward Islands	13	13	12	11	13	☒	70	44	41	30	0	6	7	4	4	2	0	2	2	3	2	1	7	4	2	4	1	3	10
Crozet Islands	4	4	3	5	4	16	☒	13	14	20	0	3	5	3	3	1	0	3	3	2	1	1	3	0	1	1	0	1	7
Kerguelen Islands	21	20	21	20	23	53	70	☒	70	40	0	12	12	9	6	4	0	3	3	3	3	2	11	8	4	5	2	3	14
Heard Island	8	9	9	10	11	33	50	48	☒	30	0	7	5	5	3	2	0	3	3	3	2	2	7	3	3	4	2	4	10
Bouvet Island	4	3	3	5	3	13	40	15	16	☒	8	11	19	11	7	6	4	10	10	5	5	4	7	0	1	0	0	1	5
Peter I Island	0	0	0	0	0	0	0	0	0	5	☒	5	14	6	6	7	5	3	3	6	7	8	4	0	0	0	0	0	0
South Georgia	16	20	16	17	23	13	30	24	19	60	42	☒	70	55	41	38	29	34	32	31	35	35	26	3	2	1	1	1	14
South Sandwich Islands	7	7	5	6	8	7	20	9	5	40	50	29	☒	29	23	22	13	19	17	16	19	20	13	0	1	1	1	1	10
South Orkney Islands	11	13	11	13	14	9	30	17	14	55	50	52	67	☒	60	55	55	45	44	46	54	54	34	2	1	1	2	2	10
South Shetland Islands	12	14	12	13	16	13	40	17	11	50	67	54	74	83	☒	72	62	57	54	57	64	62	40	3	2	2	3	2	12
Antarctic Peninsula	10	11	8	9	13	7	20	11	8	45	83	53	74	81	76	☒	70	66	63	69	76	76	39	3	1	2	2	2	7
Weddell Sea	1	1	1	2	0	0	0	0	0	15	33	21	23	42	34	36	☒	40	39	38	41	42	28	0	0	0	1	0	2
Dronning Maud Land	2	3	3	3	5	4	30	6	8	50	25	31	42	44	40	44	51	☒	92	47	53	50	33	0	1	0	1	1	5
East Ant	2	3	3	3	5	4	30	6	8	50	25	32	42	46	41	45	54	100	☒	48	54	52	35	0	1	0	2	2	5
The Ross Sea	6	8	5	7	10	13	30	9	14	45	83	52	67	81	72	82	88	85	80	☒	87	87	43	2	2	1	2	2	7
Bellingshausen Sea E	5	7	5	5	9	4	10	7	8	30	75	42	56	68	58	66	68	69	65	63	☒	94	39	2	1	1	1	1	5
Bellingshausen Sea W	4	7	5	5	9	2	10	6	5	25	83	42	58	67	56	65	68	65	62	62	92	☒	38	1	1	1	0	1	5
NZ Sub-Antarctic Islands	16	16	15	19	17	18	30	22	22	40	33	29	35	39	33	31	42	39	38	28	35	34	☒	13	11	10	10	5	21
Chatham Islands	9	11	8	7	9	11	0	17	11	0	0	3	0	2	2	2	0	0	0	1	2	1	14	☒	24	22	10	6	19
New Zealand	21	18	17	24	19	22	40	35	32	15	0	7	9	6	5	4	3	3	3	5	4	3	39	86	☒	58	29	18	43
Kermadec Islands	8	9	8	11	10	20	20	20	22	5	0	3	5	2	3	3	0	1	1	2	2	2	18	38	28	☒	14	10	24
Tasmania	10	7	6	9	7	7	10	9	11	5	0	2	5	4	4	3	3	2	4	3	2	1	21	19	16	16	☒	48	19
South Africa	8	6	6	10	6	20	20	19	32	10	8	3	7	5	4	3	1	2	5	4	3	3	15	16	14	17	66	☒	45
Tristan da Cunha Islands	10	7	8	10	10	9	30	11	11	10	0	6	9	4	4	2	1	2	2	2	2	2	8	7	4	5	3	6	☒

Gastropoda

	Southern Chile	Magellan Strait	Tierra del Fuego	Southern Argentina	Falkland Islands	Prince Edward Islands	Crozet Islands	Kerguelen Islands	Heard Island	Bouvet Island	Peter I Island	South Georgia	South Sandwich Islands	South Orkney Islands	South Shetland Islands	Antarctic Peninsula	Weddell Sea	Dronning Maud Land	East Ant	The Ross Sea	Bellingshausen Sea E	Bellingshausen Sea W	NZ Sub-Antarctic Islands	Chatham Islands	New Zealand	Kermadec Islands	Tasmania	South Africa	Tristan da Cunha Islands
Southern Chile	☒	32	32	5	21	3	4	2	0	0	0	3	0	2	2	1	1	2	1	1	0	0	0	0	0	0	0	0	0
Magellan Strait	31	☒	41	7	18	9	11	6	0	0	0	5	0	4	3	5	2	3	2	3	0	0	0	0	0	0	0	0	0
Tierra del Fuego	57	77	☒	11	42	16	12	8	0	0	0	10	0	7	3	7	4	3	2	4	13	0	0	0	0	0	0	0	0
Southern Argentina	23	37	30	☒	30	16	16	12	0	5	6	14	0	13	8	11	6	6	6	6	13	0	2	2	1	0	0	0	0
Falkland Islands	26	23	29	8	☒	9	8	8	0	5	0	10	0	7	2	11	2	1	1	3	0	0	1	0	0	0	0	0	0
Prince Edward Islands	2	5	5	2	4	☒	25	19	8	0	6	6	3	6	6	5	3	5	6	5	13	0	1	0	0	0	0	0	0
Crozet Islands	5	13	8	4	8	59	☒	59	33	14	12	10	3	7	12	11	7	10	11	9	13	0	1	0	0	0	0	0	0
Kerguelen Islands	3	10	7	4	10	59	80	☒	67	9	18	16	7	14	19	14	9	11	12	10	13	0	1	0	0	0	0	0	0
Heard Island	0	0	0	0	0	3	5	8	☒	0	6	1	3	6	4	3	1	1	2	1	0	0	1	0	0	0	0	0	0
Bouvet Island	0	0	0	0	1	0	4	2	0	☒	6	2	7	1	2	4	3	1	1	1	0	0	0	0	0	0	0	0	0
Peter I Island	0	0	0	0	0	3	3	3	8	5	☒	3	7	5	7	7	6	7	5	7	0	0	0	0	0	0	0	0	0
South Georgia	7	13	13	7	18	28	20	23	17	14	24	☒	20	35	32	29	16	17	15	17	25	0	1	0	0	0	0	0	0
South Sandwich Islands	0	0	0	0	0	3	1	2	8	9	12	4	☒	7	15	12	5	6	7	7	13	50	0	0	0	0	0	0	0
South Orkney Islands	3	5	5	4	8	16	8	12	42	5	24	20	20	☒	30	29	14	11	17	14	25	0	0	0	0	0	0	0	0
South Shetland Islands	3	5	3	3	3	19	16	19	33	9	41	22	50	36	☒	47	23	27	31	32	50	0	0	0	0	0	0	0	0
Antarctic Peninsula	2	8	7	4	16	16	16	15	25	18	47	21	43	37	51	☒	23	28	29	31	38	0	1	0	0	0	0	0	0
Weddell Sea	5	8	8	4	6	22	21	19	17	27	71	24	37	36	51	46	☒	68	61	59	38	50	0	0	0	0	0	0	0
Dronning Maud Land	3	5	3	2	1	16	12	10	8	5	41	11	20	12	25	24	30	☒	36	37	25	0	0	0	0	0	0	0	0
East Ant	3	5	3	3	3	28	21	18	25	9	47	15	37	30	46	41	43	57	☒	61	38	100	0	0	0	0	0	0	0
The Ross Sea	3	8	5	3	6	22	17	15	17	5	65	17	37	25	48	43	42	59	61	☒	38	50	0	0	0	0	0	0	0
Bellingshausen Sea E	0	0	1	0	0	3	1	1	0	0	0	1	3	2	4	3	1	2	2	2	☒	0	0	0	0	0	0	0	0
Bellingshausen Sea W	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	1	1	0	☒	0	0	0	0	0	0	0
NZ Sub-Antarctic Islands	2	0	1	2	3	9	3	4	17	0	0	1	0	1	1	2	0	0	1	0	0	0	☒	28	14	1	1	0	0
Chatham Islands	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	29	☒	19	4	2	0	0
New Zealand	2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	67	84	☒	27	6	2	0
Kermadec Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	4	6	☒	2	1	0
Tasmania	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	5	4	7	☒	1	0
South Africa	5	2	2	0	1	0	1	1	0	5	0	1	3	0	2	1	1	1	1	1	0	0	1	1	1	4	1	☒	0
Tristan da Cunha Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	☒

Bivalvia

	Southern Chile	Magellan Strait	Tierra del Fuego	Southern Argentina	Falkland Islands	Prince Edward Islands	Crozet Islands	Kerguelen Islands	Heard Island	Bouvet Island	Peter I Island	South Georgia	South Sandwich Islands	South Orkney Islands	South Shetland Islands	Antarctic Peninsula	Weddell Sea	Dronning Maud Land	East Ant	The Ross Sea	Bellingshausen Sea E	Bellingshausen Sea W	NZ Sub-Antarctic Islands	Chatham Islands	New Zealand	Kermadec Islands	Tasmania	South Africa	Tristan da Cunha Islands
Southern Chile	☒	36	27	13	31	20	18	14	0	0	0	14	11	16	9	9	6	10	9	4	14	0	2	1	0	0	0	0	0
Magellan Strait	31	☒	42	16	39	45	45	32	33	33	25	30	37	39	21	28	17	50	19	20	7	14	5	1	1	0	0	0	0
Tierra del Fuego	28	50	☒	21	53	40	55	32	33	42	38	44	53	55	36	40	26	70	26	30	14	14	5	1	1	0	0	0	0
Southern Argentina	19	25	28	☒	39	25	27	39	33	8	25	26	21	26	19	21	14	20	8	11	0	14	4	1	1	0	0	0	0
Falkland Islands	23	34	39	21	☒	40	36	32	0	8	13	33	42	32	30	28	22	40	15	20	7	14	2	0	0	0	0	0	0
Prince Edward Islands	6	16	12	6	16	☒	27	36	0	0	0	23	21	16	9	11	12	30	8	7	7	0	3	0	0	0	0	0	0
Crozet Islands	3	9	9	3	8	15	☒	14	0	17	13	14	21	16	11	13	11	40	9	11	7	0	2	0	0	0	0	0	0
Kerguelen Islands	6	16	13	12	18	50	36	☒	100	17	13	33	26	26	19	17	17	30	13	13	0	14	6	1	0	0	0	0	0
Heard Island	0	2	1	1	0	0	0	11	☒	0	0	5	0	3	2	2	2	0	0	0	0	0	1	0	0	0	0	0	0
Bouvet Island	0	7	7	1	2	0	18	7	0	☒	75	19	32	29	19	23	15	30	21	24	14	14	1	0	0	0	0	0	0
Peter I Island	0	4	4	2	2	0	9	4	0	50	☒	9	11	19	11	15	9	10	9	13	21	29	0	0	0	0	0	0	0
South Georgia	9	23	28	12	29	50	55	50	67	67	50	☒	84	74	55	55	43	90	42	43	29	0	5	0	0	0	0	0	0
South Sandwich Islands	3	13	15	4	16	20	36	18	0	50	25	37	☒	42	36	36	25	90	28	33	29	14	2	0	0	0	0	0	0
South Orkney Islands	8	21	25	9	20	25	45	29	33	75	75	53	68	☒	57	57	40	90	40	50	29	14	2	0	0	0	0	0	0
South Shetland Islands	6	18	25	10	29	20	45	32	33	75	63	60	89	87	☒	79	54	90	53	72	43	29	2	0	0	0	0	0	0
Antarctic Peninsula	6	23	28	11	27	25	55	29	33	92	88	60	89	87	79	☒	54	90	51	67	36	29	2	0	0	0	0	0	0
Weddell Sea	6	20	25	10	29	40	64	39	33	83	75	65	84	84	74	74	☒	100	72	83	71	57	1	0	0	0	0	1	0
Dronning Maud Land	2	9	10	2	8	15	36	11	0	25	13	21	47	29	19	19	15	☒	15	20	14	0	1	0	0	0	0	0	0
East Ant	8	18	21	4	16	20	45	25	0	92	63	51	79	68	60	57	58	80	☒	76	57	43	2	0	1	0	0	0	0
The Ross Sea	3	16	21	6	18	15	45	21	0	92	75	47	79	74	70	66	58	90	66	☒	64	57	1	0	1	1	0	0	0
Bellingshausen Sea E	3	2	3	0	2	5	9	0	0	17	38	9	21	13	13	11	15	20	15	20	☒	71	0	0	0	0	0	0	0
Bellingshausen Sea W	0	2	1	1	2	0	0	4	0	8	25	0	5	3	4	4	6	0	6	9	36	☒	0	0	0	0	0	0	0
NZ Sub-Antarctic Islands	3	9	7	4	4	15	18	21	33	8	0	12	11	6	4	4	2	10	4	2	0	0	☒	28	17	3	1	0	0
Chatham Islands	2	2	1	1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39	☒	35	4	2	0	0
New Zealand	2	4	3	3	2	5	9	4	0	0	0	2	5	3	2	2	2	10	4	4	0	0	63	91	☒	23	5	0	0
Kermadec Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	2	5	☒	1	2	0
Tasmania	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	3	4	☒	0	0
South Africa	0	0	0	0	2	0	0	4	33	0	0	0	0	0	0	0	3	0	2	2	7	0	0	0	0	6	0	☒	0
Tristan da Cunha Islands	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	☒

Table 4.3. Matrices showing the percentage of the total species from each region shared with each of the other regions.

RESULTS

Taxon counts and endemism

My study included geographical occurrence data for 1318 species of bivalves, 4656 species of gastropods, 1465 species of cheilostomes and 167 species of cyclostomes. For all groups other than the cyclostome bryozoans, New Zealand had the highest recorded number of species and genera, followed by Tasmania and South Africa (Table 4.1). Within Antarctic waters the Weddell Sea was a hotspot of species richness for bivalves (67 species, 36 genera) and gastropods (214 species, 86 genera), while the largest numbers of cyclostomes (34 species, 14 genera) were found along the West Antarctic Peninsula and of cheilostomes (176 species, 81 genera) in the Ross Sea. The largest area in this study was the East Antarctic (over 2 million km^2), four times larger than the next largest region. Regions such as New Zealand, the New Zealand sub-Antarctic islands, South Africa, the Ross Sea and Weddell Sea are all of comparable sizes, covering 550,000–650,000 km^2. Smaller island groups and islands cover less than 100,000 km^2 and these areas tended to have the smallest numbers of recorded species, e.g. Bouvet and the Prince Edward Islands. The Kermadec Islands, the smallest area included in the study, showed above average species numbers for the three groups for which data were available. The relationship between area and species numbers for the Gastropoda and Cheilostomata was significant (ANOVA associated with regression: all $F_1 > 4.6$, $P < 0.05$); for the Bivalvia this relationship was not significant ($F_1 < 7.7$, $P \sim 0.05$), but was suggestive of an increasing trend; and for the Cyclostomata there was no clear relationship ($F_1 < 4.1$, $P > 0.05$).

The large number of species in New Zealand is also reflected in its large numbers of species not shared with the other regions, ranging between 37% and 65% for the different classes (Table 4.2), a finding that was also true, to a lesser extent, for the other northern regions. In contrast, the number of endemic species (unique to one region) was much lower in regions within the SO. Remote islands such as the Prince Edward Islands (11–25%) and the Tristan da Cunha Islands (17–100%) show high levels of endemic species.

Within the PF, only the Gastropoda showed any regional endemism, with two geographical exceptions: South Georgia and the Weddell Sea, both with relatively high rates of endemism for all four classes. Of all the Antarctic regions, Bouvet Island showed the highest levels of endemism for both the Gastropoda (50%) and the Bivalvia (14%). No gastropods, bivalves or cyclostomes and only c. 8% of cheilostomes recorded from Heard Island were endemic. Comparison of the percentage of endemism between the four study classes and, based on literature data, the pycnogonids and cephalopods, showed that combining the Antarctic regions into one larger region dramatically increased the percentage of endemism. Most rates of Antarctic species endemism ranged between c. 43% (bivalves) and c. 56% (cheilostomes) with the exception of the gastropods which showed relatively high endemism at c. 74%. The percentage endemism for the larger SO zone (Antarctic and sub-Antarctic Islands) showed the same pattern as for the Antarctic, with most regions increasing by between < 1% and > 6%; however, the percentage for the cheilostomes actually decreased slightly. Once again, Gastropoda (79%) showed a far higher percentage endemism, almost 19% greater than the next highest taxon, the Cephalopoda (60%).

Gastropoda had the highest number of regions that contained endemic species (27 out of 29) (Table 4.2), while cyclostome bryozoans only had endemic species in half of the regions they were recorded in. Figure 4.2a shows the Gastropoda to have the highest number of species restricted to a single region (3664), followed by Bivalvia (915) and Cheilostomata (572), with Cyclostomata the lowest (52). Bryozoans had the species with the highest number of occupied regions (Cheilostomata in 24 and Cyclostomata in 23 regions), i.e. they were the most ubiquitous. Gastropoda were found in a maximum of 14 regions and Bivalvia in 16. All classes showed a marked decrease in the number of species found as the number of regions increased. Figure 4.2b shows the same data but as a percentage of the overall number of species within each class. Gastropoda had the highest percentage of species restricted to a single region (80%), followed by Bivalvia (74%), with a drop to the Cheilostomata (44%) and the Cyclostomata (36%). All classes showed a decrease in the percentage of total species with an increasing number of regions. Gastropoda showed the most rapid decrease with only 1.6% of species found in more than four regions. Similarly, Bivalvia had only 4% of species found in more than four regions, contrasting strikingly with Cheilostomata at 17% and Cyclostomata at 24%.

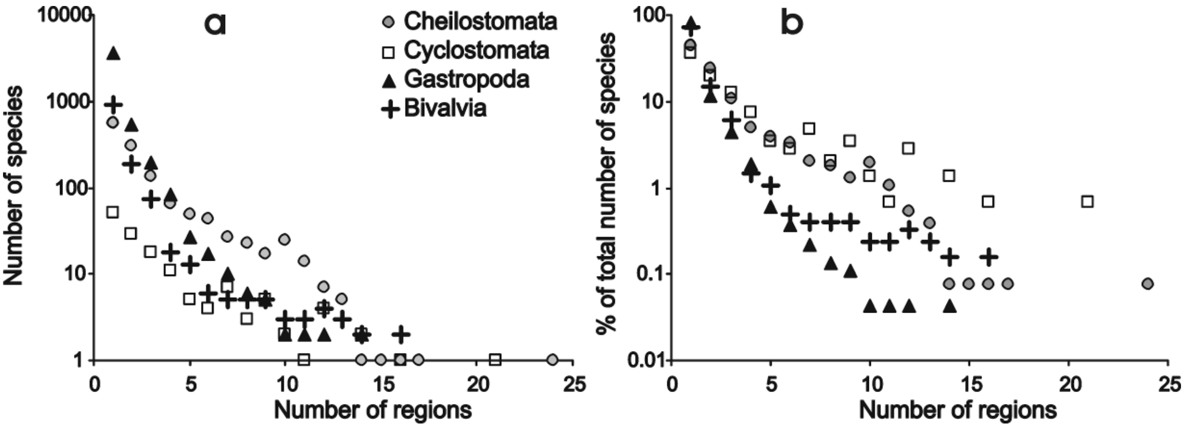


Figure 4.2. Numbers (a) and percentages (b) of species per class found only within a given number of regions.

There were significant correlations between the number of SO endemic species and overall species numbers per region (Figure 4.3). For Gastropoda and Cheilostomata these relationships were particularly strong, both showing R^2 values of > 0.95 (but differing slopes). The Bivalvia and Cyclostomata also had similar but lower R^2 values of c. 0.82. All had P values of less than 0.001.

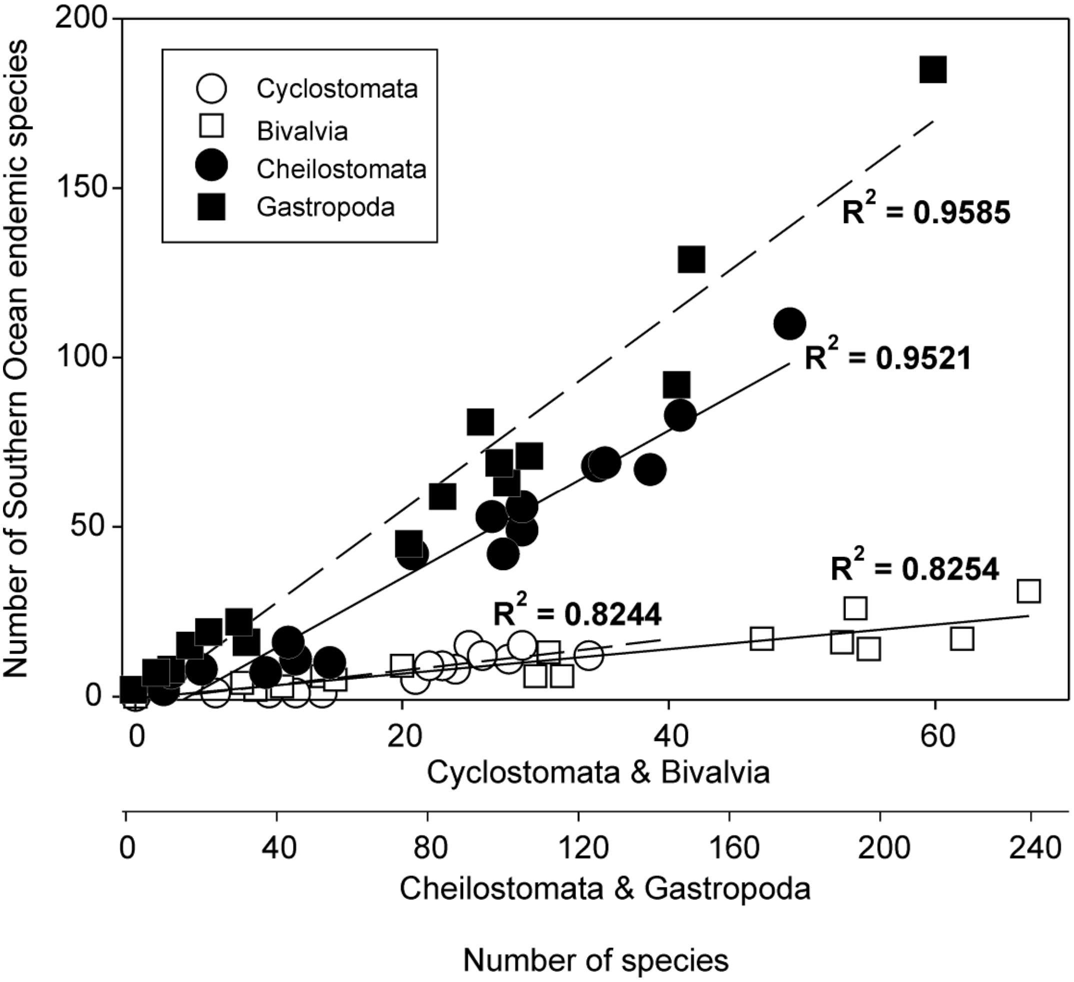


Figure 4.3. Relationships between the number of species per region and the number of Southern Ocean endemic species per study class. The key to classes and the R^2 of relationships are shown on the figure. The associated F and P values of each ANOVA are: Gastropoda F=346.3, P<0.001; Bivalvia F=70.91, P<0.001; Cheilostomata F=298.36, P<0.001 and Cyclostomata F=70.43, P<0.001.

Figure 4.4 shows the percentage of species in each region made up of SO endemic species in a logical biogeographical order: starting with those regions closest to South America followed by those progressively further away in a clockwise circumpolar direction (following west-wind drift) and starting with the sub-Antarctic islands then moving inside the PF. The Gastropoda, Cheilostomata and Cyclostomata all showed an increase in the proportion of SO endemic species per region the further each region was from South America. In contrast, the Bivalvia showed no geographical trend or pattern. Using the Spearman rank correlation coefficient (rs), there was strong evidence for an increase with the biogeographical regional sequence for the Cyclostomata (rs = 0.68, $P = 0.011$), the Cheilostomata (rs = 0.79, $P < 0.001$) and the Gastropoda (rs = 0.90, $P < 0.001$), but not for the Bivalvia (rs = 0.19, $P = 0.46$).

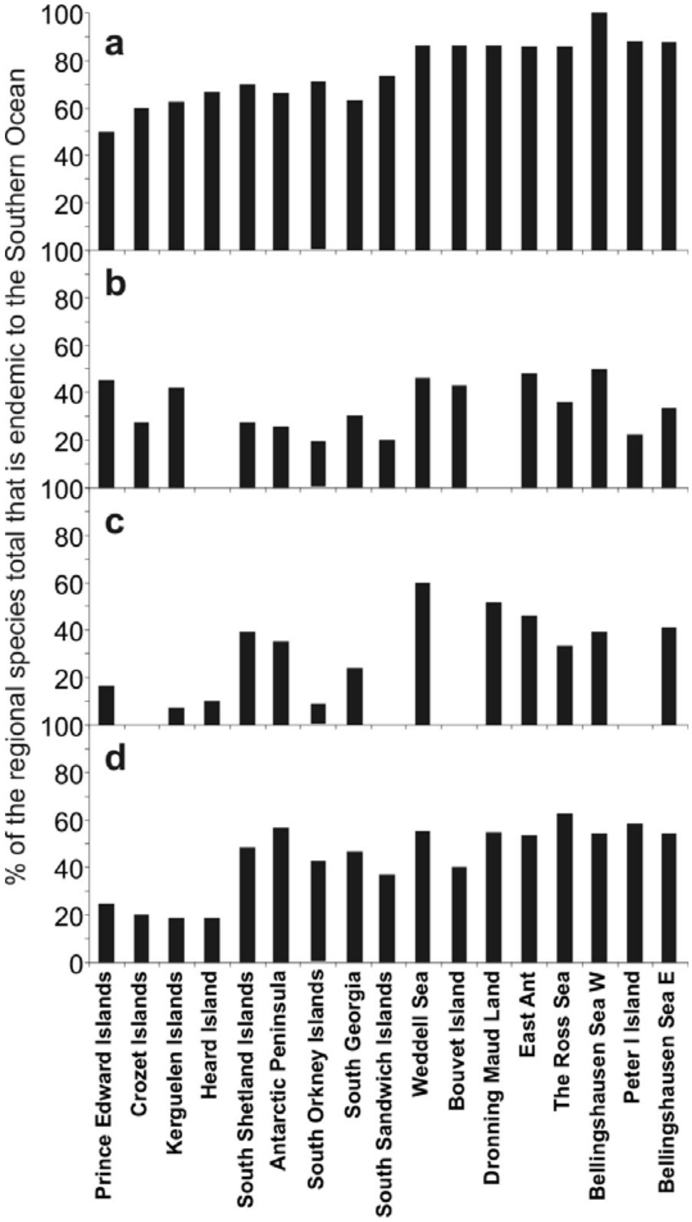


Figure 4.4. The percentage of (a) Gastropoda, (b) Bivalvia, (c) Cyclostomata and (d) Cheilostomata species from each region made up of those endemic to the Southern Ocean. Regions are in 'geographic order', starting with the sub-Antarctic Islands outside the Polar Front, then those of the Scotia Sea and finally the Antarctic regions from those closest to South America, following the direction of the Antarctic Circumpolar Current (clockwise).

Biogeographical patterns

Centres of radiation

Using a count of how many genera within a region had their maximum number of species in that region (Table 4.4) as an indicator of species generation/radiation hotspots, New Zealand had the highest value for all four groups: Gastropods (230), Bivalvia (59), Cheilostomata (54) and Cyclostomata (5). South Africa and Tasmania had the next highest numbers except in the case of the Cyclostomata, for which they showed 1 and 0 genera, respectively. Within the SO these hotspots varied between the different classes. For the Gastropoda, the Weddell Sea contained over 30% more genera with their maximum number of species than any other SO region (32 in total). The Bivalvia had hotspots in the South Shetland Islands (eight genera), the Antarctic Peninsula (six genera) and the Weddell Sea (five genera). The Cheilostomata showed significantly higher numbers in the Ross Sea (18 genera), more than double that of the next SO region. The Cyclostomata had far smaller numbers than the other classes with a maximum of three genera in both the Antarctic Peninsula and Dronning Maud Land. Sampling is not uniform around the SO, and discrepancies of sampling intensity are a source of error for all works on biogeography; these are addressed in Clarke et al. (2007). Clarke et al. (2007) found sampling of the continental shelf fauna is reasonably full and extensive, although new species are still being described and there are significant gaps in sampling off Wilkes Land and in the Bellingshausen and Amundsen Seas. Species richness was highest in those areas that have been subject to the most intense research activity and this pattern remained even after correction for sampling intensity.

Table 4.4. Count of the number of genera per study region that show the maximum-recorded number of species for that genus in that area.

Region	Gastropoda	Bivalvia	Cheilostomata	Cyclostomata
Southern Chile	4	8	8	1
Magellan Strait	5	6	8	1
Tierra del Fuego	10	7	9	4
Southern Argentina	33	8	6	0
Falkland Islands	2	4	6	3
Heard Island	2	0	1	0
Prince Edward Islands	1	0	2	1
Crozet Islands	9	0	0	0
Kerguelen Islands	14	2	3	1
Bouvet Island	3	0	1	0
Peter I Island	1	0	1	0
South Georgia	17	3	6	0
South Sandwich Islands	5	0	2	0
South Orkney Islands	10	0	4	0
South Shetland Islands	17	8	11	2
Antarctic Peninsula	13	6	8	3
Weddell Sea	32	5	2	2
Dronning Maud Land	16	0	4	3
East Ant	17	4	4	2
The Ross Sea	20	3	18	1
Bellingshausen Sea E	0	0	6	1
Bellingshausen Sea W	0	0	6	1
NZ Sub-Antarctic Islands	26	8	7	1
Chatham Islands	26	7	5	0
New Zealand	230	59	54	5
Kermadec Islands	34	4	14	0
Tasmania	103	24	13	0
South Africa	131	36	29	1
Tristan da Cunha Islands	0	1	1	2

Regional relationships

In order to analyse faunal similarities between the 29 regions the species–region data matrices were analysed by applying multivariate statistics. Using the results of the primer analysis, NMDS (Figure 4.5) and ANOSIM (Table 4.5), three significant groupings were shown that held true for all four classes. The groupings were South America, the Antarctic and New Zealand and each region was assigned to a grouping. The Tristan da Cunha Islands were judged to be different enough from all other regions that they were not included in this analysis. The results of the cluster analysis (not shown) indicated that for each of the different classes, some regions, usually islands, showed affinities with different major groupings (Table 4.6). Bouvet Island showed most variation, as the fauna there had differing affinities in all four possible different groups. Kerguelen, Crozet and the Prince Edward Islands showed a South American 'signature' for most classes, except for the Gastropoda for which they were classed as Antarctic. The Antarctic islands of South Georgia, Heard Island, South Orkneys and South Sandwich Islands all grouped with South America for the Cyclostomata data. The sub-Antarctic islands of New Zealand grouped with New Zealand except in the case of the Cheilostomata, for which they grouped with the Antarctic. The ANOSIM tests (Table 4.5) showed that these groupings (South America, the Antarctic and New Zealand) were statistically strong, with nine results showing a P-value of less than 0.1%, indicating a significant difference between the large-scale groupings. The three results for the Cyclostomata had a P-values of 0.2% and 0.3%, indicating that the groupings were strong and significant with a slight increase in the probability of a type 1 and 2 error respectively and is linked to the lower numbers of species found in this group. The difference in the number of permutations for the Cyclostomata is due to some regions lacking sampling or records for this group.

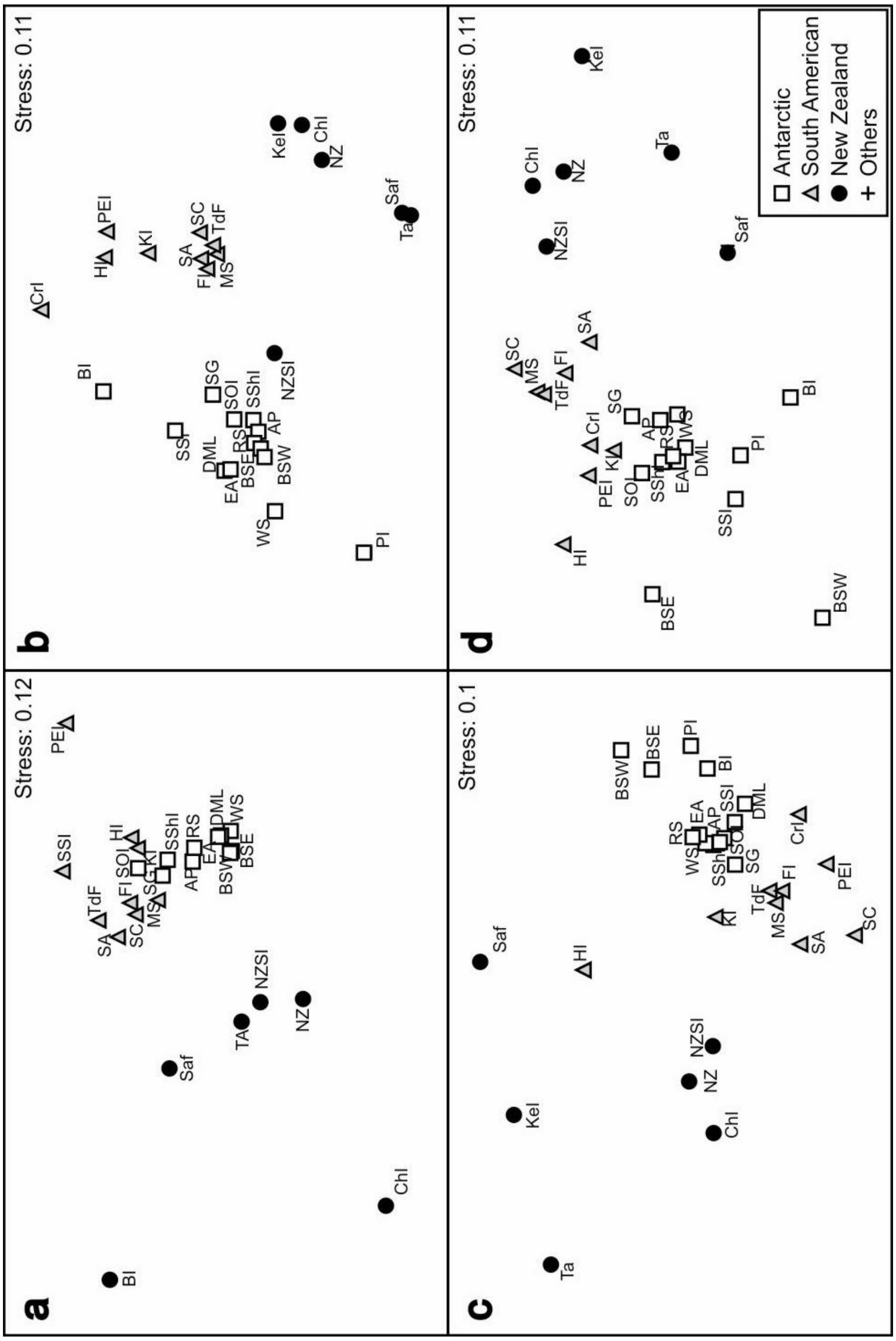


Figure 4.5. Similarity of (a) Cyclostomata, (b) Cheilostomata, (c) Bivalvia and (d) Gastropoda between regions and major areas using non-metric multidimensional scaling (NMDS) applied to species data. Region abbreviations are as in Figure 4.1. Key to patterns is included in the figure.

Table 4.5. Results of ANOSIM tests for major groupings of regions. ANT= Antarctic, SAM= South American & NZ= New Zealand. The R-statistic is a measure of the similarity of assemblages, and reflects the degree of separation of assemblages: the closer the value to 1, the greater the difference in assemblage composition (Clarke & Warwick 2001).

	Groups	R Statistic	Significance Level %	Possible Permutations	Actual Permutations	Number >= Observed
Cyclostomata	SAM, ANT	0.37	0.2	125970	999	1
	SAM, NZ	0.674	0.3	1287	999	2
	ANT, NZ	0.62	0.2	6188	999	1
Cheilostomata	SAM, ANT	0.865	0.1	497420	999	0
	SAM, NZ	0.832	0.1	5005	999	0
	ANT, NZ	0.862	0.1	27132	999	0
Bivalvia	SAM, ANT	0.577	0.1	497420	999	0
	SAM, NZ	0.737	0.1	5005	999	0
	ANT, NZ	0.937	0.1	27132	999	0
Gastropoda	SAM, ANT	0.419	0.1	497420	999	0
	SAM, NZ	0.824	0.1	5005	999	0
	ANT, NZ	0.859	0.1	27132	999	0

Faunal provinces

Matrices of percentage similarity between the 29 regions for each of the four classes were used to produce groupings of regions based upon a 50% or greater similarity level (Table 4.3). Mapping the grouped regions identified a total of six different zones that were not represented by the large-scale faunal patterns in the bryozoan and molluscan study taxa (Figure 4.6). For comparison, faunal patterns based on biogeographical data for the Pycnogonida (Munilla & Soler, 2009) were displayed in the same way (Figure 4.6d). The resulting large-scale patterns show both similarities and differences between classes. With the exception of the Gastropoda, all groups show the Antarctic regions to cluster discretely. The Gastropoda data for the Antarctic were split between East and West Antarctica, with areas of overlap in the Weddell and Bellingshausen seas. New Zealand was not shown to strongly interact or overlap with the Antarctic or South America for any of my example classes, and only interacted with South Africa and Tasmania in the case of the Cyclostomata. The sub-Antarctic islands were separate groupings for the Pycnogonida and Gastropoda, a subset of South America for the Cheilostomata, and combination of Antarctic and South American for the Cyclostomata and Bivalvia. The regional data for South America showed no interaction with that of the Antarctic for the Gastropoda, Pycnogonida or Cheilostomata but did show regions of overlap with islands within and outside the PF for the Cyclostomata and Bivalvia. Bouvet Island, well within the PF, had a strong affinity with South Africa for the Cyclostomata.

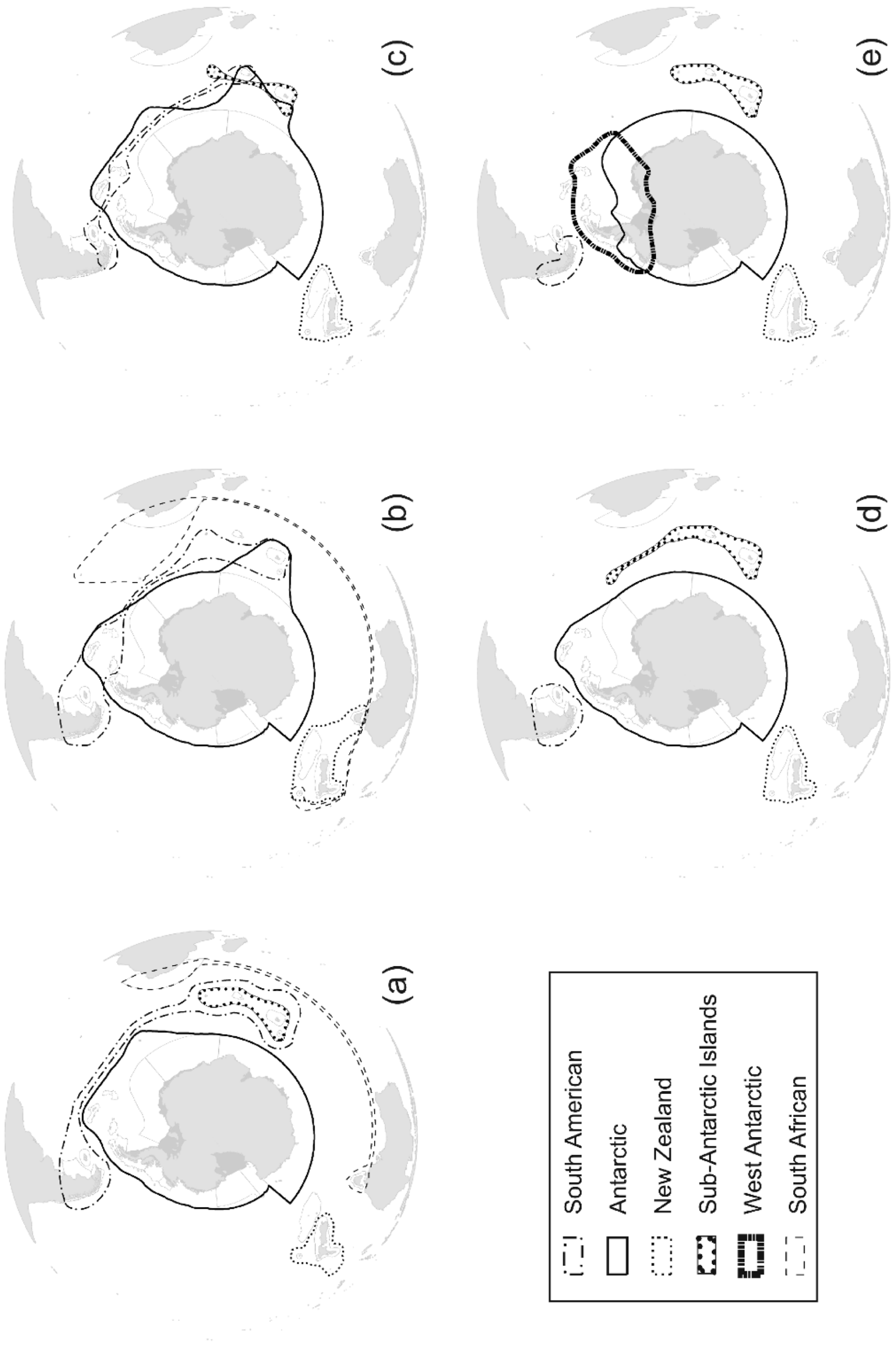


Figure 4.6. Large-scale faunal patterns in (a) Cheilostomata, (b) Cyclostomata, (c) Bivalvia, (d) Pycnogonida and (e) Gastropoda. The patterns are based upon regions being grouped at a 50%, or greater, sharing of species. The key to patterns is included in the figure.

DISCUSSION

Patterns in southern polar and temperate shelf richness

The description and underlying causes of a supposed global latitudinal gradient in species richness generated considerable ecological discussion throughout the latter half of the last century (Rohde, 1992; Gaston, 2000). Research in the marine realm in the last decade has increasingly exposed asymmetry in biodiversity and biogeography between the Northern and Southern Hemispheres (Crame, 2000; Valdovinos et al., 2003; Chown et al., 2004; Barnes & Griffiths, 2008), and these studies, amongst others, have shown that a strong component of the Northern Hemisphere/Southern Hemisphere asymmetry is high southern polar richness. The current study focused on the organization of southern polar richness in several model taxa at species and genus levels. I show that the most striking broad-scale patterns to emerge from species counts (of model taxa) per region are a strong east–west hemispheric asymmetry, also noted by Crame (2000) and Gray (2001). In bivalve and gastropod molluscs and cheilostome bryozoans, richness was typically low within the SO compared with Indo-West Pacific areas immediately to its north. In my model taxa the South American regions have a similar or even smaller number of species to those within the SO, far lower than those regions found in the Indian and western Pacific Oceans. In contrast to temperate and tropical regions, the SO shows no sign of this east–west disparity, possibly due to the homogenizing effect of the Antarctic Circumpolar Current (ACC) and relatively uniform water temperatures and physical conditions

(Arntz et al., 1994) or the continuous coastline and continental shelf around all latitudes. Only the cyclostome bryozoans, the most poorly studied of my model taxa, showed a relatively uniform distribution, with no obvious effect of latitude or geography. In striking contrast to other taxa reported to date, the highest richness of cyclostomes was in South America and the Antarctic Peninsula.

Island species richness typically increases with geographical area and decreases with isolation (MacArthur & Wilson, 1967). Although the number of species in this study did increase with increasing geographical area (Table 4.1), this was less extreme in the South American and SO regions than in the more diverse Eastern Hemisphere regions. The Kermadec Islands, despite being the smallest of my described regions, had significantly more recorded species than all but one of the South American and the SO regions, which are between c. 3 and c. 3000 times greater in area, respectively. It seems likely that this is explained by the Kermadec Islands being close to the Wallacean biodiversity hotspot of the Indo-West Pacific (Roberts et al., 2002). In contrast the 'New Zealand sub-Antarctic islands' region gives smaller numbers of species than expected for its apparent size due to the large area of open ocean between the widely dispersed and relatively small islands; however, most sampling has been concentrated in close proximity to the land. The relatively even distribution of species around the SO means that the East Antarctic region, with its vast area and similar number of species to smaller, neighbouring regions, does not appear to fit the rule. The degree to which this reflects sampling intensity is unclear, but the seas around New Zealand sub-Antarctic islands and especially East Antarctica are amongst the more poorly studied.

For my model taxa, and others (e.g. brachiopods; see Walsh, 1996), the seas around New Zealand are very rich. New Zealand's shelf has many factors that should promote such richness, including its geographical proximity to the Indo-West Pacific diversity hotspot. It has a complex geological history with a wide range of rock types and ages (Cooper & Millener, 1993; Swenson et al., 2001) and spans a wide latitudinal range; factors which tend to increase the number of niches for its size. Such factors, coupled with New Zealand having broken away from Gondwana far earlier than the other study areas at c. 100 Ma (Weaver et al., 1994), make it less surprising that it has a rich and endemic fauna. McDowall (2004) suggests that, like the region, the biota of New Zealand has a highly complex origin, including both the vicariant speciation of an ancient Gondwanan fauna and the more recent dispersal from neighbouring Australia. Antarctica and the SO have long been considered highly isolated due to the ACC and the PF (but see Clarke et al., 2005) but levels of regional endemism for my study taxa within these areas are uniformly lower than found in New Zealand. The simplest explanation could be that the high endemism of New Zealand is expected, given its high levels of richness and the strong relationship between endemism and richness (e.g. Tilbrook & De Grave, 2005).

Patterns of endemism

High endemism is typically associated with localities old enough for taxa to have evolved there but isolated enough that they have not spread elsewhere. In the sea this becomes complicated by the ability of some propagules to travel considerable distances, in extreme cases across oceans (Scheltema, 1971). Of my model taxa, few bryozoans have planktotrophic larvae (which can disperse widely) and at high latitudes the same is true for gastropod and bivalve molluscs (Thorson's rule; see Mileikovsky, 1971). Gastropod molluscs tend to have particularly high levels of ecological and geographical endemism (and richness) at isolated localities (e.g. Bouchet et al., 2002). My data showed this also holds true around the Antarctic, with the gastropods having the highest richness of my model taxa and being the only class to show any significant regional endemism. South Georgia was notably rich in endemics, across all studied taxa, and this may be explained in a similar way to the richness around New Zealand. Although South Georgia may be isolated now, it was close to South America just 10 Ma and it is both old and large. Surprisingly, young Bouvet Island (c. 1.39 Ma) (Engleskjon & Jørgensen, 1986) showed the highest levels of endemism for the molluscs within the Antarctic. Linse (2006) found that many of this small, remote island's mollusc species had strong connectivity with the deep sea and this apparently high level of molluscan endemism may reflect a paucity of sampling of the surrounding deep water, the probable source of much of the island's shelf fauna. Heard Island, another remote island within the PF, displayed unusually low rates of endemism, with only the Cheilostomata showing any endemic species at all; I suggest this is due to the continuity of shelf connections of the Kerguelen Plateau between Heard Island and the Kerguelen Islands. The majority of species of my studied taxa found at Heard Island are also recorded at the Kerguelen Islands, a biogeographical oddity as these islands lie either side of the PF today (Moore et al., 1999), but in the past both have been on the same side of the PF as it migrated north and south of its current position (Gendron-Badou et al., 1997). During ice ages the shelf around both Heard Island and the Kerguelen Islands was in the SO and in some interglacial periods they were both in the southern Indian Ocean. As a result the fauna of Heard Island seems to be mainly a subset of that around the Kerguelen Islands.

Ranges of species vary greatly between taxonomic classes, and this was reflected in my results. The Gastropoda showed the most limited dispersal, with 80% of species restricted to a single region and less than 1.6% found in four or more regions. In strong contrast to the Gastropoda, the Cyclostomata appeared to be widely dispersed, with only 36% of species restricted to a single area and 24% of species found in more than four regions. I suggest that, in part, this is due to the reproductive strategy of cyclostomes, which involves sexual reproduction followed by cloning of the zygotes before mass broadcast release. The Cyclostomata have a short-lived free-swimming larval stage (Hayward & Ryland, 1985), which could be extended in Antarctic species (Barnes & Clarke, 1995), and this method of reproduction may reduce potential variation between offspring and could lead to low species numbers with large ranges.

When the Antarctic and the SO are considered as single units the percentage endemism for both is far greater than that of their component parts. Past estimates of endemism south of the PF (Antarctic) by Arntz et al. (1997) and Barnes & De Grave (2000) suggested endemism of between 75% and 90% for all of my study taxa. New data for the same region reveal that endemism is lower, except in the Gastropoda (Table 4.2). Data for the Pycnogonida (Munilla & Soler, 2009) and Cephalopoda (Collins & Rodhouse, 2006) support a general trend for classes to have Antarctic endemism of between about 42% and 56%, revealing a previous overestimation. Higher levels of endemism in the Gastropoda are not unexpected, as this class typically shows very high levels of endemism elsewhere (Bouchet et al., 2002).

Typical levels of endemism of 42–56% are comparable with those of other large, isolated regions such as New Zealand. These levels apply well to classes, but patterns can change greatly when the analysis is done at lower taxonomic levels. For example, within the class Cephalopoda the orders show very different polar endemism, as the Teuthida (squid) have just 12.5% endemism whilst most Octopoda present (79.4%) are endemic to the Antarctic (Collins & Rodhouse, 2006). This is a reflection of the 'lifestyle' differences between the two groups: squid are highly mobile and usually pelagic whereas octopus are usually benthic and non-migratory. It is likely, however, that the cephalopods represent an extreme example of differences in lifestyle, but endemism can differ even across taxonomic levels of groups with similar lifestyle characteristics (e.g. suborders in bryozoans; see Tilbrook & De Grave, 2005).

New data show that a generalized endemism value of around 50% also holds true for ascidians (44%; see Primo & Vázquez, 2007) and some lower taxonomic levels, e.g. sea anemones (50% endemic) (Rodriguez et al., 2007), which is comparable with other large isolated regions such as New Zealand. Isolated regions where data are sparse, such as Bouvet Island and Peter I Island, often appear to be outliers. These small regions of shelf area may be of scientific interest, particularly as they show the influence of age and isolation on Antarctic faunas, although even with increased sampling they are unlikely to change my overall view of SO biogeography. The greatest unknown lies in the deep sea, a little-studied habitat with a potentially great influence as a source and dispersal route for much of the SO fauna (Brandt et al., 2007b, Strugnell et al., 2008).

Our view of SO benthos has changed much over the last decade, including my understanding of their distribution. It is now clear that many more shelf species occur across wider ranges and environmental conditions than was previously thought. Lower levels of endemism have important implications for issues such as ecosystem structure, functioning and vulnerability. As endemic species constitute at least half of the SO benthos I looked for patterns in the distribution of these species in my studied taxa and found that the numbers of SO endemic species per region correlated very well with the total number of species per region in my data. Strong correlation of endemism with richness has also been reported from similar taxa at low latitudes (e.g. Tilbrook & De Grave, 2005), and as previously poorly sampled areas are better studied, I predict that more endemics will be found in proportion to known numbers of species. This correlation can be interpreted as implying that no single region is a hotspot for endemic species or can be seen as a distinct area of endemic species generation. The level of SO endemism with its even distribution suggests that species are being generated all around the SO and disperse relatively quickly. Alternatively, the poor and very patchy nature of the fossil record coupled with environmental homogeneity and strong pan-Antarctic transport makes it hard to establish whether new species are generated in particular places and spread, or are evenly generated around the Antarctic. For example, South Georgia may be a centre of high endemism either because isolation limits dispersal opportunities of the species generated there or due to genuine higher generation of species, or both.

Several authors (Dell, 1972; Brandt, 1991; Arntz & Ríos, 1999; Linse, 2002) have suggested strong links and exchange of species between South America and the Antarctic. There are a number of mechanisms for potential exchange into and out of the SO and some indigenous species are still in the process of recolonization since the Last Glacial Maximum (Clarke et al., 2005; Barnes et al., 2006b). Measuring the proportion of species in each region accounted for by SO endemic species can be used to assess the influence of other regions upon the SO. The observed increase in prominence of SO endemic species with distance from South America coupled with no influence from the Eastern Hemisphere regions suggests that species are entering the Antarctic via the Scotia Sea and the sub-Antarctic islands and are transported clockwise by the ACC. This could also imply that many species have entered the SO since the establishment of the ACC and its apparent isolation. No pattern was observed for the Bivalvia, which can be linked to the fact that they show the lowest rate of Antarctic endemism and tended to have species with large latitudinal and longitudinal ranges (Clarke et al., 2007a).

Biogeographical patterns

Centres of radiation

In my study, New Zealand stood out as a place of very high species generation across all groups, an observation that is probably due to the lengthy isolation and other features of New Zealand (discussed above) providing time for much vicariant speciation. Within the SO there was no single dominant region across taxa – each faunal class showed different patterns. The Weddell Sea appears to be a significant area for radiation in the mollusc classes, whereas the Ross Sea seems to be a focus for the cheilostomes. These two areas represent the potential meeting points for the ancient faunas of East and West Antarctica, and this overlap in species could lead to hotspots of species per genus. Another possible explanation for the observed hotspots is the effect of the level of specialist taxonomic expertise that has worked in each region. The Ross Sea was for a long time a focus for Antarctic cheilostome work through the combined efforts of American, New Zealand and Italian expeditions.

Regional relationships

Ordinations, and other similarity analyses, have been an increasingly utilized and powerful tool to investigate underlying trends in biogeography (Ramos, 1999; Barnes & De Grave, 2000; Linse et al., 2006). Results in the current study suggested that all my regions clustered into three major groupings: South America, New Zealand and Antarctic. My data support the findings of previous biogeographical studies over several decades in demonstrating a strong similarity between South America and the Antarctic (Linse, 2002; Primo & Vázquez, 2007), far greater than either has with New Zealand. Although the major components that defined these groupings remained constant there was considerable variation between classes when it came to the various island regions; isolated Bouvet Island was the only region to fit into all three groupings. The sub-Antarctic islands of Kerguelen, Crozet and Prince Edward islands showed a South American signature for the bryozoans and the bivalves, despite all of them being geographically closer to the Antarctic and South Africa. The west-wind drift and the ACC disperses organisms in the Southern Hemisphere in a clockwise direction from South America towards islands such as Bouvet. The Gastropoda of the sub-Antarctic islands, however, do not show an affinity with South America; instead they group with the Antarctic. The Kerguelen Plateau stretches to within c. 200 km of continental Antarctica (at 3000 m depth); during its geological history, spanning c. 110 Myr the Kerguelen Plateau has moved very little in relation to Antarctica (Frey et al., 2000). It has, however, changed position relative to sea level, sometimes well above sea level (Frey et al., 2000), meaning that the seafloor around the plateau was much shallower in the past and has since subsided due to cooling of the oceanic crust and upper mantle with time. This close proximity to the continent, through relatively shallow water, would possibly allow mobile (crawling) animals such as the gastropods to colonize the Kerguelen Plateau from Antarctica, and vice versa. In the more ubiquitous Cyclostomata, island groups from within the PF group with South America, including South Georgia, Heard Island, the South Orkneys and South Sandwich Islands. It is possible this is related to their unusual reproductive strategy of polyembryony, but the link or mechanism is not clear.

The New Zealand sub-Antarctic islands showed a strong New Zealand signature for three of my study taxa, and also for echinoderms (Dawson, 1970) and ascidians (Primo & Vázquez, 2007). In contrast, however, the Cheilostomata of the region clustered strongly with Antarctic regions. The New Zealand sub-Antarctic islands share 43% of their species with the Ross Sea, whereas in the other study taxa only 0–17% of species were shared (Table 4.3). Although the reason for this is obscure, it seems likely that it is connected with the prevalent currents, which flow northwards out of the Ross Sea and East Antarctica to these islands. It is possible that cheilostomes rafted on macroalgae in warmer interglacial periods.

Faunal provinces

The similarity between any two given regions can be quantified as a single, overall figure, although it is often advantageous to consider the direction of that relationship. Describing the similarity between the regions as two numbers (the percentage of one region found at another and vice versa) can indicate potential points of origin and the direction of species dispersal. Using this method it is possible to show regions that are of great importance to others but are not themselves dominated by the shared components of those regions. Conversely, this method identifies regions that can be considered as subsets of other regions, e.g. the relationship between Heard and Kerguelen islands. It is also possible to highlight groups of regions that have strong faunal connections and the potential mechanisms for those connections.

The large-scale patterns observed using this directional method support the idea of a largely homogeneous Antarctic fauna. Three of my four studied taxa as well as the Pycnogonida (Munilla & Soler, 2009) arguably show the SO as a 'single functional unit'. Only the Gastropoda showed any differentiation between (the historically separate) areas of the Antarctic (East and West). My results, however, do not show a clear division between the two areas, and the Bellingshausen and Weddell seas act as areas of considerable overlap.

As reported for some other taxa (see Primo & Vázquez, 2007), I found that the Antarctic and South American faunas did not show strong faunal relationships with New Zealand, possibly due to its distance from the ACC, the main vector for species dispersal in the SO. South America's influence upon the sub-Antarctic islands via west-wind drift is clearly seen in three of the model classes: the Cyclostomata, Cheilostomata and Bivalvia. For the Gastropoda and Pycnogonida these islands appear to be a separate grouping. A strong Antarctic influence on the fauna of the Kerguelen Plateau is also apparent for the cyclostomes and bivalves, while for the widespread cyclostomes and bivalves the influence of South America reaches within the PF, affecting the islands in the north of the Scotia arc. The only other evidence for external influences within the PF comes from the Cyclostomata of Bouvet Island; only two species are currently recorded from the island, both of which are also found in South Africa. Two potential mechanisms to explain this are deep-sea dispersal and the incursion of the Agulhas Current across the PF (Lutjeharms et al., 2003). Meaningful conclusions are limited by the small numbers of species involved and the paucity of sampling in the adjacent deep sea.

CONCLUSIONS

The accepted view of SO benthic biogeography has in some ways changed little since the key works of Ekman (1935, 1953), Hedgpeth (1971) and Dell (1972). Unlike those ideas previously proposed, I show regions to differ depending upon the class of animals being considered (Figure 4.6). Excluding the lack of a South Georgia subprovince, the Gastropoda show the greatest similarity to the previously suggested zones, including some differences between east and west. Patterns in all of the other taxa studied suggested a single Antarctic province and a definite distinction between the sub-Antarctic islands influenced by South America and those of New Zealand, confirming the original suspicions of Ekman and Hedgpeth that their observed split between the faunas of East and West Antarctica was an artefact of sample distribution available at the time.

Although there is clear regional and local variation in the Antarctic marine fauna (Linse et al., 2006; Clarke et al., 2007a) when compared with its Southern Hemisphere neighbours, the SO seems to show very few regional patterns. The level of faunal homogeneity, or at least a lack of common boundaries to species, implies that very few barriers to dispersal exist within Antarctic waters. I suggest that much of this homogeneity is driven by the similarity of conditions and the ACC which transports animals in a clockwise direction around the continent. Strong evidence exists for a long-term influence of the ACC upon SO benthic biogeography. All four of the current study taxa, as well as echinoids (David et al., 2005), pycnogonids (Munilla & Soler, 2009) and ascidians (Primo & Vázquez, 2007) show varying degrees of influence of the west-wind drift. Even the highly endemic, mostly non-planktonic, Gastropoda showed less of an influence of South American species with increased distance in the direction of the ACC. In my other study classes (Bivalvia, Cyclostomata and Cheilostomata), the fauna of the sub-Antarctic islands of Prince Edward, Crozet and Kerguelen were derived from South American origins. This study supports previous findings of strong biogeographical links between the Antarctic and South America, but there is little evidence for a relationship between either of these regions and New Zealand/Australia (Tasmania). This is a potential explanation for the comparatively low species numbers in the SO, with the PF acting as a barrier to the species from the richer Eastern Hemisphere and no equivalent of the Scotia arc or sub-Antarctic islands down-current to act as a gateway.

Most investigations of biogeography examine patterns in one particular taxon but then discuss a generalized pattern. A key aim of the current study was to use multiple classes to determine degrees of generality and exceptions. My four model taxa all showed the potential to be 'outliers' during this study. The Cyclostomata showed a near 'opposite' pattern of richness to the other groups as most species occurred in South America and the Antarctic Peninsula (Table 4.1). The Cheilostomata were alone in showing strong links between the New Zealand sub-Antarctic islands and the Antarctic. Only the Bivalvia showed no pattern of decreasing influence of South American species with distance. The Gastropoda alone showed very high levels of endemism, the sub-Antarctic islands grouping with the Antarctic and some degree of east–west split in the Antarctic fauna. In general some biogeographical commonality emerges. It is now clear that previous estimates of Antarctic endemism (see, e.g. Arntz et al., 1997) were too high. For my study classes, a figure in the region of 50% species endemism seems realistic.

A key biogeographical question is whether the Antarctic is cut off or just far away from potential colonists. For South American species to reach the Antarctic requires crossing large distances of deep water, in some areas aided by a rapid (10 cm s−1) current in the direction of the Scotia arc and sub-Antarctic islands. However, for Eastern Hemisphere species the Antarctic appears both remote and cut off by the PF, which acts as a barrier even to any species that could cross the deep water. From within the PF the main route out of the Antarctic would be via Antarctic bottom water that flows northwards into neighbouring oceans but this (slow) route would be restricted to species capable of surviving at abyssal depths.

CHAPTER 5 - BIODIVERSITY AND BIOGEOGRAPHY OF SOUTHERN OCEAN PYCNOGONIDS.

[The data in this chapter are also presented in: Griffiths, H.J., Arango, C.P., Munilla, T. & McInnes, S.J. (in submission) Biodiversity and biogeography of Southern Ocean pycnogonids. Ecography.]

Chapter 5 - BIODIVERSITY AND BIOGEOGRAPHY OF SOUTHERN OCEAN PYCNOGONIDS.

INTRODUCTION

Sea spiders (Arthropoda; Pycnogonida) have a worldwide distribution and are often regarded as a characteristic component of Antarctic habitats (Arnaud & Bamber, 1987). Pycnogonid species tend to be of larger maximal size in colder and deeper waters compared to temperate and tropical waters (Hedgpeth, 1969) and are usually more abundant, particularly around Antarctic shelves. These features make them a common and conspicuous component of Southern Ocean (SO) benthic samples, in contrast to the typical rarity of reports from elsewhere probably due to their small size and low abundance. The Antarctic pycnogonid fauna appears to be more diverse compared to that at lower latitudes; 20% of the total species known are found in Antarctic and/or Sub Antarctic waters, possibly being the most speciose area for pycnogonids in the world (Munilla & Soler, 2009). Comparing the percentages of known living species on a global scale, it has been suggested pycnogonids are better represented around Antarctica than speciose groups as poylchaete worms (~12%), amphipods (~8-14%), echinoderms (4.9%), Porifera (6.2%), fish and gastropod molluscs (<2%) (Munilla, 2001; Barnes & Peck, 2008). In contrast, for many other groups e.g. the decapod crustaceans (Thatje & Arntz, 2004) the waters of the SO are poor in species on a global scale. Despite the diversity and abundance of Pycnogonida in Antarctic benthos and the fact that they have been studied more extensively than those from other regions, we are still far from understanding their distribution and diversity patterns. These patterns might be crucial to understand the evolutionary history of sea spiders in the Southern Ocean and around the globe.

Antarctic pycnogonids have been described and illustrated since the earliest scientific expeditions such as the American Expedition of Nathaniel Palmer (1829-30), H.M.S. Challenger (1872–76) and R.R.S. Discovery (1925–27). Taxonomists linked with these early explorations set about cataloging new and spectacular forms of sea spiders found in trawling and dredging samples (Eights, 1835; Hoek,1881; Gordon, 1932). A complete account of the work done since late 1800's covering more than 172 years and more than 40,000 specimens collected is summarised in Munilla and Soler (2009). Today about 270 species, representing all extant lineages, of pycnogonids are found in the SO. Endemism (to Antarctica) and circumpolarity have been described as common characteristics of the Antarctic pycnogonid fauna, as for other groups including the molluscs (Linse et al., 2006) and bryozoans (Barnes & Griffiths, 2007). Some previous studies have attempted to map the distribution of pycnogonid taxa, notably Stock (1957), Hedgpeth (1969) and Pushkin (1993). Stock looked at the distribution of the mainly Antarctic family Austrodecidae, proposing species corridors, migration and speciation through isolation. Hedgpeth in particular, used these distributions in efforts to define proposed biogeographic patterns or provinces within the Southern Hemisphere. The most recent studies (Munilla, 2001; Munilla & Soler 2009; Griffiths et al., 2009) analyse pycnogonid distributions based upon species lists accumulated from the literature for predefined regions based upon geographic, maritime or political boundaries.

The study presented here assesses the biogeographic patterns derived from the most current sample records of pycnogonids from the SO and neighbouring areas. I examined the distribution and bathymetric ranges of all pycnogonid species from high southern latitudes. By combining these datasets, they allowed us to draw conclusions regarding biogeographic regionalisation and towards their possible ecological and evolutionary drivers. I aimed to investigate regional species richness and how much apparent regional richness can be explained by differences in sampling effort, and how much is due to true localized species hotspots.

MATERIALS AND METHODS

All available data on the occurrence of pycnogonids in the Southern Ocean, and adjacent oceans, have been collated into the SOMBASE (Griffiths et al., 2003), which started as the Southern Ocean Mollusc Database in 2000 and now holds georeferenced information on several SO phyla including bryozoans, isopods, sponges and corals. At present, SOMBASE contains over 6,600 records of occurrences of pycnogonid taxa (Figure 5.1a) and is updated on a regular basis, when new records are made available. The current pycnogonid records were compiled from all available published and unpublished datasets and their taxonomic and systematic status checked by taxonomic experts. The data are going back as far as the early scientific expeditions such as Challenger (1881) and Discovery (1932) but also include the latest identifications and species lists from several of the 2009/10 Census of Antarctic Marine Life expeditions. The latter incorporate distribution records from previously un-sampled regions like of Pine Island Bay in the Amundsen Sea (JR179, BAS unpublished cruise report). All pycnogonid distribution data used in my analyses are freely available through the Scientific Committee on Antarctic Research Marine Biodiversity Information Network (http://www.scarmarbin.be).

The present study comprises distribution information of 332 species of pycnogonids from 1837 sample locations around continental Antarctica, the sub-Antarctic Islands, South America, and New Zealand. The dataset also includes partial records for South Africa and Australia. These records are not comprehensive and are included when the original dataset held distribution information on species shared with the Southern Ocean, South America and/or New Zealand to ensure that the entire distribution range for Southern Ocean species was represented. Each record required a taxonomic identification to species level, a latitudinal and longitudinal location (as accurate as possible) and a depth (where provided in the literature or cruise report).

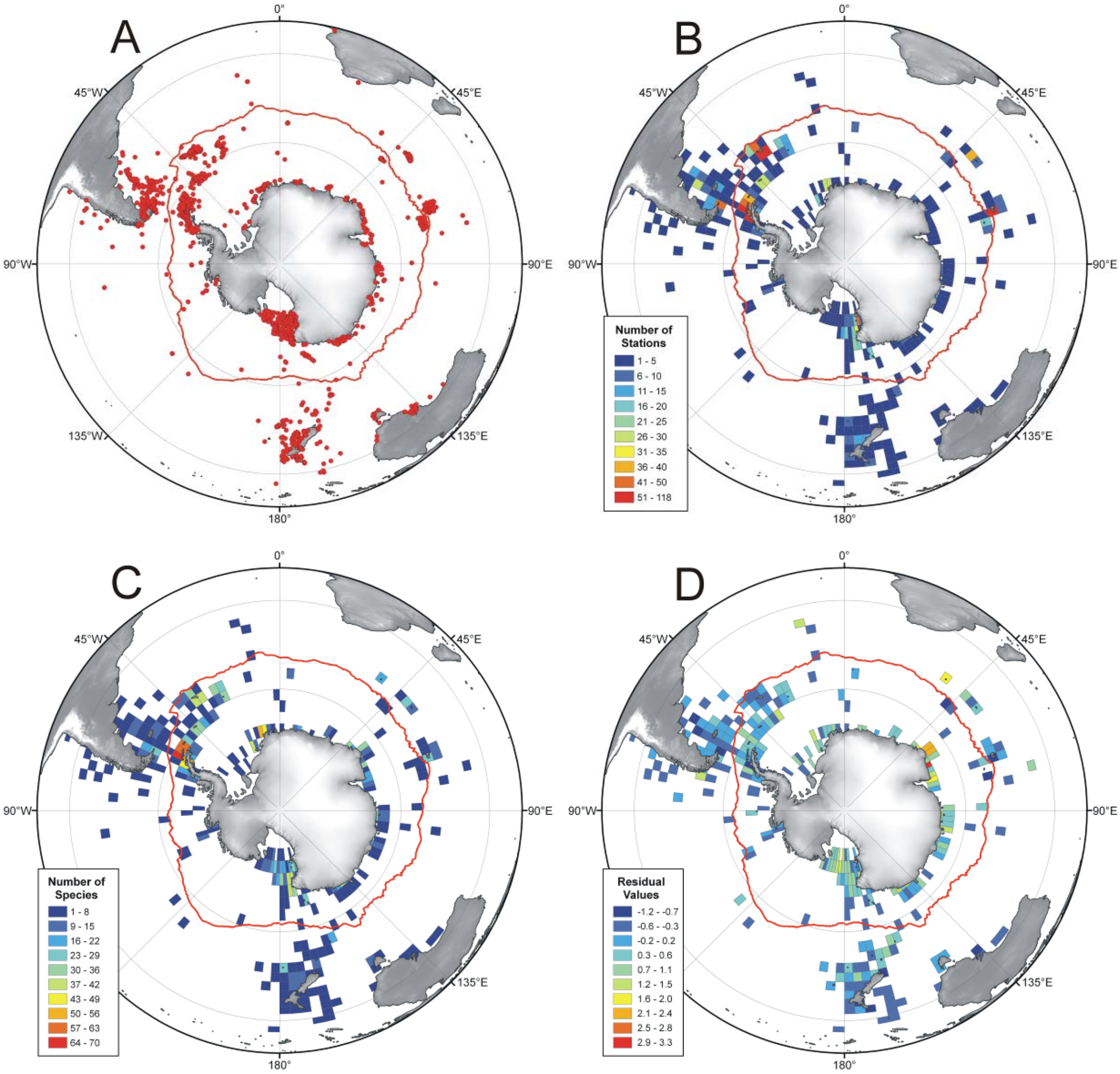


Figure 5.1. Maps quantifying pycnogonid distribution in the Southern Ocean and neighbouring regions. a) The distribution of sample locations for pycnogonids in the Southern Ocean and neighbouring regions. b) The number of pycnogonid sample stations (unique combinations of latitude and longitude) recorded from each 3° by 3° grid cell. c) The number of pycnogonid species collected from each 3° by 3° grid cell. d) The residuals from the regression mean of number of pycnogonid species v number of stations from each 3° by 3° grid cell. Red line represents the mean position of the Polar Front.

Species Richness

To compare regional species numbers and quantify sampling intensity I divided the Southern Hemisphere into a series of grid cells of three degrees of latitude by three degrees of longitude (Figure 5.1 b-d). I refer to all grid cells within the Polar Front (PF) as Antarctic. The term Southern Ocean is used when referring to the area south of the PF (Antarctic area) and the sub-Antarctic islands which lie outside the current PF but are influenced by it, e.g. the Prince Edward Islands, Crozet Islands and Kerguelen Islands (Griffiths et al., 2009).

The number of distinct species per grid cell was calculated by using queries in MS Access which only counted each species once per grid, independent of how many times it had been recorded in a given grid cell. For the purpose of this investigation I regard a sampling station as a unique combination of latitude and longitude. By this approach I remove the problem of duplicating records which may appear in more than one of the data sources used but add the problem associated with historical expeditions giving a single location for multiple methods of sampling, which would lead to an underestimation of sampling effort for some areas. However, most of these expeditions do not differentiate between apparatus used to catch each specimen, simply giving pooled results by locality. Statistical analysis was carried out with Minitab, version 15 (Minitab Inc., State College, PA, USA). The model 1 least-squares regression was used to avoid residuals being correlated with the independent variable. All logarithmic transformations were natural (Naperian) logarithms. The residual values from the mean were used to identify areas which were significantly richer or poorer in species than would be expected having a given number of stations. The species only found in a single grid cell were identified and used to produce a count of endemic or single record species per grid cell. I also examined the number of species that were endemic to both the Antarctic and the Southern Ocean.

Rarefaction analysis was carried out using the species–area option in PRIMER (Clarke & Warwick, 2001), with 999 iterations, on the best sampled grid cells from different regions within the study area.

Species Ranges

Latitudinal and longitudinal ranges were calculated for all species that had been recorded at three or more stations. Latitudinal ranges were calculated by subtracting the lowest, most southerly value, from the highest value, the most northerly one. Calculation of longitudinal ranges have to take into account the fact that the Southern Ocean covers the full 360 degrees from 180° west to 180° east. To avoid taxa with a limited range but spanning 0° or 180° longitude from falsely appearing as circumpolar in distribution, I calculated the minimum continuous arc that included all distribution points for a given species. This was done by calculating all of the possible longitudinal distances between consecutive records to obtain the largest gap. The value of this gap was then subtracted from 360 to provide the longitudinal range. This method of calculating longitudinal range means that gaps in sampling will prevent any taxa from having a fully circumpolar distribution.

Species distribution records for the taxa with 3 or more records were mapped using a geographic information system (GIS) and species with similar distribution patterns were grouped together into a set of general types with the number of species in each group recorded. Two transects, one from the AP and Weddell Sea (10°W to70°W) northwards through the Scotia Sea and up into South America and the other from the Ross Sea to New Zealand, were chosen to examine any trends in species richness with latitude. Depth ranges and mean depths were calculated for each of these species from the available data.

Depth ranges for species with 3 or more records were calculated by subtracting the minimum depth from the maximum known depth for that species. The mean depth for each species was calculated from all of the stations at which that species had been found. Mean depth was based upon presence only did not include numbers of specimens per species.

Biogeographic Patterns

The multivariate statistical software PRIMER (Clarke & Warwick, 2001) was used to analyse faunal similarities between grid cells by implementing the Bray–Curtis measure performed on non-transformed, species presence/absence data. The similarity matrix was then used for cluster analysis and analysis of similarities (ANOSIM) tests. Only grid cells with three or more species present were used in the analyses.

RESULTS

In total distribution information of 332 species of pycnogonids belonging to 45 genera from 1837 sample locations were analysed.

Species Richness

The sampling records are unevenly distributed (Figure 5.1b). Some regions such as the western Weddell Sea and western Amundsen Sea show large gaps in our knowledge, with no samples recorded. The majority of the samples are found along coastal regions of the Antarctic continent and around the island groups. Deep-sea samples, away from the continental slopes, are particularly patchy in their distribution. Of the 279 cells containing data, 108 only contained a single sample station, with 86 cells containing 5 or more stations. The maximum number of stations recorded from any one grid cell was 118 from the West Antarctic Peninsula (WAP). Further sampling hotspots included South Georgia, the Kerguelen Islands, the south western Ross sea and the tip of South America.

Species counts per grid cell (Figure 5.1c) range from 1 to 70 with the highest numbers found in the South Shetland Islands (SShI) (56-70 species). Another notable area of high species numbers was the Eastern Weddell Sea (EWS) (55 species). Species numbers north of the PF were generally lower than those around Antarctica with maximum values of 22 species for the tip of South America, 28 species for the Kerguelen Islands and 24 species for the Antipodes Islands off New Zealand. 68 of the 279 investigated cells contained records of only a single species and 138 cells contained 5 or more species.

The data for South Africa were not included in the regression and residual analysis because I used a general species list for the region, geo-referenced to a single location, and are not representative of the local diversity patterns. Maps of the residuals reveal a few discrete areas where pycnogonid species richness appears to be high even after correction for sampling intensity, namely part of East Antarctica (48-72° E) and the Prince Edward Islands (Figure 5.1d). These are regions where low numbers of samples, one or two, have yielded relatively high numbers of species. Some cells which had notably low residual values, indicating fewer species overall, were some of the better sampled cells of South America, New Zealand, Kerguelen and South Georgia.

Comparison of regional species richness by rarefaction (Figure 5.2) shows increases in species numbers per grid cell with increasing sampling. The cells from north of the PF; South America, New Zealand and the Sub-Antarctic Islands, showed the lowest rate of species accumulation with increased sampling and all appeared to head towards a plateau of less than 30 species. Cells in the group labeled "Typical Antarctic" included the South Orkney Islands, the Ross Sea, South Georgia, South Sandwich Islands and one cell from the WAP, with predicted asymptotes between 35 and 50 species. Notably the WAP cell that appears in this grouping does not include any of the SShI or any of the Bransfield Strait but is the most sampled cell looked at in the whole study. The third grouping, "Rich Antarctic", is comprised of cells from two geographic regions; the SShI and the Weddell Sea. The Weddell Sea have the steepest slope of any of the curves, indicating a particularly high degree of local species richness, but tend to plateau off between 50 and 60 species. The SShI cells have a less steep slope than the Weddell Sea but do not reach asymptote as early (>60 species), indicating a lower level of local richness but a higher level of regional richness.

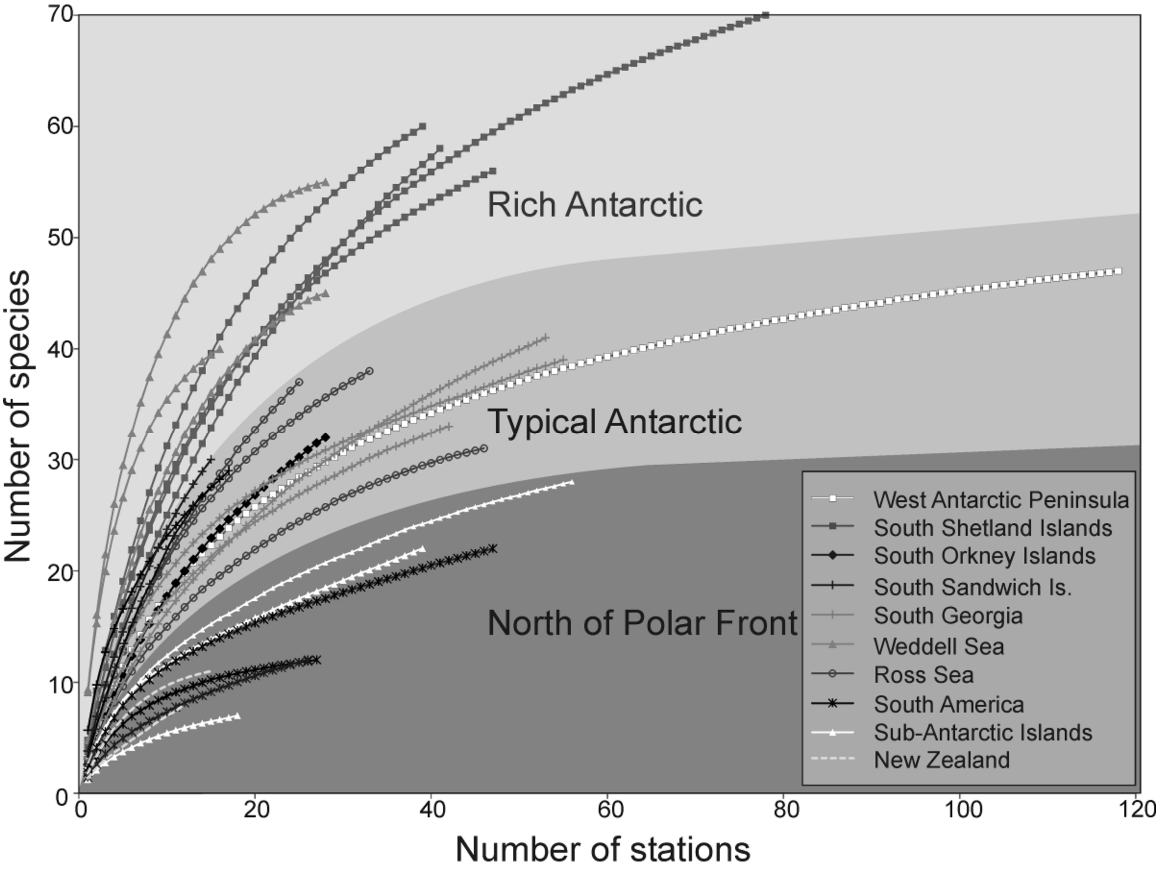


Figure 5.2. Rarefaction curves showing accumulation of pycnogonid species for selected 3° by 3° grid cells from the Southern Ocean and neighbouring regions.

Endemism

I examined how many species are endemic to a particular region/ grid cell. Once I removed the species that had only ever been recorded once or twice, the distribution patterns (not shown) of species endemic to a single grid cell showed no discernible trend or pattern. The 59 cells that contained endemic species were randomly spaced around the study area, with between one and three endemic species per cell. Given the relatively small size of my grid cells, for a species to qualify as endemic it would have to have latitudinal and longitudinal ranges of less than three degrees. The recent study by Munilla and Soler (2009) has already quantified endemism on larger scales for the SO, based upon a dataset containing the published data records, and my findings do not change their results of 108 endemic species in the Antarctic.

Species Ranges

The longitudinal range distributions of the pycnogonids were dominated by species with very limited ranges. Of the 332 examined species, a large number was represented by few samples, e.g.149 species were represented by less than 3 records. The 183 species had 3 or more distribution records and included 65 species with limited ranges (Figure 5.3a), 48 species with ranges of less than 30° of longitude, and large numbers of species with broad longitudinal ranges, 70 species >200°. The maximum longitudinal range was 312° and was recorded for two species, *Austropallene cornigera* (Möbius, K., 1902) and *Colossendeis megalonyx* Hoek, 1881, with a further 5 species having ranges above 300°.

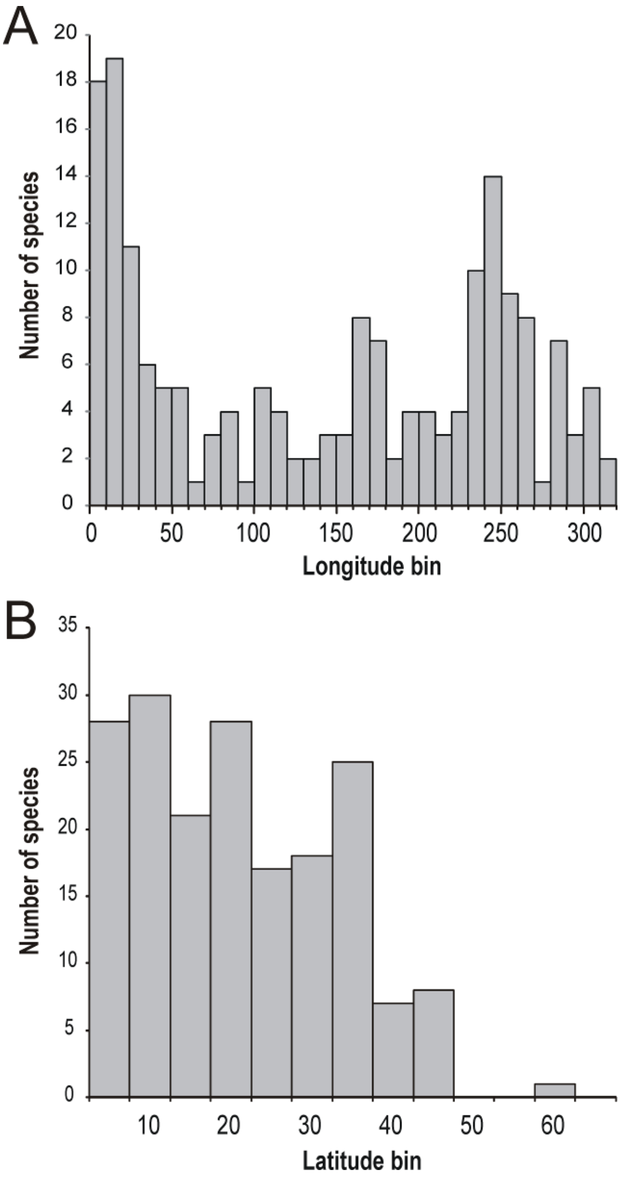


Figure 5.3. Biogeographical range sizes in the pycnogonid species found at three or more locations of the Southern Ocean and neighbouring regions. Data are shown separately for a) longitudinal range and b) latitudinal range. The range size is the difference between the maximum and the minimum range points; it does not imply that the organism is found everywhere in between.

The distribution of latitudinal ranges (Figure 5.3b) resembled the longitudinal ones as it is dominated by the majority of taxa having too few sample records to draw meaningful conclusions. Of the 183 species with 3 or more samples there were more or less equal numbers of species (17–30) in each range bin class up to 35°. The species with the widest latitudinal range was *Achelia serratipalpis* (Bouvier, 1911), with a range of 58°. There does not appear to be any evidence for strong latitudinal diversity gradients within the pycnogonids. The study of two transects (results not shown), one from the AP and Weddell Sea (10°W to70°W) northwards through the Scotia Sea and up into South America and the other from the Ross Sea to New Zealand, showed some evidence for greater local richness within the PF even after correction for sampling effort but no strong latitudinal trend. A lack of samples at certain bands of latitude due to the absence of continuous north to south continental shelf coupled with the meandering nature of the PF, allowing Antarctic species from South Georgia to be found at the same latitude as species north of the PF in South America, may be hiding any latitudinal trends even if they do occur.

When the individual distribution patterns were compared using Bray-Curtis measure of similarity in PRIMER using the latitudinal and longitudinal range sizes and the geographical mid-points of those ranges, 14 distinct distribution patterns emerged (Figure 5.4a-h). Half of these patterns represented 5 or fewer species, with the others representing between 10 and 74 species. The seven more regional patterns (Figure 5.4a.) represent 41 species that appear to have very localized distributions and are endemic to a single region e.g. Ross Sea, New Zealand, South Georgia etc. figures 5.4b-5.4d represent 18 species whose distributions seem to center around the Scotia Sea, northern Antarctic Peninsula and the tip of South America with the three groups differing in the direction in which the ranges extended from the center (south westward, south eastward and northwards). The smallest pattern (Figure 5.4e) represents three species, one from the coast of continental East Antarctica and two from the sub-Antarctic that have narrow latitudinal ranges but wide longitudinal ranges between 58°E and 176°E. In contrast, figure 5.7f represents the largest number of species, 73, which show a wide distribution both latitudinally and longitudinally and could be described as cosmopolitan within this dataset. This classification does not distinguish between those species confined to south of the PF and those also found further north. The final two patterns (Figures 5.4g and h) represent species whose longitudinal range spans about half of the hemisphere either starting or ending in the Scotia Sea region. Figure 5.4g includes 22 species from inside and outside the PF that have their most westerly distribution somewhere South of New Zealand or Tasmania and extends eastward through about 180° to the tip of South America or the Scotia arc. Figure 5.4h shows almost the opposite pattern to Figure 5.4g, with 14 species originating in either southern South America or the Scotia arc and extending eastwards as far as the Sub-Antarctic Islands of Heard and Kerguelen. Almost all of the aforementioned patterns, with the exception of the Ross Sea, NZ, Australia and sub-Antarctic Islands endemics (Figure 5.4a and 4e (32 species in total)), overlap in the region of the Scotia Sea.

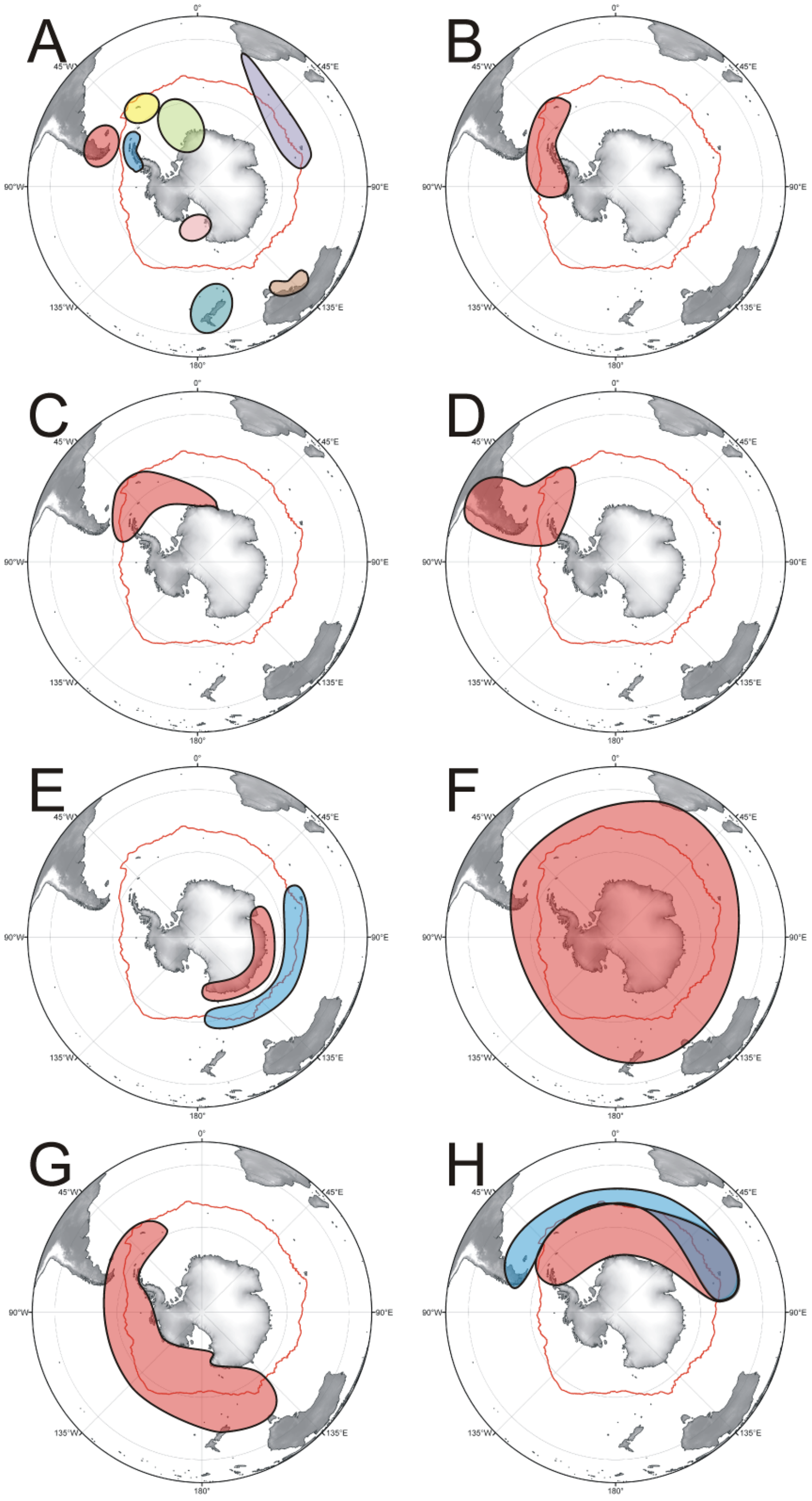


Figure 5.4. General patterns in the distribution of pycnogonid species found at three or more locations in the Southern Ocean and neighbouring regions. A-H are the eight major types of distribution patterns observed.

To examine the extent and nature of eurybathy and depth restrictions in the pycnogonids I looked at the depth ranges and the mean depth at which each species is found. The depth ranges of species found at three or more locations (Figure 5.5) varied from species that had only been recorded at a few locations and only from a narrow depth range, e.g. *Achelia quadridentata* (Hodgson, 1910) and *Tanystylum brevipes* (Hoek, 1881), to species such as *Colossendeis megalonyx* which were very well sampled and had a depth range of over 5,600m. The majority of the mean depths of species were shallower than 500m, ~72% of the species. The vast majority of the 183 species found at three or more locations, 170, were found at least once in waters shallower than 1,000m. Twelve species were only recorded below 1,000m and, of these, four were restricted to depths below 3,000m. The bathymetric ranges of the pycnogonids show a high degree of eurybathy, with 65% of species having a depth range of greater than 500 m and 37% of species having a range of greater than 1,000 m. The midpoint of the majority of species' depth range was deeper than the mean depth at which they were found. Only 17% of species had a mean depth below that of the midpoint of the range, and 21% of species had a mean depth over 1,000 m shallower than the midpoint. Depth range did not strongly correlate with either latitudinal or longitudinal ranges.

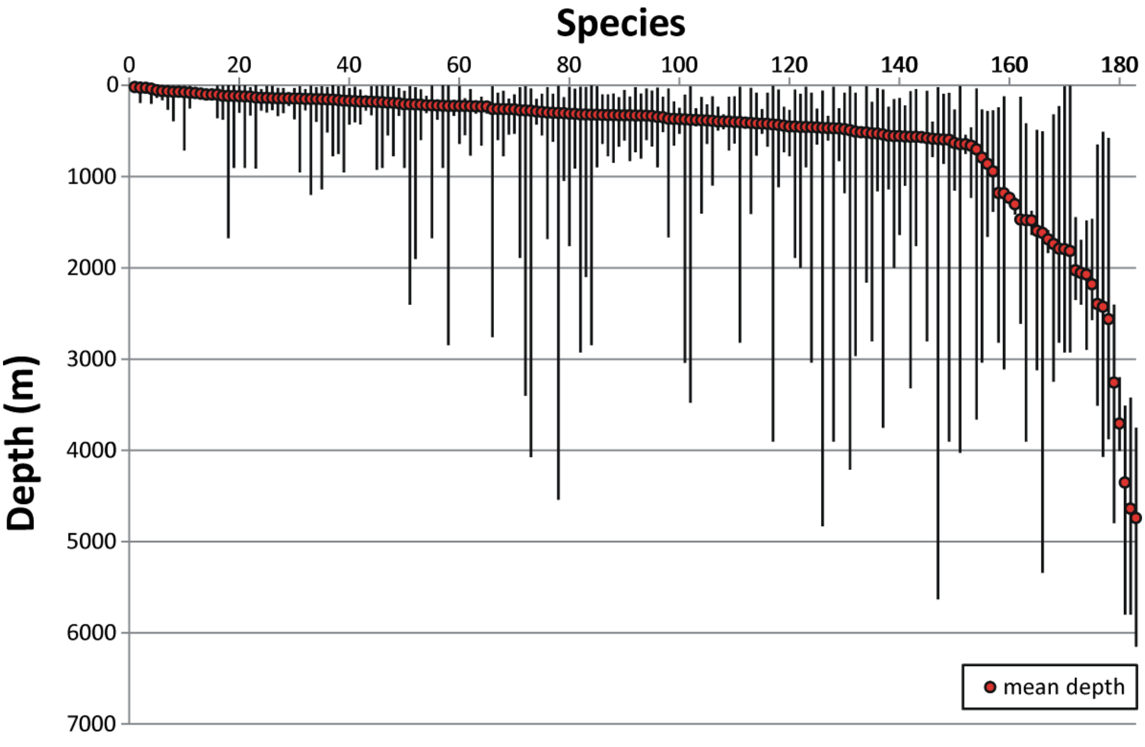


Figure 5.5. Depth ranges and mean depths of pycnogonid species found at three or more locations in the Southern Ocean and neighbouring regions.

Biogeographic Patterns

In order to analyse the similarity of the sample locations and to find clustering groups based on their species composition, a multivariate analysis was performed in PRIMER. The results of the PRIMER multivariate analysis of the species composition of all cells containing 3 or more species (Figure 5.6a) were mapped onto their geographic locations (Figure 5.6b). The results show 5 distinct geographic groupings with a cutoff point of 22% similarity. The largest cluster, group 1, is contains cells that are exclusively found within the PF on the continental shelf or around islands. Group 2 was also only found within the PF but always in areas of deep water (>1,000m). Group 3 comprised solely of cells from the continental shelf of South

America. Group 4 represents cells from around the sub-Antarctic Islands of Heard, Kerguelen, Prince Edward and Crozet. The fifth group made up of two branches (a & b) group is exclusively found in the waters around New Zealand and its neighboring islands. Many of the less well sampled cells, usually containing the lowest numbers of species, showed no geographic affiliation in their species composition. This is probably due to the low sampling effort meaning that only the more common, cosmopolitan species are reported.

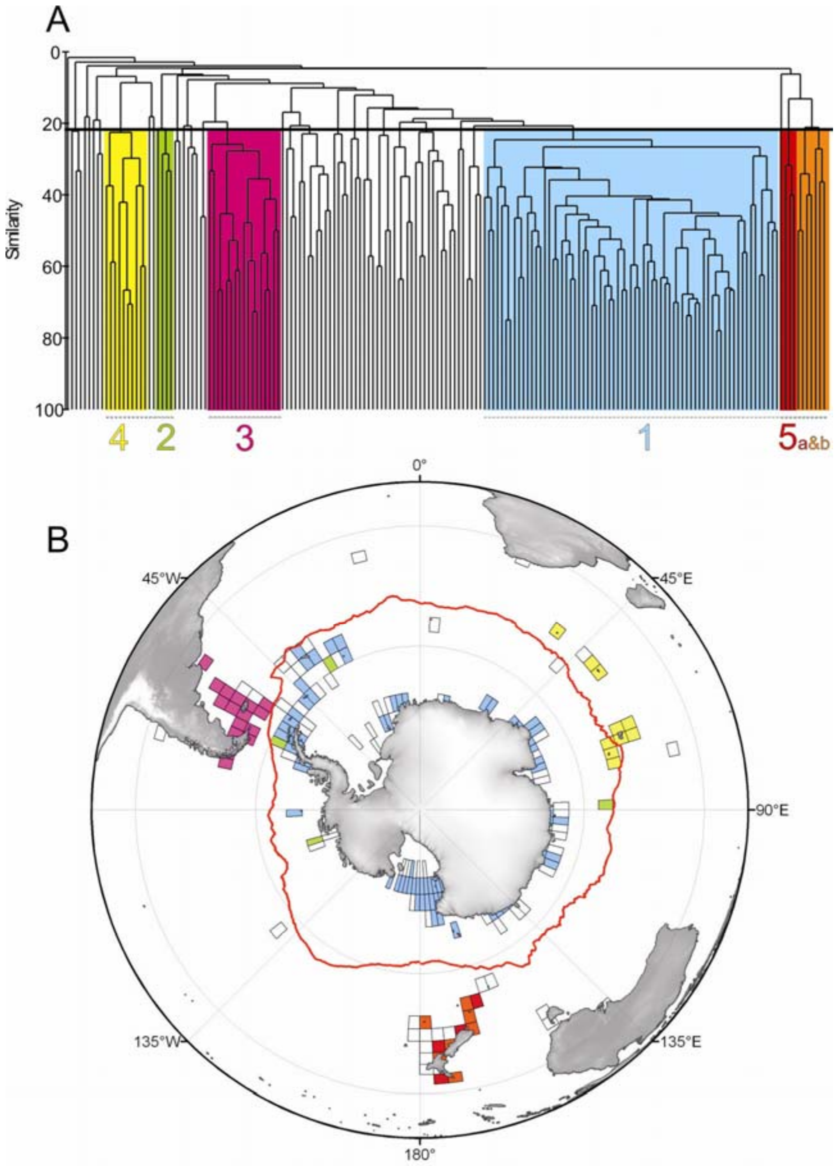


Figure 5.6. Large scale biogeogrpahic relationships in species assemblages for 3° by 3° grid cells that contain three or more species of pycnogonid. a) Cluster analysis of the percentage faunal similarity between cells. b) A geographic representation of the relationships shown in Figure 5.6a. The colours represent the geographic regions; Antarctic (blue), Antarctic Deep (green), South American (pink), Sub-Antarctic (yellow) and New Zealandean (red/orange).

DISCUSSION

The main questions addressed by this chapter tackle the broad-scale biogeographical or macroecological patterns in the distribution of the pycnogonids. Although the pycnogonids are among the groups better represented by the limited deep sea sampling (Brandt et al., 2004), the vast majority of records, 93%, are from water shallower than 1,000 m. The continental shelf in Antarctica is deep and previous work has defined the shelf region as anywhere down to 1,000 m (Clarke et al., 2007a). Therefore it can be said that any major patterns observed from this dataset represent those found on the continental shelf.

Species Richness

For the pycnogonids, as with other taxa, previous works have examined species richness and distributions based upon predefined geographic sub-regions, with these regions being defined by maritime areas such as seas or archipelagos (Barnes & De Grave, 2000; Munilla & Soler, 2009) or by previously described biogeographic regions such as those proposed by Hedgepeth (1969) over thirty years ago (Arnaud, 1974; White, 1984; De Broyer & Jazdzewski, 1996; Clarke & Johnston, 2003; Rodriguez et al., 2007). When attempting to quantitatively assess the distribution of species numbers the differences in area and sampling intensity for the different regions has made meaningful comparison difficult. Added to this, many of the previous studies have used different, often subjective definitions of their study areas and how and where data is split geographically, e.g. how islands are grouped together into single regions. I used the three degrees of latitude by three degrees of longitude grid cells to divide up the Southern Hemisphere into comparable sections (Clarke et al., 2007a). Although the area of the cells in the north of the study is greater than those in the south I did not attempt an equal area cells approach on the basis that the amount of topographic variation within cells meant that you could never completely compare like with like, with the area of continental shelf per cell varying depending on location. With some of the regions used to amalgamate data by previous studies varying in size from 639,681 km^2 in the Weddell Sea to 2,626 km^2 at Bouvet Island it is possible that for the larger locations the spatial scale at which the data is examined may mask local details and patterns (Clarke et al., 2007a).

Much of the pattern observed in species richness is a reflection of sampling effort, with the best sampled regions being home to the most species. However, even when I attempted to correct for sample effort some unexpected hotspots appeared. The region of which had the highest concentration of high residual values was East Antarctica (48-72° E). With further investigation into the samples which produced these results I can state that these are cell which have low sample numbers and many of these samples come from the British, Australian and New Zealand, Antarctic Research Expedition (BANZARE) (Gordon, 1944) and include stations where a single list of specimens is given for a location but multiple sample methods were used. Not enough information is available to determine which animals were caught using each piece of equipment and only a single geographic location is provided. I must conclude that simple correction for the number of samples taken is only part of the story: equally important is the thoroughness of that sampling, the methods used to sample and subsequent taxonomic work.

Perhaps a more effective way of comparing regional species richness between different geographic areas is with rarefaction curves (Gotelli & Colwell, 2001). This method allows comparisons between cells with different numbers of samples, however, it does require several samples to be taken from each cell used thus excluding the majority of cells from the study area. The first obvious pattern to emerge from the rarefaction curves is the relative paucity of species in regions outside PF. This is perhaps unsurprising as the Antarctic is known to be richer in species than its neighbouring regions (Munilla & Soler, 2009). Using this method of comparison some areas of Antarctica are significantly richer than others. Other than for a single cell from the WAP, which falls within the "typical Antarctic" grouping despite being adjacent to the South Shetland Island cells, there is a high degree of similarity in the shape of the curves from the same geographic regions. These cells can therefore be taken as representative of the larger geographic regions that they are from. Perhaps surprisingly when compared to other studies, the EWS has the steepest initial curves of any geographic region, indicating high local species richness. Other studies, such as Munilla and Soler (2009), do not show the EWS region as particularly species rich, this is because they do not include the most recent data from the two Polarstern cruises (1996 and 2003), recording 80 species (Soler et al., 2009). The highest overall species numbers were from the cells surrounding the SShI and the curves for these cells had not yet reached asymptote. These four cells contain far more species for a given number of samples than neighbouring cells such as those from the South Orkney Islands or the WAP cell immediately south west of the SShI (the most sampled cell in this study). This indicates that the SShI/Bransfield Strait region is a species richness hotspot for pycnogonids.

The SShI and Bransfield Strait region is diverse both in its marine biology and its physical environment. The region has a highly varied geomorphology and geology including deep troughs, canyons, shelf, slopes, abyss, embayments, cold seeps and a range of sediment types from soft silt to hard bedrock. The region is also very interesting oceanographically. On the sea floor the region is dominated by two major water masses (Clarke et al., 2009), the northern side of the islands has relatively warm Circumpolar Deep Water (0 to ~2 °C) and on the southern side, inside the Bransfield Strait, colder Weddell Sea Bottom Water (0 to -2°C). These two water masses have very different chemical properties (Orsi & Whitworth, 2004). The region between Elephant Island and the King George Island is an important location for the meeting of these water masses. The surface waters of the region are not the most productive known from the Southern Ocean but have been shown to be a region where the highest percentage of particles from the plankton reach the sea floor (Kim et al., 2004), providing a rich source of food for the benthos. The SShI and the northern tip of the AP were among the places to be deglaciated on the shelf after the last glacial maximum around 19k years ago (Heroy & Anderson, 2007), and there is some question over the maximum northern extent of grounded ice in this region (Heroy & Anderson, 2005). The glaciological evidence for a potentially ice free area makes the SShI and northern AP a candidate location for a marine shelf refuge during the Last Glacial Maximum.

Species Ranges

Pycnogonids are obligate brooders, for most species it is known (except Colossendeids) that males carry fertilised eggs and larval stages, that later on can become parasites on, usually sessile, invertebrates (review in Arnaud & Bamber, 1987). This type of reproduction could be considered to be in conflict with the wide geographic ranges reported for many pycnogonid species (if these hold true after further molecular work). Wide ranging brooding species in many invertebrate groups are relatively common in Antarctica, however, in many occasions these proposed wide distributions might prove to be result of poorly detailed taxonomic discrimination at species level or cryptic speciation processes only evident with fast-evolving molecular markers (Held & Leese, 2006).

The longitudinal and latitudinal range patterns shown by the pycnogonids (Figures 5.3a & b) are very similar to those shown by the bivalve molluscs (Clarke et al., 2007a). One possible explanation could lie in the fact that both groups contain relatively high numbers of wide ranging species which may in fact be groups of distinct but morphologically similar species or species complexes. An example from the bivalves of a circum-Antarctic species that appears to show cryptic speciation based upon location and geographic isolation is *Lissarca notorcadensis* (Linse et al., 2007). Molecular work by Krabbe et al. (2010) on pycnogonid specimens from a relatively limited geographic area of the SO (maximum of 1,000 km apart) suggests that one of the widest ranging species, *Colossendeis megalonyx,* includes cryptic species. Although evidence in the most commonly found species of SO pycnogonid, *Nymphon australe* Hodgson 1902, suggests low genetic divergence between populations across similar distances on the Antarctic Peninsula (Mahon et al., 2008) and even across distant Antarctic locations (Arango et al., in press). These somewhat contrasting results on genetic diversity and differentiation in widely distributed species of Antarctic pycnogonids show it is not possible to generalize explanations for pycnogonid distributions.

Both *C. megalonyx* and *N. australe* have been recorded from water shallower than 20m down to the deep-sea. In Antarctica the hostile shallow benthic environment tends to be dominated by macrobenthic species with planktotrophic development due to their ability to quickly recolonize ice-disturbed haibats (Poulin, 2002). As only 6.8 % of Antarctic pycnogonid species are found exclusively shallower than 100m (Munilla, 2001) it is not surprising that this group seems unhindered by the lack of a planktonic life stage. Species such as *N. australe* have been shown to have wide geographic ranges for genetic haplotypes (Mahon et al., 2008) indicating that there must be some mechanism for gene flow. The most recent work on *N. australe* by Arango et al. (in press) has shown it to be a single identifiable circumpolar species but with significant genetic differentiation between distant locations e.g. WAP, EWS and East Antarctica. The lightweight body and large surface area to volume ratio of *N. australe* might allow for dispersal by some of the strong currents that surround the Antarctic continent. This would also explain why the larger and heavier *C. megalonyx* shows greater variation over similar distances.

The pycnogonids have a high degree of eurybathy but the mean depths for species are usually shallower than the mid-point of their range. This is largely due to most benthic sampling having been carried out in water shallower than 500 m (Griffiths et al., in press). As with latitudinal and longitudinal ranges, bathymetric ranges are a subject of debate because of the latest advances in molecular work. Molecular analysis of *C. megalonyx*, which has the widest bathymetric range of any of the species studied, could not determine a depth based separation of clades based upon the available evidence (Krabbe et al., 2010).

From the various distribution patterns (Figure 5.4) representing the species found at 3 or more locations it is possible to say that ~82.5 % of species fit to a pattern that includes the Scotia Sea, more specifically the SShI. Other studies (Stock, 1957; Hedgpeth, 1969; Munilla, 2001) have suggested Antarctica as a center of radiation for the group. Munilla and Soler (2009) proposed the Scotia Sea as center of retention of the circumpolar current fauna and dispersion to other zones from Antarctic waters. I would go as far as proposing the Scotia Sea, in particular the SShI and the northern AP as a center of radiation for pycnogonids and a potential refuge during the last glacial maximum. This idea is supported by the high numbers of species found in the region, the steep species accumulation curves and the poorer but similarly sampled neighbouring areas (Figures 5.1c and 5.2) and the glacial history of the region (Heroy & Anderson, 2007). Other groups, such as the octopods, have been shown to have survived and radiated outwards from the SShI. These include the circumpolar species, *Pareledone aequipapillae,* which has colonized the Antarctic shelf in a clockwise direction from the SShI round to the Amundsen Sea (Allcock et al., in press). The SShI are also reported to be a hotspot for speciation in the octopods (Allcock et al., in press).

These patterns include a large number of widely distributed, circumpolar or cosmopolitan species (~40% of all species found at three or more locations (Figure

5.4f). As previously mentioned, molecular techniques have begun to question the validity of some of these wide ranging species. With increased molecular analysis it is likely that many of these patterns will break down into a collection of smaller patterns based upon a range of determining factors such as oceanography, bathymetry, water temperature, habitat type and geographic isolation. If the environmental factors responsible for cryptic speciation can be clearly identified within a group, e.g. strict separation between clades on different islands, it would be possible go back to the database and re-assign the recorded specimens. For regions, depths or habitats where different clades are found side by side with no apparent boundaries it would be impossible to determine the genotype of the animals in the database without re-examining the original specimens. This issue is not confined to the pycnogonids, with species previously thought of as circumpolar from a range of phyla having been recently split based upon molecular evidence: crinoids (Wilson et al., 2007), molluscs (Linse et al., 2007; Wilson et al., 2009), and isopods (Held, 2003; Held & Wägele, 2005; Raupach & Wägele, 2006).

Biogeographic Patterns

The results of the biogeographic analysis strongly suggest a distinct but relatively homogeneous Antarctic shelf fauna for the pycnogonids. These results agree with those of Munilla and Soler (2009), and the overall pattern of a distinct Antarctic fauna with very little similarity to that of New Zealand and greater similarity to that of southern South America echoes patterns already shown for the bryozoans and molluscs (Griffiths et al., 2009) and the ascidians (Primo & Vázquez, 2007). This analysis also identified a separation between the Antarctic shelf fauna and that of the deep sea within the PF. Previous work from the EWS region (Soler et al., 2009) also shows a distinction between the faunal composition of samples taken from the shelf (<848 m) and those collected from deeper water (900-1,866 m). The low level of similarity between the distinct grouping of the sub-Antarctic Islands (Prince Edward, Crozet, Kerguelen and Heard) and the other geographic regions implies that the remoteness and geographical isolation of these islands has led to a regional fauna, potentially derived from both Antarctic and South American populations (Munilla, 2001) through west-wind drift but also including 24 regionally endemic species (Munilla & Soler, 2009). The separation of New Zealand implies that, as in other taxa (Griffiths et al., 2009), independent radiation has occurred in this region due to its early separation from Gondwana and proximity to the Indo-West Pacific diversity hotspot.

How such biogeographic patterns will change with increasing material available, better taxonomic resolution and molecular data is uncertain, however it is unlikely, given the results I have already, that the large scale differences between Antarctica and its neighbouring continents will change. Within these studies the PF seems to be an effective barrier to gene-flow, both in the pycnogonids (Krabbe et al., 2010) and in other groups including brooding ophiuroids (Hunter & Halanych, 2008) and broadcast-spawning nemerteans (Thornhill et al., 2008), suggesting that the number of species endemic to the Antarctic is likely to increase and the level of similarity to South America will decrease. It must also be noted that in some species which are thought to show cryptic speciation, e.g. the mollusc *Doris kerguelensis*, the opposite has been found with the same haplotypes being found on both sides of the PF (Wilson et al., 2009). The effect of these cryptic species on the pattern within the Antarctic is harder to predict. For the pycnogonids, bryozoans, bivalves, ascidians and gastropods there seems to be little evidence, based upon current morphological taxonomy, for biogeographic sub-regions within the PF (Griffiths et al., 2009). Undiscovered cryptic species, within all of these groups, may be useful to revealing local and regional patterns caused by the glacial cycles, bathymetry, oceanography, geomorphology or habitat preferences. However, unless many of these species evolved and radiated in response to the same physical drivers of speciation there may not be common cryptic distribution patterns across taxa.

CONCLUSIONS

The Antarctic pycnogonid fauna, given our current level of knowledge, is distinct and the richest in the world. The high level of Antarctic endemism (Munilla & Soler, 2009) coupled with a lack of any obvious biogeographic sub-regions implies that species have evolved and become widely dispersed in the region.

The SShI is the most species rich area in Antarctica and is a center of radiation for pycnogonids in the Southern Hemisphere and was potentially a refuge for species during the last glacial maximum.

New molecular advances have started to change our understanding of circumpolar and cosmopolitan species proposing cryptic speciation. Some of these biogeographic patterns may change with increased knowledge of pycnogonid diversity (both species and genetic). How much these patterns are likely change in the pycnogonids is unclear, it seems probable that the overall pattern, of a rich Antarctic fauna distinct from that of its neighbours, will remain true and even strengthen. Pycnogonid species numbers in the Antarctic are likely to increase with further sampling, taxonomic work and molecular data, helping to gain a better understanding of global pycnogonid diversity, distribution and evolutionary history.

CHAPTER 6 - GEOGRAPHIC RANGE SHIFT RESPONSES TO CLIMATE CHANGE BY ANTARCTIC BENTHOS: WHERE WE SHOULD LOOK.

[The data in this chapter are also presented in: Barnes, D.K.A., Griffiths, H.J. & Kaiser, S. (2009) Geographic range shift responses to climate change by Antarctic benthos: where we should look. Marine Ecology Progress Series, 393: 13-26]

Chapter 6 - GEOGRAPHIC RANGE SHIFT RESPONSES TO CLIMATE CHANGE BY ANTARCTIC BENTHOS: WHERE WE SHOULD LOOK.

INTRODUCTION

For the last few million years the dominant climatic pattern has been an alternation of states between long and cold ice ages (towards glacial maxima) and brief warmer inter-glacials. Environment characteristics are now rapidly changing, especially in the Antarctic Peninsula (AP) which is warming by ~3.5°C per century (Vaughan et al., 2003). Although sea surface temperatures have increased slightly in the Bellingshausen and Scotia Seas (Meredith & King, 2005; Whitehouse et al., 2008), the main marine effect measured to date is a regional reduction in fast ice (Zwally et al., 2002). Projected climate change impacts around the AP would seem very severe given characteristics of the marine fauna such as extreme long life (see Arntz et al., 1994) and stenothermy (Peck, 2005a). The present chapter focuses on where and at what taxa to look at in order to detect range shift responses to environmental change. Species each have thermal optima, and an upper and lower tolerances for the habitats in which they occur. Warming or cooling will change the location of their limits and optima. Species have a varying ability to alter their ranges in response to climate, with a lag phase depending on their mobility. Such dispersal may be through gametes, larvae, adult mobility or rafting by sessile adults. Typically such range shifts involve northward or southward migrations and are evident for fauna both extant and in the past (Roy et al., 2001; Thomas & Lennon 1999; Beaugrand et al., 2002; Mieszkowska et al., 2007). In the UK for example, northward range shifts driven by climate change have now become very striking and a concern in the popular media (e.g. in butterflies: Clay-Jones & Bignell, 2008;). Terrestrial data sets are of course more comprehensive but these too have comparability problems and unlike the SO seabed are potentially influenced by many interacting variables; e.g. biological introductions (of the study species, their predators, competitors and food plants), and land use.

Despite the considerable number and severity of direct anthropogenic impacts on biodiversity, projected climate change probably represents the greatest extinction risk to organisms in the future (Thomas et al., 2004), especially in the polar regions (Peck, 2005a). Most described polar biodiversity occurs in the sea, and most of that is benthic and on the continental shelf (Clarke & Johnston, 2003; Barnes et al., 2009a; but see Brandt et al., 2007b). I argue that the threat to survival is particularly pertinent to the rich Antarctic benthos for a number of reasons: for several million years the thermal climate of the SO has remained remarkably constant and cool (Zachos et al., 2001) giving rise to a biota with depressed upper heat tolerances (Somero & DeVries, 1967); Antarctic shelf species may be more thermally sensitive than their narrow thermal survivability envelope indicates because certain critical functions (such as predator avoidance) are even more stenothermal (Peck, 2005a). These traits, together with typically slow growth, long time to first reproduction and limited dispersal ability (Poulin et al., 2002), i.e. a slow generational turnover, will pose major challenges for adaptation of Antarctic shelf benthos. As the options of tolerance and adaptation in Antarctic benthos seem limited (but see Barnes & Peck, 2008), the alternative responses are migration or extinction. To avoid extinction many organisms around the AP, one of the fastest warming regions, must migrate deeper or along linear coast to reach lower temperatures.

Using fossil evidence from Seymour Island, Aronson et al. (2009) speculate there will be drastic range changes in Antarctic benthos driven by near future warming. However the fossil record around Antarctica is poorly represented in space, time and scientific effort compared with modern data, which also have the advantages of better taxonomic resolution and potential linkage to oceanographic and ecophysiological data. Range change by modern species should be most easily detected at range edges, so I used geographic information from the Southern Ocean Mollusc Database (SOMBASE) and Scientific Committee on Antarctic Research Marine Biodiversity Information Network (SCAR-MarBIN) international databases (Griffiths et al., 2003; DeBroyer & Danis, 2008) to assess where the geographic limits for Antarctic benthic marine species exist. These data are collected and entered by the international scientific community and include thousands of records spanning expeditions from the 1800s to present day. I then analysed these data to look for hotspots where the geographic limits of different Antarctic species coincide (areas where many species reach the edge of their northern or southern range).

As many Antarctic species are considered to be widespread (Clarke & Johnston, 2003), their southernmost limits should abut onto the most southerly land-continental shelf interfaces (and thus be unlikely to change and of little use to monitor). I therefore hypothesised that most southern polar marine species would have their southernmost geographic limits in the southern Weddell and Ross Seas. I expected that a key hotspot of southern limits would be the southernmost tip of South America, and that it will be important to monitor species from this area as the first potentially successful (non-indigenous) invaders of the SO. Secondly, I hypothesized that hotspots of northernmost limits would be around the boundary of the Polar Front (PF), the strongest jet of the Antarctic Circumpolar Current and generally taken to demark the edge of the SO (also see Chapter 1). Under projected regional warming scenarios, my expectation is that northernmost limits will shift southwards. Finally I considered which species (identified in hotspots of southern and northern range limits) are likely to represent the best model for monitoring change.

METHODS

Study area

The current study focused on the continental shelf fauna of the South Atlantic, South Indian, South Pacific and Southern Ocean (SO) areas. The study area is approximately south of 20° S, however South Africa and South Australia were not considered as the records for their faunas are incomplete (in SOMBASE). The northernmost boundary of the SO (my main area of interest) was defined as the Polar Front (PF); however the PF area is complex, with dynamic eddies crossing it north and southwards, it is graduated (i.e. a zone) and also mobile (see Moore et al., 1999). These authors show that the PF can migrate 10 to 100s of km even over short time scales (such as a decade), and will wander much more substantially with glacial-interglacial cyclicity. There are few shelf areas underlying or close to the PF zone, but those that there are, such as the Kerguelen Plateau (KP), can vary between being outside the SO (as is currently the case) to straddling the boundary or lying inside. The southernmost boundary for species in the study area was the edge of the Antarctica continent and, for the purposes of the current investigation, the edges of ice shelves. I appreciate that there is considerable shelf underlying some ice shelves, particularly in the Weddell and Ross Seas, and several drill-holes and remote vehicle observations have revealed a limited fauna in situ (Riddle et al., 2007). Neither of the databases used in this study contain under-shelf records, but if more extensive under-ice investigations are carried out or the geographic limit of major ice shelves retreat, many species may be recorded further south than the southernmost limits considered here. Furthermore, even shelf areas under ice shelves do not represent potential absolute southernmost limits, as large parts of the West Antarctica land mass would be flooded if the overlying ice sheet melts, being both below sea level and without the coastal shield of higher ground (Bamber et al., 2009).

Protocol

To identify appropriate study taxa, I evaluated the number and area coverage of records for different potential model taxa in the SOMBASE and SCARMarBIN databases (cf. Griffiths et al., 2003; DeBroyer & Danis, 2008). Each 'record' is a species reported from a georeferenced sample (such as a trawl, epi-benthic sledge, grab, core, SCUBA dive or ROV video), compiled and checked from the published literature and scientific cruise data by an international network of taxonomic editors for the wider scientific community to use. However the number of samples taken using each of these sampling methods differed in each box (defined below), which represents a source of error. It was determined that the most comprehensive records were for the shelled gastropod and bivalve molluscs, amphipod crustaceans, ophiuroid echinoderms and hexacoral cnidarians. The location of each record of each species of these model taxa is geo-referenced in each database (positions are linked to a Geographical Information System (GIS)). Records for shelled gastropods (n = 9003 records), bivalves (n = 5011), amphipods (n = 6406), ophiuroids (n = 1977), and hexacorals (n = 243), were used from the 989, 448, 829, 82 and 182 species listed in the SOMBASE and SCAR-MarBIN databases for each taxon respectively. Species lists recorded by locality (e.g. for 'South Georgia' or 'South Orkney Islands') were also examined to determine geographic range limits for cheilostome bryozoans (from SOMBASE), ascidian chordates (from P. Carmen, unpublished data) and fish (from M. Belchier and M. Collins, unpublished data). Thus the range of taxa considered by the current study is broadly representative of the spectrum of mobility and reproductive strategies amongst high latitude fauna (e.g. see known data for Antarctic species in www.scarmarbin.be/).

I divided the study area into a series of similar boxes, each 3 × 3 degrees of latitude and longitude (for more details of such methodology, see Clarke et al., 2007a). I first determined the number of boxes containing records of each taxon (471 in total), and then considered geographic patterns of species range limit hotspots. I found that there were data for benthic species from 199 of the 308 (65%) boxes over Antarctic shelf areas. The geographic range of the study and the number of boxes for which SOMBASE and SCARMarBIN contained data is shown in figure 6.1. Patterns of record intensity and richness (species number) are an important context to range limit hotspots, as potential range limit hotspots detected by this method must be a subset of sample or species richness hotspots. I counted the number of species having their most southerly limit within each box to identify hotspots. However many of these records were of species which were only recorded in a single box; I therefore confined my data to species found in at least 3 boxes. I then repeated this process for northernmost limits, but using just the strongest SO datasets: those for the gastropod and bivalve molluscs. Rarefaction analysis was carried out using the species–area option in PRIMER (Clarke & Warwick, 2001), with 999 iterations, on the best sampled grid cells from different regions within the study area.

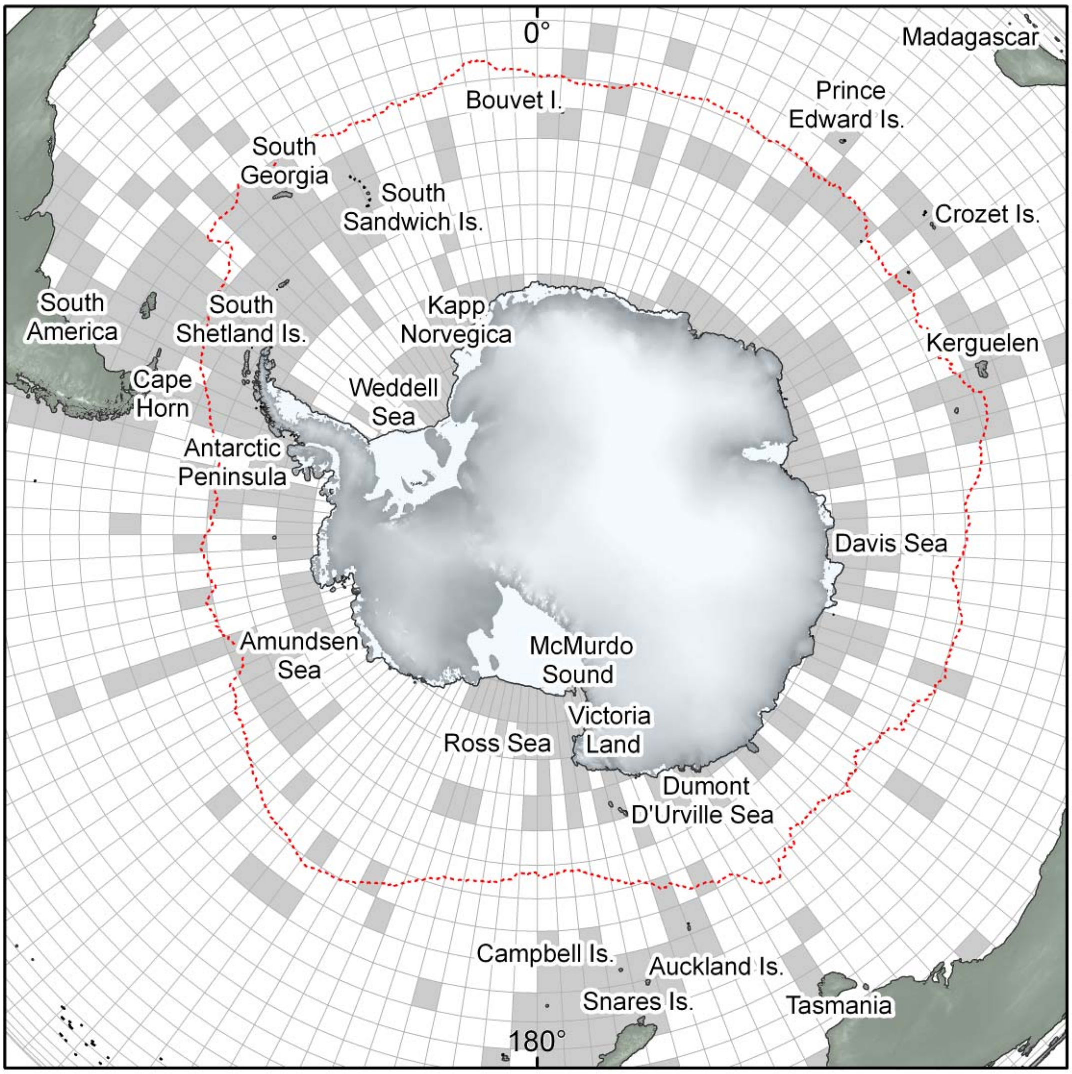


Figure 6.1. Study region: Antarctica, the Southern Ocean and southern temperate areas. Grey rectangles: areas (3 · 3° boxes) of the study region for which data exists in the SOMBASE and SCAR-MarBIN databases for the study groups used. Dashed line: Polar Front

I used the stronger data sets of shelled gastropod and bivalve species to investigate the range patterns of species found at different latitudes by dividing the study area into 10° latitudinal 'bins'. The total latitudinal range of every species was measured. For each latitudinal 'bin' the number of species with particular ranges was counted (summarized into 5° groups). To consider which species might be most appropriate for monitoring range changes in response to projected warming, I examined, as an example, the particular species limited at the South Georgia hotspot.

To test how effective my protocol was for detecting hotspots of range limits rather than simply reflecting sample effort, I constructed both rarefaction curves and examined residuals.

RESULTS

I found strong a pattern in the intensity of records, showing a concentration of research effort around the Scotia arc, AP, Weddell and Ross Seas (Figure 6.2a). Just as evident was the lack of records in the Amundsen and Davis Seas, and along the East AP; therefore any true southern limits existing in these locations will not be found by the current study. Patterns of gastropod species richness within the geographic boxes (Figure 6.2b) were significantly correlated to those for the number of records (Figure 6.2a: Pearson correlation $r = 0.726$, $p < 0.001$). Relationships between the number of records, species richness and range limits are shown for gastropod data in Figure 6.3. In both of these plots 4 points are clearly above the 95% prediction intervals (i.e. the residuals are considerably greater than expected values). These 4 points map to the same 3 × 3° (latitude × longitude) areas; the areas highlighted as range limit hotspots in figure 6.2c,d; rarefaction curves provided further support for the robustness of the hotspots identified. Rarefaction curves for gastropod data from 4 example locations further showed that range limits increased with sampling, but accumulated 4 to 14 times faster in hotspots than in other 3 × 3 degree areas within the same regions (see figure 6.4). It is notable that numbers of range limits approached, or were at, asymptote at non-hotspot areas, whereas at 3 of the hotspots they did not approach asymptote. Thus despite significant relationships between gastropod range-limit data and those for both record and species numbers, there was strong support for the validity of all hotspots identified.

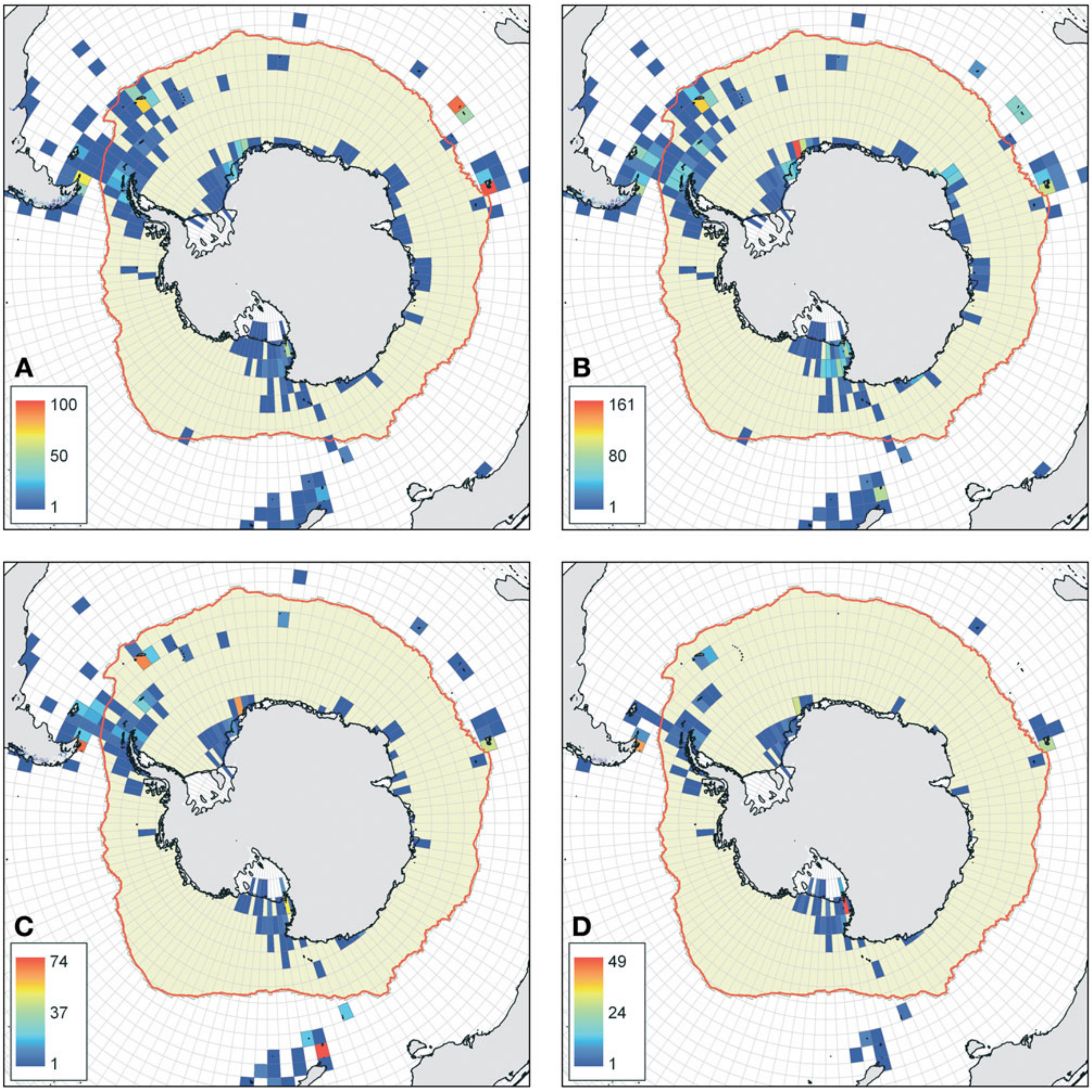


Figure 6.2. Gastropod mollusc richness at high southern latitudes. (A) Numbers of records (the number of separate samples with gastropods reported), (B) numbers of species, (C) southernmost limits, (D) southernmost limits for species present in more than 2 boxes. Data from SOMBASE and SCAR-MarBIN databases

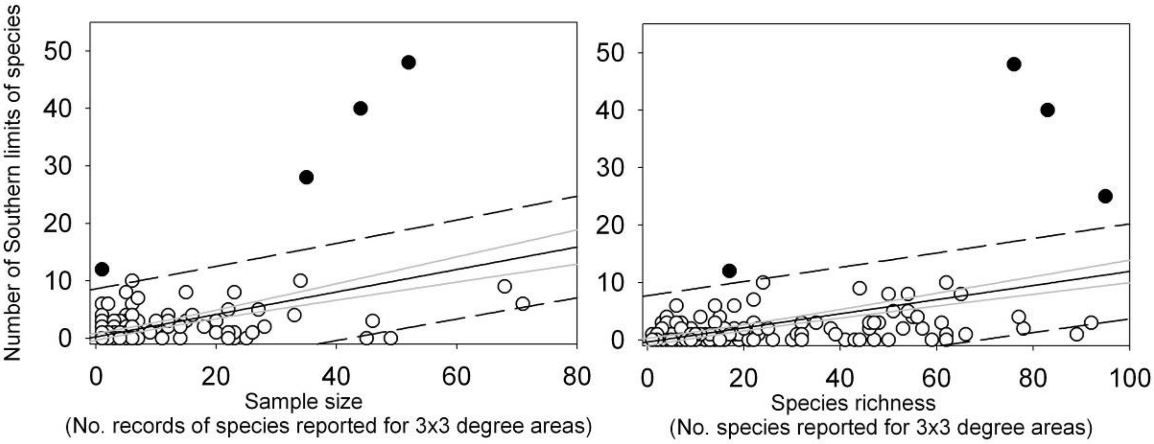


Figure 6.3. Relationship between sample intensity ($R^2 = 28$, $P < 0.001$), species richness ($R^2 = 33$, $P < 0.001$) and southern range limits per geographic sampling area for gastropod molluscs. Solid black line: Significant regressions, grey line: 95% confidence interval, dashed black lines: 95% prediction lines. Filled circles: Hotspots of (southernmost) range limits; these are points with residuals above the upper 95% prediction line.

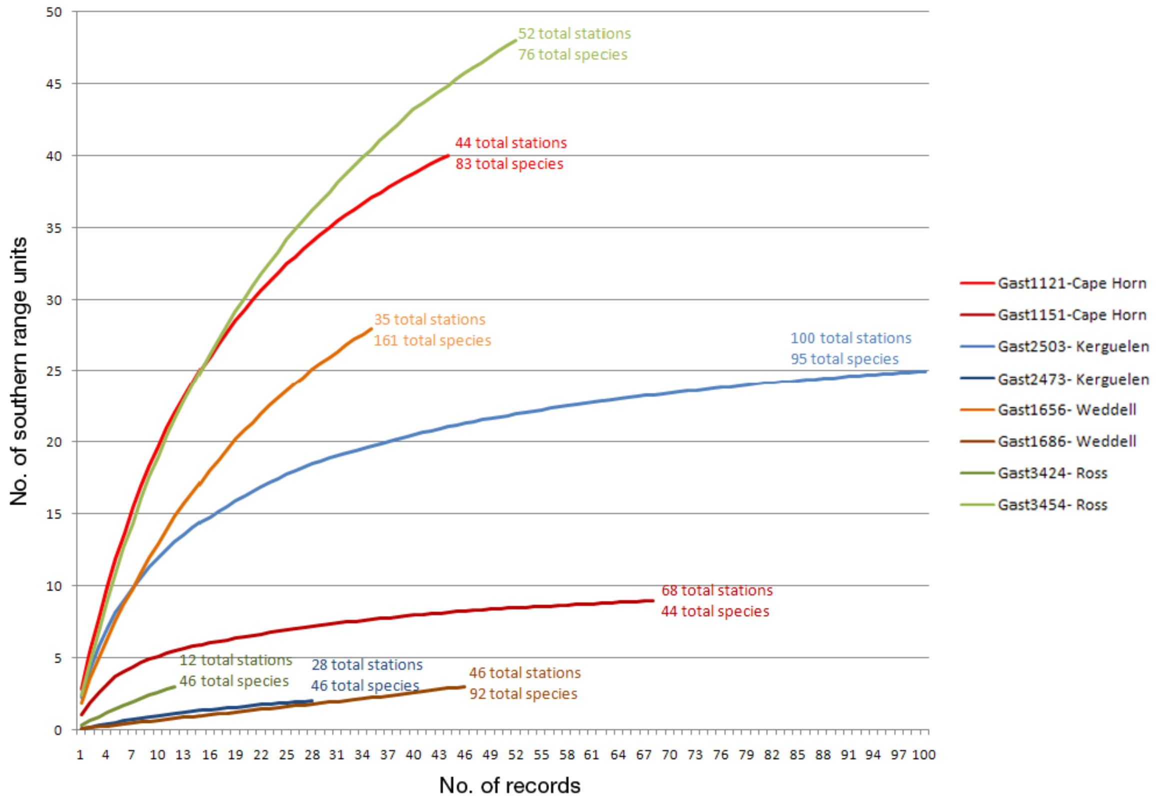


Figure 6.4. Rarefaction curves showing accumulation of (southern) range limits in hotspot and non-hotspot areas for gastropod molluscs (lighter shades = hotspot, darker shades = non-hotspot). Data are for 4 example areas; Cape Horn, Kerguelen Plateau, Weddell Sea and Ross Sea, as shown in the legend

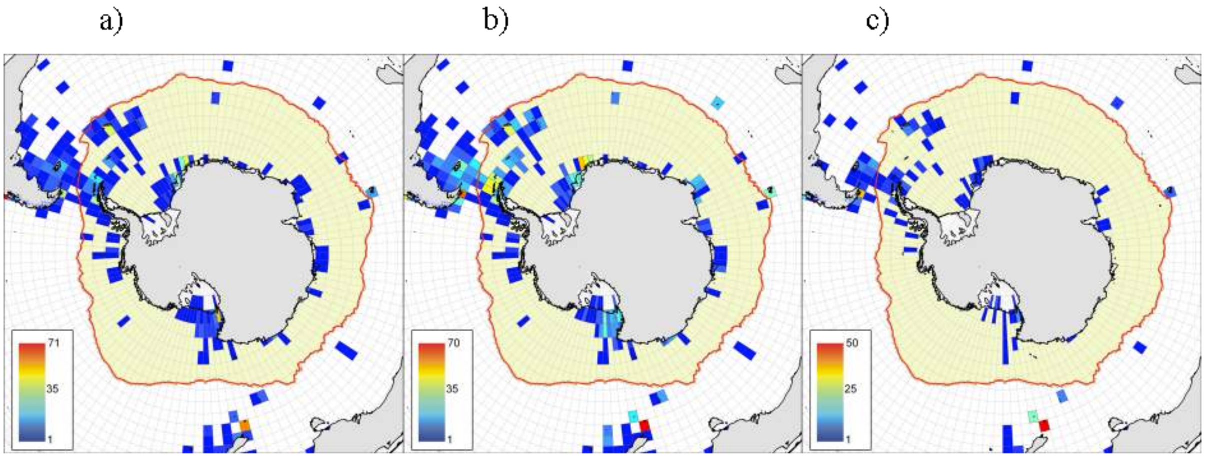


Figure 6.5. Bivalve mollusc richness at high southern latitudes. (a) Numbers of records (the number of separate samples with bivalves reported), (b) numbers of species, (c) southernmost limits. Data from SOMBASE and SCAR-MarBIN databases.

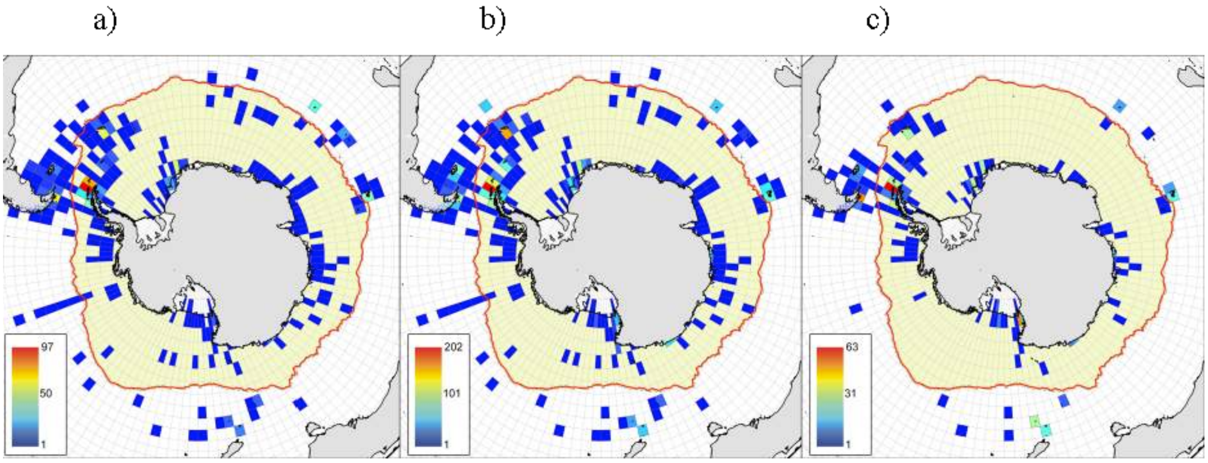


Figure 6.6. Amphipod crustacean richness at high southern latitudes. (a) Numbers of records (the number of separate samples with amphipods reported), (b) numbers of species, (c) southernmost limits. Data from SCAR-MarBIN database.

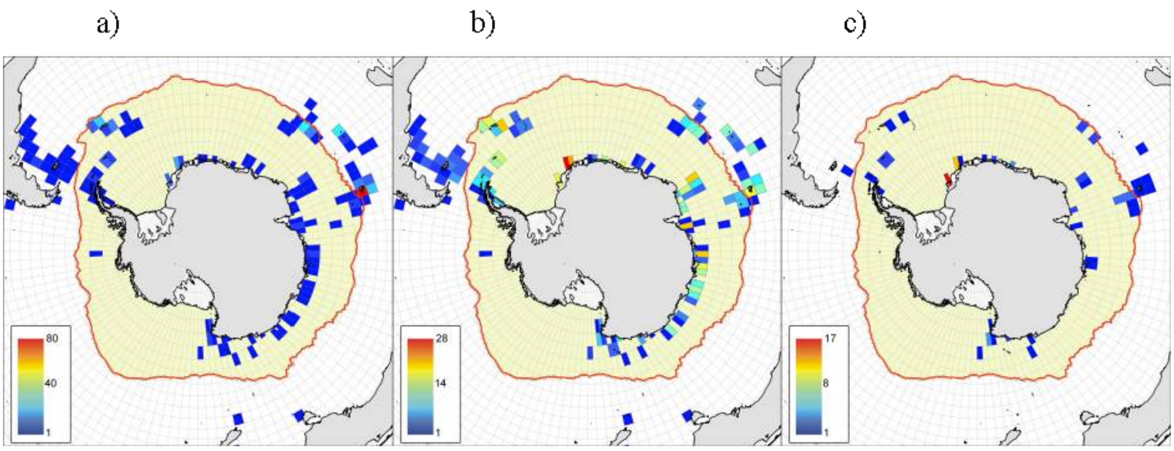


Figure 6.7. Ophiuroid echinoderm (brittlestar) richness at high southern latitudes. (a) Numbers of records (the number of separate samples with ophiuroids reported), (b) numbers of species, (c) southernmost limits. Data from SCAR-MarBIN database.

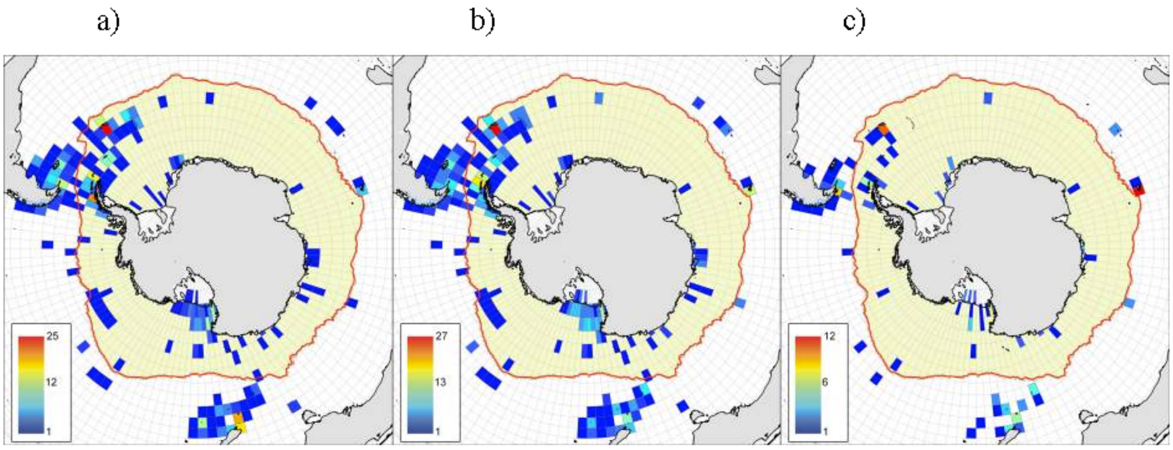


Figure 6.8. Hexacoral cnidarians (hard coral) richness at high southern latitudes. (a) Numbers of records (the number of separate samples with hexacorals reported), (b) numbers of species, (c) southernmost limits. Data from SCAR-MarBIN database.

Patterns in other Southern Ocean study taxa also revealed hotspots. The number of records of species, numbers of species and numbers of southernmost limits of species for bivalve molluscs are shown in figures 6.5a–c respectively. This process was repeated for amphipod crustaceans to reveal records of species (Figure 6.6a), numbers of species (Figure 6.6b) and numbers of southernmost limits of species (Figure 6.6c); for ophiuroid echinoderms (Figures 6.7a-c) and hexacoral cnidarians (Figures 6.8a-c). As with gastropods, for each of the taxa studied there were significant (Pearson) correlations between the number of range limits and species richness, and the number of records and species richness. The relationships for the bivalve molluscs, amphipods, ophiuroids and hexacorals are each shown in figure 6.9. In each plot there are a few points considerably above the 95% prediction intervals (red lines, figure 6.9) and in every case of each taxon these were the hotspots identified previously (shown in figure 6.10). It is clear that the residuals for hotspots are highly positive compared with other (non-hotspot) data, which in contrast lie within 95% prediction intervals.

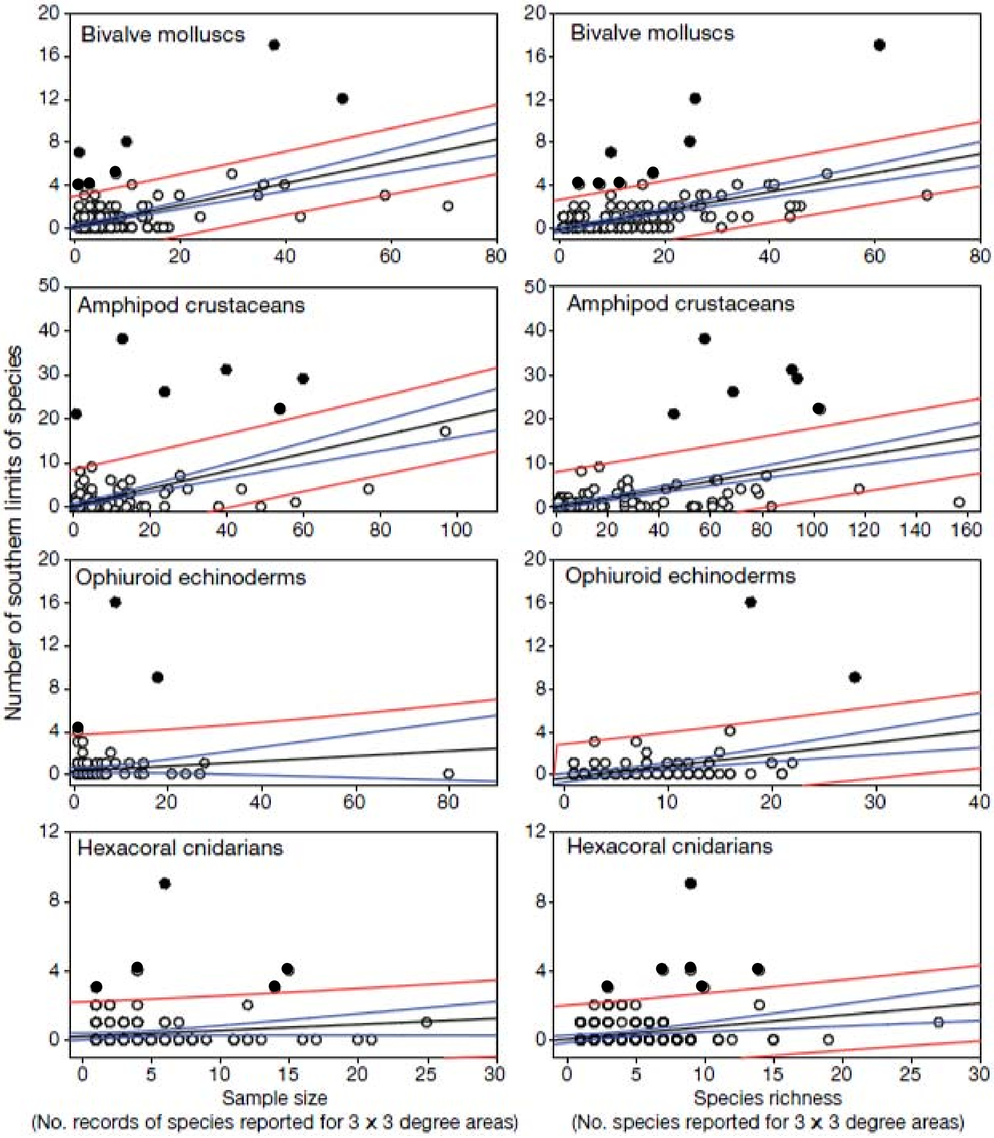


Figure 6.9. Relationship between sample intensity, species richness and southern range limits per geographic sampling area for bivalve molluscs ($R^2 = 29$, $P < 0.001$; $R^2 = 32$, $P < 0.001$), amphipod crustaceans ($R^2 = 25$, $P < 0.001$; $R^2 = 30$, $P < 0.001$), ophiuroid echinoderms ($R^2 = 1$, $P = 0.19$; $R^2 = 14$, $P < 0.001$) and hexacoral cnidarians ($R^2 = 1.4$, $P = 0.06$; $R^2 = 6.2$, $P = 0.001$). Solid black line: Significant regressions, blue lines: 95% confidence interval, and red lines: 95% prediction lines. Filled circles: hotspots of (southernmost) range limits all lie above the upper 95% prediction line.

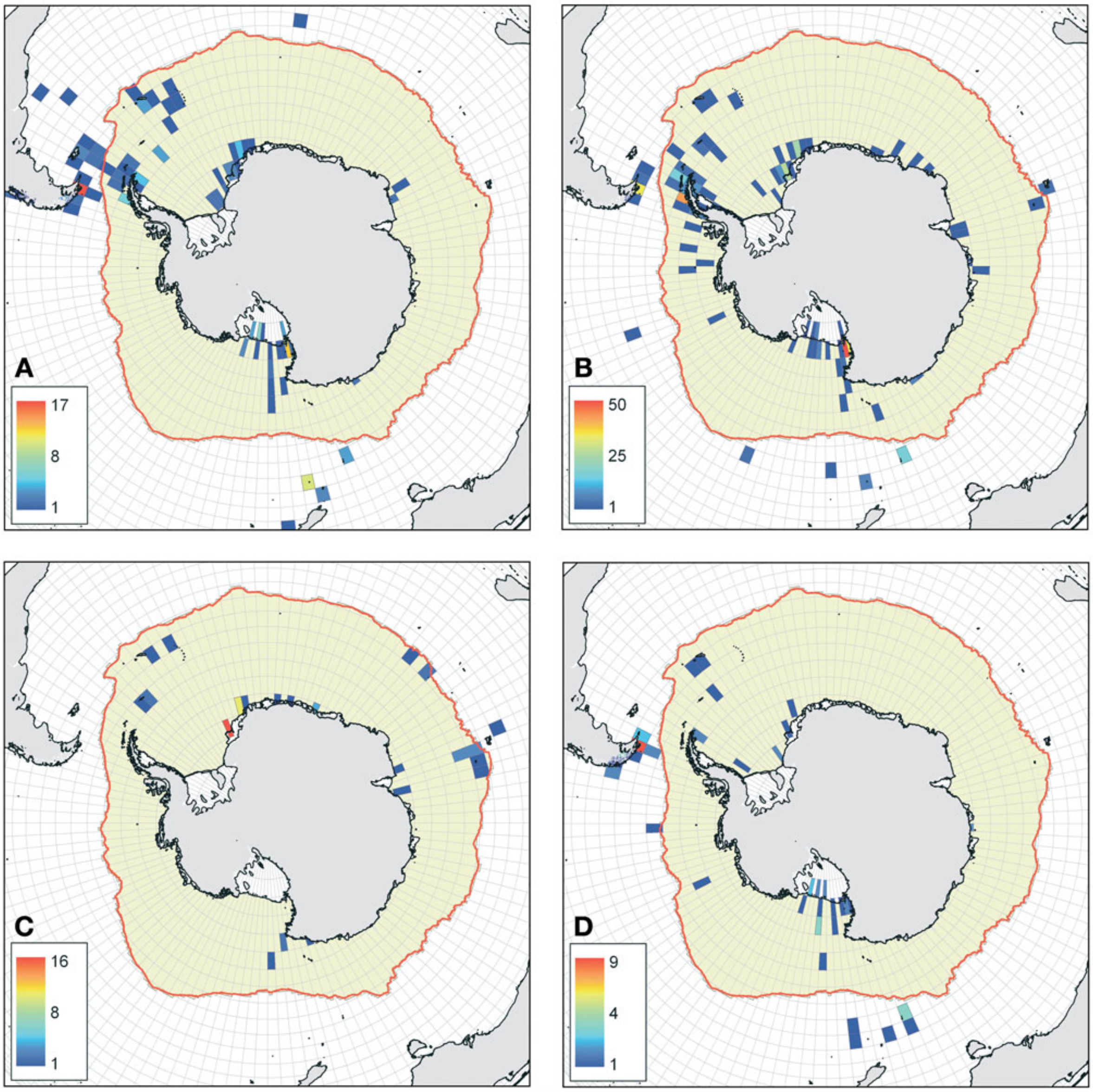


Figure 6.10. Number of species at their southernmost limit at high southern latitudes (for species occurring in more than 2 boxes) by 3°x3° ·box for (A) bivalves, (B) amphipods, (C) ophiuroids, and (D) hexacorals. Data from SOMBASE and SCAR-MarBIN databases

Southernmost limits

There were few southernmost limits identified in most of the boxes for which there were records, but there were hotspots found in 6 of the boxes (Figure 6.2c): southernmost Cape Horn, South Georgia, Kapp Norvegica, East Kerguelen, Snares/Auckland Islands (southern New Zealand), and McMurdo Sound (southern Ross Sea). When species only present in 1 or 2 boxes were removed, far fewer boxes were found to contain recorded range limits; for example, hotspots disappeared from isolated islands such as the South Sandwich and Crozet archipelagos, and Bouvet Island (Figure 6.2d-the same 4 hotspots as supported by figures 6.4 & 6.10). South Georgia, and Snares/Auckland Islands disappear from the 6 hotspots, leaving 4 key areas where southernmost gastropod limits are concentrated. However, of these southern limit hotspots it is judged that 2 are particularly important; at southernmost Cape Horn the fauna are amongst the most likely non-indigenous SO invaders in the future; distinctive examples include *Calliostoma modulestum*, the *Fissurella* limpets *F. nigra, F. oriens* and *F. picta* and *Nacella* limpets *N. magellanica and N. mytilina*. At the second key southern limit hotspot, the Kerguelen archipelago, there is one of the longest continuous extents of N–S shelf area, which also represents the only shelf area to cross the PF. On this basis it is argued that the fauna there has amongst the greatest potential for southward range shifts (by dispersing southwards along the Kerguelen Plateau). Example gastropod species with southern limits at Kerguelen Islands include *Aforia lepta, Magarella expansa*, and 3 *Trophon* snails (*T. declinans, T. scolopax and T. septus*). Although fewer species have geographic limits in the northwest AP and South Georgia, these are also important areas being adjacent to the only significant regions of SO warming to date (Meredith & King, 2005; Whitehouse et al., 2008).

Patterns of bivalve record intensity were approximately similar to those seen for gastropods, and included some similar hotspots; however, they differed in the presence of hotspots of sampling (no. of records) in central Chile and west AP, and their absence in Kerguelen and the Crozet Islands (see figure 6.5a–c). Richness of species showed an essentially similar pattern to sample intensity, with the exception of richness hotspots around the South Shetland Islands (Figure 6.5b). In contrast to gastropod richness, the boxes with most species were southernmost Cape Horn and Snares/ Auckland Islands, which were also the only 2 strong centers of southernmost range limits (Figure 6.5c). However when species only found in 2 boxes or fewer were removed, 4 southern limit hotspots became apparent; southernmost Cape Horn, southern Ross Sea, Campbell Islands and the western AP (Figure 6.10a-the same 4 hotspots identified by residuals in figure 6.9). At Cape Horn bivalve species at their southern limit included *Chlamys patagonica, Ensis macha, Gaimardia trapesina* and *Mytilus edulis*.

Amphipod record intensity and richness showed similar patterns, with key areas being the South Shetland Islands, South Georgia, southernmost Cape Horn and Kapp Norvegica (Figure 6.6a,b). The hotspots for southernmost limits reflected these key areas, except for the additional hotspot of McMurdo Sound (Figure 6.6c). With the removal of species found in fewer than 3 boxes, similar southern limit hotspots to those of the molluscs were apparent: McMurdo Sound, the western AP, southernmost Cape Horn, and Kapp Norvegica (Figure 6.10b-the same 4 hotspots identified by residuals in figure 6.9). Distinctive amphipod species with southernmost limits at Cape Horn include 3 *Gameropsis* species (*G. longitarsus, G. dentifera* and *G. typica*), 3 *Gondogeneia* species (G. *gracilicauda, G. macrodon* and *G. ushuaiae*) and *Jassa alonsoae*. At Anvers Island (western AP) a number of distinctive amphipod species reach their known southern limits, including *Bovallia gigantea, Monoculodes antarcticus* and 4 *Oradarea* species.

The patterns of record intensity and richness found in ophiuroids differed with respect to each other, and to those in other previous groups (gastropods, bivalves and amphipods). The only strong record hotspot (the number of separate samples with ophiuroids reported) was East Kerguelen, but many hotspots of richness were apparent around Kapp Norvegica, South Georgia, the eastern Antarctic coast (from 55 to 110° E) and the Kerguelen Islands (Figure 6.7a,b). These were not reflected in the southernmost limits, of which there were just 2 hotspots in the southern Weddell Sea and nearby Kapp Norvegica (Figure 6.7c). Removal of species occurring in fewer than 3 boxes altered this pattern little (Figure 6.10c-the same 2 hotspots identified by residuals in figure 6.9). The final group to be examined for hotspots was the hexacorals, which showed similarities in terms of record intensity and richness (especially to the gastropod and amphipod patterns). The hotspots of record intensity and richness were South Georgia, the northwest AP, south of New Zealand, and East Kerguelen. Of these South Georgia and East Kerguelen were also hotspots of southern limits, as was (to a lesser extent) southernmost Cape Horn (Figure 6.8a,b). However, as shown by the bivalves, once species restricted to fewer than 3 boxes are removed, only southernmost Cape Horn was a strong southern limit hotspot (Figure 6.10d-the same single hotspot identified by residuals in figure 6.9). In summary, southernmost Cape Horn was the most consistent southern limit hotspot, except in the case of ophiuroids. Gastropod, bivalve and amphipod patterns had similarities: e.g. McMurdo

Sound (southern Ross Sea) was also an important hotspot of southern limits. So in all 5 study taxa, there were clear range limit hotspots, all of which were identified as those in which the number of range limits was anomalously high for the level of sampling (see Figures 6.3, 6. 4, 6.9).

Northernmost limits

I rejected analyses of northern limits for amphipods, ophiuroids and hexacorals due to the scarcity of data north of the PF, focusing instead on gastropod and bivalve molluscs. For the gastropods, South Georgia was by far the strongest hotspot of northern limits (for species which occurred in at least 3 boxes: figure 6.11a); the Crozet Islands, Kerguelen Islands, and Scotia arc were minor northern limit hotspots for gastropods. The locations of northern limits in bivalves were similar, but Prince Edward Island and the South Sandwich Islands emerged as the strongest hotspots, with Kerguelen Island and South Georgia and an area on the Patagonian shelf as minor hotspots (Figure 6.11b). The northern range limit hotspots identified in figure 6.11 were supported as these were the obvious anomalies in plots of range limits by sample intensity (Figure 6.12). Thus, the archipelagos of South Georgia and Kerguelen were consistently key places for northern limits of southern polar fauna, as well as having many southernmost limits of temperate fauna.

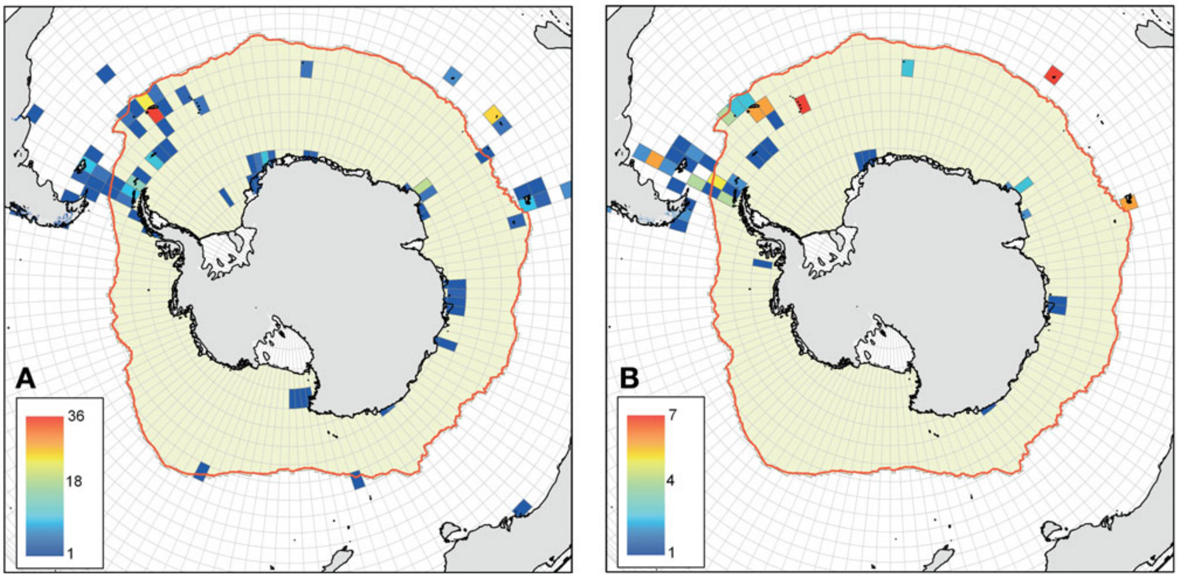


Figure 6.11. Number of mollusc species at their northernmost limit at high southern latitudes (for species occurring in more than 2 boxes) by 3 · 3° box. (A) Gastropods, (B) bivalves. Data from SOMBASE and SCAR-MarBIN databases

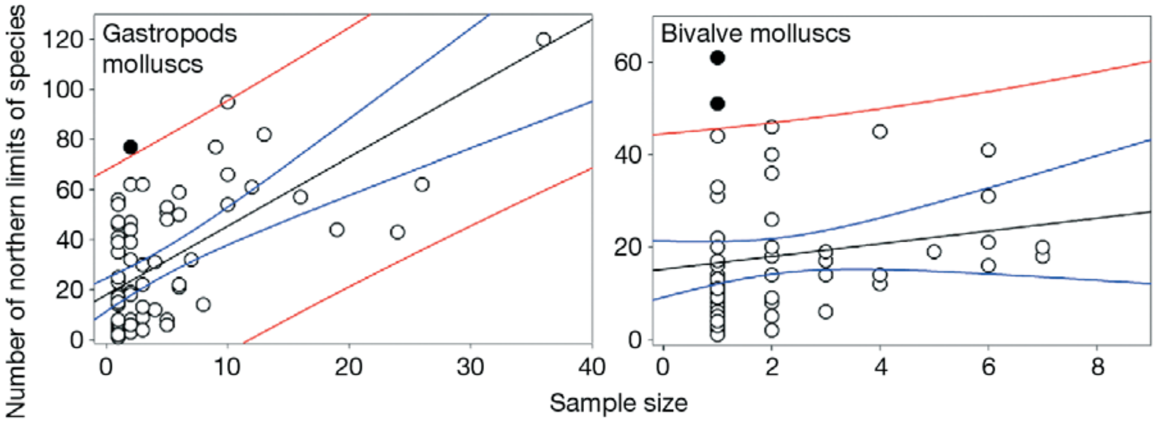


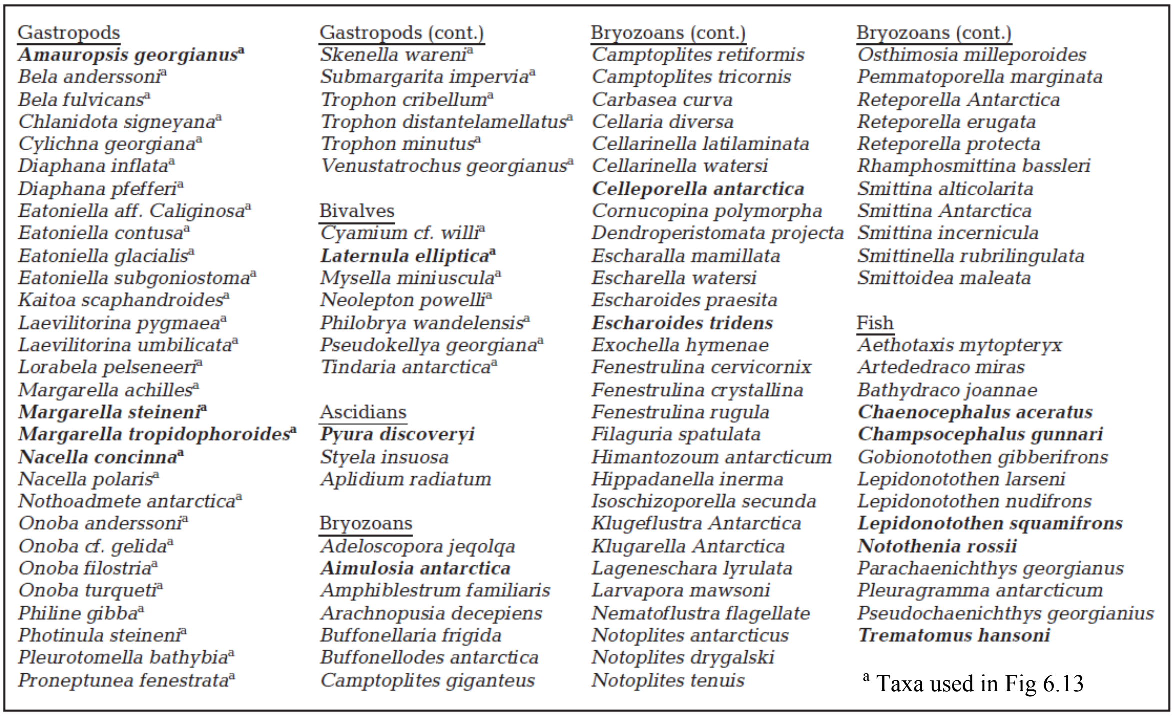
Figure 6.12. Relationship between sample intensity and northern range limits per geographic sampling area for gastropod and bivalve molluscs. Solid black line: Significant regressions, blue lines: 95% confidence interval, and red lines: 95% prediction lines. Hotspots of (northernmost) range limits, shown by filled circles, all lie above the upper 95% prediction line

A hotspot of range limits-South Georgia as an example

I selected one example location, South Georgia, to investigate further because (a) analyses showed it was one of the few locations of southern and northern limits across taxa, (b) recent warming has been demonstrated, (c) it has amongst the warmest waters in the SO (Barnes et al., 2006a) raising potential survivability of non-indigenous invaders, and (d) it is regularly accessed by both scientists and tourist (thereby providing increased possibilities for monitoring, but also transport opportunities for non-indigenous organisms to reach it). Although not a southern limit hotspot, figures 6.2d & 6.10 show that some of the 5 study taxa are at their southernmost limit at South Georgia. Analysis of cheilostome bryozoan data in SOMBASE shows that it is the southern limit for 12 species, including *Chaperiopsis acanthina, C. orbiculata* and *C. rotunda* as well as *Electra longispina* (notable for having dispersive planktonic larvae). I also found that 6 species of ascidian (e.g. *Molgula malviniensis* and *M. setigera*, P. Carmen, unpublished data), and at least 4 species of fish (*Patagonotothen guntheri, Protomyctophum choriodon, Electrona subaspera* and *Mancopsetta maculate*; M. Collins, unpublished data) have southern limits at South Georgia. I suggest that South Georgia is key for surveying range shift in marine biodiversity because of the density of species northernmost limits there (as opposed to southernmost). Northernmost limits are more useful in monitoring and detecting changes in species ranges scientifically, as it is easier to establish the gradual disappearance of a specific species than it is to survey for potential new arrivals (as would occur with a shift in southern range limit); this is especially true in Antarctica where confidence in complete species lists is still poor. Although only 3 ascidians have northern limits in South Georgia (Table 6.1), it is clear that many gastropods and bivalves do reach their northernmost limit there (Figures 6.2d &

6.10a), as well as additionally representing the northern edge of the range for 47 different cheilostomes (Table 6.1). For many species with southern or northern limits at South Georgia, database records show them to be both abundant and present in shallow shelf areas; some of these common and abundant species are particularly easy to recognise and identify, and thus I suggest that they are potentially the best model indicators to monitor (see species in bold, Table 6.1).

Table 6.1. Species of benthic taxa with northernmost limits at South Georgia. Data are from SOMBASE, except ascidians courtesy of P. Carmen (unpublished data) and fish from M. Collins (unpublished data). Taxa in bold are those I suggest to be key species for monitoring range shift.



Gastropods

- ***Amauropsis georgianus***[a]
- *Bela anderssoni*[a]
- *Bela fulvicans*[a]
- *Chlanidota signeyana*[a]
- *Cylichna georgiana*[a]
- *Diaphana inflata*[a]
- *Diaphana pfefferi*[a]
- *Eatoniella aff. Caliginosa*[a]
- *Eatoniella contusa*[a]
- *Eatoniella glacialis*[a]
- *Eatoniella subgoniostoma*[a]
- *Kaitoa scaphandroides*[a]
- *Laevilitorina pygmaea*[a]
- *Laevilitorina umbilicata*[a]
- *Lorabela pelseneeri*[a]
- *Margarella achilles*[a]
- ***Margarella steineni***[a]
- ***Margarella tropidophoroides***[a]
- ***Nacella concinna***[a]
- *Nacella polaris*[a]
- *Nothoadmete antarctica*[a]
- *Onoba anderssoni*[a]
- *Onoba cf. gelida*[a]
- *Onoba filostria*[a]
- *Onoba turqueti*[a]
- *Philine gibba*[a]
- *Photinula steineni*[a]
- *Pleurotomella bathybia*[a]
- *Proneptunea fenestrata*[a]

Gastropods (cont.)

- *Skenella wareni*[a]
- *Submargarita impervia*[a]
- *Trophon cribellum*[a]
- *Trophon distantelamellatus*[a]
- *Trophon minutus*[a]
- *Venustatrochus georgianus*[a]

Bivalves

- *Cyamium cf. willi*[a]
- ***Laternula elliptica***[a]
- *Mysella miniuscula*[a]
- *Neolepton powelli*[a]
- *Philobrya wandelensis*[a]
- *Pseudokellya georgiana*[a]
- *Tindaria antarctica*[a]

Ascidians

- ***Pyura discoveryi***
- *Styela insuosa*
- *Aplidium radiatum*

Bryozoans

- *Adeloscopora jeqolqa*
- ***Aimulosia antarctica***
- *Amphiblestrum familiaris*
- *Arachnopusia decepiens*
- *Buffonellaria frigida*
- *Buffonellodes antarctica*
- *Camptoplites giganteus*

Bryozoans (cont.)

- *Camptoplites retiformis*
- *Camptoplites tricornis*
- *Carbasea curva*
- *Cellaria diversa*
- *Cellarinella latilaminata*
- *Cellarinella watersi*
- ***Celleporella antarctica***
- *Cornucopina polymorpha*
- *Dendroperistomata projecta*
- *Escharalla mamillata*
- *Escharella watersi*
- *Escharoides praesita*
- ***Escharoides tridens***
- *Exochella hymenae*
- *Fenestrulina cervicornix*
- *Fenestrulina crystallina*
- *Fenestrulina rugula*
- *Filaguria spatulata*
- *Himantozoum antarcticum*
- *Hippadanella inerma*
- *Isoschizoporella secunda*
- *Klugeflustra Antarctica*
- *Klugarella Antarctica*
- *Lageneschara lyrulata*
- *Larvapora mawsoni*
- *Nematoflustra flagellate*
- *Notoplites antarcticus*
- *Notoplites drygalski*
- *Notoplites tenuis*

Bryozoans (cont.)

- *Osthimosia milleporoides*
- *Pemmatoporella marginata*
- *Reteporella Antarctica*
- *Reteporella erugata*
- *Reteporella protecta*
- *Rhamphosmittina bassleri*
- *Smittina alticolarita*
- *Smittina Antarctica*
- *Smittina incernicula*
- *Smittinella rubrilingulata*
- *Smittoidea maleata*

Fish

- *Aethotaxis mytopteryx*
- *Artededraco miras*
- *Bathydraco joannae*
- ***Chaenocephalus aceratus***
- ***Champsocephalus gunnari***
- *Gobionotothen gibberifrons*
- *Lepidonotothen larseni*
- *Lepidonotothen nudifrons*
- ***Lepidonotothen squamifrons***
- ***Notothenia rossii***
- *Parachaenichthys georgianus*
- *Pleuragramma antarcticum*
- *Pseudochaenichthys georgianius*
- ***Trematomus hansoni***

[a] Taxa used in Fig 6.13

Range widths with latitude

I found that species at higher (southern) latitudes tended to have broader latitudinal ranges (Figure 6.13). I observed that both gastropods and bivalves showed a similar pattern of a high number of small ranging species (0–5 and 5–10°) in lower latitudes (30–60° S). At higher latitudes (60–80° S) the majority of species had ranges greater than 10° of latitude. The bias towards small ranging species in the north of the study area may be exaggerated due to the geographic limits of the dataset: the full northern ranges of many species were not represented, and the majority of species in the dataset are those with records further south.

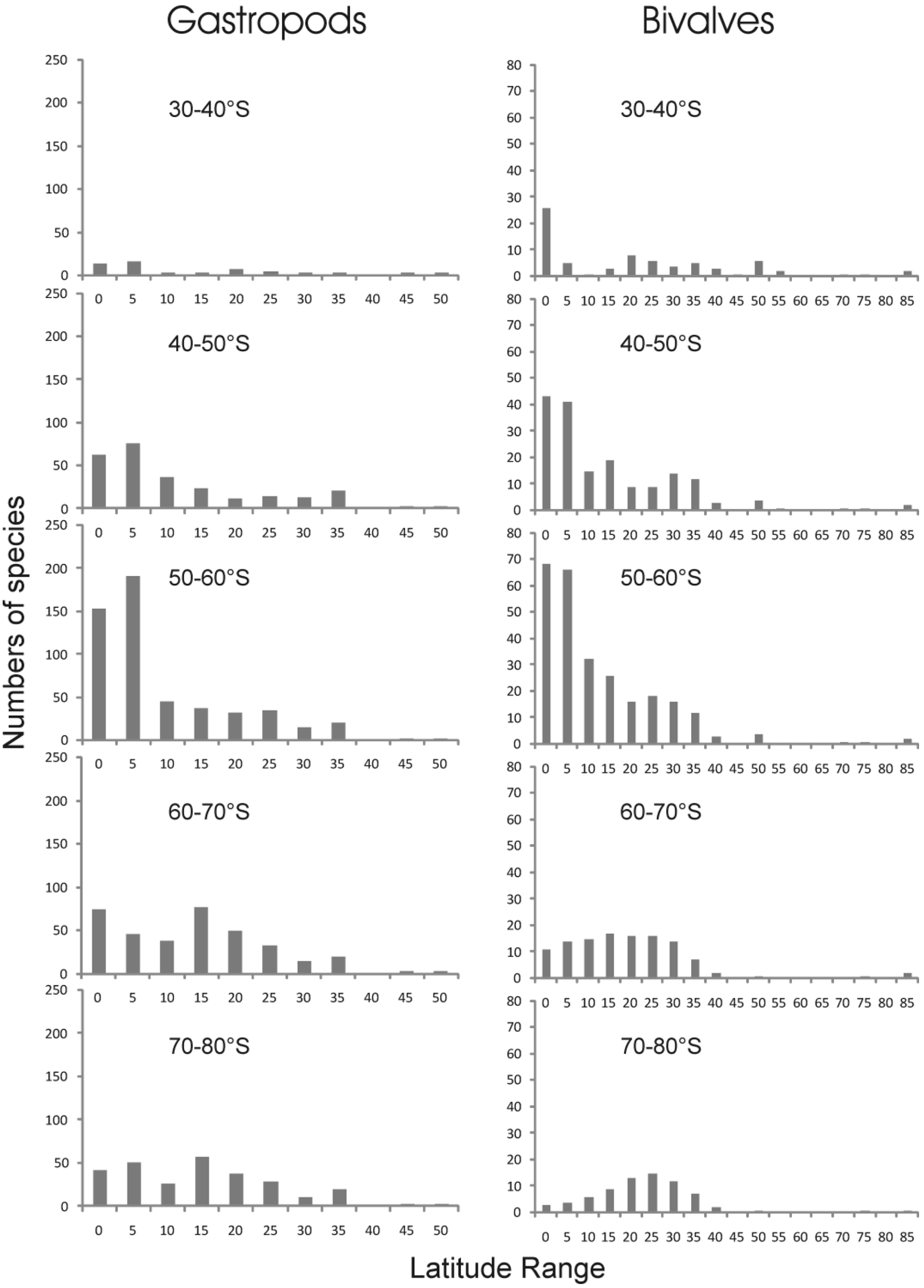


Figure 6.13. Range widths of species of gastropod and bivalve molluscs. Numbers of species with range width grouped by 10° latitude bins. Data from SOMBASE and SCAR-MarBIN databases

DISCUSSION

The response of biota to recent, rapid, regional warming is likely to include some degree of toleration, adaptation, migration and extinction. The balance of these responses will be complex and depend on local change, habitat, community, species and individual characteristics (Brooker et al., 2007; Poloczanska et al., 2008). I consider that the dominant response in the Southern Ocean (as elsewhere) will be migration; but science in the region has focused on the ability to tolerate or adapt and also, in the popular media, on extinction (Ahlstrom & Napper, 2002). Species ranges around Antarctica drastically changed in response to varying climate in the past, and Aronson et al. (2009) suggest that they will alter radically in the near future. The current study is the first to quantify southern and northern range limits, and geographic hotspots of these limits, and to identify which modern taxa have the best geographic information. I consider there is an urgent need to focus survey effort in the most appropriate areas and taxa in order to most rapidly detect responses to warming in Antarctica's rich biodiversity. I accept that there is considerable bias in Antarctica data (sample size varies considerably between areas, and some range limit hotspots are close to research stations); but both residuals of record intensity versus range limits (Figures 6.3, 6.9) and rarefaction curves (Figure 6.4) show hotspot independence from sampling. Error margins will be considerable, perhaps for decades: location and depths of recent and planned scientific cruises, coupled with the long lag time for species level identifications, means observed patterns are unlikely to be significantly updated in the near future. Given the thermal sensitivity experimentally derived for some benthos (Peck, 2005a) and the rapid temperature change in the region (Vaughan et al., 2003), I suggest that it is important to start monitoring now rather than waiting for spatial coverage of records to approach that in places such as the North Atlantic.

Models have been developed for a few temperate species to test predicted responses of species to climate change with some success (Lima et al., 2007). The same authors show that where the model failed to predict a lack of northward range shift, there was a gap of unsuitable habitat; again this highlights the complexity of response, and the importance of ground-truthing. The most documented response to climate change has been either a northward or southward range shift (Thomas & Lennon 1999, Roy et al., 2001, Beaugrand et al., 2002), but Antarctic continental shelves and slopes are isolated from elsewhere. Victoria Land (VL), AP, and the Kerguelen Plateau (KP) are the only major linear shelves around Antarctica (Figure 6.14a). The temperature gradient along VL and AP is negligible or bidirectional (Figure 6.14b), so the most potential for thermally-driven range shifts lies along the KP.

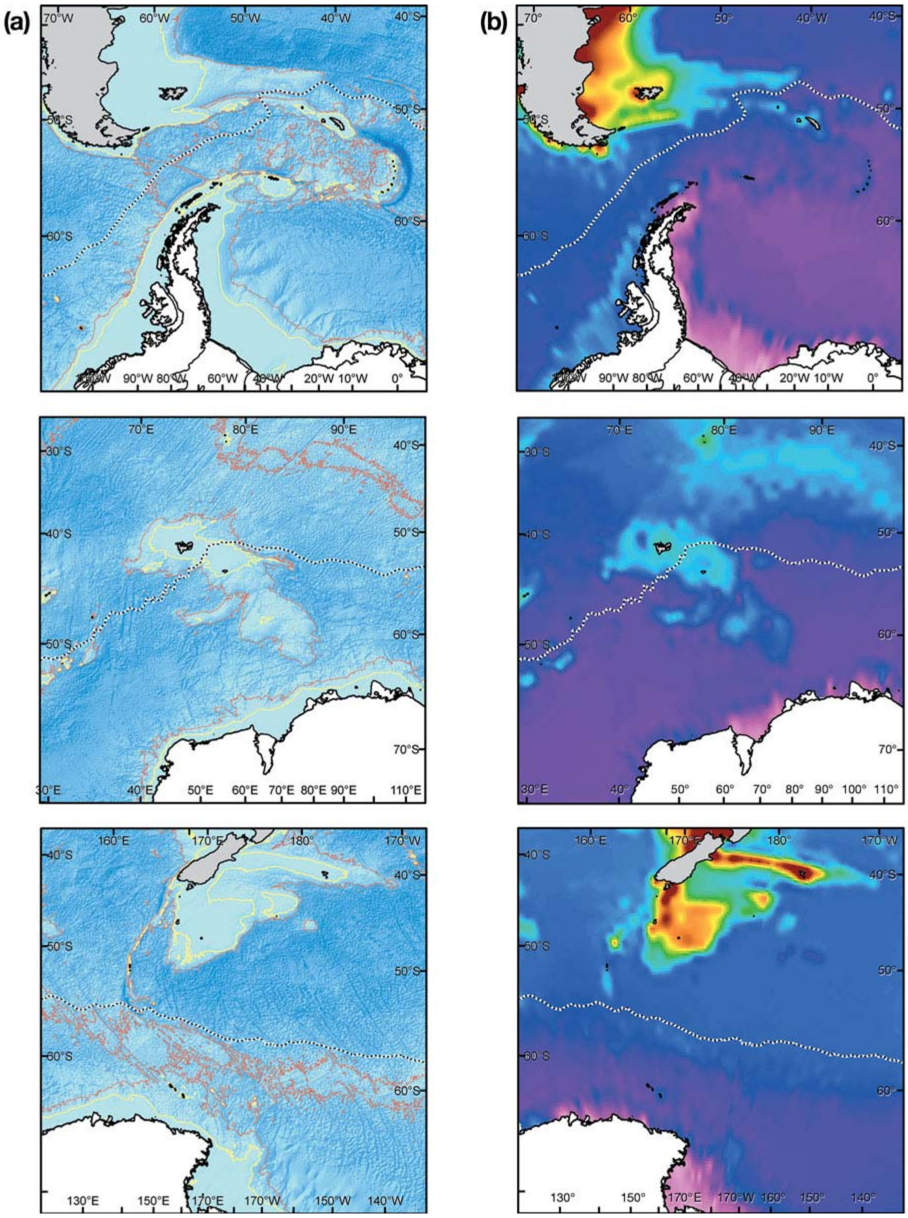


Figure 6.14. (a) Bathymetry and (b) seabed temperature of the 3 major regions of linear (north-south aligned) coast around Antarctica. From top to bottom these are the Antarctic Peninsula, the Kerguelen Plateau and Victoria Land (in text as AP, KP and VL respectively). In (a) the 1000 and 3000 m contours are shown as well as continental shelf areas in light blue. In (b) seabed temperature scale is from negative (light pink) to cool (blues) and warm (green, yellow,orange). Sea temperature data are from Clarke et al. (2009). The dashed line indicates the Polar Front

Marine warming has recently been detected in the AP and Scotia arc (Meredith & King 2005, Whitehouse et al., 2008), so I argue that the immediate priorities should be the generation of range limit baselines, and the identification of hotspots and model taxa. I hypothesised above that hotspots of southern range limits for Antarctic benthos would be in the southern Weddell and Ross Seas, and this was broadly true for the taxa studied (Figures 6.2 & 6.10). These areas are amongst the most southerly of any shelf areas; however, other than under-ice shelf environments of the Weddell and Ross Seas, there is no possibility for southward range shift and thus escape from future warming is limited to migration to deeper waters. Cape Horn was the strongest southern range limit hotspot in my data for temperate species (with the exception of ophiuroids, due to few records in SCAR-MarBIN; this probably reflects a focus on the Antarctic for this dataset). Amongst the species at Cape Horn there are likely to be many key potential invaders of the SO, and probably only the lack of continuous shelf, the abrupt oceanographic change at the PF, and the direction of the currents prevent southward range spread as invaders. The Scotia arc may act as stepping-stones south for plants, terrestrial invertebrates and microbes through dispersal on extreme wind events (Marshall, 1996) as well as for birds, but genetic evidence to date suggests benthos disperses from the Antarctic Peninsula out to the Scotia arc, rather than vice versa (e.g. Linse et al., 2007). Marine organisms may disperse southwards as larvae in mesoscale eddies or in ship ballast water, or as adults on debris or ship hulls (Lewis et al., 2006) but so far only a non-indigenous algae seems to have established (Clayton et al., 1997). So the ‘bottleneck’ of temperate species at their southern limit at Cape Horn (as was expected), is likely to increase as a hotspot as other species migrate southwards from the Patagonian shelf. As the northern limits for different species shift southwards, it is also likely to be the focus point for shrinking range sizes (until a chance event allows species to cross the PF and so establish themselves in the SO). It is likely that a similar situation exists along the South African coast, although only 22 non-indigenous species are currently known there (Griffiths et al., 2009). Adults (e.g. Ralph et al., 1976) and larvae (Thatje & Fuentes, 2003) of non-indigenous species have travelled into the SO, but have seemingly been unable to complete life-cycles.

True geographic limits for even the more obvious large Antarctic macro- and megafauna are still being established. For example, the BIOPEARL I scientific cruise of 2006 found the hexacorals *Balanophyllia malouinensis* (in the Falkland Trough) and *Flabellum curvatum* (at Elephant Island, north Antarctic Peninsula) both south of their previously known southern limit (British Antarctic Survey unpublished data). Likewise, new southern limits have also been recently established in the region for a number of species in other taxa (e.g. bryozoans: Lopez de la Cuadra & Garcia Gomez, 2000). Despite this, in terms of detecting response to warming, it will be clearly easier to monitor the disappearance of species from a site (i.e. retreating northern limits) than to survey for whichever new species might arrive (i.e. increasing southernmost limits). In areas with well established baselines, such as for terrestrial fauna in Europe, monitoring arrivals of species in new areas is easier (Clay-Jones & Bignell, 2008) but the statistics of detecting first presences is complex. Although my data set was not as strong for investigation of northern range limits, I argue that examination and monitoring of these is more important (than southern limits).

My second hypothesis was that the present and past boundary of the PF would mark hotspots of northernmost limits. The patterns found in gastropod and bivalve molluscs confirmed this (Figure 6.11), as did non-georeferenced data of ascidians, bryozoans and fish (Table 6.1). The PF has long been suggested to be a major discontinuity, and thus a northern limit for much SO biodiversity (e.g. Ekman, 1953). New molecular approaches show that some species with ranges apparently crossing the PF are actually separate cryptic species each side (Hunter & Halanych, 2008). Only 3 shelf areas are just south (one grid box in the methods reported here) of the PF, South Georgia, Bouvet and Heard islands. Of these only South Georgia is both old and large (so should be biodiverse), which explains it emerging as a strong hotspot of northernmost limits (Figure 6.11, Table 6.1). Hotspots of northern limits of SO fauna north of the PF, such as at KP, reflect that the PF regularly wanders north of sub-Antarctic islands (Moore et al., 1999) or is permanently north during glaciations (Frank et al., 2000).

The main question posed by the current study was where to concentrate effort to detect responses in biodiversity to projected southern polar warming. The current study suggests 2 key areas are most appropriate for monitoring marine benthic response to warming: South Georgia and Kerguelen. This is mainly because the data showed them to be the strongest hotspots for southern and northern range limits across taxa (Table 6.1, figures 6.2, 6.10, 6.11). The proximity of a marine biological research station and the presence of a discrete shelf should make detecting the disappearance or appearance of species easier at South Georgia. In contrast, Kerguelen is the only major shelf area which crosses the PF or which has a strong thermal gradient (Figure 6.14). Other criteria for site suitability include how well the local fauna is known and where invaders are most likely to arrive. Amongst the most important vectors are shipping, and the website www. iaato.org/tourism_stats.html lists the most visited sites. Two sites are by far the most visited, Goudier Island (Port Lockroy) and Deception Island (Port Foster) (Lynch et al., 2010); the latter of which is the only known site for established marine aliens in the SO (Clayton et al. 1997).

Establishment of sites to focus attention and surveys is clearly a crucial first step, after which the species to study seems most important as neither the taxonomic expertise nor the effort is available to consider all taxa, or even all species within a given taxon. Irrespective of whether the taxa selected here are or are not the most sensitive indicator taxa, they are currently amongst the best taxa to monitor for response to change on the basis of their having the most geographic and bathymetric information available. At local scale this will differ with site: for example data from this study showed that ophiuroid data were the strongest for the Kerguelen region, but poorest for Cape Horn. Specific species, which are listed here with range edges at South Georgia, include some (in bold in Table 6.1) which have many ‘indicator’ characteristics (such as being common, abundant, presence in shallows and at known sites, and ease of recognition). Furthermore some of these potential model species for monitoring of range change have been widely studied internationally as model Antarctic benthic organisms (e.g. *Laternula elliptica*), and some of these have already been established as very thermally sensitive at the edge of their range (e.g. *Nacella concinna*, Morley et al., 2009b).

Several species are highlighted as potentially good indicator species to monitor (for South Georgia: the gastropods *Margarella steineni* and *Nacella concinna*, the bivalve

Laternula elliptica, the ascidian *Pyura discoveryi*, the bryozoans *Aimulosia antarctica*, *Celleporella antarctica* and *Escharoides tridens* and the fish *Chaenocephalus aceratus, Champsocephalus gunnari, Lepidonotothen squamifrons, Notothenia rossii* and *Trematomus hansoni*. The depth ranges of these species are *M. steineni* (1–53 m), *N. concinna* (0–195 m), *L. elliptica* (0–1100 m), *P. discoveryi* (46–2350 m), *A. antarctica* (0–1500 m), *C. antarctica* (6–229 m), *E. tridens* (13–200 m), *C. aceratus* (5–770 m), *C. gunnari* (0–700 m), *L. squamifrons* (10–900 m), *N. rossii* (5–350 m) and *T. hansoni* (6–549 m: SOMBASE, SCARMarBIN, FISHBASE, JR109 and JR144 unpublished scientific cruise data, and other authors unpublished data). There is an increasing body of work on the thermal tolerance of Antarctic species, but what constitutes a limit is complex. The wide physiological literature suggests a short term experimental limit of 5 to 10°C (Peck et al., 2009a). However the longer term limits are narrower and some such as the bivalve *Limopsis marionensis* seem unable to survive beyond an upper temperature of 2°C (Pörtner et al., 1999). Of the key species identified, *N. concinna* and *L. elliptica* are unable to survive more than 3 months at 3°C (Peck et al., 2009a). Fish such as *Chaenocephalus aceratus* and *Notothenia rossii* have a limit at 6°C (Somero & DeVries, 1967), but these may not have fully acclimated (L. Peck pers. comm.). The functional limits for many of these species are even lower, but in all cases, the limit depends on the rate of warming. Arguably the knowledge most needed is how much temperature rise an individual of a species can cope with, such that they can complete a life cycle and produce a viable F1 generation; this is currently unknown for any Antarctic species. Identifying the identity and location of species at range limits should make geographic and taxonomic targeting of future physiological work more productive for elucidating likely responses to climate change.

Meaningful interpretation of any apparent range shift data on any model species will depend, not just on linkage to physiological data on thermal biology, but also on prior establishment of their phylogeographic status by location. This is crucial, as it has become apparent that (as elsewhere) some widespread southern polar species are actually complexes of at least 2 species (e.g. see Hunter & Halanych, 2008). Cryptic speciation also occurs with depth (e.g. in *N. concinna*: Carla de Aranzamendi et al., 2008) and it is likely that many range shifts will be bathymetric as well as geographic. This is particularly the case at South Georgia where there are no connected shelf areas for organisms to migrate south, and where water temperature decreases by up to 6°C with depth (Holeton et al., 2005).

Finally I considered the range sizes (rather than range limits) of southern polar benthos because of the linkage to past survival success during times of environmental change (Roy et al., 2001), but also because, like (and partly because of) limit shifts, I expect these to change with warming. The smaller latitudinal ranges, which were found in gastropod and bivalves at lower latitudes, which seem to suggest some support for Rapoport's Rule (Stevens, 1989), (Figure 6.13) may be due to differing rate of temperature change with latitude (Figure 6.15). Sea temperature increases 3.34°C with each 10° decrease in latitude north of 55° S. Mean sea temperature only decreases 0.76°C with each 10° latitude south of 55° S. Temperature is not the only variable that changes less at higher southern latitudes (salinity would be another example), and thus larger geographic range sizes at higher latitudes may simply reflect greater similarity of environmental conditions. Bivalves showed a stronger pattern than gastropods because they tend to be wider ranging (Clarke et al., 2007a) whereas gastropods tend to be more endemic to small areas (Linse et al., 2006). Bivalves may thus be amongst the best taxa to watch with respect to SO invasion (e.g. see Ralph et al., 1976). With a southern limit hotspot at Cape Horn, the sites most visited by ships (such as Deception I) will be amongst the most likely places for bivalve invaders to arrive.

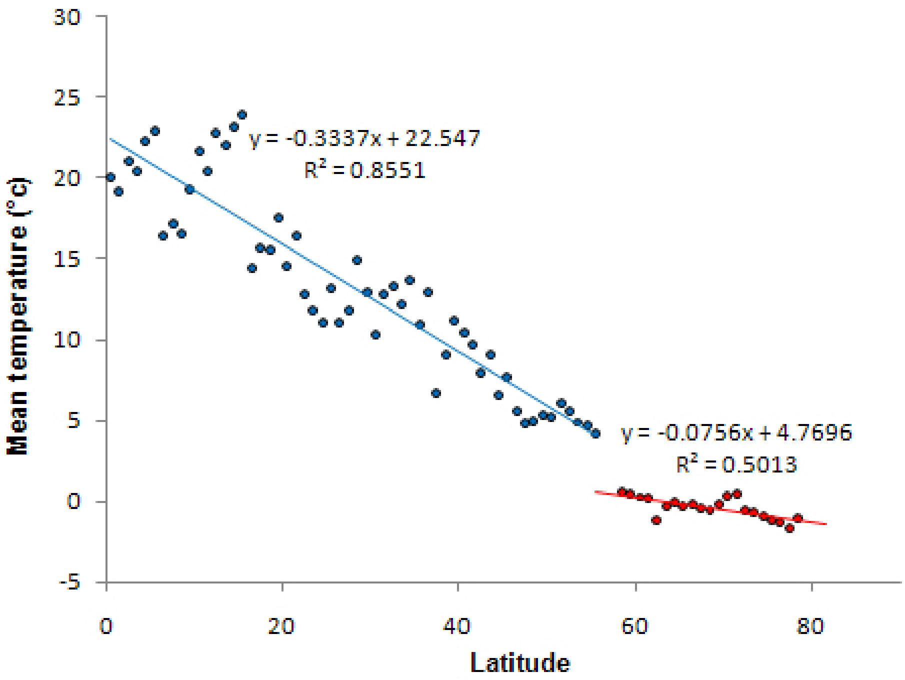


Figure 6.15. Mean temperature for the sea floor down to 1000 m for each latitudinal band (data from Clarke et al. 2009)

CONCLUSIONS

Most of Antarctica's biodiversity occurs on the continental shelf, and the most likely response to rapid warming is by species changing their ranges. The quality and quantity of data are much better for some areas and taxa than others, and both of these have been highlighted here; this information is within openly-accessible databases (such as SCAR-MarBIN). Range shifts of Antarctic marine benthic species will not necessarily be along continental shelf areas aligned N–S because temperature does not always decrease southwards along them and, apart from the Kerguelen Plateau, they have no continuity with cool temperate areas. The current chapter, the first account of baselines of northern and southernmost limits of Antarctic taxa, shows that Cape Horn is a range limit hotspot and bottleneck for southernmost species, and thus potential alien invaders. I suggest that South Georgia and the Kerguelen Plateau are amongst the best areas to monitor range shifts for a variety of reasons, but in both cases it is likely that detecting shrinking northernmost limits will be easier to achieve and to test potential predictive models with. Bivalves seem to be a good candidate group to use as indicators but there are a number of key species across a variety of classes which fulfill major criteria, such as being easily identifiable, widespread and abundant. Because of strong bathymetric temperature gradients at both of these localities, bathymetric migration seems at least as likely as geographic migration given the supposedly high level of eurybathy in Antarctic shelf taxa.

GENERAL CONCLUSIONS

GENERAL CONCLUSIONS

Main findings of the study

This thesis describes Southern Ocean marine biogeographic patterns and trends across a range of scales; temporal, spatial and taxonomic resolution. Although previous studies have defined biogeographic classifications for the Antarctic marine fauna based on pre-set geographic regions, none have had access to comprehensive databases of georeferenced marine species records before. In some cases the findings of this study support those of previous works; in others the results suggest a different picture of a unified Antarctic benthos with no obvious biogeographic sub-regions. The principal findings are as follows:

- Our knowledge of the biodiversity of the Southern Ocean is largely determined by the relative inaccessibility of the region. The location of scientific bases heavily influences the distribution pattern of sample and observation data, and the logistical supply routes are the focus of much of the at-sea and pelagic work. Taxa such as molluscs and echinoderms are well represented at species level within existing datasets with high numbers of georeferenced records. Other taxa, including the species-rich nematodes, are represented by just a handful of digital records.

- Our knowledge of biodiversity at high taxonomic levels is also patchy but seems to be high in point samples, particularly from accessible regions such as the Scotia Sea. Fifteen phyla and 29 classes of macro- and megafauna were present in 29 Scotia Sea samples, many of which occurred at all sites. Even at remote and geologically young sites richness was high. These 15 phyla represented all but three phyla of the total that could realistically be expected to occur in samples and, furthermore, up to 12 different phyla within some single trawls. Similarities in trawled faunas often did not reflect isolation, oceanography or habitat.

- In the wider analysis, setting the detailed Scotia Sea biodiversity results into the Southern Ocean context; the Scotia Sea and parts of the Weddell, Ross and East Antarctic seas were the most sampled areas. A preliminary analysis of the SCAR-MarBIN database indicates that the pattern of sampling hotspots is driven principally by bird and mammal observations, whereas records of benthic species drive the overall pattern in species richness. Analyses of the complete data set reveal important biases in the data: most samples have been taken in shallow water (< 700 m) and are either concentrated around shore-based research stations, or in the open ocean, close to regular ship transit routes. These data provide a useful benchmark for the future, enabling ventures such as CAML to assess their impact on knowledge of biological diversity. It also highlights areas that are most under-sampled, such as the deep sea and the Amundsen Sea. Likewise the density of records, and therefore apparent strength of patterns, differed strongly between classes of animals.

- Unlike the biogeographical schemes previously proposed, this thesis shows that the evidence for biogeographical regions in the Southern Ocean differ depending upon the class of animals being considered. Despite this some general rules seem viable, including species endemism rates of around 50%, a single Antarctic province and a definite distinction between the sub-Antarctic islands influenced by South America and those of New Zealand. The level of faunal homogeneity within the Polar Front implies that very few barriers to dispersal exist within Antarctic waters. I suggest that much of this homogeneity is driven by the similarity of conditions and the Antarctic Circumpolar Current (ACC) which transports animals in a clockwise direction around the continent. This study supports previous findings of strong biogeographical links between the Antarctic and South America, but there is little evidence for a relationship between either of these regions and New Zealand or Australia (Tasmania). It is clear that some detailed focus on individual classes of benthos is needed as well as across-class syntheses.

- Examination of the sea spiders (pycnogonids) identified a distinct and unified Antarctic shelf fauna which was different to that of the deep-sea around Antarctica, the sub-Antarctic islands, South America or New Zealand. Within the Antarctic, the South Shetland Islands was the most speciose region and a probable center of radiation for the pycnogonids. No latitudinal gradients in species richness were detected. The distribution patterns observed were based upon classical taxonomy and could change with new insights from molecular techniques. Even with the potential for cryptic species, it is suggested that the large-scale biogeographic trends observed in the pycnogonids should hold true. The detailed knowledge of current ranges of taxa can be used to investigate the potential response of life to the drastic environmental changes in much of West Antarctica.

- The ranges of several Southern Ocean benthic taxa (bivalve and gastropod molluscs, amphipods, ophiuroids and hexacorals) were investigated with respect to geographic limits. Southern Patagonia, South Georgia and the Kerguelen archipelago had amongst the most range-limit hotspots in the study taxa. Shifts of Southern Ocean endemics are likely to be mainly range contractions (southward movement of northernmost limits), whilst species with ranges crossing the Polar Front may become ‘new’ Southern Ocean endemics. Species with southernmost limits north of the Polar Front should begin to penetrate the Southern Ocean, either as returning natives (expelled during glaciations) or invasive non-indigenous species. Monitoring range shifts in only a few suggested key places and taxa should give powerful insights into biodiversity responses to climate change and gauge tolerance vs. migration.

The biogeographic patterns detected by this study for the large geographic scale of the Southern Ocean and its neighbours are largely driven by geological, glaciological and oceanographic processes over millions of years, as described by Croizat (1964). Therefore it is not surprising that Antarctica shares its greatest number of species with its nearest and most recently separated neighbour, South America. However Antarctica has been isolated long enough to evolve high levels of endemic species, many endemic genera and a few endemic families. This isolation has led to the observed single Antarctic bioregion or province. The factors responsible for Antarctica's isolation, the extremely cold water temperatures and powerful ACC, are also key to the wide distributions of many of its marine species. My study clearly demonstrates the role of the ACC in transporting and dispersing many benthic taxa around the continent and out to the sub-Antarctic islands. Whilst forming a barrier to dispersal to many species from outside the Southern Ocean, the ACC is not impermeable and there is evidence for species having entered the Antarctic from South America through the Scotia arc and the sub-Antarctic islands. The low faunal similarities between Antarctica and Australia and New Zealand may be a reflection of a lack of a similar pathway across the ACC in the Eastern Hemisphere. A potential route for species to leave the Southern Ocean is via the Antarctic bottom water which flows northwards into all of the neighbouring ocean basins. Such routes in and out of the Southern Ocean will determine how the Southern Ocean benthos will be affected by climate change. This study has identified the key geographic areas and taxa to look for species range shifts related to such changes. Future challenges lie in truly understanding this Antarctic region and how, when and where this endemic speciation occurred and if these broad-scale patterns hold true at a more local scale.

Directions for future research

The patterns observed in this thesis are typically associated with large scale geographic features on a continental or oceanic scale. A greater challenge will be to look for the smaller patterns within these patterns which are caused by equally important factors on a much smaller scale. Habitat heterogeneity is known to be important for species diversity (Gutt & Piepenburg, 2003), but little is understood about the impact of biogeographic patters at this scale upon the bigger picture. Linking communities and individual species to habitat types will allow us to predict, using physical parameters, the distributions of species, even for previously un-sampled regions of Antarctica.

Among the major challenges facing Antarctic marine biogeographers today is the integration of the latest molecular phylogeographic and taxonomic results with the wealth of existing species distribution data based on collections spanning the last two centuries but not suitable for molecular analysis. Whilst the molecular results provide us with high resolution snapshots of the evolution of selected Antarctic species and even populations, at present there are few published and it will take many decades for the numbers of genetically sequenced specimens to reach a point where I can do any sort of comprehensive circumpolar analysis (Grant & Linse, 2009; Grant et al., in submission). However, there are studies which examine the phylogeography of Antarctic marine species at a regional scale (Krabbe et al., 2010; Hunter & Halanych, 2008; Mahon et al., 2008) and others which have used small numbers of widely distributed samples to show examples of cryptic species (Wilson et al., 2007, 2009; Held, 2003; Held & Wägele, 2005; Raupach & Wägele, 2006; Linse et al., 2007). The next step would be to look for patterns in the distributions of these cryptic species to see if they can be explained by physical parameters such as depth, temperature, water masses or geographic distance. If such an explanation can be found then there is the potential to retrospectively assign species to a clade or cryptic species and there is even potential to predict the likelihood of finding new related species in un-sampled regions such as the Amundsen Sea or the deep sea.

Using the latest tools, such as GeoPhyloBuilder extension for ArcGIS (www.nescent.org), to integrate phylogenetic patterns with a Geographical Information System (GIS) will enable phylogeographers to visualise and interpret how and where evolution and dispersal have taken place and what mechanisms lead to current distribution patterns. Molecular clocks can be used to date these separations and will help to explain divergence times linked to past geological and glaciological events (Strugnell et al., 2008).

Biogeographic analyses, based on both, species collection records and if available their molecular genetic analysis, have an important role to play in the future conservation of Antarctic marine living resources. Many of the criteria used by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) for assigning Vulnerable Marine Ecosystems (VMEs) in Antarctica are based upon the presence of key habitat-forming species such as sponges and corals (Martin-Smith, 2009). Until now there has not been a comprehensive georeferenced database of all recorded habitat-forming species known from the Southern Ocean. Such a database is currently under construction as part of SOMBASE and will provide the fisheries regulators and scientists with the most advanced data to help protect the Antarctic benthos. This database will also be used for future biogeographic studies of these taxa and will also feed into models of seafloor community distributions both as members of those communities and as habitats for those communities.

The legacy of such large databases and analyses is to provide a robust benchmark against which future change can be assessed. This wealth of knowledge is all publicly available through the SCAR-MarBIN web portal and will continue to grow as future results become available, serving as a tool for the whole scientific community.

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