

Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca

Katrin Linse*, Huw J. Griffiths, David K.A. Barnes, Andrew Clarke

British Antarctic Survey, Natural Environmental Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, UK

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Abstract

For many decades molluscan data have been critical to the establishment of the concept of a global-scale increase in species richness from the poles to the equator. Low polar diversity is key to this latitudinal cline in diversity. Here we investigate richness patterns in the two largest classes of molluscs at both local and regional scales throughout the Southern Ocean. We show that biodiversity is very patchy in the Southern Ocean (at the 1000-km scale) and test the validity of historical biogeographic sub-regions and provinces. We used multivariate analysis of biodiversity patterns at species, genus and family levels to define richness hotspots within the Southern Ocean and transition areas. This process identified the following distinct sub-regions in the Southern Ocean: Antarctic Peninsula, Weddell Sea, East Antarctic—Dronning Maud Land, East Antarctic—Enderby Land, East Antarctic—Wilkes Land, Ross Sea, and the independent Scotia arc and sub Antarctic islands. Patterns of endemism were very different between the bivalves and gastropods. On the basis of distributional ranges and radiation centres of evolutionarily successful families and genera we define three biogeographic provinces in the Southern Ocean: (1) the continental high Antarctic province excluding the Antarctic Peninsula, (2) the Scotia Sea province including the Antarctic Peninsula, and (3) the sub Antarctic province comprising the islands in the vicinity of the Antarctic Circumpolar Current.

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1. Introduction

Clines of biodiversity from the tropics to the poles have long been considered to be one of the most fundamental patterns in spatial organisation of organisms. Although there are clearly changes along gradients other than latitude, patterns in terrestrial mammals, reptiles, birds, insects and vascular plants

seem predominantly explained by distance from the equatorial region or a correlate of this (Gaston and Spicer, 2004). In the marine environment, however, robust data have taken much longer to gather and are still lacking for many major groups. Present data indicate a strong poleward decline in diversity for northern hemisphere marine taxa (Clarke and Lidgard, 2000; Crame, 2000; Roy et al., 1996; Roy et al., 1998; Stehli et al., 1967).

One of the earliest taxa to be used to investigate trends in marine biodiversity has been the Mollusca, or more specifically the bivalves and gastropods,

*Corresponding author. Tel.: +44 1223 221631;
fax: +44 1223 221257.

E-mail address: kl@bas.ac.uk (K. Linse).

and data from these remain important today. However, recent evidence from both of these classes has shown that patterns in the southern hemisphere are quite different from those in the north (Valdovinos et al., 2003) and that longitudinal patterns of richness are just as strong as those with latitude (Crame, 2000). Until recently a major difficulty in the establishment of truly global patterns of marine diversity has been the paucity of data for high southern latitudes, that is, the undersampling of the Southern Ocean and southernmost Atlantic, Indian and Pacific oceans. In the past decade or so, marine sampling intensity in these regions has started to approach the levels elsewhere in the world, and our view of global patterns of marine diversity is changing. The Southern Ocean constitutes ~8% of the world's ocean surface area, ~2% of the global coastline, and ~11% of global continental shelf. Recent sampling has revealed considerably higher southern polar diversity than in the northern polar region (Arntz et al., 1994; Brey et al., 1994; Gutt et al., 2000), and many taxa have higher than expected richness relative to ocean area. Pycnogonids, polychaetes, ascidians, amphipods and bryozoans are all particularly speciose around Antarctica (17.5%, 12.2%, 9.4%, 8.3% and 8.1% of global species, respectively) (Clarke and Johnston, 2003). Though <1% of world species of gastropods occur in southern polar waters, richness is higher than reported from most of subtropical and temperate South America (west coast) (Valdovinos et al., 2003).

Taxa tend to form characteristic groupings by region, and the science of biogeography have grown to identify and characterise such groupings and the environmental conditions that cause them. As with biodiversity studies, research and analysis of patterns in biogeography historically have advanced faster in the terrestrial than in the marine realm, particularly in botany. For example, plant assemblages have been grouped by climatic factors such as precipitation, temperature and humidity to form 'zones'. In the sea, broad biogeographic regions have been erected by similarities in the known faunal groupings (Briggs, 1974; Dell, 1972; Hedgpeth, 1969). As with large-scale patterns in biodiversity, one of the main taxa used to elucidate such similarity were the molluscs. A recent classification of marine biogeography has been based on a combination of water-column physics and ocean-colour data from Coastal Zone Colour Scanner (CZCS) imagery (Longhurst, 1995; Longhurst et al.,

1995). These analyses partition the global ocean into four major 'biomes', Trades, Westerlies, Polar and Coastal, and each of these is further subdivided into a total of 50 provinces. Of these, two occur south of the Polar Front (PF). The Antarctic Province lies between the PF at about 50°S and the Antarctic Divergence at 60–65°S; it thus comprises the southern branch of the powerful Antarctic Circumpolar Current (ACC) (Deacon, 1982; Orsi et al., 1995). South of the Antarctic Divergence lies the Austral Polar province, which comprises essentially the seasonally ice-covered seas surrounding the coast of Antarctica. Immediately to the north of the PF lies the Subantarctic Water ring province, part of the Antarctic Westerlies Biome, and including the northern branch of the ACC (Deacon, 1982; Orsi et al., 1995; Heywood and King, 2002). The oceanographic context is important to understanding the evolution of the Antarctic fauna: for example the ACC (the West Wind Drift in the early biogeographic literature) is highly influential to the links between the Magellanic region and the Subantarctic island faunas around the margins of the Southern Ocean (Barnes and De Grave, 2001; Helmuth et al., 1994; O'Hara, 1998). Furthermore, Antarctica's long geographic and oceanographic isolation have been critical to the evolution of the high levels of endemism that characterise many marine taxa.

The early studies of the Southern Ocean marine fauna defined subregions based on several ideas. Regan (1914), Nybeling (1947) and Powell (1951) focussed on the distribution of model taxa, such as fish or molluscs. Earlier still, Waite (1916) and Norman (1937) used taxon distribution in combination with geological data, and later Ekman (1935, 1953) relied on oceanographic evidence. Common to all these approaches was latitudinal division into a Subantarctic/low Antarctic zone, and an Antarctic/high Antarctic zone. In terms of longitude, the major divisions proposed were either into East and West Antarctica, or into four quadrants. Later studies (Holdgate, 1960; Knox, 1960; Hedgpeth, 1969) divided the sub-Antarctic zone (north of the PF, in those days termed the Antarctic Convergence) into the Magellanic region, the Tristan da Cunha/Gough Island Archipelago and the Kerguelenian region. They further divided the Antarctic zone into a continental and South Georgia district. The scheme proposed by Hedgpeth (1969, 1970) was widely accepted although Dell (1972) argued against fine distinctions in the Antarctic region and

discussed the problems of fitting isolated islands into regional patterns. Since these seminal studies our knowledge on the distributions and diversity of the Antarctic marine fauna has increased through intensive sampling in recent years (Arntz et al., 1997; Clarke and Johnston, 2003), but the biogeographic patterns of Southern Ocean molluscs have not been re-examined.

With the recent increase in biodiversity and biogeographic studies, there has been a marked increase in the amount of distributional data for Southern Ocean marine organisms, and this has led to the traditional faunal/floral lists becoming too large and unmanageable. Relational databases have begun to take the place of the faunal/floral catalogues in biodiversity and biogeographical studies (Budd et al., 2001; Hill et al., 2000; Rosenberg, 1993; Peat, 1998; Zhang et al., 2000). The advantage of relational databases is that they can store and link distributional data with the information of abundance, ecology and environment that are needed to analyse and explain patterns in biodiversity and to test ecological and biogeographic hypotheses (Grassle and Stocks, 1999). Relational databases can handle vast amounts of data and complicated queries relatively quickly, and deliver raw data matrixes for multivariate analyses. Several such databases have been created, including marine molluscan databases from different geographic regions (Griffiths et al., 2003; Rosenberg, 1993) and the database of Indo-Pacific Marine Molluscs housed by the Academy of Natural Sciences, Philadelphia). Linking relational databases to a Geographical Information System (GIS) creates a powerful tool to analyse large-scale biogeographic patterns (e.g., Markwick, 2002; Markwick and Lupia, 2002; Griffiths et al., 2003; Myers and Worm, 2003; OBIS: www.iobis.org; Census of Marine Life: www.coml.org).

Here we analyse one of the most comprehensive regional databases yet assembled for any taxon, the Southern Ocean Molluscan Database (SOMBASE: Griffiths et al., 2003), to investigate richness and biogeographic trends in two related molluscan taxa, gastropods and bivalves. We hypothesise that their biogeographic patterns in Antarctica are determined primarily by historical factors and that the comparison of biogeographic patterns between the ecologically different taxa gastropods and bivalves will show similar trends in biodiversity and biogeography and that biogeographic regions will be in accordance with those of Hedgpeth (1969) and Dell

(1972). To test these hypotheses we have investigated patterns of southern polar biodiversity in the shelled gastropod and bivalve molluscs from the local, through regional to global scale.

2. Material and methods

2.1. Geographic areas

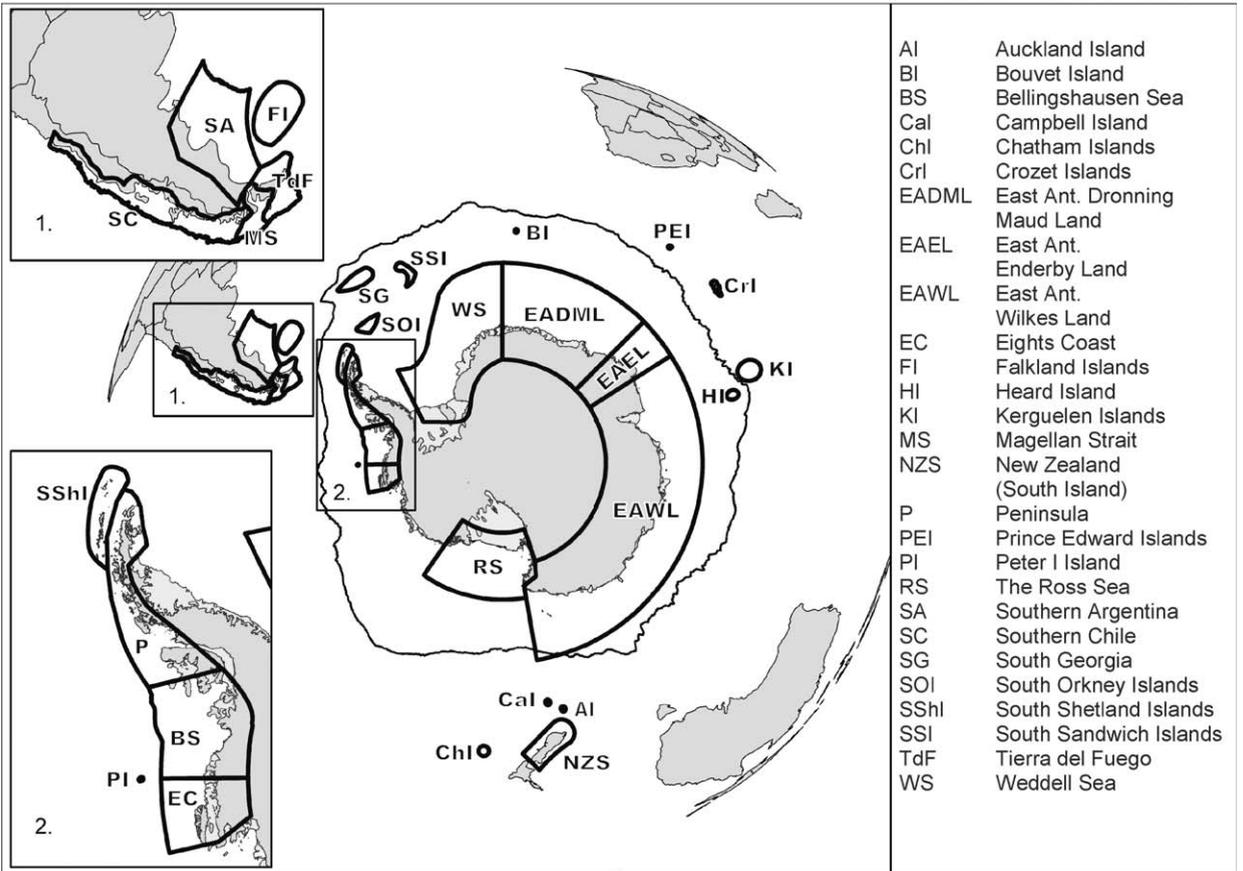
We investigated data availability for all major areas within the Southern Ocean (waters south of the PF), the sub-Antarctic islands, the Magellan region of South America and the southern New Zealand islands. Within the Southern Ocean 12 sub-regions were defined based on multivariate analysis of the recent diversity records in shelled gastropods and bivalves (Clarke et al., under review). For our biogeographic analysis we used these 12 sub-regions the Weddell Sea, East Antarctica—Dronning Maud Land, East Antarctic—Enderby Land, East Antarctic—Wilkes Land, Ross Sea, West Antarctic (Eights Coast, Bellingshausen and Amundsen Seas), Antarctic Peninsula, South Shetland Islands, South Orkney Islands, South Sandwich Islands, Bouvet Island, and South Georgia, as well as Heard and Peter I islands. The neighbouring areas included in our recent study were the Prince Edward, Crozet, Chatham, Auckland, Kerguelen archipelagos, Campbell Island and the Magellan region, subdivided into the Falkland Islands, Tierra del Fuego, Strait of Magellan, Atlantic and Pacific coasts of the Magellan region. The ocean areas of the neighbouring areas and sub-regions within Antarctica were written into polygons, which defined the geographic range of each area using GIS (ArcGIS 8.2) (Fig. 1A).

2.2. Data source and definitions

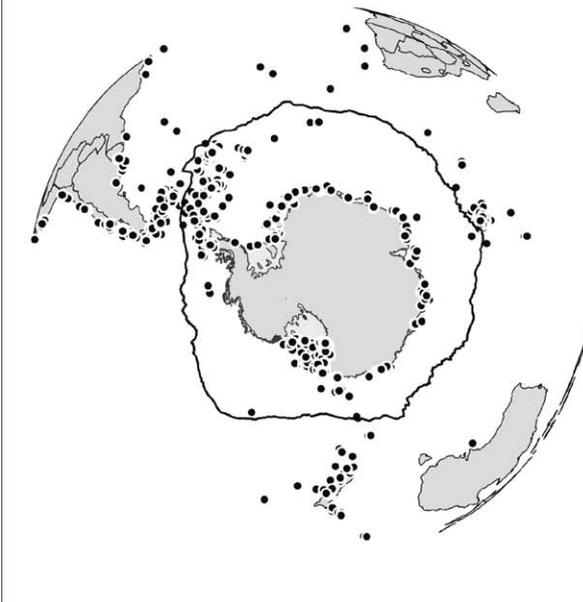
Biogeographic data from the Southern Ocean and neighbouring areas were regularly updated in SOMBASE (Griffiths et al., 2003). For comparability of data between areas, and to minimise the sample effort bias, only distribution records for shelf species of shelled gastropods and bivalves were included (Fig. 1B, C). We defined ‘shelf’ species as those occurring in waters between 0 and 1000 m (Clarke and Johnston, 2003). Therefore species, that are recorded only from depths deeper than 1000 m were excluded from the analyses presented here.

To assess the Antarctic species richness in relation to global richness patterns in shelled gastropods and

(A)



(B)



(C)

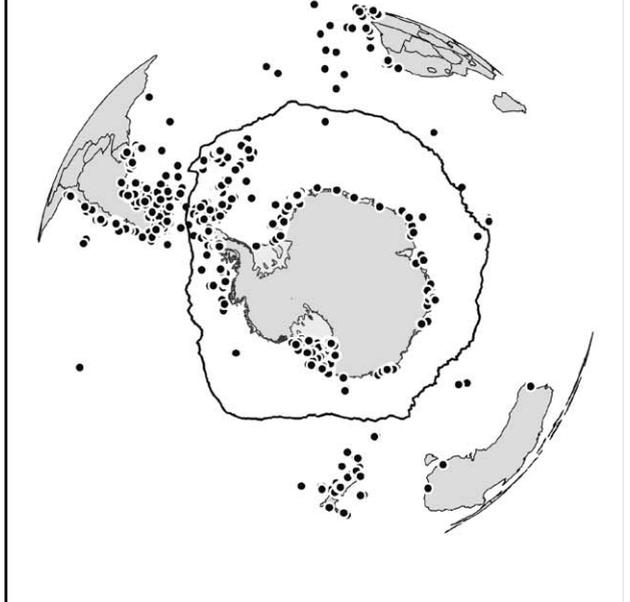


Fig. 1. Maps of Southern Ocean and surrounding with neighbouring continents overlaid with Polar Front: (A) Biogeographic areas, (B) shelled gastropod records and, (C) Bivalve records.

bivalves, we assembled species richness per zone data using published diversity records for gastropods (Spencer and Willan, 1995; Roy et al., 1998; Higo et al., 1999; Bouchet et al., 2002; Valdovinos et al., 2003; CLEMAM database, 2005; OBIS Indo-Pacific Molluscan Database,) and bivalves (Crame, 2000).

2.3. Data analysis

Raw species-distribution data for the Southern Ocean and neighbouring areas were analysed by probing SOMBASE in selected fields, such as taxonomic level, defined depth range, or defined area polygons, then using the query results for GIS or multivariate analysis in either ArcGIS (ESRI, 2002) or PRIMER 5 (Clarke and Warwick, 2001). The methodologies used for the different analysis are described below.

2.3.1. Taxon distribution patterns

For the analysis of distribution patterns at different taxonomic levels (family, genus, species), taxon counts for each of the pre-defined areas were done by using a spatial join between the data points and the geographic polygons, which defined the extent of each of the areas under investigation. The database created included a table containing the species data, sample sites, and the area in which the sites were located. To avoid counting a single taxon more than once per area, a second query was created to reduce the list to the first occurrence of a taxon in an area. Once this second query was extant, a third query (taxa per area query) was entered to count the number of taxa per area. This analysis was done six times to assess the taxon area richness for gastropod families, genera and species, and bivalve families, genera and species separately.

To analyse the number of shelf taxa only, the steps in the analysis were very similar to that just described. On the initial query, only species known from less than 1000 m depth (the Antarctic continental shelf is unusually deep Clarke and Johnston, 2003) were selected by adding the pre-defined depth range to the table. This was done by using bathymetric data for the entire study area, the Southern Ocean and neighbouring areas, and using a location based GIS selection to produce a list of species found in areas less than or equal to 1000 m depth. The analysis was run six times for each of the different taxonomic units studied.

2.3.2. Diversity centres

Numbers of species per genus and number of species per family were compared between study areas to investigate any general patterns. Only species-rich families and genera, or those judged to have radiated significantly within the Southern Ocean, were included in this analysis. The shelled gastropod families we selected were: Buccinidae, Turridae, Trochidae, Naticidae, Rissoiidae, Muricidae, Cerithiidae, Eatoniellidae, Diaphanidae, Cyclostrematidae, and Cancellariidae. The genera we selected were: *Prosipho*, *Pareuthria*, *Chlanidota*, *Trophon*, *Margarella*, *Falsimargarita*, *Eatoniella*, *Diaphana*, and *Toledonia*. Likewise the bivalve families we selected were: Nuculanidae, Sareptidae, Philobryidae, Limopsidae, Limidae, Pectinidae, Montacutidae and Cuspidariidae; and the bivalve genera we selected were *Nucula*, *Yoldiella*, *Philobrya*, *Lissarca*, *Adacnarca*, *Limopsis*, *Limatula*, *Mysella*, and *Cuspidaria*.

2.3.3. Estimating endemism

We defined endemic taxa assuming that taxa were not found beyond the limits of our database (SOMBASE). Thus we designated a taxon as endemic if it only occurred in one of our pre-defined areas. The identifications of taxa that were only found in one area were based on the taxon per area richness lists produced for the taxon distribution patterns analysis (see Section 2.3.1). Any taxon found in only one area was then assumed to be endemic. This method uses the entire database, not just the selected areas, to ensure that occurrences in regions outside the polygons are not ignored. The level of endemism per area was then displayed as taxon numbers and also as a percentage of the total taxon number per area.

2.3.4. Biogeographic relationships

We used the software package PRIMER 5 (Clarke and Warwick, 2001) to analyse biogeographic relationships amongst shelled gastropods and bivalves in our study areas. The analysis was based on the distributions of shelf species only, but on all records of these species, including those records from deeper than 1000 m depths. The species-per-area lists produced by the taxa-per-area query (see Section 2.3.1) were used as the data matrix for PRIMER 5. Faunal similarity between areas was measured by quantitative Bray-Curtis similarities (Bray and Curtis, 1957) of non-transformed binary (presence-absence) data. Non-metric

multidimensional scaling (nMDS) and cluster analysis were applied to resemblance data to display faunal similarities in two-dimensions. The data matrixes for shelled gastropods and bivalves were analysed both separately and pooled.

3. Results

3.1. Southern Ocean gastropod and bivalve richness

From our 27 study areas in the Southern Ocean and adjacent regions approximately 895 shelled gastropod and 379 bivalve species are known to date. Our results highlight the very poor knowledge of the Amundsen Sea fauna, and also that certain other areas have been so poorly sampled (e.g., the Bellingshausen Sea) that the diversity values are of little meaning. We examined shelf (0–1000 m depth) patterns, but taxon lists in most areas (e.g., South Orkney Islands, Strait of Magellan or the Ross Sea) differed little between shelf and all depths (Table 1).

Molluscan taxon richness differed between shelf and all depths at the South Sandwich Islands, the South Shetland Islands, and in the Weddell Sea. Typically larger (shelf) areas, e.g., the Weddell Sea, Ross Sea, Tierra del Fuego and East Antarctic–Wilkes Land, were richest, followed by the larger islands (Falkland Islands, South Georgia, and the Kerguelen Islands). The small and most isolated islands, such as Bouvet Island, the Prince Edward Islands, and Campbell Island, exhibited the lowest richness. The three richest areas of our study areas were South Georgia (199 species/107 genera/62 families) and those on the margins of west and east Antarctica: the Weddell Sea shelf (279/119/65) and the Ross Sea (192/111/57).

The Southern Ocean areas had higher species per family (median 2.7:1) and species per genus (median 1.66:1) ratios than areas north of the Southern Ocean (medians 1.88:1 and 1.27:1 respectively). The Weddell Sea and Tierra del Fuego, for example, had similar numbers of genera and families, but the

Table 1
Molluscan taxon numbers (Shelled gastropods & bivalves) per area

Area	Species		Genera		Families	
	Shelf	All depths	Shelf	All depths	Shelf	All depths
Auckland Island	123	123	85	85	50	50
Bellingshausen Sea	11	11	9	9	7	7
Eights Coast	6	6	3	3	3	3
Bouvet Island	36	36	31	31	24	24
Campbell Island	47	47	43	43	32	32
Chatham Islands	5	5	5	5	5	5
Crozet Islands	74	74	43	43	29	29
East Ant. Enderby Land	110	110	69	69	44	44
East Ant. Wilkes Land	164	167	92	95	54	55
East Ant. Dron. Maud Land	105	105	63	63	34	34
Falkland Islands	126	126	82	82	51	51
Heard Island	15	15	12	12	9	9
Kerguelen Islands	129	129	78	78	49	49
Magellan Strait	116	116	89	89	54	54
New Zealand (South Island)	70	72	64	66	40	42
Peninsula	130	131	80	81	47	47
Peter I Island	3	3	3	3	2	2
Prince Edward Islands	52	52	44	44	37	37
South Georgia	199	206	107	112	62	65
South Orkney Islands	112	112	73	73	46	46
South Sandwich Islands	40	60	33	48	24	34
South Shetland Islands	133	160	78	90	49	56
Southern Argentina	26	26	24	24	20	20
Southern Chile	125	125	96	96	62	62
Ross Sea	192	194	111	113	57	58
Tierra del Fuego	178	178	107	107	63	63
Weddell Sea	279	301	119	126	65	69

Weddell Sea was much richer in species. The dominant trends in taxon richness in the pooled shelf dataset were also apparent in individual analyses for shelled gastropods (Appendix A) and bivalves (Appendix B). For almost every study area and at all taxonomic levels gastropods were much richer than bivalves. Southern Ocean study areas

had higher ratios of gastropod to bivalve taxa (median 2:1 species) than areas to the north (median 1.46:1).

There were, however, distinct differences in the richness patterns both between the shelled gastropod and bivalves, and also within these two groups, at different taxonomic levels (Fig. 2). Shelled

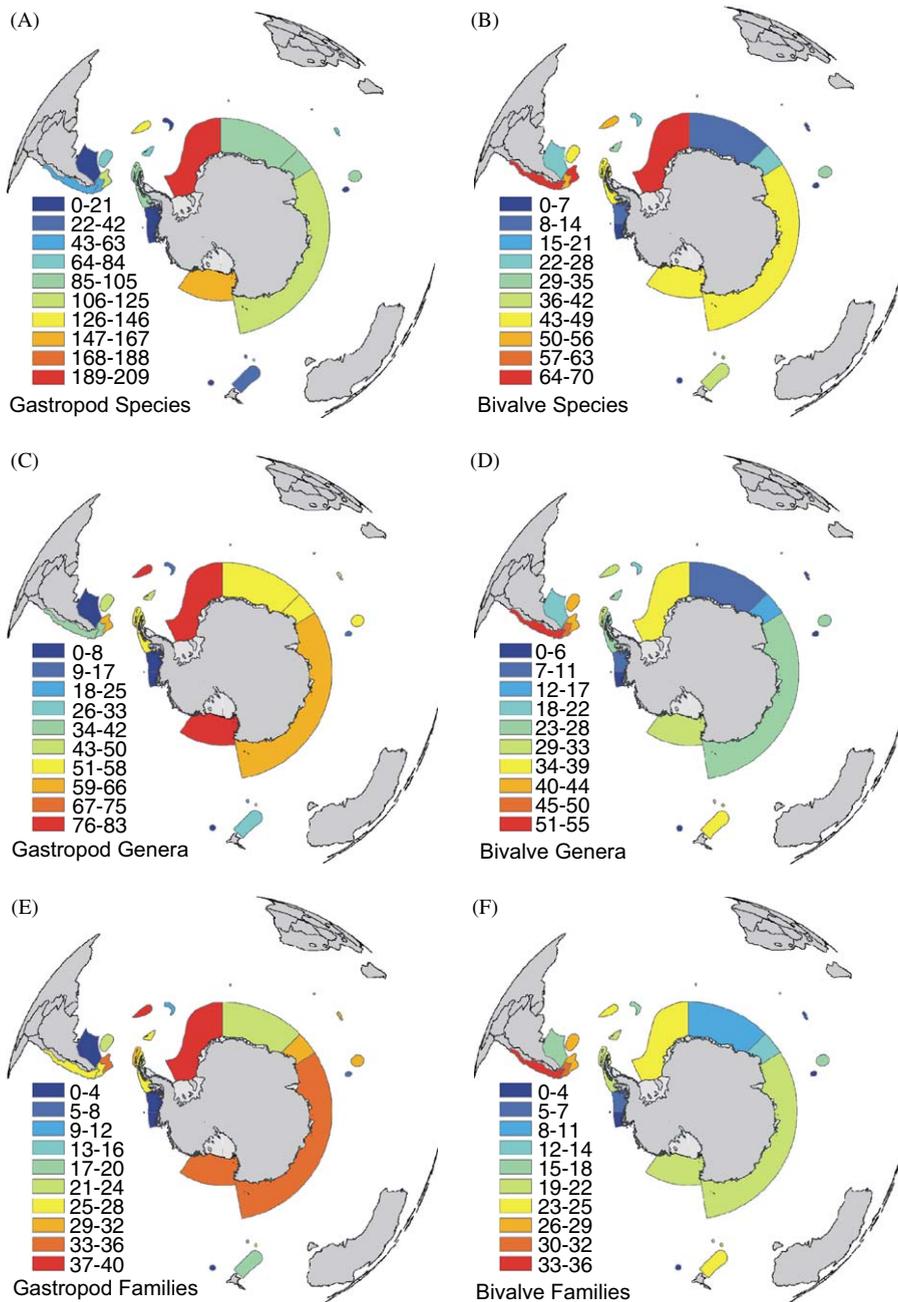


Fig. 2. Hotspots of taxonomic richness in pre-defined areas of the Southern Ocean and neighbouring areas; (A) gastropod species, (B) bivalve species, (C) gastropod genera, (D) bivalve genera, (E) gastropod families, (F) bivalve families.

gastropods had higher richness levels in high Antarctic areas than bivalves, and two areas of East Antarctica were impoverished in bivalve taxa but mid-richness levels in gastropods (Fig. 2). Areas identified as having the highest taxonomic diversity ('hotspots') differed depending on the taxonomic level of the analysis. For example South Georgia patterns of richness were moderate at species level

but high at generic and familial levels in shelled gastropods, whereas species richness was higher than generic or familial levels in bivalves (Fig. 2).

3.2. Centres of diversity in the Southern Ocean

Analysis of species richness in families and genera of shelled gastropods and bivalves revealed that

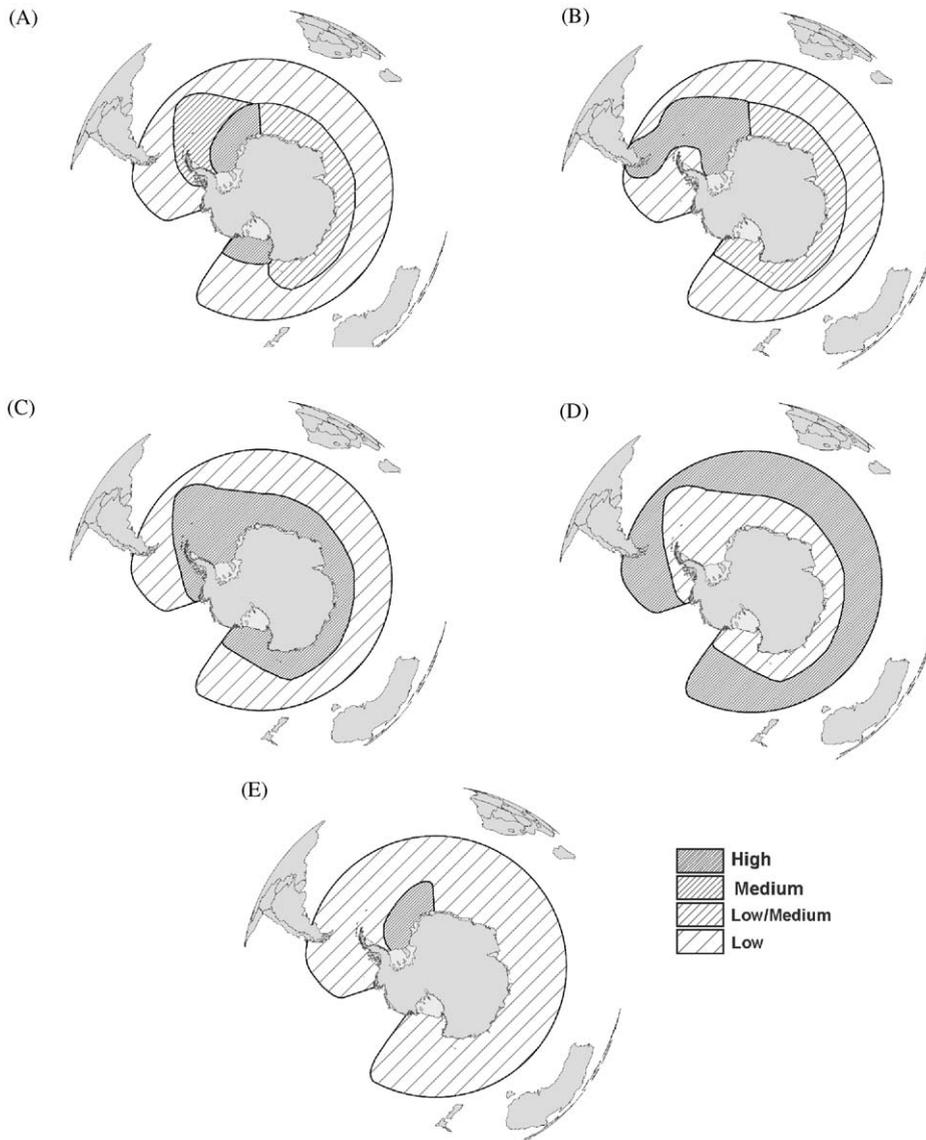


Fig. 3. Distribution centres of high-latitude southern marine molluscs. Areas of high to low richness of families/genera. The specific taxa are Cyclostrematidae, Buccinidae, Sareptiidae, Turridae, Diaphanidae, Naticidae and Cuspidariidae, and *Toledonia* and *Cuspidaria* (A), Rissoidae, Trochidae, Philobryidae, Muricidae and Eatoniellidae, and *Pareuthria*, *Eatoniella* and *Trophon* (B), Limidae and Montacutidae and *Mysella*, *Limatula*, *Yoldiella*, *Prosipho*, and *Falsimargarita* (C), Pectinidae, Nuculidae, Volutidae, Mytilidae, Gaimardiidae or Condylocardiidae (D), and Limopsidae, Cancellariidae, and Cerithiidae, *Philobrya* and *Limopsis* (E). The shading represents levels of species richness from high to low.

most were encompassed by just five overall patterns (Fig. 3). The families Cyclostrematidae, Buccinidae, Sareptiidae, Turridae, Diaphanidae, Naticidae and Cuspidariidae, and the genera *Toledonia* and *Cuspidaria* had the Weddell and Ross Seas as centres of taxon richness (Fig. 3A), with richness decreasing towards the Scotia arc, Antarctic Peninsula region, and East Antarctica, and lowest in the sub-Antarctic, Magellanic and other areas. A second pattern apparent was a richness centre spanning the Weddell Sea to Magellanic areas, through the Scotia arc (Fig. 3B). The families Rissoidae, Trochidae, Philobryidae, Muricidae, and Eatoniellidae, and the genera *Pareuthria*, *Eatoniella* and *Trophon* all exhibited this pattern. The third pattern was high Southern Ocean richness coupled with low richness in the sub-Antarctic and other northern areas (Fig. 3C). The families Limidae and Montacutidae, and the genera *Myseilla*, *Limatula*, *Yoldiella*, *Prosipho*, and *Falsimargarita* showed this type of distribution. Conversely, the third distribution type was a high richness north of the PF and low richness south of it. This was shown by the families Pectinidae, Nuculidae, Volutidae, Mytilidae, Gaimardiidae and Condylocardiidae (Fig. 3D). Finally, the families Limopsidae, Cancellariidae, and Cerithiidae, and the genera *Philobrya* and *Limopsis* had a centre of richness in the Weddell Sea (Fig. 5E).

3.3. Endemism

The species level of Antarctic endemism for both shelled gastropods and bivalves within the Southern Ocean was approximately 75% (Table 2). At generic and familial levels this was reduced to 13.2% and 0%, respectively. Comparison of regional endemism within and outside the Southern Ocean showed no obvious patterns, though with the exception of South Georgia, areas within the Southern Ocean had low rates of species endemism (4.5–19.7%). Species level endemism in areas outside the PF varied between 2.7% (Crozet Islands) and 23% (Tierra del Fuego). The two highest levels of endemism amongst our study areas were at South Georgia and Bouvet islands; apart from latitude and being within the PF, these two areas have little in common. South Georgia is a large, old island whereas Bouvet is a small, young one. At genus level none of our study areas north of the PF had endemics and only five areas within the Southern Ocean did (Table 2). Seven of the ten genera,

Table 2
Molluscan endemic taxa (Shelled gastropods & bivalves) per area

Area	Species		Genera		Families	
	N	%	N	%	N	%
Bellingshausen Sea	1	9.1	0	0.0	0	0.0
Eights Coast	0	0.0	0	0.0	0	0.0
Bouvet Island	13	36.1	0	0.0	0	0.0
Crozet Islands	2	2.7	0	0.0	0	0.0
East Ant. Enderby Land	5	4.5	0	0.0	0	0.0
East Ant. Wilkes Land	17	10.4	0	0.0	0	0.0
East Ant. Dron. Maud Land	20	19.0	0	0.0	0	0.0
Falkland Islands	23	18.3	0	0.0	0	0.0
Heard Island	0	0.0	0	0.0	0	0.0
Kerguelen Islands	21	16.3	0	0.0	0	0.0
Magellan Strait	21	18.1	0	0.0	0	0.0
Peninsula	7	5.4	2	2.5	0	0.0
Peter I Island	0	0.0	0	0.0	0	0.0
Prince Edward Islands	9	17.3	0	0.0	0	0.0
South Georgia	65	32.7	2	1.7	0	0.0
South Orkney Islands	22	19.6	3	4.1	0	0.0
South Sandwich Islands	2	5.0	0	0.0	0	0.0
South Shetland Islands	6	4.5	0	0.0	0	0.0
Ross Sea	22	11.5	1	1.0	0	0.0
Tierra del Fuego	41	23.0	0	0.0	0	0.0
Weddell Sea	55	19.7	2	1.7	0	0.0
Sum Southern Ocean	464	75.2	27	13.2	0	0.0

(*Anderssonia*, *Antistreptus*, *Eatoniopsis*, *Kaitoa*, *Munditia*, *Pickenia* and *Tropidomarga*), which only occurred in one area of the Southern Ocean, did so along the Scotia arc/Antarctic Peninsula range. *Dickdellia* and *Intortia* were only found in the Weddell Sea, and *Murdochella* only recorded in the Ross Sea.

There were far more endemic species of shelled gastropods than bivalves (Fig. 4, Appendix C). Only in the Strait of Magellan and Tierra del Fuego was the number of endemic bivalve species higher than that of gastropods. Just two bivalve genera, *Adamussium* and *Ptychocardia*, were endemic to the Southern Ocean, but neither were endemic to any of the individual study areas. In contrast to bivalve patterns, the Weddell Sea and South Georgia were the two hotspots of endemism in gastropods (Fig. 4A, C).

3.4. Analysis of zoogeographic relationships

Multivariate analysis of the 27 study areas at the three selected taxonomic levels revealed three major biogeographic regions at high southern latitudes. These were the Magellan region, Southern Ocean,

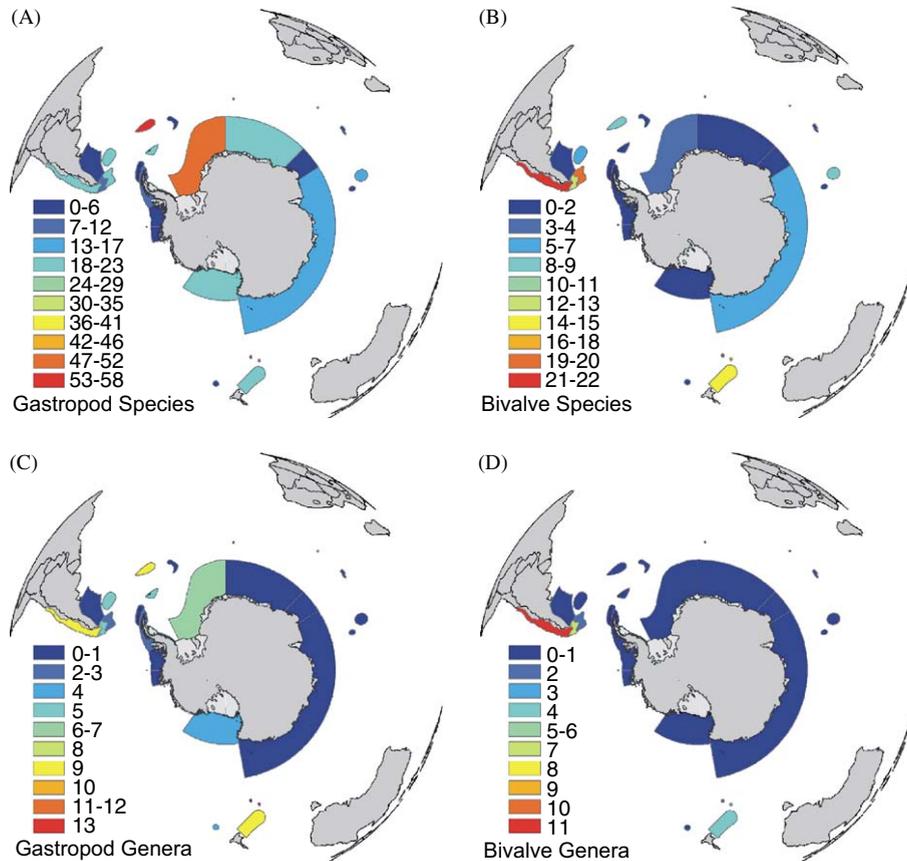


Fig. 4. Patterns of endemism in high-latitude southern marine molluscs with taxon and taxon level. The taxa are, (A) gastropod species, (B) bivalve species, (C) gastropod genera, (D) bivalve genera. The coloured scale bar represents numbers of endemic taxa.

and New Zealand. This pattern emerged both with the pooled data and with separate analyses for shelled gastropod and bivalve data (Figs. 4 and 5). Pooled and separate analyses also suggested that there were five main outliers: Bellingshausen Sea, Eights Coast, Chatham Islands, Heard Island and Peter I Island, all of which are poorly sampled locations. At the family level the regions split at ~60% similarity level, whereas at generic level divergence occurred at ~45% similarity. At the species level the split occurred at between 20 and 25%, depending on whether the shelled gastropod and bivalve data were considered separately or combined (Fig. 4, Table 3).

Separate analyses of shelled gastropod data showed similar area relationships to analyses of pooled data at species and genus level, but not at family level (Table 3). A cluster at the family level with New Zealand affinities split at ~40% from a large cluster combining most other areas. At 65%

similarity this cluster separated into three Magellanic groups, Southern Chile, Falkland Islands, and Strait of Magellan/Tierra del Fuego, and two Antarctic ones, one of which was East Antarctica and the other was the Antarctic Peninsula, Scotia arc islands, Kerguelen, Crozet, and Prince Edward Islands. At genus level, three major clusters separated at 40% similarity, centred around New Zealand, South America and Antarctica. Bouvet, Heard and the South Sandwich Islands clustered separately. Within the Antarctic generic cluster three sub-groups formed separating into East, West (including the Scotia arc islands), and sub-Antarctic islands (Kerguelen, Crozet, and Prince Edward Islands). In contrast, at species level these sub-Antarctic islands had formed a separate cluster alongside those of New Zealand, South American, and Antarctic clusters.

Separate analyses of the bivalve data showed patterns similar to the pooled data, with two

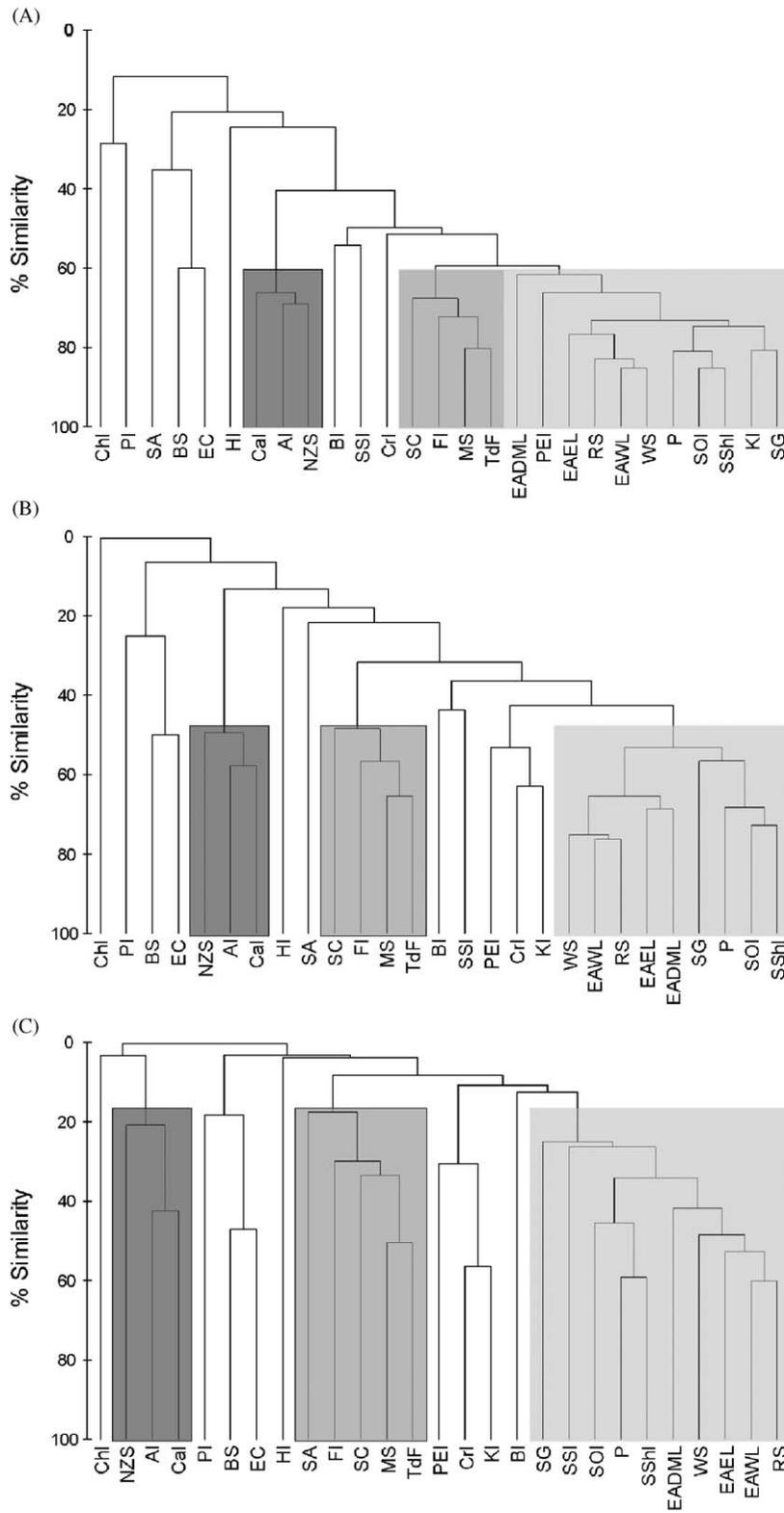


Fig. 5. Biogeographic relationships of high-latitude southern marine molluscs with taxonomic level. The taxonomic levels are (A) Combined families, (B) Combined genera, (C) Combined species. The colours represent the regions, New Zealandan (dark), South American (mid) region and Southern Ocean (light).

Table 3

Biogeographic relationships of high latitude regions based on southern marine molluscs, combined and separated for bivalves and gastropods, with taxonomic level

	CombSp	CombGen	CombFam	BivSp	BivGen	BivFam	GastSp	GastGen	GastFam
Bouvet Island	A	A	O	A	A	A	O	O	O
Crozet I	I	A	O	/	/	/	I	A	ASA
East Ant. Enderby Land	A	A	A	A	A	A	A	A	ASA
East Ant. Wilkes Land	A	A	A	A	A	A	A	A	ASA
East Ant. Dronning Maud Land	A	A	A	A	A	A	A	A	ASA
Kerguelen I	I	A	A	SA	SA	SA	I	A	ASA
Peninsula	A	A	A	A	A	A	A	A	ASA
Prince Edward I	I	A	A	SA	O	SA	I	A	ASA
South Georgia	A	A	A	A	A	A	A	A	ASA
South Orkney I	A	A	A	A	A	A	A	A	ASA
South Sandwich I	A	A	O	A	A	A	A	O	O
South Shetland I	A	A	A	A	A	A	A	A	ASA
The Ross Sea	A	A	A	A	A	A	A	A	ASA
Weddell Sea	A	A	A	A	A	A	A	A	ASA
Auckland Island	NZ	NZ	NZ	NZ	NZ	NZ	NZ	NZ	NZ
Campbell Island	NZ	NZ	NZ	NZ	NZ	NZ	NZ	NZ	NZ
New Zealand (South Island)	NZ	NZ	NZ	NZ	NZ	NZ	NZ	NZ	NZ
Bellingshausen Sea	O	O	O	O	O	O	/	/	/
Eights Coast	O	O	O	O	O	O	/	/	/
Chatham I	O	O	O	O	O	O	O	O	O
Heard Island	O	O	O	O	O	O	O	O	O
Peter I Island	O	O	O	O	O	O	O	O	O
Falkland I	SA	SA	SA	SA	SA	SA	SA	SA	SA
Magellan Strait	SA	SA	SA	SA	SA	SA	SA	SA	ASA
Southern Argentina	SA	O	O	SA	SA	SA	O	O	O
Southern Chile	SA	SA	SA	SA	SA	SA	SA	SA	SA
Tierra del Fuego	SA	SA	SA	SA	SA	SA	SA	SA	ASA

A	Antarctic
SA	South America
O	Other
I	Islands
ASA	Antarctic/South America
NZ	New Zealand

notable exceptions. The Kerguelen and Prince Edward Islands (Table 3) fit within the Antarctic cluster in the pooled dataset and gastropod data, but within the South American cluster in the separate bivalve analysis. The Antarctic cluster at all taxonomic levels was split further into two sub-groups, as in the separate shelled-gastropod analysis. However, these groupings differed from each other: in the bivalves, the Scotia arc islands and Antarctic Peninsula grouped with the Weddell and Ross Seas as one sub-group. The other sub-group

comprised the East Antarctica—Dronning Maud Land, Bouvet Island and East Antarctica—Wilkes Land.

4. Discussion

4.1. Geotectonic, palaeogeographic and hydrodynamic processes

The geological history of Antarctica and its isolation are directly linked to the break-up of the

supercontinent of Gondwana and so therefore is the history of the Antarctic marine fauna. Before geographical patterns can be considered, however, it is important to bear in mind the historical context, given the dramatic change in environment of the Southern Ocean over the last few 10s of millions of years. Although the fossil record of this fauna is highly fragmentary, molluscan fossils are known from the Mesozoic to the Holocene (e.g., Zinsmeister and Macellari, 1988; Zinsmeister et al., 1989; Stilwell and Zinsmeister, 1992; Stilwell, 2002; Wrona, 2003; Stilwell et al., 2004).

During the Mesozoic (248–65 Ma BP), the supercontinent of Gondwana broke into five major fragments, the continental blocks of Antarctica, Australia, India, South America, and Africa, and several minor fragments, e.g., the West Antarctic microcontinental fragments of Antarctic Peninsula, Thurston Island, and Marie Byrd Island (Lawver et al., 1992). Seafloor spreading commenced in the South Atlantic, off the western margin of Australia and between India and Antarctica, and the macrocontinental blocks drifted away from each other opening shallow and deep-water basins around Antarctica (Lawver et al., 1992; Lawver and Gahagan, 2003), but at this time the ACC system was not yet in existence. In Cretaceous Antarctica (144–65 Ma BP) the taxonomic composition of the molluscan fauna was quite different from that known today. Suspension feeding bivalves, ammonites (cephalopods) and hyoliths dominated the marine molluscs in terms of abundance and richness, whilst gastropods were less important (Stilwell, 2002; Stilwell, 2003; Wrona, 2003). Amongst the Cretaceous fauna, only the bivalve genus *Malletia*, a deposit feeder, is represented today.

After the *K–T* boundary (65 Ma BP) the composition and richness changed dramatically. Since then gastropod taxa have dominated the fossil record, and especially carnivorous forms with planktonic development. In contrast the suspension-feeding taxa largely disappeared. The Early Palaeocene fauna of Seymour Island (northern Antarctica Peninsula), the oldest records for this period, comprise 18 species of bivalves belonging to 11 families and 36 species of gastropods from 17 families (Stilwell, 2003). Six of these genera (*Nucula*, *Thyasira*, *Bittium*, *Amauropsis*, *Melanella* and *Probuccinum*) are still extant, as are 13 families. During the Early Eocene (50 Ma BP) a major current ran southwards along the eastern margin of Australia, passing the West Antarctic microcontinental frag-

ments, and then northwards along the west coast of South America at the same time an easterly flowing wind-driven current was initiated in the Weddell Sea. A trans-Antarctic current from the Ross Sea to the Weddell Sea, separating the West Antarctic microcontinental fragments from the East Antarctic, may have been present during the Eocene (50–33.7 Ma BP) and possibly as late as mid-Miocene (15 Ma BP) (Lawver and Gahagan, 2003). Patterns of fossil richness in the La Meseta Formation from Seymour Island show a strong Eocene radiation of the molluscan fauna (e.g., Stilwell and Zinsmeister, 1992; Zinsmeister, 1984; Zinsmeister and Camacho, 1982). More than 170 species and 110 genera of gastropods, bivalves and scaphopods were present, with the dominant families being nuculanid, malletiid mytilid, mactrid and venerid bivalves together with naticid, struthiolariid, buccinid and turrid gastropods. Only 12 genera of this fauna are still represented in the Southern Ocean, most of the remaining genera occur in the seas north of the PF.

With the opening of the Drake Passage as a deep-water connection between the Pacific and Atlantic Oceans in the Early Oligocene (30 Ma BP), the present circum-Antarctic current system was generated (Lawver and Gahagan, 2003). Since then the ACC system has isolated the Southern Ocean marine fauna to present time (Clarke and Crame, 1989, 1992). During the Cenozoic, seawater temperatures cooled, an ice cap covered most of the Antarctic continent, and the continental shelf molluscan fauna underwent further compositional shifts and extinction events (Clarke, 1990; Clarke and Crame, 1989). The variable extent of the ice cap influenced the accessibility of shelf habitats, forced the marine fauna to react to these changes in habitat availability and lead to the creation of a “biodiversity pump” (Clarke and Crame, 1992). Taxa, which are typically adapted to warmer, temperate waters (bivalves such as mytilids, ostreids, mactrids and venerids together with gastropods such as struthiolariiids, fids, and mitrids), disappeared from the Southern Ocean. In contrast, other taxa (e.g., philobryid bivalves and buccinid and turrid gastropods) radiated extensively (Crame, 1996, 1997, 1999). Pliocene fossils (5.3–1.8 Ma BP) from Cockburn Island are assumed to be the latest shallow marine records from an interglacial before Antarctica reached its present cold state (Stilwell, 2002). Three of the five reported species there, *Nacella concinna*, *Adamussium colbecki* and

Laternula elliptica, are still extant and are circum-Antarctic in distribution.

4.2. Biogeographic zones

The coasts and seas around Antarctica have tended to be pooled into one large unit for large-scale spatial analyses of biodiversity. Initial views and ideas of Southern Ocean biogeography were shaped using molluscs as a model taxon (Hedgpeth, 1969; Dell, 1972). Despite being a large area, early analyses split the Southern Ocean into a small number of relatively broad areas and suggested the ACC (West Wind Drift in the older literature) to be important. These areas were the coasts of East Antarctica, Ross Sea, Weddell Sea, Antarctic Peninsula, Scotia arc, and a subregion for South Georgia. Following Briggs (1974) this picture has been continually updated with new findings and detailed work in new areas (e.g., Zelaya, 2000; Linse, 2002). Data from other marine taxa, such as the cheilostome bryozoans (Moyano, 1996; Barnes and De Grave, 2000) and polychaetes (Cañete et al., 1999; Glasby and Alvarez, 1999), have enabled some broad comparison of diversity centres and affinities with the more detailed mollusc data. In addition, other taxa such as the demosponges and hexactinellid sponges have been analysed at a coarser scale (Tabachnik, 1994; van Soest, 1994). Such analyses have confirmed the strong links between the southern South America (Magellanic) coast, the sub-Antarctic, and the high Antarctic. Thus a picture has emerged of a fairly isolated and different Southern Ocean fauna, but with strong links with regions immediately to the north. The strongest affinity seems, unsurprisingly, to be with the last land mass attached to Antarctica (see van Soest, 1994; Moyano, 1996; Cañete et al., 1999; Barnes and De Grave, 2000; Linse, 2002; Montiel, 2005; Montiel et al., 2005).

Clearly for molluscs, as is the case for bryozoans (Barnes and De Grave, 2000 and encrusting taxa in general, Barnes and De Grave, 2001) and probably other taxa, there are very different levels of richness between areas within the Southern Ocean. Some areas of apparently low richness, such as the Bellingshausen and Cosmonauts seas, are quite possibly an artefact of poor sampling intensity (Clarke et al., under review). Overall our analyses indicate similar geographic patterns of richness in the gastropods and bivalves at species level in the Southern Ocean (Fig. 2), with South Georgia, the Weddell and Ross seas as hotspots.

A reason for increased benthic diversity might be (seasonally) high food availability. The waters around South Georgia, one of the diversity hotspots in our data, are known for their high pelagic productivity (Atkinson et al., 2001), and this might drive increased richness of the underlying benthic fauna. The shelf areas around the Antarctic continent are seasonally covered by sea-ice, but show high primary productivity in spring and summer, especially in the Ross, Weddell and Davis Sea areas (SeaWiFS data), initiated by the break-up of the pack ice (Brierley and Thomas, 2002 and references therein). The role and importance of pelagic-benthic coupling on taxon diversification processes is unknown at the moment, but we know that the benthic fauna is dependent/reacting on pelagic productivity influx (Arrigo et al., 1998; Gutt, 2000; Peck et al., 2005; Isla et al., 2005). A further reason for similar, high richness and taxa composition between the Ross and Weddell seas might be the existence of marine pass-ways during Pleistocene ice sheet collapses (Scherer et al., 1998) that enabled geneflow between these disjunct Antarctic seas. North of the Southern Ocean (particularly the Chilean coast), and at genus and family levels, richness patterns were more different between these two classes of molluscs. At generic and familial levels gastropods were especially rich along the Chilean coast whilst bivalves were richest at South Georgia and the Weddell Sea.

Our data have revealed five major geographic diversity patterns (Fig. 3), spreading from the (1) Weddell Sea, (2) Weddell and Ross Seas, (3) Weddell Sea, Scotia arc, and Magellanic, (4) high-Antarctic and (5) Subantarctic. The latter two patterns clearly support the initial ideas of high-latitude southern biogeography (Hedgpeth, 1969; Dell, 1972) as well as the new oceanographically based scheme (Longhurst, 1998). Other major patterns, such as those of the Cyclostrematidae, Buccinidae, Sareptiidae, Turridae, Diaphanidae, Naticidae, Cuspidariidae, Rissoidae, Trochidae, Philobryidae, Muricidae and Eatoniellidae families and a few other genera (Fig. 3A and B), show similarity with those of non-molluscan taxa, particularly the cheilostome bryozoans. These are the taxa that relate the Atlantic sector of Antarctica with the Scotia arc and Magellanic South America, that is they link Antarctica to its past. The Weddell Sea appears to have played a central role in the evolution of many molluscan genera and species.

Our multivariate analyses of faunal similarity between regions (Fig. 5) clustered species, families and genera into the accepted three major biogeographic regions, namely South America, New Zealand, and Antarctic. Overall similarity in the patterns observed in bivalves and shelled gastropods: sub Antarctic and Antarctic faunas were closely linked despite some sub-Antarctic islands being north of the PF. Secondly there was a strong indication of the historical importance of the ACC, in that the Prince Edward and Kerguelen archipelagos were more closely linked to South America in the bivalves but to Antarctica in the gastropods. Thirdly there was the similarity of pattern at family, genus and species, contrasting with the very different levels of endemism at each of these taxonomic levels. We conclude that Antarctic and sub Antarctic bivalve and shelled gastropod molluscs are closely linked across the PF, and quite distinct from other high-latitude southern regions at multiple taxonomic levels.

Perhaps the most surprising result to emerge from our analyses is the grouping of the Prince Edward and Kerguelen archipelagos with the regions south of the PF for the shelled gastropods and with South America for the bivalves, suggesting very different evolutionary histories for these two groups. Although these islands currently lie north of the PF, it has not always been this way: sediment cores indicate that during glacial periods the PF has migrated northwards by at least four degrees (Gendron-Badou et al., 1997). The differences between the two taxa may indicate that the gastropods and bivalves colonised the islands at different times, when the islands were on different sides of the PF.

In order to determine whether the patterns in molluscan biogeography we detected are similar to those in other Antarctic marine invertebrates, we compared our results with those published on bryozoans (Barnes and De Grave, 2000, with additions for the Weddell Sea by Gutt et al., 2000) and on the peracarid crustaceans taxa amphipods (De Broyer and Jazdzewski, 1993), cumaceans (Brandt et al., 1999), isopods (Brandt et al., 1999), mysids (Brandt et al., 1998), and tanaidaceans (Schmidt, 1999). In the bryozoans, the Southern Ocean sub-regions with the highest species richness are the South Shetland Islands and the Weddell Sea, whilst the Ross Sea shows low species richness. In general species richness in bryozoans is higher in the non-Antarctic regions (Barnes and De Grave, 2000).

The studies on the peracarid crustaceans are all based on the zoogeographical zonation of the Southern Ocean as presented in De Broyer and Jazdzewski (1993). This zonation identified an East Antarctic sub-region that comprises our six sub-regions Weddell Sea, East Antarctica—Dronning Maud Land, East Antarctic—Enderby Land, East Antarctic—Wilkes Land, Ross Sea, West Antarctic (Eights Coast, Bellingshausen and Amundsen Seas). Our data are hardly comparable for those sub-regions, as their East Antarctic sub-region comprises a much wider area and includes our richness hotspots of the Weddell and Ross Seas. The highest richness for the different peracarid taxa is reported from the East Antarctic region. If data for the Ross and Weddell Seas also are presented (Brandt et al., 1999), their species numbers indicate a high species richness in these areas. The South Shetland Islands are a hotspot for species richness in isopods (Brandt et al., 1999) and South Georgia for mysids (Brandt et al., 1998).

4.3. Endemism

Trends in endemism have been particularly well studied in the terrestrial realm, especially in vertebrates and vascular plants. At one extreme, some species are restricted to one very small area, although they may be very abundant at that location (local endemics). Remote oceanic islands tend to have the world's most distinctive floras. Thus 91% of plants native to the Hawaiian Islands are endemic, and values for other island groups are similar (for example 90% in Papua New Guinea, 80% in Madagascar, and 76% in New Caledonia). By contrast, regions that are not geographically isolated have lower proportions of endemic species for example, less than 4% of the native vascular plant species of the United Kingdom are endemic (www.rbghkew.org.uk/gowild/wildfacts/biodiversity.html).

Marine organisms have been thought to be much more widely distributed than terrestrial species because they encounter fewer physical barriers to dispersal. Typically levels of endemism in marine faunas are not as high as those described for terrestrial vascular plants, but they may follow similar patterns: for example coastal amphipod faunas around isolated islands may be highly endemic (Myers, 1997). Even deep-water hexactinellid sponges have high levels of endemism around isolated southern Australasia and Antarctica

compared with regions such as the north Atlantic (Tabachnik, 1994). Levels of endemism for the Southern Ocean fauna as a whole vary between taxa, but are comparatively high (Arntz et al., 1997; Clarke and Johnston, 2003). Studying peracarid isopods, Brandt (1991, 1999) found endemism rates of 88% for species, 21% for genera, and 0% for families in the Antarctic. The Antarctic fish fauna shows similar rates for endemism on species level with 88%, but very high rates with 76% for genera (Andriashev, 1987). Barnes and De Grave (2000), for example, found 83% of cheilostome bryozoan species were endemic to Antarctica (but only 8% of genera and none of the families). Our data for molluscs have revealed similar patterns: 75% endemism at the species level, 13% at the genus level, and 0% at the family level. Overall at the species level, molluscan endemism is intermediate compared with other marine invertebrate groups in the Southern Ocean (Arntz et al., 1997). Since the first studies (Dell, 1964, 1972) on endemism in Antarctic molluscan species, the extent has increased from 64% (Dell, 1964) to 78% (Arntz et al., 1997), mainly through the discovery of new species (Egorova, 1982; Dell, 1990; Numanami, 1996). That our recent estimate (75%) is slightly lower than that given by Arntz et al. (1997) is because of recent discoveries of what were previously thought to be Antarctic endemics on the deeper shelf and slope of the Magellan region (Linse, 1997, 2002; Brandt et al., 1999).

The level of endemism for molluscs in adjacent the Magellan region is lower with 50% (Linse, 1997) and equals the rates for peracarid amphipods, cumaceans, isopods and mysids (48–52%; Brandt, 1999) and fish (52%; Norman, 1937). At the generic level molluscan endemism is high compared with bryozoans, but lower than found in isopods (Brandt, 1991) and hexactinellid sponges (28%) (Tabachnik, 1994), and only a one-sixth that of the Southern Ocean fish fauna. It would seem that Antarctica has been isolated long enough for the evolution of new genera but not long enough for new families. We agree with Eastman (2005) that the high levels of endemism in the marine realm classify the Antarctic as distinctive evolutionary area.

Although several authors have calculated endemism figures for taxa of interest in the Southern Ocean, there have been very few studies of geographic structure within that endemism. In his revision of the molluscan fauna from the Ross Sea

Dell (1990) reported 25 (13%) endemic species, while this number dropped in our study to 22 species (11.5%). Numanami (1996) found 21 gastropods species (23.3%), mostly new described ones, to be endemic, for her study area with is included in our East Antarctic—Dronning Maud Land sub-region. Only one of these species has been found else since then. In contrast to the high overall level, we found typically low rates of regional endemism especially in the bivalves (Fig. 4). Only in South Georgia and Weddell Sea gastropods were levels of endemism elevated, mirroring the patterns in richness (Fig. 2). The high levels of species and generic richness in Ross Sea gastropods however, were not, reflected in endemism levels.

4.4. Large scale patterns in species richness

In a recent global-scale analysis, the terrestrial realm has been divided into eight biogeographic regions, 14 biomes and 867 ecoregions (Olson et al., 2001). Mapping family-level data for equal-area grid cells for terrestrial mammals, reptiles, amphibians and seed plants, Williams et al. (1997) and others have shown a general latitudinal trend of distinctly higher equatorial species richness. But such results also showed a longitudinal trend that species richness was lower in the equatorial Africa than in equatorial Asia and America. Dividing the marine realm proved to be much more difficult, as marine organisms tend to be much more widely distributed than terrestrial species, encounter fewer obvious physical barriers to their distribution and dispersal, and live in a much more three-dimensional environment with a strong advective component. The marine realm was, historically, divided into regions on the basis of physical characteristics such as temperature or surface currents (Couper, 1983; Hayden et al., 1984). More recently Longhurst (1998) has classified the marine realm into four biomes and 50 provinces, on the basis of water-column physics and remotely sensed ocean colour.

It has long been assumed that the decline in terrestrial diversity from equator to poles would be mirrored in the sea, although the robustness of this conclusion was limited by the very poor sampling in the polar regions (Clarke, 1992). Molluscan data have been central to the development of our picture of marine diversity, but even so, few detailed patterns have been reported away from the Americas. We have therefore undertaken a detailed analysis of molluscan diversity patterns in a region

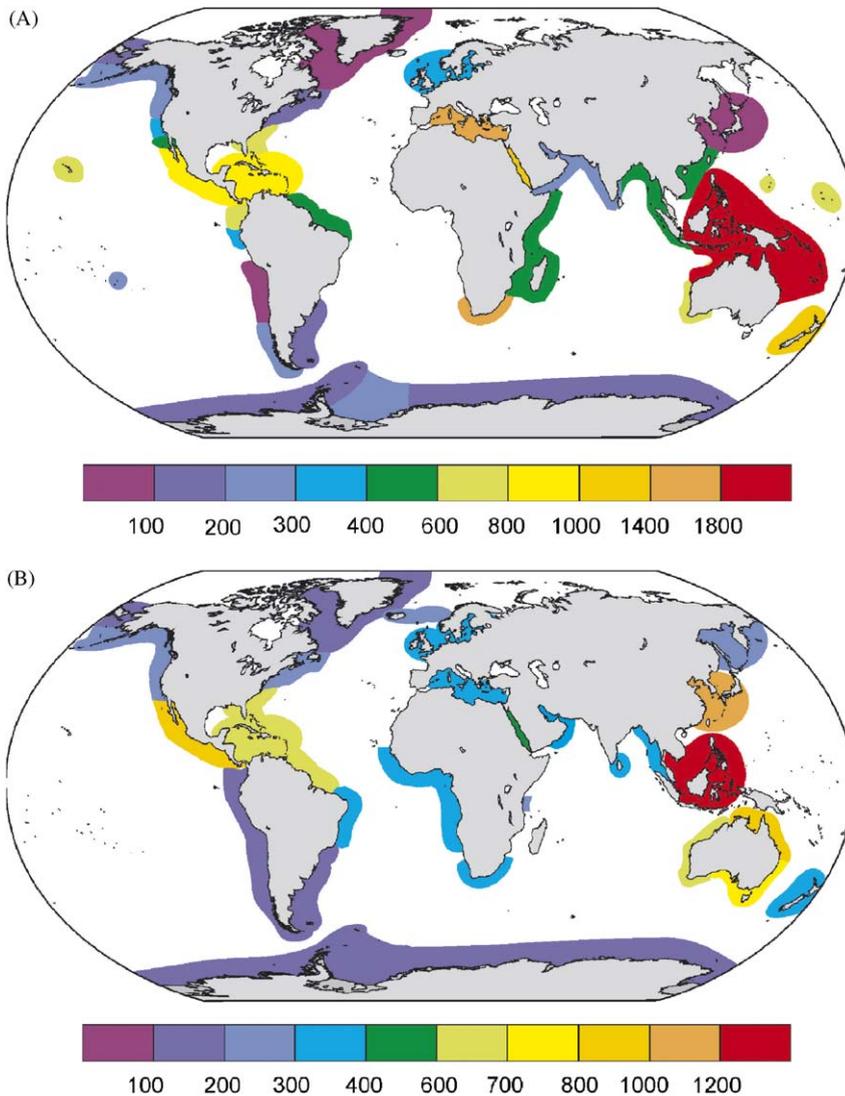


Fig. 6. Global distribution of species richness in gastropods (A) and bivalves (B). Gastropod data are from Spencer and Willan (1995), Roy et al. (1998), Higo et al. (1999), Bouchet et al. (2002), Valdovinos et al. (2003), CLEMAM database, OBIS Indo-Pacific Molluscan Database, R. Willan pers. comm. and this study. Bivalve data are from Crame (2000) and this study.

of the world that has traditionally been regarded as poorly sampled, but which is critical to the establishment of global patterns of marine diversity.

At a global level species richness is not distributed evenly across the marine environment; it varies with latitude, longitude and bathymetry, and it has also varied through evolutionary time. In no phylum has this been better demonstrated than the molluscs (see Roy et al., 1998; Crame, 2000; Stilwell, 2003; Valdovinos et al., 2003). The increasing availability of robust global datasets has, in the last few decades, begun to enable analysis of species level

patterns on continental and global scales. On the basis of our analyses and previous work on global scale patterns in marine molluscan diversity we set the Southern Ocean data into the global context (Fig. 6). Globally there is a strong degree of hemispherical asymmetry in richness patterns. Longitudinal variability is as strong as latitudinal, and there is a clearly defined centre of species richness in the Indo-West Pacific region. Our gastropod data reveal a moderately impoverished southern polar fauna, whereas our bivalve data do not alter the general pattern established by Crame

(2000) (Fig. 6). The poorly studied areas are the same for shelled gastropods and bivalves. The importance of hemispherical asymmetry in richness patterns has been increasingly noticed in a variety of marine taxa including hexactinellid sponges (Tabachnik, 1994), brachiopods (Walsh, 1994), and bivalves (Crame, 2000; Valdovinos et al., 2003). For example, the number of most major taxa is greater than would be expected given Antarctica's proportion of the world's coastline (~2%). Pycnogonids, polychaetes, holothurians, ascidians and bryozoans are all richer than would be expected on the basis of the area of the Southern Ocean (~8%). Probably the most realistic comparison, however, is on the basis of shelf area, as this is where most research has been undertaken both in Antarctica and elsewhere. By shelf area, many taxa are much richer than would be expected in the Southern Ocean and much more so than in the Arctic, contributing to strong hemispherical asymmetry (Arntz et al., 1994; Brey et al., 1994; Clarke and Johnston, 2003). Such differences between the two polar marine faunas is perhaps not so surprising considering the asymmetry in environmental factors such as sea temperature, seasonal freshening, basin age and geological history, bathymetry and bottom substrata as well as other factors (see Dunton, 1992; Chown et al., 2004).

Although latitudinal patterns typically attract most of the discussion about large-scale distributions, demonstration of considerable longitudinal variability is decades old. Stehli and Wells (1971) showed that hermatypic coral generic richness to be quite different between east and west continental seaboard, and similar patterns also have become apparent in demosponges (van Soest, 1994), decapod crustaceans (Boschi, 2000), bivalves (Crame, 2000), and sabellid polychaetes (Giangrande and Licciano, 2004).

4.5. Conclusions

Our results show that much of Antarctica's coast, which has been formerly seen as one large biogeographic zone, can be clearly separated into many sub-regions. Species richness and endemism of both

gastropods and bivalves vary distinctively between these subregions of what has long just been clumped together as 'East Antarctica' (Dell, 1972; De Broyer and Jazdzewski, 1993).

Multivariate analyses of the continental shelf benthic molluscan fauna of the Southern Ocean revealed the existence of three major biogeographic provinces within Antarctica, namely: (1) the continental high Antarctic province, (2) the Scotia Sea province including the Antarctic Peninsula, and (3) the Subantarctic islands province.

These current biogeographic patterns are the result of historical extinction, radiation and dispersal events. Ecological factors, such as reproduction mode, dispersal ability and feeding mode, obviously will have influenced the distributional success of genera and species. To further our understanding of the distribution and diversity of marine molluscs and other taxa, the next logical steps are to analyse taxon records through time and geographic links to ecological factors such as reproductive and feeding strategies. Unfortunately too few sites with fossil records of marine shelf habitat are known from Antarctica to allow us to compare past and present patterns in biogeography directly. It should be possible, however, to map reproductive trends of molluscs on regional scales.

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Appendix A. Shelled gastropod taxon numbers per area

Shelled gastropod taxon numbers per area shown in Table A1.

Table A1
Shelled gastropod taxon numbers per area

Area	Species		Genera		Families	
	Shelf	All depths	Shelf	All depths	Shelf	All depths
Auckland Island	73	73	46	46	26	26
Bellingshausen Sea	0	0	0	0	0	0
Eights Coast	0	0	0	0	0	0
Bouvet Island	22	22	20	20	14	14
Campbell Island	23	23	20	20	14	14
Chatham Islands	4	4	4	4	4	4
Crozet Islands	74	74	43	43	29	29
East Ant. Enderby Land	85	85	53	53	30	30
East Ant. Wilkes Land	119	121	66	68	33	34
East Ant. Dron. Maud Land	94	94	52	52	24	24
Falkland Islands	77	77	42	42	24	24
Heard Island	12	12	9	9	7	7
Kerguelen Islands	98	98	54	54	31	31
Magellan Strait	60	60	41	41	25	25
New Zealand (South Island)	34	34	30	30	17	17
Peninsula	85	86	53	54	28	28
Peter I Island	2	2	2	2	1	1
Prince Edward Islands	32	32	27	27	22	22
South Georgia	146	147	75	75	40	40
South Orkney Islands	80	80	47	47	27	27
South Sandwich Islands	16	30	15	26	9	15
South Shetland Islands	85	102	50	58	29	33
Southern Argentina	2	2	2	2	2	2
Southern Chile	61	61	41	41	26	26
Ross Sea	147	149	81	83	36	37
Tierra del Fuego	111	111	64	64	35	35
Weddell Sea	209	221	83	87	40	42

Appendix B. Bivalve taxon numbers per area

Bivalve taxon numbers per area shown in [Table B1](#).

Table B1
Bivalve taxon numbers per area

Area	Species		Genera		Families	
	Shelf	All depths	Shelf	All depths	Shelf	All depths
Auckland Island	50	50	39	39	24	24
Bellingshausen Sea	11	11	9	9	7	7
Eights Coast	6	6	3	3	3	3
Bouvet Island	14	14	11	11	10	10
Campbell Island	24	24	23	23	18	18
Chatham Islands	1	1	1	1	1	1
Crozet Islands	0	0	0	0	0	0
East Ant. Enderby Land	25	25	16	16	14	14
East Ant. Wilkes Land	45	46	26	27	21	21
East Ant. Dron. Maud Land	11	11	11	11	10	10
Falkland Islands	49	49	40	40	27	27
Heard Island	3	3	3	3	2	2

Table B1 (continued)

Area	Species		Genera		Families	
	Shelf	All depths	Shelf	All depths	Shelf	All depths
Kerguelen Islands	31	31	24	24	18	18
Magellan Strait	56	56	48	48	29	29
New Zealand (South Island)	36	38	34	36	23	25
Peninsula	45	45	27	27	19	19
Peter I Island	1	1	1	1	1	1
Prince Edward Islands	20	20	17	17	15	15
South Georgia	53	59	32	37	22	25
South Orkney Islands	32	32	26	26	19	19
South Sandwich Islands	24	30	18	22	15	19
South Shetland Islands	48	58	28	32	20	23
Southern Argentina	24	24	22	22	18	18
Southern Chile	64	64	55	55	36	36
Ross Sea	45	45	30	30	21	21
Tierra del Fuego	67	67	43	43	28	28
Weddell Sea	70	80	36	39	25	27

Appendix C. Endemic taxa per area for shelled gastropods and bivalves

Endemic taxa per area for shelled gastropods and bivalves shown in Table C1.

Table C1
Endemic taxa per area for shelled gastropods and bivalves

Area	Shelled Gastropoda				Bivalvia			
	Species		Genera		Species		Genera	
	N	%	N	%	N	%	N	%
Bellingshausen Sea	0	0.0	0	0.0	1	9.1	0	0.0
Eights Coast	0	0.0	0	0.0	0	0.0	0	0.0
Bouvet Island	11	50.0	0	0.0	2	14.3	0	0.0
Crozet Islands	2	2.7	0	0.0	0	0.0	0	0.0
East Ant. Enderby Land	5	5.9	0	0.0	0	0.0	0	0.0
East Ant. Wilkes Land	12	10.1	0	0.0	5	11.1	0	0.0
East Ant. Dron. Maud Land	20	21.3	0	0.0	0	0.0	0	0.0
Falkland Islands	18	23.4	0	0.0	5	10.2	0	0.0
Kerguelen Islands	14	14.3	0	0.0	7	22.6	0	0.0
Magellan Strait	8	13.3	0	0.0	13	23.2	0	0.0
Peninsula	6	7.1	2	3.8	1	2.2	0	0.0
Peter I Island	0	0.0	0	0.0	0	0.0	0	0.0
Prince Edward Islands	4	12.5	0	0.0	5	25.0	0	0.0
South Georgia	58	39.7	2	2.6	7	13.2	0	0.0
South Orkney Islands	22	27.5	3	6.3	0	0.0	0	0.0
South Sandwich Islands	1	6.3	0	0.0	1	4.2	0	0.0
South Shetland Islands	5	5.9	0	0.0	1	2.1	0	0.0
Ross Sea	22	15.0	1	1.2	0	0.0	0	0.0
Tierra del Fuego	22	19.8	0	0.0	19	28.4	0	0.0
Weddell Sea	51	24.4	2	2.4	4	5.7	0	0.0
Sum Southern Ocean	395	79.6	25	15.7	69	57	2	4.3

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