

# How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs

Andrew Clarke\*, Huw J. Griffiths, Katrin Linse, David K. A. Barnes and J. Alistair Crame

British Antarctic Survey, NERC, Madingley Road, High Cross, Cambridge CB3 0ET, UK

## ABSTRACT

The aim of this study was to use data for gastropod and bivalve molluscs to determine whether the fauna of the Southern Ocean is sufficiently well known to establish robust biogeographical and macroecological patterns. We chose molluscs for this work because they have been collected by almost every biological expedition to Antarctica, and are relatively well known taxonomically. 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. The low species richness of the Southern Ocean molluscan fauna compared with many tropical sites is confirmed, and is related principally to the absence of the large number of rare taxa that characterize some tropical assemblages. There is as yet no convincing evidence for a latitudinal cline in molluscan diversity within the Southern Ocean. Multivariate analyses defined biogeographical provinces very similar to those established previously, though they also identified a number of finer-scale sub-provinces including a small area of high diversity off Enderby Land. Most Southern Ocean gastropods and bivalves are rare, with limited distributions; relatively few taxa have circumpolar distributions.

## Keywords

Antarctica, biogeography, macroecology, mollusc, latitude, diversity.

Correspondence: Andrew Clarke, Biological Sciences, British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK.  
E-mail: accl@bas.ac.uk

## INTRODUCTION

The resurgence of interest in biological diversity and the rise of the discipline of macroecology (Brown, 1995) have intensified the search for broad patterns in nature. A particular focus for ecologists has been the documentation of global patterns in diversity, and on land this process is well advanced. The combination of remote sensing, detailed ecological work on the ground, powerful databases, and innovative software means that we now possess a detailed picture of the global distribution of terrestrial plant diversity (Barthlott *et al.*, 1996; Francis & Currie, 2003). Furthermore, these data are of sufficient quality to allow critical testing of macroecological hypotheses (Hawkins *et al.*, 2003; Currie *et al.*, 2004). The invaluable legacy of professional and amateur natural history in Europe, North America, Australia, and New Zealand has meant that most terrestrial

vertebrates and some of the more charismatic invertebrates are also well mapped, at least in some parts of the world.

The situation is very different in the sea. The ocean is vast and difficult to sample, and as a result our knowledge of marine diversity lags far behind that on land. While most animal phyla are marine and benthic, the majority of described species are terrestrial (and many of these are insects). In consequence, discussions of biogeography and biological diversity have tended to centre on the terrestrial realm. There is a pressing need to test the generality of concepts developed on land by determining to what extent, if any, they apply in the sea; but such tests are hampered severely by our relatively poor knowledge of marine diversity.

We therefore selected a well-known group of marine organisms, benthic molluscs, from a relatively well-sampled area, the Southern Ocean, and attempted to answer three questions:

**Table 1** The Southern Ocean benthic environment. The fractal nature of coastlines and depth contours means that all data depend on the length scale used. The area of the deep sea was calculated by subtraction, and so ignores mid-ocean ridges within the Southern Ocean. All data are from version 4.1 of the Antarctic Digital Database (ADD Consortium, 2000), and hence are updated from Clarke & Johnston (2003).

Coastline	
Length (km)	45,317
Ice shelf coastline (km)	18,877 (42%)
Ice coastline (km)	20,972 (46%)
Rock coastline (km)	5468 (12%)
Continental shelf (< 1000 m depth)	
Area not beneath ice shelves in 2002 (km <sup>2</sup> )	$2.97 \times 10^6$
Area beneath ice shelves in 2002 (km <sup>2</sup> )	$1.63 \times 10^6$
Total shelf area (km <sup>2</sup> )	$4.59 \times 10^6$
Continental slope (area between 1000 m and 3000 m isobaths)	
Total slope area (km <sup>2</sup> )	$2.35 \times 10^6$
Deep sea (area > 3000 m depth)	
Total deep sea area (km <sup>2</sup> )	$24.86 \times 10^6$

- 1 How well do we know the fauna?
- 2 What basic biogeographical and macroecological patterns can we establish from these data?
- 3 How do these patterns compare with those elsewhere?

## METHODS

We selected molluscs for this study because they have been collected by all the major oceanographic expeditions to have worked in the Southern Ocean, and almost all scientific reports emanating from these expeditions have volumes or sections dedicated to gastropods and bivalves. Furthermore, collection and taxonomic work continues today, and molluscs are one of the best-known groups of Antarctic benthic marine invertebrates.

All available data on the occurrence of shelled gastropod and bivalve molluscs in the Southern Ocean, and adjacent oceans, have been collated into the Southern Ocean Molluscan Database, SOMBASE (Griffiths *et al.*, 2003). SOMBASE is a spatially explicit relational database containing over 12,000 records of occurrences of molluscan taxa. It is linked to a geographical information system (GIS) and the combination provides a powerful tool for the analysis of spatial patterns in distribution.

## Some definitions

We use the Southern Ocean as defined by oceanographers, namely all waters south of the mean position of the Polar Front (PF, referred to as the Antarctic Convergence in earlier literature) (Orsi *et al.*, 1995; Trathan *et al.*, 1997). This corresponds to the Antarctic Polar Biome as defined using water column physics, biogeochemical variables, and ocean colour data by Longhurst (1998), and matches broadly the Antarctic marine environment as viewed by most biogeographers. A problem comes with those islands that are very close to, or straddle, the mean position of the PF. The position of the PF has changed through geological time and some islands currently on or outside the present PF will have been within the Southern Ocean in the past. For the purposes of this study, we have excluded Îles Kerguelen and Îles Crozet, but included South Georgia (which lies well inside the PF). This is somewhat arbitrary in that the evolutionary history of both Îles Kerguelen and Îles Crozet will necessarily be tied to that of the

Antarctic, but it does simplify the current analyses. More detailed work has elucidated the role of these two island groups in the evolutionary history of the Southern Ocean molluscan fauna (Linse *et al.*, 2006).

To examine depth trends in molluscan diversity we also need to define the continental shelf, continental slope, and deep sea. This is because the criteria used generally do not apply within the Southern Ocean: a combination of depression by the weight of continental ice and scour by previous extensions of the ice sheet means that the continental shelf around Antarctica is unusually deep. Large areas of the Antarctic continental shelf lie at depths between 500 m and 700 m, and in some places depths exceed 1000 m. This contrasts with a typical depth of 60–100 m for most continental shelves elsewhere (Walsh, 1988). On the basis of extensive bathymetric work in the Southern Ocean, we have defined the continental shelf as all depths down to 1000 m, the continental slope as all depths between 1000 m and 3000 m, and the deep sea as > 3000 m. This follows the definitions established in Clarke & Johnston (2003), and some basic statistics are given in Table 1.

## Statistical analysis

To quantify sampling intensity we divided the Southern Ocean into a series of boxes, each with the same number of degrees of latitude and longitude ( $0.5 \times 0.5$ ,  $1 \times 1$ ,  $1.5 \times 1.5$ ,  $2 \times 2$ ,  $3 \times 3$ ,  $4 \times 4$ , and  $5 \times 5$ ). Considerations of spherical geometry mean that these boxes vary in area depending on latitude, but this variation is relatively small within the Southern Ocean. We then determined the number of boxes that contained samples of benthic molluscs, with gastropods and bivalves tallied separately. We also analysed boxes on the continental shelf, continental slope, and deep-sea separately. Where a box contained the isobath marking the boundary between two depth zones, the box was assigned to whichever depth category occupied the greater area in that box. This can, of course, lead to misclassification of a few samples (for example a sample from the bottom of the continental slope being counted in a deep-sea box), but errors from this are believed to be small.

Statistical analysis was carried out with Minitab, version 14 (Minitab Inc., State College, PA, USA). In all cases, model

**Table 2** Families of gastropod and bivalve molluscs represented by 10 or more species in the Southern Ocean. Data from SOMBASE. For each family, data are the number of genera and the number of species. Also shown are the number of species reported by Clarke & Johnston (2003); \*Indicates families not listed by Clarke & Johnston (2003) (C&J) because they contained < 10 species in their compilation. The difference between these two compilations indicates the rapid growth in our knowledge of Southern Ocean molluscs over recent years.

Family	Genera	Species	Species (C&J)
<b>Bivalves</b>			
Philobryidae	3	20	13
Cuspidaridae	3	13	*
Sareptidae	2	12	*
Cyamidae	4	10	*
Limidae	1	10	*
Limopsidae	1	10	*
<b>Gastropods</b>			
Buccinidae	18	83	84
Turridae	15	49	45
Trochidae	13	36	41
Naticidae	10	34	29
Rissoiidae	7	31	24
Muricidae	3	24	23
Eatoniellidae	1	22	15
Diaphanidae	3	20	15
Cyclostrematidae	7	19	15
Littorinidae	4	17	14
Cerithiidae	3	14	22
Cancellaridae	3	12	10
Lamellaridae	3	11	12
Zeratulidae	5	11	*
Eulimidae	4	10	10
Total bivalves		158	110
Total gastropods		549	530

1 least-squares regression was used to avoid residuals being correlated with the independent variable. All logarithmic transformations were natural (Napierian) logarithms.

For analyses of faunal similarity, a similarity matrix was constructed for continental shelf samples only, using a Bray–Curtis

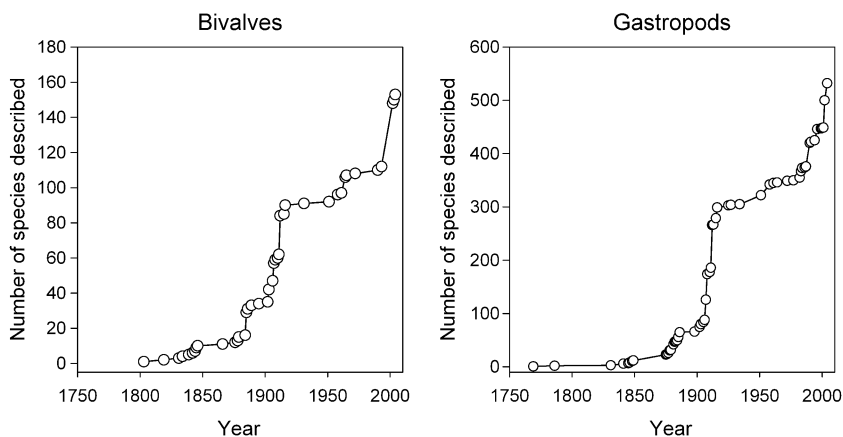
index based on presence/absence data; standard clustering routines used to establish the major biogeographical regions. Data were clustered using PRIMER (version 5), and regions defined by a threshold of 60% similarity. Rarefaction analysis was carried out using the species–area option in PRIMER, with 999 iterations.

Longitudinal ranges were calculated both clockwise and anticlockwise and the minimum value was chosen unless the presence of samples between the range boundaries indicated otherwise. This procedure was necessary to avoid taxa with a limited range but spanning 0° or 180° longitude from appearing erroneously to be circumpolar in distribution.

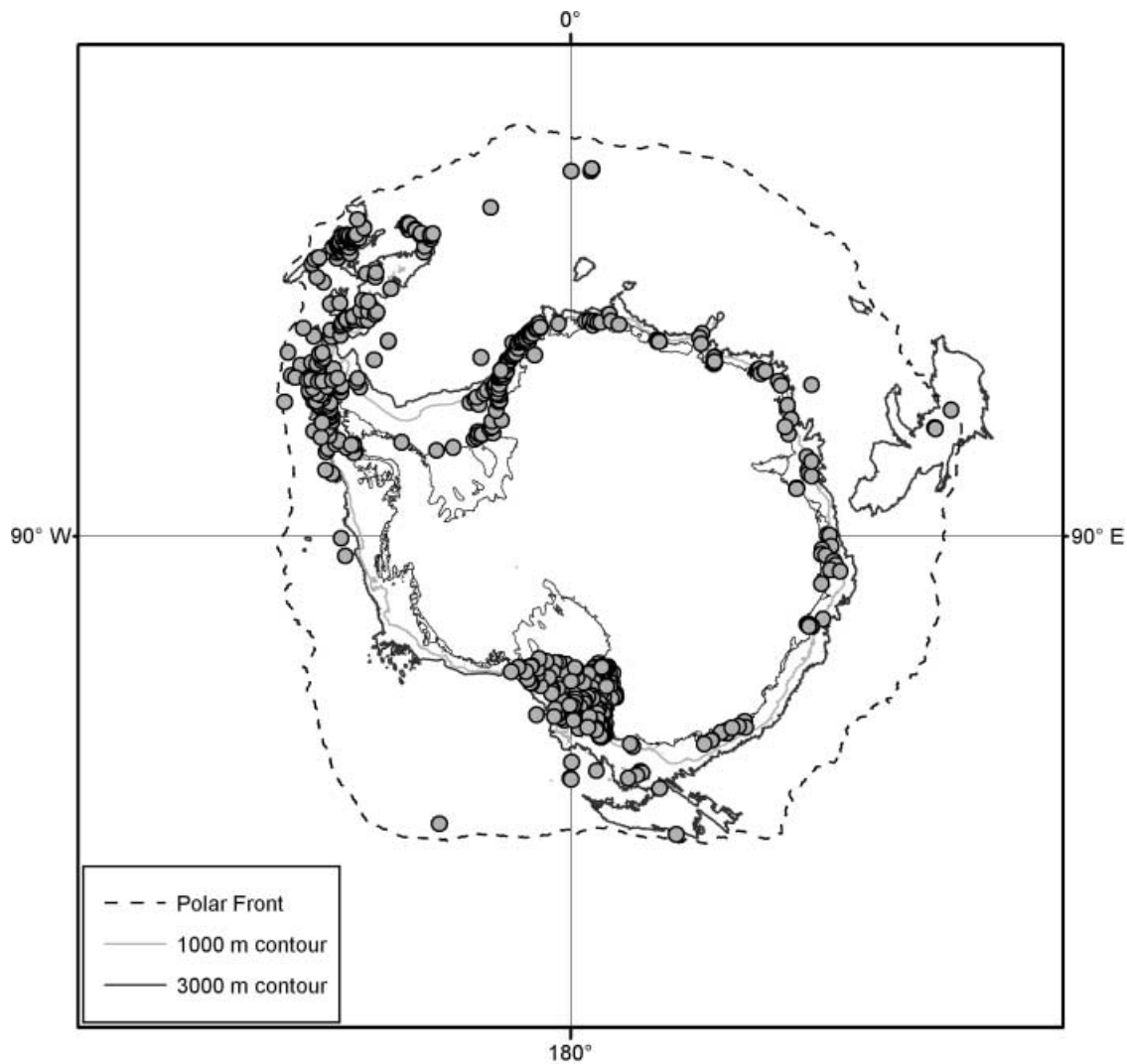
## RESULTS

Before we can undertake analyses of biogeographical or macroecological patterns, we need to ascertain how good our sampling is. The critical factors here are the extent to which the fauna has been described, and how extensive the sample coverage has been.

Clarke & Johnston (2003) compiled a list of > 4100 described species of benthic marine invertebrate from the Southern Ocean, of which 530 were shelled gastropods and 110 were bivalves. Addition of new data and subsequent taxonomic revisions has increased these totals to 549 and 158, respectively. The main families of gastropods and bivalves currently known from the Southern Ocean are listed in Table 2, and this differs slightly from the compilation by Clarke & Johnston (2003). Most of these changes are the result of new sampling (Linse, 2004, 2006), but some also follow from recent molecular work (e.g. Page & Linse, 2002; Held & Wägele, 2005; Raupach & Wägele, 2006) and taxonomic revisions (Zelaya, 2005; Zelaya & Ituarte, 2002, 2003; Zelaya *et al.*, 2006). It is, of course, only possible to guess at how many taxa remain to be discovered, but a good indication of how well the fauna has been described is given by the time-course of species description (Fig. 1). This shows clearly that although the earliest expeditions described many species, the bulk of Southern Ocean molluscs were described following oceanographic work in the late nineteenth and early twentieth centuries. There have also been important additions in the past two decades, associated mainly with international work undertaken through SCAR



**Figure 1** Time-course of cumulative species description for Southern Ocean molluscan species, with data shown separately for bivalves and gastropods. Updated from Clarke & Johnston (2003). Note the two periods of important taxonomic work in the early and late twentieth century.



**Figure 2** Map showing the distribution of sample locations for gastropod molluscs in the Southern Ocean. Isobaths are shown to mark the edge of the continental shelf (1000 m) and an arbitrary transition from continental slope to deep sea (3000 m). Also shown is the mean position of the Polar Front, which is the northern boundary to the Southern Ocean. The database contains > 7000 locations, so not all data can be distinguished because many locations overlap when plotted at this scale.

(Scientific Committee for Antarctic Research). It is likely that the two most important factors in the near future will be exploration of deeper waters (Brandt *et al.*, 2004, 2007; Harasewych & Kantor, 2004; Linse, 2004; Schwabe, 2006) and further work on molecular phylogenetics.

### How thoroughly have we sampled the Southern Ocean?

The distribution of all molluscan samples recorded in SOMBASE is shown in Fig. 2; this indicates that the continental shelves have been fairly well sampled, though there are still some unsampled areas. In particular the coasts of Wilkes and Marie Byrd Land have been poorly sampled, the latter because the dense ice of the Amundsen and Bellingshausen Seas restricts ship access.

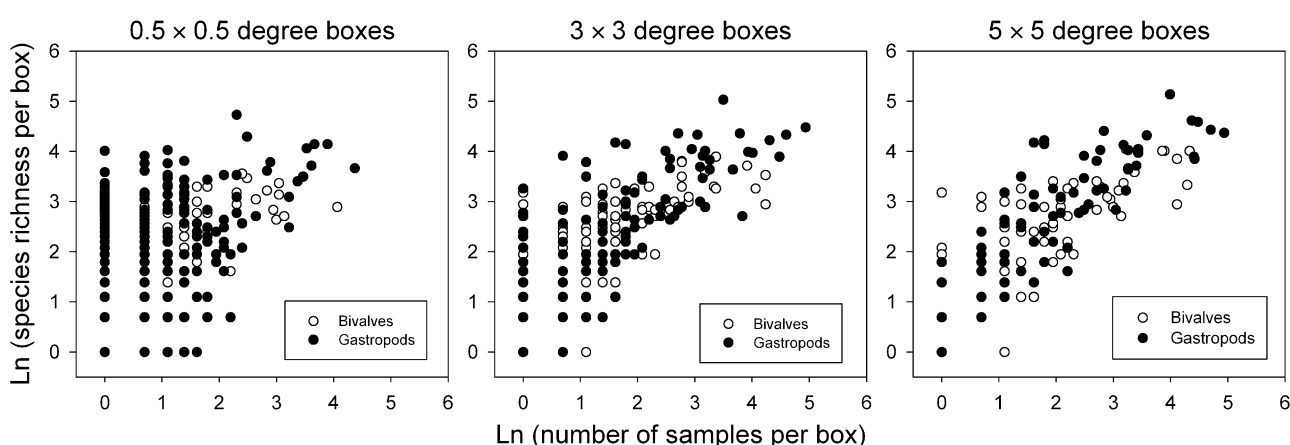
To quantify sampling intensity more formally, we divided the Southern Ocean into lat/long boxes of varying sizes (see Methods).

Most samples come from the continental shelf, and as would be expected the apparent fraction of the Southern Ocean for which we have samples increases with box size (Table 3): at a box size of  $1^\circ \times 1^\circ$ , < 3% of boxes contain samples, whereas at a box size of  $5^\circ \times 5^\circ$  degrees, almost 30% of boxes contain samples. This is a well-known effect when counting point samples within boxes, and it emphasizes the need for a careful and objective setting of box sizes for subsequent analyses.

The spatial distribution of sampling intensity (Fig. S1 in Appendix S1) shows that the Subantarctic islands and the western Antarctic Peninsula have been relatively well sampled, though many boxes contain only small numbers of samples, even at large spatial scales of aggregation (see map in Supplementary Material). The eastern Weddell Sea and the Ross Sea have also been well sampled, as have many parts of coastal Antarctica around the continent. There are, however, significant gaps in those areas that are difficult of access, such as Eastern Antarctica (notably the

**Table 3** Sample coverage in the Southern Ocean. Data show the total number of latitude/longitude boxes in the Southern Ocean ( $N$ ), with number of those boxes containing samples of molluscs. Data are presented separately for gastropods and bivalves, and divided into shelf, slope, and deep sea. The units of size for the sample boxes are degrees.

Box size	$N$	Number of boxes with samples of gastropods			Number of boxes with samples of bivalves		
		Shelf	Slope	Deep	Shelf	Slope	Deep
0.5	49,159	356	72	33	295	59	32
1	12,414	243	66	33	212	57	32
1.5	5575	191	63	33	171	53	31
2	3154	158	56	31	133	47	30
3	1434	114	52	29	106	44	26
4	811	90	47	27	79	42	25
5	524	70	43	24	66	35	26



**Figure 3** Relationship between species richness per box and number of sample locations in that box. Data are tallied for three spatial scales, with gastropods (filled symbols) and bivalves (open symbols) plotted separately. Note logarithmic transformation of both variables.

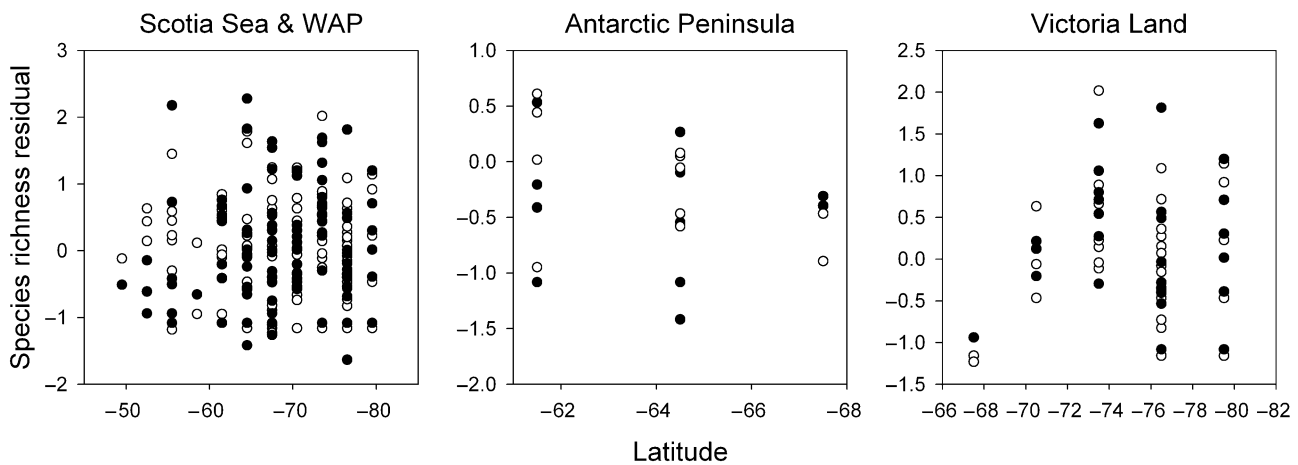
coast of Wilkes Land between the research stations of Casey and Dumont d'Urville, roughly  $110^{\circ}$  E to  $140^{\circ}$  E), and the Bellingshausen and Amundsen Seas (roughly  $140^{\circ}$  W to  $90^{\circ}$  W). The patchy nature of sampling is also indicated by the frequency distribution of species richness per box: at the finest sampling scale ( $0.5^{\circ} \times 0.5^{\circ}$ ), most boxes contain fewer than 10 species, and relatively few boxes contain more than 20 species (see Fig. S3).

Thus while the time-course of species description implies that we may have sampled a considerable proportion of the fauna, at least from the continental shelf, the geographical spread of samples indicates that coverage is less than ideal spatially. Together with the relatively small number of locations with a high species richness, this suggests that sampling error may dominate any macroecological or biogeographical patterns we establish, unless we can correct for that error in some way.

### Sampling error

The major source of error in establishing broad-scale patterns of diversity comes from variability in sampling intensity: the more samples are taken from an area, the more rare species are sampled.

The influence of sampling intensity on richness can be seen for Southern Ocean molluscs by plotting the species richness in a given box as a function of the number of samples in that box. For both gastropods and bivalves, the species richness in a box was a strong function of the number of samples in that box, and this pattern was found at all spatial scales investigated (Fig. 3). As the spatial scale of the analysis (box size) increased, the distribution of the data about the regression line improved, but at the same time the spatial resolution decreased (Fig. 3). At a spatial scale of  $0.5^{\circ} \times 0.5^{\circ}$  most boxes contained very few samples, and the species richness per box was highly variable because of marked differences in the thoroughness with which those samples were collected and analysed. At this spatial scale most data fall on the left-hand side of the graph, and the distribution of residuals is highly unsatisfactory. At the largest spatial scale used in this analysis,  $5^{\circ} \times 5^{\circ}$ , residual distribution is much improved for gastropods, but less ideal for bivalves. The model 1 least-squares regression line for these plots may be used as a description of the dependence of species richness on sampling intensity, and hence the residuals represent a first-order estimate of species richness corrected for sampling intensity (Clarke & Lidgard, 2000).



**Figure 4** Variation in species richness with latitude for three sites in Antarctica, the Scotia Sea, and western Antarctic Peninsula combined, the western Antarctic Peninsula alone, and Victoria Land (Ross Sea). Data are residuals from regression of observed species number on sample number, and were calculated separately for all spatial scales studied. Data plotted here are for  $3^\circ \times 3^\circ$  boxes, which represent the optimum balance between spatial scale in relation to the length of the latitudinal transect, and residual variance. There was no statistically significant relationship between either absolute species richness or residual species richness and latitude at any spatial scale for either gastropods or bivalves (all  $P > 0.05$ ).

Maps of these residuals reveal a few discrete areas where molluscan species richness appears to be high even after correction for sampling intensity, namely South Georgia, the northern Antarctic Peninsula, the inner Ross Sea, the eastern Weddell Sea, and East Antarctica (see Fig. S4). These are all regions where sampling has been particularly intensive and thorough, and so it is perhaps not surprising that they are the most species-rich. We 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 and subsequent taxonomic work. Even after first-order correction for sampling intensity, the resultant spatial patterns of species richness are still linked clearly to those areas of Antarctica where taxonomic work has been particularly thorough.

Despite these obvious difficulties, the first-order corrected data are the best we currently have. We have therefore used these to look for broad-scale patterns in diversity.

### Broad-scale patterns in diversity

Three large-scale patterns in diversity are potentially important within the Southern Ocean, namely latitudinal clines, depth clines, and biogeographical regions.

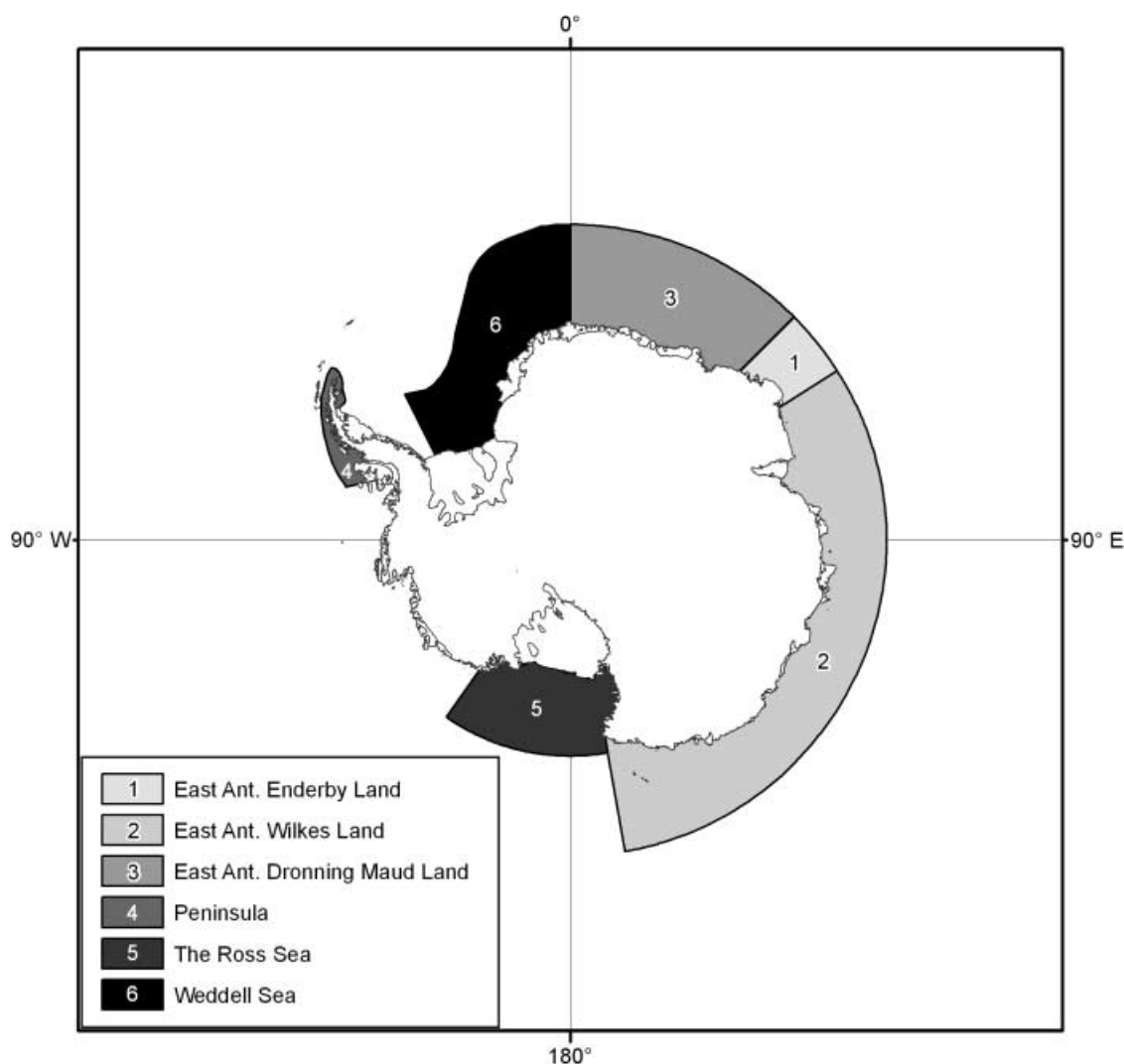
Although the Southern Ocean covers a range of about 30 degrees of latitude, the concentration of sampling on the continental shelf means that the presence or absence of a latitudinal cline in diversity within the Southern Ocean can be determined only in the two areas where the shelf runs meridionally, namely the Antarctic Peninsula and the eastern Ross Sea (Victoria Land).

There was no indication of the existence of a significant latitudinal cline in diversity in the complete data set, when using residuals calculated from sample/richness regressions at any spatial scale (Fig. 4a; all  $P > 0.05$ ). Data for the Antarctic Peninsula

alone suggest the existence of a cline in bivalve but not in gastropod species richness, though any trend is confounded by the small number of boxes that cover the relevant region, and the marked variability of the data (Fig. 4b; data at other spatial resolutions are similar). The maximum species richness of both gastropods and bivalves does show a statistically significant ( $P < 0.05$ ) cline with latitude, which might suggest that improved sampling might reveal an underlying decrease in molluscan species richness with latitude along the Antarctic Peninsula. Taken overall, present data, however, give no statistical support to the existence of such a cline.

A more complex pattern is exhibited by data for the Ross Sea (Fig. 4c). Here both gastropods and bivalve residuals show a steep cline from  $68^\circ$  S to  $74^\circ$  S, but with richness increasing with latitude (that is, the reverse of the normal pattern). At latitudes above about  $74^\circ$  S richness shows no trend with latitude. The reverse cline along Victoria Land at the outer reaches of the Ross Sea may represent inadequate sampling, which should be redressed through current work by German, American, Italian, and New Zealand biologists in this area (Cummings *et al.*, 2006; Thrush *et al.*, 2006).

The highly inadequate sampling away from the continental shelves (Fig. S5) makes the distinguishing of any depth clines in the Southern Ocean very difficult. Certainly the number of species reported from the continental slope and the deep sea is far fewer than on the shelf, but the number of samples is also fewer (see Supplementary Material). Any conclusions regarding depth clines in Southern Ocean benthic molluscs would thus be premature. Indeed the most recent sampling indicates that the deep sea molluscan fauna of the Southern Ocean may be richer than suspected. Agassiz trawl, epibenthic sledge, and box core samples taken in 2002 from 21 locations in the Scotia Sea and northern Weddell Sea at depths ranging from 774 m to 6348 m collected



**Figure 5** Map of the Southern Ocean showing the major biogeographical zones identified for continental shelf molluscs. Details of these zones are given in Table 4.

40 species of deep-water bivalves. These belonged to 17 families, and at least seven species were new to science. These new samples suggest that current data underestimate bivalve species richness in the Southern Ocean deep sea quite significantly, and that there may be no cline in bivalve species richness with depth (Brandt & Hilbig, 2004; Linse, 2004; Brandt *et al.*, 2007).

Previous work has established a series of biogeographical regions for the Southern Ocean (Hedgpeth, 1969, 1970; Dell, 1972). These were established on the basis of distribution patterns in the entire marine benthic fauna, though molluscs were often important in determining the final patterns, and they have largely stood the test of time and the advent of new knowledge (Linse, 2002). We used the molluscan data in SOMBASE to test the extent to which patterns of similarity in the species composition of boxes matched these previously established patterns.

Cluster analysis based on presence/absence data suggested a series of biogeographical regions for continental shelf molluscs

that are highly consistent with those established previously. The most significant differences are the division of the continental shelf fauna of East Antarctica into a series of smaller sub-regions, and the indication of distinct richness hotspot in the Enderby Land region (Fig. 5). We propose that on the basis of this analysis of molluscan distributions, the most appropriate biogeographical classification for the Southern Ocean continental shelf benthos is a division into three major provinces and 11 smaller regions or sub-provinces (Table 4). The proposed provinces are essentially identical to those established previously (Hedgpeth, 1969, 1970; Dell, 1972) with the finer-scale subdivisions being the novel outcome of our analysis. The sub-provinces proposed here are somewhat similar to the arbitrary sectors considered by Clarke & Johnston (2003) but differ in being defined more objectively. The biogeographical distribution of Southern Ocean molluscs is examined in more detail elsewhere (Linse *et al.*, 2006). This finer-scale analysis further subdivides the Western Antarctic Peninsula sub-province (Table 4) into three regions:

**Table 4** Faunal regions of the Southern Ocean continental shelf, as indicated by multivariate analysis of molluscan data. Longitudes are not given for well-defined island groups. SR = species richness (gastropod and bivalve molluscs combined).

Province/sub-province	Longitude	SR
Continental High Antarctic		
Weddell Sea (includes eastern Antarctic Peninsula and Princess Martha Coast)	62.5° E–0°	279
Dronning Maud Land	0°–45° E	105
Enderby Land	45° E–55° E	110
Wilkes Land (includes Mawson and Ingrid Christensen Coasts, to Cape Adare)	55° E–170° E	164
Ross Sea (Cape Adare to Cape Colbeck, including Victoria Land)	162° E–145° W	192
Marie Byrd Land and Amundsen Sea (Cape Colbeck to Pine Island Bay)	145° W–115° W	(no data)
Antarctic Peninsula and Scotia Sea		
Eights Coast (includes easternmost Amundsen Sea)	115° W–80° W	6
Western Antarctic Peninsula*	80° W–60° W	130
South Orkney Islands		192
Islands of the West Wind Drift		
South Georgia		99
South Sandwich Islands		40

\*Linse *et al.* (2006) divide this sub-province further into three finer-scale regions: Bellingshausen Sea, the main western Antarctic Peninsula, and the South Shetland Islands.

the Bellingshausen Sea, the main Antarctic Peninsula, and the South Shetland Islands.

### Macroecological patterns

We also examined the data for macroecological patterns. The semiquantitative sampling that characterizes most taxonomic work on Southern Ocean benthos somewhat limits the analyses that can be performed, but patterns that can be examined are species abundance distributions and geographical range size distributions.

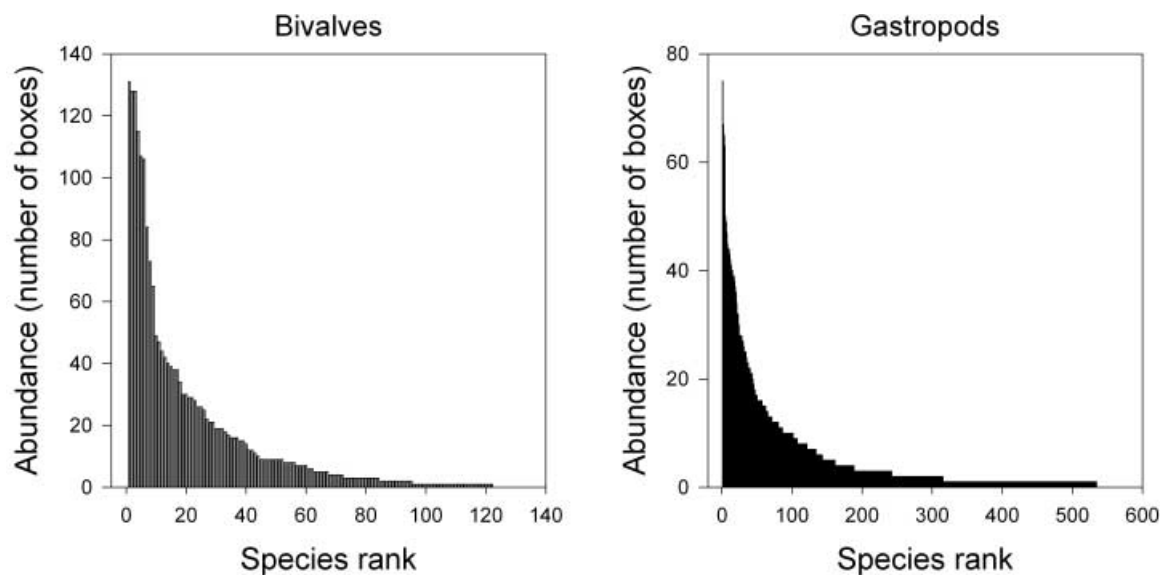
Few samples of benthic molluscs taken in the Southern Ocean have been fully quantitative, a notable exception being the study of shallow-water gastropods at Signy Island by Picken (1980). Nevertheless the number of samples taken overall is quite large, and we can therefore use the number of samples in which a given species is found as a rough index of overall abundance. Using this approach, the species abundance curve shows a very typical pattern: a few species are common and found in most boxes, whereas most species are rare and found only occasionally (Fig. 6). In the entire data set, 223 species (182 gastropods, 41 bivalves) have been reported only once, and 100 species (85 gastropods, 15 bivalves) twice. This suggests that sufficient sampling has been undertaken to reveal the broad structure, and that the species abundance structure in the Southern Ocean is qualitatively similar to that elsewhere. Further sampling and taxonomic work will undoubtedly change the details, but probably not the broad structure.

The second analysis undertaken was that of geographical range. The Southern Ocean is a somewhat atypical biogeographical entity, in that it spans a relatively small latitudinal range and is completely circumpolar. The latitudinal range of Southern Ocean molluscs is constrained by the Polar Front to the north and the Antarctic continent to the south, a maximum range of ~28 degrees of latitude. Some taxa have, however, been reported both inside and outside the Southern Ocean, and so for this analysis, the complete latitudinal range was calculated.

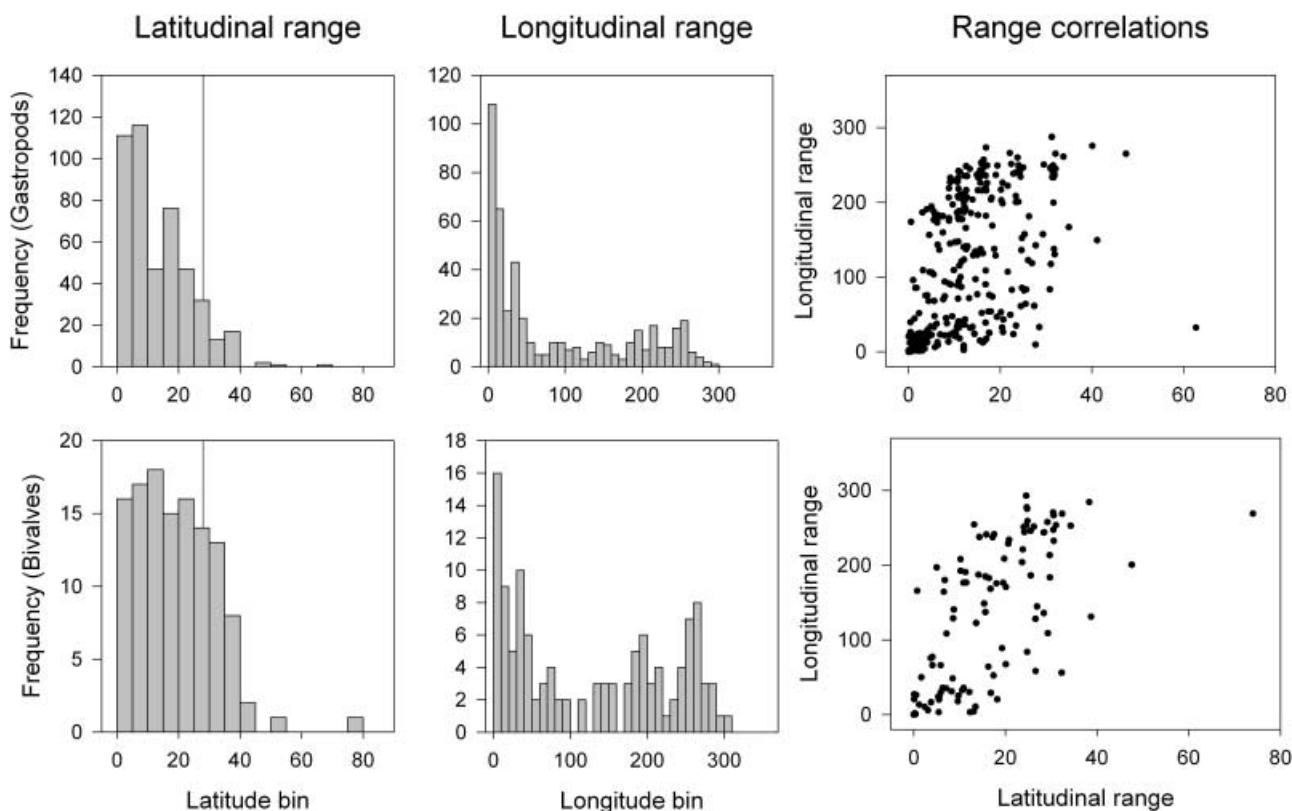
The frequency distribution of latitudinal ranges (Fig. 7) differs between gastropods and bivalves. In gastropods, most taxa show very limited latitudinal ranges (< 10°), as would be expected with most species only being recorded very few times. Relatively few gastropods have ranges that take them outside the Southern Ocean, and the taxa with the widest latitudinal ranges were *Kerguelenatica bioperculata*, *Antarctoneptunea aurora*, and *Iothia coppingeri*. The frequency distribution of latitudinal ranges in bivalves was quite different with more or less equal numbers of species (14–18) in each range bin class up to 35° (Fig. 7). The two bivalves with the widest latitudinal ranges were *Dacrydium albidum* and *Limatula simillima*.

The longitudinal range distributions of both gastropods and bivalves were dominated by taxa with very limited ranges, again being the result of most taxa being represented by few samples. Perhaps more surprising is that very few taxa were widely distributed (Fig. 7). The method of calculating longitudinal range used here means that gaps in sampling will prevent any taxa from having a fully circumpolar distribution. Nevertheless, it is striking

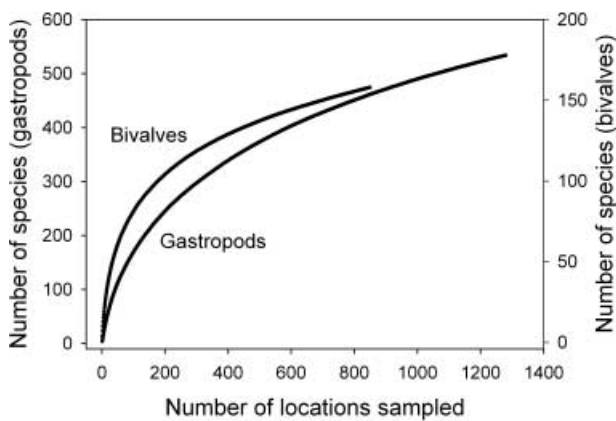




**Figure 6** Species abundance plots for Southern Ocean continental shelf bivalve and gastropod molluscs (data for  $0.5^\circ \times 0.5^\circ$  boxes). Species are ranked according to the number of boxes in which they are found (which is a crude proxy for abundance). These plots show that relatively few species are found widely, and most species are found in very few boxes.



**Figure 7** Biogeographical range sizes in Southern Ocean continental shelf gastropods and bivalves. Data are shown separately for latitudinal range and longitudinal range. Latitudinal ranges were calculated for the entire range of the species, including the distribution outside the Southern Ocean where relevant. The vertical line shows the maximum latitudinal range possible for a species ranging from the continent to the Polar Front ( $\sim 28^\circ$ ). The maximum longitudinal range ( $360^\circ$ ) represents a fully circumpolar species. The range size is the difference between the maximum and the minimum range points; it does not imply that the organization is found everywhere in between (and for a shallow water species this would be highly unlikely since most of the Southern Ocean is deep sea).



**Figure 8** Rarefaction curves for Southern Ocean gastropods and molluscs. The different shapes for the gastropod and bivalves are most likely related to differences in species abundance structure (Gray *et al.*, 2004).

how few taxa have ranges even approaching circumpolar. This proportion is greater in bivalves, possibly partly the result of the lower number of species overall, and the slightly different species abundance structure. It is very likely that as sample coverage and intensity improves, more taxa will prove to be circumpolar but present data suggest that truly circumpolar molluscan taxa in the Southern Ocean are the exception rather than the rule.

There were significant correlations between longitudinal and latitudinal range extents for both gastropods and bivalves when the complete data sets were analysed (Fig. 7).

## DISCUSSION

The basic question tackled in this paper is whether we know the benthic molluscan fauna of the Southern Ocean sufficiently well to infer broad-scale biogeographical or macroecological patterns.

Although the spatial coverage of samples around Antarctica is fairly good, important gaps remain in East Antarctica and also particularly in the Bellingshausen and Amundsen Seas (Fig. 2). While this coverage is probably sufficient to allow reasonably robust conclusions concerning the continental shelf fauna, data for deeper water are especially sparse. We are thus highly constrained in our ability to draw meaningful conclusions about the Antarctic deep-sea, but material from recent deep-sea expeditions is starting to improve matters greatly (Brandt & Hilbig, 2004; Linse, 2004; Schrödl *et al.*, 2006; Schwabe, 2006; Brandt *et al.*, 2007). Such data will be of enormous importance to understanding the evolutionary history of the Southern Ocean fauna, which has involved frequent movement of taxa between the continental shelf and the deep sea (Brandt & Hilbig, 2004; Raupach *et al.*, 2004). Access in the west to the extensive sampling undertaken by the Former Soviet Union would also be of enormous benefit (Vinogradova, 1997; Malyutina, 2004).

The time-course of species description (Fig. 1) implies that new taxa are still being described at a significant rate. Rarefaction

analyses of extent data for the Southern Ocean also imply that we may be far from having described most molluscan taxa, in that neither the gastropod nor the bivalve curves are approaching an asymptote (Fig. 8). However, this analysis must be treated with some caution: firstly, the non-quantitative nature of most sampling has meant that we have had to use frequency of occurrence (that is, the number of sites at which a given species has been recorded) as a proxy for abundance, and secondly, the shape of a rarefaction curve is affected strongly by species abundance structure (Ugland *et al.*, 2003). The latter is likely to be a major factor in the different shape of the curves for Southern Ocean gastropods and bivalves.

It has long been known that, a few large taxa notwithstanding, many Southern Ocean molluscs are small (Nicol, 1966, 1978). This has meant that a number of difficult groups of small taxa remain to be thoroughly worked up, and many species probably remain to be described. This is particularly true of the fauna of the continental slope and deep sea. It is also likely that the continued application of molecular techniques will reveal further cryptic species (Page & Linse, 2002; Lörz *et al.*, 2007; Linse *et al.* in press), although this process is not unique to the Southern Ocean for the identification of cryptic species using molecular techniques is increasing the species richness everywhere (Bickford *et al.*, 2007).

Despite these difficulties, we probably know the molluscan fauna of the Antarctic continental shelf as well as many shelves elsewhere in the world (Clarke & Johnston, 2003). We can therefore draw cautious conclusions for comparison with lower latitude faunas. The most important of these is that the relatively low species richness of gastropod and bivalve molluscs on the Southern Ocean continental shelves is real, and not an artefact of insufficient sampling. Richness is particularly low for bivalves. Although molluscan taxa undoubtedly remain to be discovered, these additions will not increase Antarctic molluscan diversity to levels approaching those of many tropical locations.

## Macroecological patterns

The species abundance patterns reported here are qualitatively similar to those of assemblages elsewhere, being dominated by rare (or at least rarely sampled) taxa. The quantitative patterns are, however, very different. In a detailed 2-year study of shallow-water gastropods at Signy Island, Antarctica, Picken (1980) recovered only 31 taxa in 138,650 individuals. In contrast Bouchet *et al.* (2002) found 2187 gastropod species in only 81,558 individuals. This indicates that tropical molluscan assemblages differ from those at high latitudes in their very large proportion of rare species. It is far from clear whether this striking difference between polar and some tropical assemblages has any consequences for ecosystem function.

Our analyses have shown that relatively few Antarctic gastropods or bivalve molluscs are common, and few are widely distributed (Table 5). The range abundance structure is undoubtedly influenced by the species abundance pattern, but the most striking result of the analyses is the low number of truly circumpolar taxa. Even using a very lax definition of circumpolar distribution to

Family	Number of species in SO
Ranking based on median number of boxes occupied by all species in the family	
Gastropods	
Capulidae	1
Trochacidae	1
Trichotropidae	9
Zerotulidae	11
Eulimidae	11
Bivalves	
Thraciidae	1
Siliculidae	2
Laternulidae	1
Sareptidae	8
Montacutidae	6
Ranking based on maximum number of boxes occupied by any single species in the family	
Gastropods	
Volutidae	9
Buccinidae	97
Lepetidae	5
Trochidae	41
Scissurellidae	8
Bivalves	
Philobryidae	22
Carditidae	5
Limopsidae	8
Limidae	8
Thraciidae	1

**Table 5** The most widely distributed families of gastropod and bivalve molluscs in the Southern Ocean (SO), based on the number of lat/long boxes in which individual species have been recorded. Families are ranked separately based on the median number of boxes for all species within that family, and the maximum number of boxes for any species in that family. Rankings for different sizes of box are identical, but rankings based on median and maximum values differ markedly. The number of species known from the Southern Ocean is shown for each family.

allow for gaps in sampling, only eight species (three gastropods, five bivalves) have longitudinal ranges  $> 270^\circ$ , and only 146 species (103 gastropods, 43 bivalves) have ranges  $> 180^\circ$ .

### Biogeographical patterns

A latitudinal cline in species richness is one of the most widespread of biogeographical patterns in nature (Chown & Gaston, 2000; Gaston, 2000). Although data for marine taxa are far less comprehensive than for terrestrial, a similar pattern is found in the sea (Clarke & Crame, 1997). Crame (2002, 2004) has recently shown that in bivalves, the latitudinal diversity cline is dominated by the most recently evolved lineage, the heteroconchs, which have diversified in the tropical regions and spread subsequently to higher latitudes. While some lineage of gastropods have undoubtedly radiated in polar regions (Linse *et al.*, 2006), the null expectation was that molluscs would exhibit a latitudinal diversity cline within the Southern Ocean (although this expectation was also constrained by the relatively short latitudinal extent of meridional continental shelves around Antarctica).

The data for continental shelf molluscs show no significant latitudinal trends within the Southern Ocean for either gastropods or bivalves. This is true both for the complete data set ( $P > 0.05$  for both gastropods and bivalves, data not shown) and for individual analyses along the two shelf areas running approximately

meridionally, the western Antarctic Peninsula and Victoria Land (Fig. 4). These data are, however, characterized by high variance resulting from the very different levels of sampling intensity and subsequent taxonomic work at different sites. Confining the analysis to those boxes with species richness above the median value for a given latitude does indicate a strong decline in richness southwards along the western Antarctic Peninsula and Victoria Land from  $74^\circ$  to  $80^\circ$  S; this suggests that improved sampling may well change the conclusions from our initial analyses. A cline has been reported for macroalgal species richness along the western Antarctic Peninsula (Moe & Delaca, 1976), and also for the diversity of shallow-water encrusting taxa (Barnes & De Grave, 2000, 2001), but these remain the only latitudinal diversity clines reported so far for marine taxa within the Southern Ocean.

The formal similarity analyses undertaken here have largely confirmed the long-established major biogeographical regions for Antarctica, although they have refined some details (Fig. 5; Table 4). In particular they have identified finer-scale divisions within East Antarctica, and also a possible hotspot and/or zone of overlap in a relatively small area off Enderby Land.

We can conclude that our knowledge of the continental shelf benthic molluscan fauna of the Southern Ocean, though imperfect, is sufficiently strong to allow us to draw reasonably robust macroecological and biogeographical patterns. Some of the details will undoubtedly change as a result of continued sampling

and taxonomic work, particularly from regions that are presently poorly known. But we believe the broad patterns we report are reasonably robust. We believe that other well-worked groups such as echinoderms, cnidarians, crustaceans, and pycnogonids (see Clarke & Johnston, 2003) can support similar analyses; such work is currently underway to test the generality of the conclusions presented here based on molluscs alone.

## REFERENCES

- ADD Consortium (2000) *Antarctic digital data base, version 3.0. Database manual and bibliography*. Scientific Committee on Antarctic Research, Cambridge.
- Barnes, D.K.A. & De Grave, S. (2000) Biogeography of Southern Ocean bryozoans. *Vie et Milieu*, **50**, 261–273.
- Barnes, D.K.A. & De Grave, S. (2001) Ecological biogeography of southern polar encrusting faunas. *Journal of Biogeography*, **28**, 359–365.
- Barthlott, W., Lauer, W. & Placke, A. (1996) Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. *Erdkunde*, **50**, 317–327.
- Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K.L., Meier, R., Winker, K., Ingram, K.K. & Das, I. (2007) Cryptic species as a window on diversification and conservation. *Trends in Ecology & Evolution*, **22**, 148–155.
- Bouchet, P., Lozouet, P., Maestrati, P. & Heros, V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, **75**, 421–436.
- Brandt, A., de Broyer, C., De Mesel, I., Ellingsen, K.E., Gooday, A.J., Hilbig, B., Linse, K., Thomson, M.R.A. & Tyler, P.A. (2007) The biodiversity of the deep Southern Ocean benthos. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, **362**, 39–66.
- Brandt, A., De Broyer, C., Gooday, A.J., Hilbig, B. & Thomson, M.R.A. (2004) Introduction to ANDEEP (ANTarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) — a tribute to Howard L. Sanders. *Deep-Sea Research, Part II*, **51**, 1457–1465.
- Brandt, A. & Hilbig, B. (2004) ANDEEP (ANTarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) — a tribute to Howard L. Sanders. *Deep-Sea Research, Part II*, **51**, 14–16.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Chown, S.L. & Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution*, **15**, 311–315.
- Clarke, A. & Crame, J.A. (1997) Diversity, latitude and time: patterns in the shallow sea. *Marine biodiversity: causes and consequences* (ed. by R.E.G. Ormond, J.D. Gage and M.V. Angel), pp. 122–147. Cambridge University Press, Cambridge.
- Clarke, A. & Johnston, N.M. (2003) Antarctic marine benthic diversity. *Oceanography and Marine Biology: An Annual Review*, **41**, 47–114.
- Clarke, A. & Lidgard, S. (2000) Spatial patterns of diversity in the sea: bryozoan species richness in the North Atlantic. *Journal of Animal Ecology*, **69**, 799–814.
- Crame, J.A. (2002) Evolution of taxonomic diversity gradients in the marine realm: a comparison of Late Jurassic and Recent bivalve faunas. *Paleobiology*, **28**, 184–207.
- Crame, J.A. (2004) Pattern and process in marine biogeography: a view from the poles. *Modern biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L. Heaney), pp. 271–291. Sinauer, Sunderland, Massachusetts.
- Cummings, V., Thrush, S.F., Norkko, A., Andrew, N., Hewitt, J., Funnell, G. & Schwarz, A.-M. (2006) Accounting for local scale variability in benthos: implications for future assessments of latitudinal trends in the coastal Ross Sea. *Antarctic Science*, **18**, 633–644.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2004) Prediction and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.
- Dell, R.K. (1972) Antarctic benthos. *Advances in Marine Biology*, **10**, 1–216.
- Francis, A.P. & Currie, D.J. (2003) A globally consistent richness–climate relationship for angiosperms. *The American Naturalist*, **161**, 523–536.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gray, J.S., Ugland, K.I. & Lamshead, J. (2004) Species accumulation and species area curves — a comment on Scheiner (2003). *Global Ecology and Biogeography*, **13**, 473–476.
- Griffiths, H.J., Linse, K. & Crame, J.A. (2003) SOMBASE — Southern Ocean Mollusc Database: a tool for biogeographic analysis in diversity and ecology. *Organisms, Diversity and Evolution*, **3**, 207–213.
- Harasewych, M.G. & Kantor, Y.I. (2004) The deep-sea Buccinoidea (Gastropoda: Neogastropoda) of the Scotia Sea and adjacent abyssal plains and trenches. *Nautilus*, **118**, 1–42.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hedgpeth, J.W. (1969) Introduction to Antarctic zoogeography. Distribution of selected groups of marine invertebrates in waters south of 35° S latitude. *Antarctic map folio series, Folio 11* (ed. by V.C. Bushnell and J.W. Hedgpeth), pp. 1–29. American Geographical Society, New York.
- Hedgpeth, J.W. (1970) Marine biogeography of the Antarctic regions. *Antarctic ecology* (ed. by M.W. Holdgate), pp. 97–104. Academic Press, New York.
- Held, C. & Wägele, J.-W. (2005) Cryptic speciation in the giant Antarctic isopod *Glyptonotus antarcticus* (Isopoda: Valvifera: Chaetiliidae). *Scientia Marina*, **69** (Supplement 2), 175–181.
- Linse, K. (2002) The shelled Magellanic Mollusca, with special reference to biogeographic relations in the Southern Ocean.

- Theses Zoologicae*, Vol. 74. Ganter Verlag KG, Ruggell, Liechtenstein.
- Linse, K. (2004) Scotia arc deep-water bivalves: composition, distribution and relationship to the Antarctic shelf fauna. *Deep-Sea Research, Part II*, **51**, 1827–1837.
- Linse, K. (2006) New records of shelled marine molluscs at Bouvet Island and preliminary assessment of their biogeographic affinities. *Polar Biology*, **29**, 120–127.
- Linse, K., Cope, T., Lörz, A.-N. & Sands, C. (In press) Is the Scotia Sea a centre of Antarctic marine diversification? Some evidence of cryptic speciation in the circum-Antarctic bivalve *Lissarca notorcadensis* (Arcoidea: Philobryidae). *Polar Biology*
- Linse, K., Griffiths, H.J., Barnes, D.K.A. & Clarke, A. (2006) Biodiversity and biogeography of Antarctic and Sub-Antarctic Mollusca. *Deep-Sea Research, Part II*, **53**, 985–1008.
- Longhurst, A. (1998) *Ecological Geography of the Sea*. Academic Press, San Diego.
- Lörz, A.-N., Maas, E.W., Linse, K. & Fenwick, G.D. (2007) *Epimeria schiaparelli* sp. nov., and amphipod crustacean (family Epimeriidae) from the Ross sea, Antarctica, with molecular characterisation of the species complex. *Zootaxa*, **1402**, 23–37.
- Malyutina, M. (2004) Russian deep-sea investigations of Antarctic fauna. *Deep-Sea Research, Part II*, **51**, 1551–1570.
- Moe, R.L. & DeLaca, T.E. (1976) Occurrence of macroscopic algae along the Antarctic Peninsula. *Antarctic Journal of the United States*, **11**, 20–24.
- Nicol, D. (1966) Size of pelecypods in recent marine faunas. *Nautilus*, **79**, 109–113.
- Nicol, D. (1978) Size trends in living pelecypods and gastropods with calcareous shells. *Nautilus*, **92**, 70–79.
- Orsi, A.H., Whitworth, T. & Nowlin, W.D. (1995) On the meridional extent and fronts of the Antarctic circumpolar current. *Deep-Sea Research*, **42**, 641–673.
- Page, T.J. & Linse, K. (2002) More evidence of speciation and dispersal across the Antarctic Polar Front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). *Polar Biology*, **25**, 818–826.
- Picken, G.B. (1980) The nearshore prosobranch gastropod epifauna of Signy Island, South Orkney Islands. p. 148. *Department of Zoology*, University of Aberdeen, Aberdeen, Scotland.
- Raupach, M.R., Held, C. & Wägele, J.-W. (2004) Multiple colonization of the deep-sea by the Asellota (Crustacea: Peracarida: Isopoda). *Deep-Sea Research, Part II*, **51**, 1787–1795.
- Raupach, M.R. & Wägele, J.-W. (2006) Distinguishing cryptic species in Antarctic Asellota (Crustacea: Isopoda) – a preliminary study of mitochondrial DNA in *Acanthaspidia drygalskii*. *Antarctic Science*, **18**, 191–198.
- Schrödl, M., Linse, K. & Schwabe, E. (2006) Review on the distribution and biology of Antarctic *Monoplacophora*, with first abyssal record of *Laevipilina antarctica*. *Polar Biology*, **29**, 721–727.
- Schwabe, E. (2006) A new species of *Bathylepeta* Moskalev, 1977 (Mollusca: Gastropoda) from the Weddell Sea, Antarctica. *Zootaxa*, **1297**, 37–45.
- Thrush, S.F., Dayton, P.K., Cattaneo-Vietti, R., Chiantore, M., Cummings, V., Andrew, N., Hawes, I., Kim, S., Kvitek, R.G. & Schwarz, A.-M. (2006) Broad-scale features influencing the biodiversity of coastal benthic communities of the Ross Sea. *Deep-Sea Research, Part II*, **53**, 959–971.
- Trathan, P.N., Brandon, M.A. & Murphy, E.J. (1997) Characterisation of the Antarctic Polar Frontal Zone to the north of South Georgia in summer 1994. *Journal of Geophysical Research*, **102**, 10483–10497.
- Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003) The species–accumulation curve and estimation of species richness. *Journal of Animal Ecology*, **72**, 888–897.
- Vinogradova, N.G. (1997) Zoogeography of the abyssal and hadal zones. *Advances in Marine Biology*, **32**, 324–387.
- Walsh, J.J. (1988) *On the nature of continental shelves*. Academic Press, San Diego.
- Zelaya, D.G. (2005) Systematics and biogeography of marine gastropod molluscs from South Georgia. *Spixiana*, **28**, 109–139.
- Zelaya, D.G. & Ituarte, C. (2002) The identity of *Waldo parasiticus* (Dall, 1876) and description of *Waldo trapezialis* new species (Bivalvia: Galleomatoidea). *Nautilus*, **116**, 109–117.
- Zelaya, D.G. & Ituarte, C. (2003) Two new species of *Neolepton* Monterosato, 1875 (Bivalvia: Neoleptonidae) from South Georgia Islands, South Atlantic Ocean. *Nautilus*, **117**, 6–11.
- Zelaya, D.G., Silva, A. & Dias Pimenta, A. (2006) A revision of *Benthobrookula* Clarke 1961 (Gastropoda, Trochoidea) in the southwestern Atlantic. *Journal of Molluscan Studies*, **72**, 77–87.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** How well do we know the Antarctic marine fauna? Gastropod and bivalve fine-scale diversity.

This material is available as part of the online article from:

<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00380.x>

(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.