Spatial patterns of benthic diversity in molluscs from West Antarctica

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Abstract: Despite several works that have documented patterns of diversity in deep sea organisms, trends of diversity and the processes responsible for such trends still remain unclear. To date very few studies have documented the effects of variables such as latitude and longitude in deep-sea organisms in the Antarctic region. We explored the spatial patterns of diversity of benthic gastropods and bivalves in an extensive region about 2200 km long and 500 km wide from the South Shetland Islands to the Bellingshausen Sea in West Antarctica. A total of 134 species from 54 sites was recorded. Alpha diversity and beta diversity (measured as Whittaker's and Bray-Curtis similarity indices) were highly variable among areas. None of the species richness estimators measured as S_{obs}, Chao2, Jacknife1 and Jacknife2, stabilized towards asymptotic values in any area. The number of rare species was large with almost half of species represented by 1 or 2 individuals (41%) and most species (62%) restricted to 1 or 2 sites. The partial Mantel test revealed that similarity between sites increased with the decrease of depth differences, but not with horizontal separation.

Introduction

Variation in distribution and abundance is a central theme of ecology and basic to both descriptive and experimental approaches to environmental science. The deep sea supports a highly diverse benthic invertebrate fauna (e.g. Rex *et al.* 2000), with high spatial and temporal variability. Patterns of distribution of organisms, i.e. meiofauna and macrofauna, and assemblages structure vary at scales from centimetres to kilometres, respectively (e.g. Etter & Grassle 1992, Rex *et al.* 2000, Ellingsen & Gray 2002). Numerous intrinsic ecological issues require a detailed quantitative understanding of the scales at which there are predictable patterns in the abundance of organisms and the natural scales of variability in these patterns (Underwood *et al.* 2000). Understanding the processes that regulate structure and dynamics of interactions between species requires recognition of the scales at which they operate and, therefore, quantitative description of spatial and/or temporal variation in abundances and diversity (Underwood *et al.* 2000).

Most marine studies of species richness and diversity have been done at small scales, that of alpha diversity. Studies at different spatial scales are, however, needed because there are strong relationships between sampling scale and the processes that influence diversity (Huston 1994). Ecological processes operate at a small scale, i.e. within habitat, whereas evolutionary forces are presumed to operate at larger scales, i.e. regional scale (Gray 1997).

Whittaker (1960) suggested that there was a range in scales of species richness and diversity and he partitioned species diversity into alpha (or within habitat), beta (or between habitat) and gamma (larger scale) diversity. Compared with the knowledge of alpha diversity, beta and gamma diversity have been far less studied in marine systems (Ellingsen & Gray 2002). In the deep sea a shift in the emphasis in biodiversity research to studies at both local and larger scales has become important in order to understand patterns of biodiversity at larger scales (Stuart *et al.* 2003, Gage 2004, Ellingsen *et al.* 2007).

Although the traditional measure of biodiversity in ecology and conservation has been the number of species, the biodiversity of an area is much more than the 'species richness' and some of the various species present in a community are abundant and others are very rare (Harper & Hawksworth 1994). Rare species can be regarded as those having low abundance or small range size (Brown 1984). In most ecological datasets, many deep-sea species seem to be rare (e.g. Grassle & Maciolek 1992). Quantification of rare species is important for communities, macroecology and conservation (e.g. Colwell & Coddington 1994). In marine systems it has been used as an important approach in assemblages and spatial patterns (e.g. Ellingsen 2001, Shin & Ellingsen 2004). However, the proportion of rare species in a given area may vary as a function of sampling intensity, using of differential sampling techniques, spatial scale and geographical location (see Shin & Ellingsen 2004).
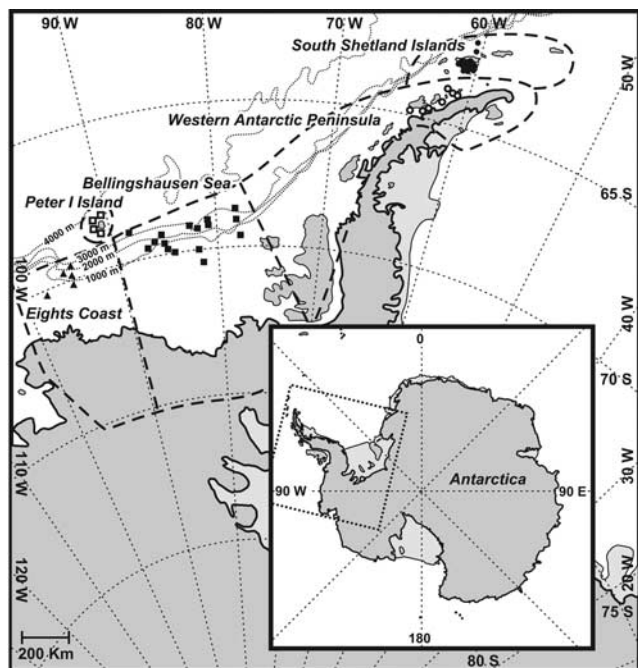
Fig. 1. Geographic position of the 54 sampling sites in the five large areas of West Antarctica from the South Shetland Islands to the Bellingshausen Sea and Eights Coast.

One of the major challenges for diversity studies in Antarctica is the assessment of possible geographic variation, i.e. latitudinal and longitudinal, and depth-related gradients of biodiversity such as those known to occur in the Northern Hemisphere (e.g. Rex *et al.* 1997, Stuart *et al.* 2003). Although several works have shown no relationship between geographic variation and/or depth and diversity in the Southern Ocean (Brandt & Hilbig 2004, Linse 2004, Brandt *et al.* 2005, Clarke *et al.* 2007, Ellingsen *et al.* 2007), this relationship has not been reported for the western Antarctica (but see Clarke *et al.* 2007). This is a not easy task for several reasons. Firstly, there are major gaps in sampling coverage of inaccessible areas, which are more or less permanently covered by ice. Secondly, assemblages are very patchy, varying at different spatial scales (Gutt & Piepenburg 2003).

The aim of this paper was to analyse patterns of alpha, beta and gamma diversity in benthic molluscs, i.e. gastropods and bivalves, from West Antarctica. In addition, we wanted to determine if variation of beta diversity, i.e. diversity between habitats, was correlated more with depth differences than with horizontal distance.

Materials and methods

Study area and sampling

The study area covers an extensive region *c.* 2200 km long and 500 km wide from the South Shetland Islands to the Bellingshausen Sea and Eights Coast on the border of Amundsen Sea (Fig. 1). The South Shetland Islands are located on the continental shelf at the northern limit of the Antarctic Peninsula and are separated from the Peninsula by the Bransfield Strait. The Bransfield Strait extends from near Clarence Island toward the south-west for *c.* 460 km to Low Island. The Strait is occupied by the Bransfield Trough, whose axial depth varies between 1100 m at the south-west margin and 2800 m just south of Elephant Island (Gordon & Nowlin 1978). The Bellingshausen Sea covers an extensive area of the continental slope and the deep sea plain along the west side of the Antarctic Peninsula between Alexander Island and Thurston Island. From a biogeographic point of view, the study area includes the sub-provinces of western Antarctic Peninsula and Eights Coast (Clarke *et al.* 2007), but the former has been previously divided into finer-scale areas of the South Shetland Islands, the main western Antarctic Peninsula, the Bellingshausen Sea and Peter I Island (Linse *et al.* 2006).

Samples were collected at 54 sites at depths ranging from 45 to 3304 m during the BENTART 95, 03 and 06 cruises aboard *RV Hespérides* (Fig. 1, Table I). During the BENTART 95 cruise, from 16 January–4 February 1995, comprehensive sampling was carried out, extending the search and analysis of benthic assemblages to the South Shetland Islands/Bransfield Strait area. During the BENTART 03 (24 January–March 2003) and BENTART 06 (2 January–16 February 2006) cruises, intensive sampling was conducted from the western Antarctic

Table I. Location and main characteristics of the areas along the study area from the South Shetland Islands to the Bellingshausen Sea and Thurston Island on the border of Amundsen Sea. Samples taken in the depth ranges 0–1000 m (shelf), 1000–3000 m (slope) and >3000 m (deep sea) are indicated. Areas: 1 = South Shetland Islands, 2 = western Antarctic Peninsula, 3 = Bellingshausen Sea, 4 = Peter I Island, and 5 = Eights Coast.

Area	Number of sites	Latitude (°S)	Longitude (°W)	Scale (km)	Depth (m)	Samples taken shelf	slope	deep sea
1	22	62.0–63.0	60.3–60.7	120 x 26	45–416	50	0	0
2	7	63.8–65.0	60.8–63.7	180 x 50	103–1056	23	3	0
3	16	68.9–70.8	77.7–88.5	364 x 295	438–3304	27	32	1
4	4	68.7–69.0	90.6–90.9	28 x 10	90–410	37	0	0
5	5	70.2–70.9	95.0–98.5	150 x 61	425–1920	9	6	0
Total	54	62.0–70.9	60.3–98.5	2200 x 500	45–3304	146	41	1

Peninsula to the Bellingshausen Sea. A complete list with information of sampling sites can be found in Arnaud *et al.* (2001) and Troncoso & Aldea (2008). Samples were collected using different sampling gears (i.e. box-corer, Agassiz trawl, epibenthic sledge, rock dredge and Nassa trap) at each site (see Aldea *et al.* 2008). Samples were sorted on deck, fixed in borax-buffered 4% formaldehyde in seawater and after one day transferred and preserved in 70% alcohol. Most specimens of gastropods and bivalves were identified to species level and only a few specimens were identified to genus or family level.

Data analyses

We prepared a complete matrix of species number and specimens per site. Alpha diversity was measured as sample species richness (SR_S) (Gray 2000), taxonomic diversity, taxonomic distinctness (Warwick & Clarke 1995) and the number of genera and families. We defined species restricted to a single site as 'uniques'; species occurring at only two sites as 'duplicates'; species represented by a single individual as 'singletons'; and species represented by only two individuals as 'doubletons' (see Colwell & Coddington 1994). The S_{obs}, representing the number of species observed in all pooled samples, the non-parametric Chao2, Jacknife1 and Jacknife2 methods (Colwell & Coddington 1994) were used to estimate the theoretical number of expected species within each area, using the EstimateS software (Colwell 1997). The 'range size' was calculated and expressed as the number of sites at which a species occurred within the study area.

Beta diversity was calculated following Whittaker (1960) as the proportion by which a given area is richer in species than the average richness of samples within it, $\beta_W = (\gamma/\bar{\alpha}) - 1$, where γ is the total number of species
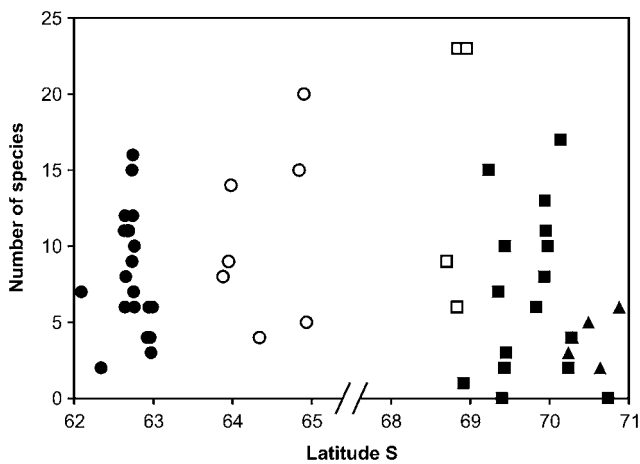

Fig. 2. Sample species richness (SR_S, alpha diversity). Samples were ordered from north (62°S) to south (71°S). Solid circles = South Shetlands Islands, open circles = western Antarctic Peninsula, solid squares = Bellingshausen Sea, open squares = Peter I Island, solid triangles = Eights Coast.

Table II. Diversity measured as SR_L, species richness in large areas (gamma diversity), SR_T = gamma diversity in total area, SR_S = sample species richness (alpha diversity), $SR_{\bar{S}}$ = mean alpha diversity, $SR_{\overline{FAM}}$ = mean number of families, $SR_{\overline{GEN}}$ = mean number of genera, Δ = mean taxonomic distinctness, Δ^* = mean taxonomic diversity, β_W = Whittaker's beta diversity; and the proportion of 'rare' species, uniques, duplicates, singletons and doubletons. CI 95% confidence intervals.

| Area | SR_L | Range | SR_S | | | | | | | 'Rare' species (%) | | | |
			$SR_{\bar{S}} \pm CI$	$SR_{\overline{GEN}} \pm CI$	$SR_{\overline{FAM}} \pm CI$	$\Delta^* \pm CI$	$\Delta \pm CI$	β_W	Uniques	Duplicates	Singletons	Doubletons
South Shetland Islands	46	2–16	8.3±1.6	7.4±1.3	6.8±1.1	88.7±2.9	73.9±4.2	4.5	37.0	6.5	28.3	6.5
Western Antarctic Peninsula	49	4–20	10.7±4.3	10.1±3.9	9.0±3.3	89.1±4.2	81.8±5.7	3.6	65.3	22.4	40.8	18.4
Bellingshausen Sea	56	0–17	6.8±2.7	6.3±2.5	5.6±2.1	76.7±18.8	68.8±17.5	7.2	50.0	23.2	30.4	12.5
Peter I Island	37	6–23	15.3±8.9	13.3±7.3	10.3±5.2	89.1±3.1	74.7±11.5	1.4	51.4	35.1	21.6	18.9
Eights Coast	18	2–6	4.0±1.4	4.0±1.4	3.8±1.3	87.7±14.7	78.4±14.4	3.5	94.4	0	72.2	11.1
Total	SR_T 134	0–23	8.3±1.5	7.5±1.3	6.7±1.0	85.1±5.9	73.9±5.7	15.2	45.5	16.4	30.6	10.4

Table III. List of species recorded in the area of study. 1 = South Shetland Islands, 2 = western Antarctic Peninsula, 3 = Bellingshausen Sea, 4 = Peter I Island, and 5 = Eights Coast.

Class to Family	Species	1	2	3	4	5
GASTROPODA						
Patellogastropoda						
Nacellidae	*Nacella polaris concinna* (Strebel, 1908)		+			
Lepetidae	*Iothia coppingeri* (Smith, 1881)		+			
Vetigastropoda						
Anatomidae	*Anatoma euglypta* (Pelseneer, 1903)			+		+
Fisurellidae	*Cornisepta antarctica* (Egorova, 1972)			+		
Emarginulinae sp.			+			
Trochidae	*Trochidae* sp. 1			+		
	Trochidae sp. 2			+		
	Antimargarita smithiana (Hedley, 1916)			+		
	Antimargarita powelli Aldea, Zelaya & Troncoso, 2009			+		+
	Calliotropis antarctica Dell, 1990			+		+
	Calliotropis pelseneeri Cernohorsky, 1977			+		+
	Calliotropis sp.			+		
	Margarella refulgens (Smith, 1907)		+		+	
	Margarella sp.	+				
	Solariella antarctica Powell, 1958			+		
	Submargarita sp.		+	+		
Skeneidae	*Brookula* sp. 2			+		
	Liotella endeavourensis Dell, 1990			+		
	Lissotesta sp.			+		
Turbinidae	*Leptocollonia innocens* (Thiele, 1912)			+		
Caenogastropoda						
Littorinidae	*Pellilitorina pellita* (Martens, 1885)		+			
Zerotulidae	*Dickdellia labioflecta* (Dell, 1990)		+			
Eatoniellidae	*Eatoniella* cf. *kerguelenensis kerguelenensis* (Smith, 1875)	+				
	Eatoniella glacialis (Smith, 1907)		+			
Rissoidae	*Onoba gelida* (Smith, 1907)		+	+	+	
	Onoba kergueleni (Smith, 1875)				+	
	Onoba turqueti (Lamy, 1905)				+	
Capulidae	*Torellia antarctica* (Thiele, 1912)		+			
	Torellia mirabilis (Smith, 1907)		+			
	Torellia planispira (Smith, 1915)	+	+			
Velutinidae	*Marseniopsis conica* (Smith, 1902)		+			
	Marseniopsis mollis (Smith, 1902)				+	
	Marseniopsis syowaensis Numanami & Okutani, 1991				+	
Naticidae	*Pseudamauropsis anderssoni* (Strebel, 1906)		+		+	
	Pseudamauropsis aureolutea (Strebel, 1908)			+	+	
	Pseudamauropsis rossiana Smith, 1907	+	+			
	Pseudamauropsis sp.	+				
	Falsilunatia delicatula (Smith, 1902)				+	+
Eulimidae	*Melanella antarctica* (Strebel, 1908)		+	+	+	
Cerithiopsidae	*Cerithiopsilla antarctica* (Smith, 1907)		+			
Muricidae	*Trophon coulmanensis* Smith, 1907	+	+			
	Trophon cuspidarioides Powell, 1951				+	
	Trophon drygalskii Thiele, 1912			+		
	Trophon echinolamellatus Powell, 1951		+			
	Trophon longstaffi Smith, 1907				+	
	Trophon sp.	+				
Buccinidae	*Buccinidae* sp. 1			+		
	Buccinidae sp. 2				+	
	Chlanidota signeyana Powell, 1951	+	+	+	+	
	Lusitromina abyssorum (Lus, 1993)					+
	Neobuccinum eatoni (Smith, 1875)	+	+	+	+	+
	Pareuthria cf. *innocens* (Smith, 1907)		+			
	Pareuthria regulus (Watson, 1882)				+	
	Probuccinum tenerum (Smith, 1907)		+			
	Prosipho cancellatus Smith, 1915		+			
	Prosipho chordatus (Strebel, 1908)				+	

Table III. Continued

Class to Family	Species	1	2	3	4	5
	Prosipho cf. *elongatus* Thiele, 1912	+				
	Prosipho hedleyi Powell, 1958				+	
	Prosipho pellitus Thiele, 1912				+	
	Prosipho pusillus Thiele, 1912				+	
	Prosipho sp.	+				
Volutidae	*Harpovoluta charcoti* (Lamy, 1910)	+	+			
Cancellariidae	*Admete* sp.	+				
Volutomitridae	*Paradmete curta* (Strebel, 1908)	+				
Conidae	*Belaturricula ergata* (Hedley, 1916)					+
	Belaturricula gaini (Lamy, 1910)		+			
Turridae	*Aforia magnifica* (Strebel, 1908)	+	+			
	Aforia multispiralis Dell, 1990		+			
	Conorbela antarctica (Strebel, 1908)			+		
	Leucosyrinx paratenoceras Powell, 1951	+		+		+
	Lorabela sp. 1				+	
	Lorabela sp. 2			+		
	Typhlodaphne innocentia Dell, 1990				+	
	Typhlomangelia principalis Thiele, 1912			+		
Opisthobranchia						
Acteonidae	*Acteon antarcticus* Thiele, 1912					+
	Neactaeonina cf. *edentula* (Watson, 1883)			+	+	
Philinidae	*Philine alata* Thiele, 1912				+	
Pleurobranchidae	*Bathyberthella antarctica* Willan & Bertsch, 1987			+		
Dorididae	*Austrodoris georgiensis* García, Troncoso, García-Gómez & Cervera, 1993		+		+	
	Austrodoris kerguelenensis (Bergh, 1884)		+			
Tritoniidae	*Tritonia antarctica* Pfeffer in Martens & Pfeffer, 1886				+	
	Tritoniella belli Eliot, 1907		+			
BIVALVIA						
Nuculida						
Nuculidae	*Nucula austrobenthalis* Dell, 1990			+		
Nuculanidae	*Nuculana inaequisculpta* (Lamy, 1906)	+				
	Propeleda longicaudata (Thiele, 1912)	+	+	+		
Yoldiidae	*Yoldia eightsi* (Couthouy, 1839)	+	+			
	Yoldiella antarctica (Thiele, 1912)			+	+	
	Yoldiella ecaudata (Pelseneer, 1903)	+		+		+
	Yoldiella oblonga (Pelseneer, 1903)			+		
	Yoldiella profundorum (Melvill & Standen, 1912)		+	+		+
	Yoldiella sabrina (Hedley, 1916)			+		
	Yoldiella valettei (Lamy, 1906)	+	+			
Malletiidae	*Malletia* sp.			+		
Siliculidae	*Silicula rouchi* Lamy, 1910	+				
Arcida						
Arcidae	*Bathyarca sinuata* Pelseneer, 1903			+		+
Limopsidae	*Limopsis knudseni* Dell, 1990			+		
	Limopsis lilliei Smith, 1915	+	+			
	Limopsis longipilosa Pelseneer, 1903			+		+
	Limopsis marionensis Smith, 1885	+		+		
	Limposis scotiana Dell, 1964	+	+			
Philobryidae	*Adacnarca limopsoides* (Thiele, 1912)	+				
	Adacnarca nitens Pelseneer, 1903	+	+	+	+	
	Lissarca notorcadensis Melvill & Standen, 1907	+	+			
	Philobrya sublaevis (Pelseneer, 1903)	+	+		+	
	Philobrya wandelensis Lamy, 1906	+				
Mytilida						
Mytilidae	*Dacrydium albidum* Pelseneer, 1903			+		
Limida						
Limidae	*Limatula hodgsoni* (Smith, 1907)	+	+	+		
	Limatula simillima Thiele, 1912			+		

Table III. Continued

Class to Family	Species	1	2	3	4	5
Ostreida						
Pectinidae	*Pectinidae* sp.			+		
	Adamussium colbecki (Smith, 1902)			+	+	+
	Hyalopecten pudicus (Smith, 1885)			+		
Propeamussiidae	*Cyclochlamys pteriola* (Melvill & Standen, 1907)			+		
	Cyclochlamys cf. *notalis* (Thiele, 1912)			+		
Venerida						
Thyasiridae	*Thyasira bongraini* (Lamy, 1910)		+		+	
	Thyasira cf. *dearborni* Nicol, 1965	+	+			
	Thyasira debilis (Thiele, 1912)	+	+	+	+	
	Thyasira falklandica (Smith, 1885)	+				
Carditidae	*Cyclocardia astartoides* (Martens, 1878)	+	+	+		+
Galeommatoidea	*Galeommatoidea* sp.			+		
	Waldo parasiticus (Dall, 1876)	+				
Galeommatidae	*Montacuta ? nimrodiana* (Hedley, 1911)	+				
	Mysella antarctica (Smith, 1907)	+				
	Mysella gibbosa (Thiele, 1912)			+		
	Mysella sp.		+			
	Pseudokellya cardiformis (Smith, 1885)	+	+			
Cyamiidae	*Cyamiocardium crassilabrum* Dell, 1964	+				
	Cyamiocardium denticulatum (Smith, 1907)	+	+		+	+
	Cyamiomactra laminifera (Lamy, 1906)	+			+	
Pholadomyida						
Lyonsiidae	*Lyonsia arcaeformis* Martens, 1885	+				
Laternulidae	*Laternula elliptica* (King & Broderip, 1831)	+			+	
Thraciidae	*Thracia meridionalis* Smith, 1885	+	+			
Cuspidariidae	*Cuspidaria infelix* Thiele, 1912	+	+	+	+	+
	Cuspidaria minima (Egorova, 1993)				+	
	Myonera fragilissima (Smith, 1885)			+		

recorded for the area or gamma diversity and $\bar{\alpha}$ is the average number of species per individual site or the average alpha diversity in the given area. The Bray-Curtis similarity coefficient (Clarke & Warwick 1994) was applied to the square root transformed data and to the presence/absence data to obtain similarity matrices using the PRIMER package (Clarke & Gorley 2005). The similarity between all pairwise permutations of sites was also used as measure of beta diversity (see Ellingsen & Gray 2002).

Gamma diversity was measured as species richness in five large areas (SR_L) previously defined statistically by Linse *et al.* (2006) and Clarke *et al.* (2007). These five areas together constituted the largest scale studied (SR_T). To investigate the problem of variability in sampling effort in more detail, gamma diversity for each area was plotted as a function of the number of samples following Clarke & Lidgard (2000).

The Kruskal-Wallis test was used to determine whether there were significant differences of alpha diversity measures among the five large zones in the study area.

Geographic distance (km) and depth distance (m) were computed between all pairwise combinations of sites. A Partial Mantel test (Anderson & Legendre 1999) was used to test the hypothesis that diversity clines correlate more with depth differences than with horizontal separation. The Partial Mantel test is a test for three matrices which estimate the correlation between matrices A (Bray-Curtis similarity matrix) and B (depth distance), while controlling the effect of a third matrix C (geographic distance) in order to remove spurious correlations (Anderson & Legendre 1999). The significance of the partial correlation coefficient was tested by permutations of the residuals (10 000 randomizations) of a null model, in which the independent variable of interest (i.e. depth differences or horizontal distance) was held constant. The statistical software package Zt, developed by Bonnet & Van de Peer (2002) was used for the analysis. In addition, the relationships between faunal patterns, using the Bray-Curtis similarity matrix, and latitude, longitude and depth (matrices computed using normalized Euclidean distance), were examined using the BIO-ENV procedure (Clarke & Ainsworth 1993).

Results

Diversity

Alpha diversity (sample species richness, SR_S) at 54 sites was highly variable, ranging from 0–23 mollusc species (Fig. 2). Mean alpha diversity ($SR_{\bar{S}}$) over the five large
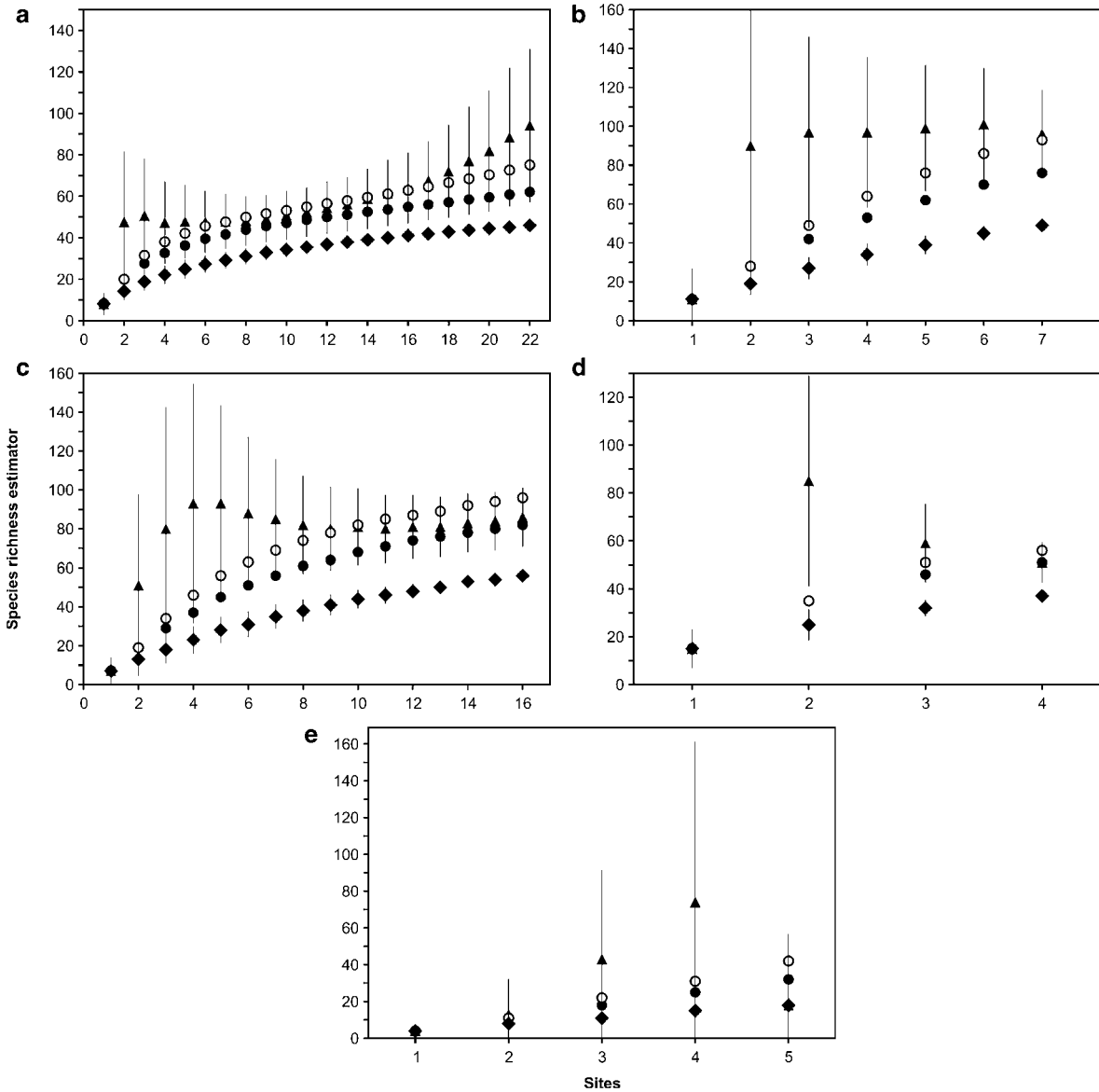
Fig. 3. Estimator of species richness for **a.** South Shetlands Islands, **b.** western Antarctic Peninsula, **c.** Bellingshausen Sea, **d.** Peter I Island, and **e.** Eights Coast. S_{obs} = solid rhombus, Chao2 = solid triangles, Jacknife1 = solid circles, and Jacknife2 = open circles. SD bars are indicated for S_{obs} and Chao2.

areas studied was the highest at Peter I Island, where the range was 6–23 species per site (Table II), followed by the western Antarctic Peninsula, whereas the lowest value was found at the Eights Coast (Fig. 2). There was no clear evidence of a relationship between $SR_{\overline{S}}$ and latitude (Table II). The western Antarctic Peninsula accounted for the highest values of taxonomic diversity (Δ) and taxonomic distinctness (Δ^*) (Table II), whereas the lowest values of taxonomic diversity and taxonomic distinctness were found in the Bellingshausen Sea. Whittaker's beta diversity (β_W) varied between 1.4 at Peter I Island, and 7.2 in the Bellingshausen Sea (Table II). The mean value of Bray-Curtis similarity was 9.34, with the highest values ranging from 70% to 63%

only between sites of the South Shetland Islands. The lowest values of similarity (4%) were between sites at Peter I Island, and one site located at Peter I Island and another one in the Bellingshausen Sea.

The total number of species (gamma diversity) observed in the 54 sites was 134 (SR_T, Table II). Gamma diversity in large areas (SR_L) was highly variable, ranging from 18 species at the Eights Coast to 56 in the Bellingshausen Sea (Tables II & III).

None of the species richness estimators stabilized towards asymptotic values in any area (Fig. 3). The highest value (mean ± SD) of the Chao2 estimator (84 ± 33) was found in western Antarctic Peninsula (Fig. 3b), whereas
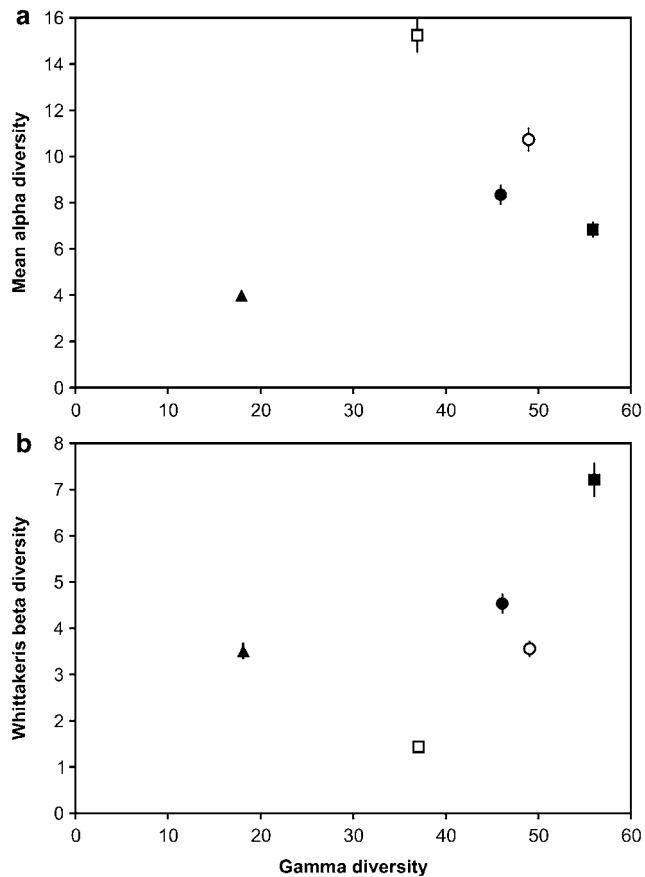
Fig. 4. Relations between gamma diversity (SR_L, species richness at large areas) and **a.** mean alpha diversity ($SR_{\bar{S}}$), and **b.** Whittaker's beta diversity ($\beta_W = (SR_L/SR_{\bar{S}}) - 1$). Bars indicate ± 95% confidence intervals. Solid circle = South Shetlands Islands, open circle = western Antarctic Peninsula, solid square = Bellingshausen Sea, open square = Peter I Island, solid triangle = Eights Coast.

Fig. 5. a. Gamma diversity pooled by the five studied areas, as a function of the number of samples in each area. **b.** Residuals around a fitted least squares regression of gamma diversity and sampling effort, both variables logarithmically transformed, plotted as a function of area. Solid circle = South Shetlands Islands, open circle = western Antarctic Peninsula, solid square = Bellingshausen Sea, open square = Peter I Island, solid triangle = Eights Coast.

the highest values (mean ± SD) of S_{obs}, Jacknife1 and Jacknife2 estimators were found in the Bellingshausen Sea (37 ± 15, 56 ± 23 and 67 ± 28, respectively; Fig. 3c). The lowest values of all indicators, S_{obs}, Chao2, Jacknife1 and Jacknife2, were observed at Eights Coast, with values of 11 ± 6, 30 ± 28, 18 ± 11 and 22 ± 15, respectively (Fig. 3e).

There was no significant relationship between gamma diversity in large areas (SR_L) and mean alpha diversity ($SR_{\bar{S}}$) ($r^2 = 0.073$, $p = 0.66$), although the southernmost area (Eights Coast) showed the lowest values for both diversity indices (Fig. 4a). Similarly, the relationship between gamma diversity and Whittaker's beta diversity (($SR_L / SR_{\bar{S}}$) - 1) was not significant ($r^2 = 0.316$, $P = 0.32$) and the lowest value of gamma diversity did not match the lowest value of beta diversity (Fig. 4b).

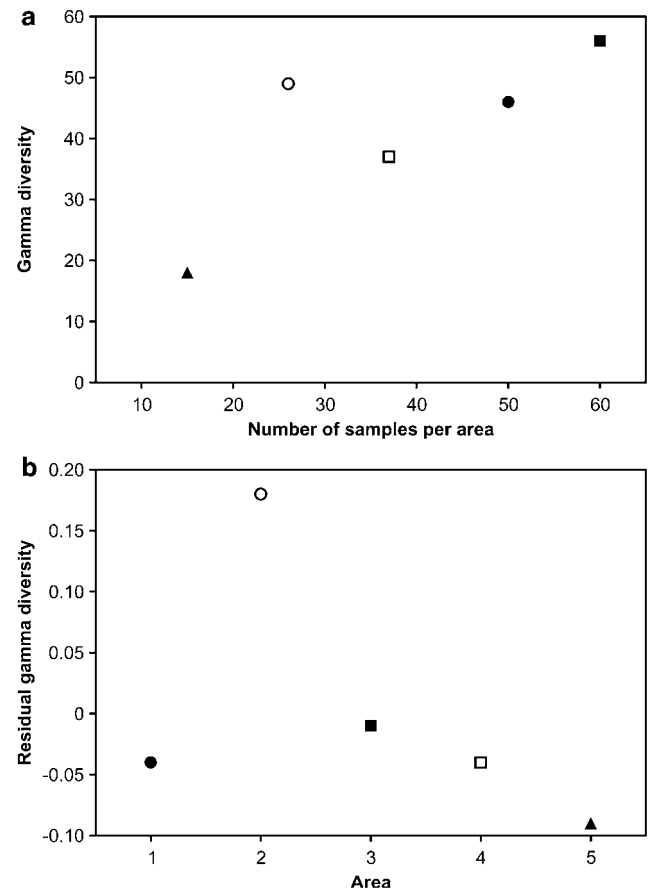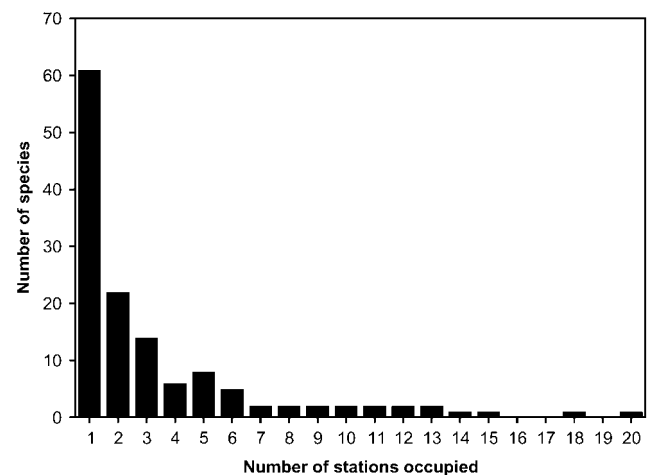The scatterplot showing the relationship between number of samples per area and gamma diversity indicated clearly

Fig. 6. Distribution of species range sizes. Range size is the number of sites occupied by a species out of a total of 54 sites.
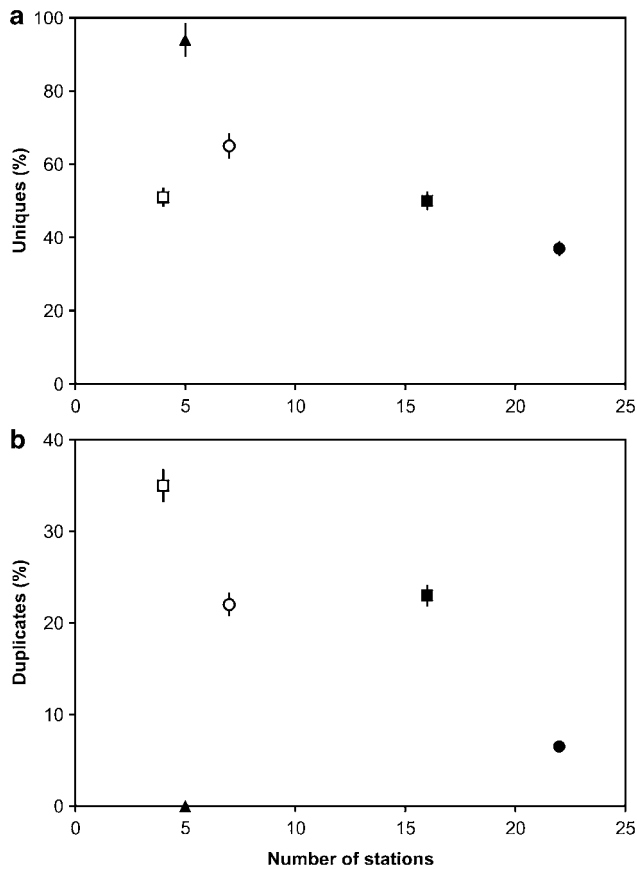
Fig. 7. Relations between number of sites and 'rare' species in each zone, **a.** uniques, species restricted to a single site, **b.** duplicates, species occurring at exactly two sites. Solid circle = South Shetlands Islands, open circle = western Antarctic Peninsula, solid square = Bellingshausen Sea, open square = Peter I Island, solid triangle = Eights Coast.
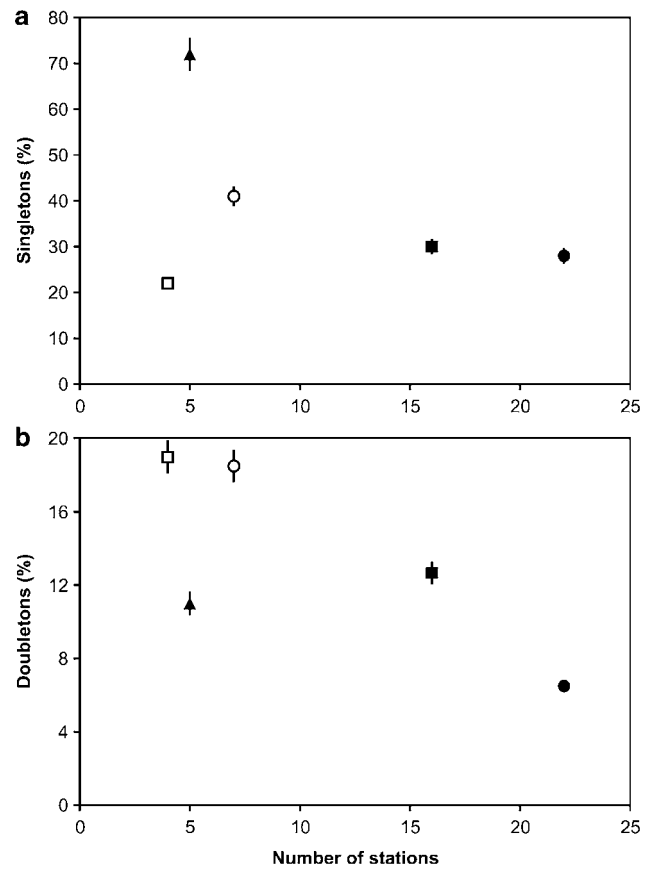

Fig. 8. Relations between number of sites and 'rare' species in each zone, **a.** singletons, species represented by a single individual, **b.** doubletons, species represented by only two individuals. Solid circle = South Shetlands Islands, open circle = western Antarctic Peninsula, solid square = Bellingshausen Sea, open square = Peter I Island, solid triangle = Eights Coast.

that calculated values of gamma diversity were not primarily a function of sampling intensity ($r^2 = 0.613$, $P = 0.12$, Fig. 5a). The residuals of the logarithmic transformation of both variables were negative, except for the western Antarctic Peninsula (Fig. 5b).

Distribution and spatial patterns

No species were present at all sampling sites (Fig. 6), although two species, *Neobuccinum eatoni* and *Cuspidaria infelix*, occurred in the all five areas, and five species, *Chlanidota signeyana*, *Adacnarca nitens*, *Thyasira debilis*, *Cyclocardia astartoides* and *Cyamiocardium denticulatum*, occurred in four areas (Table III). The most widespread

species was the tiny bivalve *Thyasira debilis* (20 sites), followed by the bivalves *Thyasira* cf. *dearborni* (18 sites), *Yoldia eightsi* (15 sites), *Nuculana inaequisculpta* (14 sites), *Cyclocardia astartoides*, *Cyamiocardium denticulatum* (13 sites), and *Cuspidaria infelix*, and the gastropods *Neobuccinum eatoni* (12 sites), *Chlanidota signeyana* and *Harpovoluta charcoti* (11 sites). The most abundant species were the bivalves *Cyamiocardium denticulatum* (654 individuals), *Adacnarca nitens* (446 individuals), *Thyasira debilis* (380 individuals), *Thyasira* cf. *dearborni* (227 individuals), and *Yoldia eightsi* (200 individuals). Conversely, 61 species, or 45.5% of the total number of species, were restricted to a single site (uniques, e.g.

Table IV. Variation of the different alpha diversity measures among the five large areas. Significant values are in bold.

Kruskal-Wallis test	Species richness	Number of genera	Number of families	Taxonomic distinctness	Taxonomic diversity
H	9.574	9.847	9.564	2.723	5.861
P-value	**0.048**	**0.043**	**0.048**	0.605	0.210

Table V. Results of partial Mantel test investigating the relationships between Bray-Curtis similarity and horizontal distance (HOR) and depth (DEPTH) in the study area. The Bray-Curtis similarity was applied to abundance data (BC_{ab}) and to presence/absence data ($BC_{p/a}$). Significant values are in bold.

Mantel test	r	P-value
(BC_{ab} x HOR).DEPTH	0.011	0.571
(BC_{ab} x DEPTH).HOR	**-0.24**	**0.002**
($BC_{p/a}$ x HOR).DEPTH	0.022	0.239
($BC_{p/a}$ x DEPTH).HOR	**-0.38**	**0.001**

Table VI. Combination of environmental variables (longitude, latitude and depth), taken K at a time; bold indicates best combination overall.

Number of variables	Correlation (pw)	Best variable combination
1	0.399	Depth
1	0.494	Longitude
1	0.511	Latitude
2	0.504	Latitude, longitude
2	**0.540**	**Latitude, depth**
2	0.513	Longitude, depth
3	0.537	Latitude, longitude, depth

Cuspidaria minima, *Cyclochlamys pteriola*, *Acteon antarcticus*, and *Solariella antarctica*, and 22 species (16.4%) were restricted to only two sites (Fig. 6) (duplicates, e.g. *Cyamiomactra laminifera*, *Limatula simillima*, *Typhlodaphne innocentia* and *Marseniopsis mollis*). Thirty one per cent (41 species) of the total number of species were represented by a single individual (singletons, e.g. *Trophon echinolamellatus*, *Belaturricula ergata*, *Hyalopecten pudicus*, and *Prosipho chordatus*), and 10% (14 species) were represented by two individuals (Table II) (doubletons, e.g. *Torellia mirabilis*, *Conorbela antarctica*, *Tritoniella belli*). At the scale of the large areas, the South Shetland Islands was the zone with the smallest percentage of uniques (37%) and the Eights Coast had the greatest (94%), whereas Peter I Island had the smallest percentage of singletons (22%) and Eights Coast the greatest (72%) (Table II).

There was no significant relationship between sampling intensity, measured as number of sites in large areas, and the relative quantity of 'rare' species measured as unique species ($r^2 = 0.469$, $P = 0.20$, Fig. 7a) and duplicate species ($r^2 = 0.087$, $P = 0.63$, Fig. 7b). The most sampled area (i.e. South Shetland) had the smallest number of uniques and a small number of duplicates, (Fig. 7a & b), and the least sampled area (i.e. Peter I Island) had the largest number of duplicates (Fig. 7b). Similarly, singletons and doubletons were not significantly related to sampling intensity ($r^2 = 0.154$, $P = 0.51$, Fig. 8a; $r^2 = 0.582$, $P = 0.13$, Fig. 8b), with the smallest number at the most sampled areas (i.e. South Shetland Islands and Bellingshausen Sea) and the largest number at the least sampled areas (i.e. Eights Coast and Peter I Island).

Some measures of alpha diversity varied significantly between areas. In particular, species richness, number of genera and families did show significant variation among areas, whereas taxonomic diversity and taxonomic distinctness did not show any variation (Table IV).

Similarity between sites (beta diversity) and relationships to horizontal and vertical distance

The Partial Mantel test between beta-diversity (measured as Bray-Curtis similarity) and depth differences, while controlling for the effect for horizontal distance, showed a significant negative correlation (Table V). In contrast, the correlation between beta diversity and horizontal separation, when the effect for depth differences was controlled, was not significant. Depth, therefore, had an effect on the beta diversity, although this effect was quite weak. These results were also corroborated by BIO-ENV analysis (Table VI).

Discussion

Besides Peracarida, the most speciose macrofaunal taxa in the Southern Ocean are Polychaeta and Mollusca (Brandt *et al.* 2007). There is, however, very little information on the patterns of diversity of these two groups at both small and large scales. Gastropods are the dominant group in terms of species number, followed by bivalves (Linse *et al.* 2006, Clarke *et al.* 2007). Furthermore, molluscs exhibit very different levels of richness between areas within the Southern Ocean (Linse *et al.* 2006).

In this study, we have to consider two main constraints. First, different gear was used so the datasets include organisms collected from the near-bottom water column, from the sediment and from within the sediment. Second, the spatial scales differed from those used in other studies in the Southern Ocean. Therefore, any comparison of biodiversity patterns with other studies is complicated, but at the same time, necessary due to the general lack of information in this particular geographic area.

Alpha, beta and gamma diversity

Although there were differences in alpha diversity between areas for species richness, number of genera and number of families, these differences were marginally significant, (Table IV). Alpha diversity showed high variability within an area and, therefore, more extensive sampling is necessary to identify regional differences and to evaluate whether alpha diversity may be impacted more by local (e.g. competition and predation) rather than by regional processes.

Values of beta diversity were high and varied among areas. The beta diversity for the whole area was high (15.2) in comparison to that reported by Ellingsen *et al.* (2007) who examined Whittaker's beta diversity for bivalves in an extensive Atlantic sector of the deep Southern Ocean. Nevertheless, the mean value of Bray-Curtis similarity (9.34%) for the whole study area could be considered low

Table VII. Species richness in large areas (diversity measured as SR_L, gamma diversity) reported for molluscs in other areas from the Southern Ocean. Cattaneo-Vietti *et al.* (2000) for Gastropoda and Bivalvia, Schiaparelli *et al.* (2006) for Polyplacophora, Gastropoda, Bivalvia and Scaphopoda and Ellingsen *et al.* (2007) for Bivalvia.

Area	Sites	Depth (m)	SR_L	Latitude (°S)	Longitude	Source
Ross	100	25–1100	56	74.5–74.9	163.9–166.2°E	Cattaneo-Vietti *et al.* (2000)
Balleny	26	70–1389	26	65.4–67.6	160.8–165.3°E	Schiaparelli *et al.* (2006)
North Ross	108	65–930	115	71.1–72.3	170.1–173.3°E	Schiaparelli *et al.* (2006)
Middle Ross	113	25–1100	36	74.6–75.5	163.9–167.3°E	Schiaparelli *et al.* (2006)
Scotia and Peninsula	29	742–6348	46	58.2–74.6	22.1–60.8°W	Ellingsen *et al.* (2007)

compared to other studies where smaller areas of study were used (e.g. Cattaneo-Vietti *et al.* 2000, Arnaud *et al.* 2001).

Gamma diversity had comparable values to those reported for different molluscs' taxa in other areas from the Southern Ocean (e.g. Cattaneo-Vietti *et al.* 2000, Schiaparelli *et al.* 2006, Ellingsen *et al.* 2007; Table VII). Nevertheless, our area of study presented the least number of sampled sites as compared to those areas previously reported. For example, the north Ross Sea had the highest value of gamma diversity (Schiaparelli *et al.* 2006) among all compared studies (Table VII), but that survey used a more intensive sampling effort, i.e. 108 sites in an area of 1° latitude x 3° longitude.

The negative values of the residuals of the fitted least-squares regression for the logarithmic transformed number of samples against gamma diversity in each area, suggested a relatively low regional diversity for that sampling effort (Clarke & Lidgard 2000). However, the western Antarctic Peninsula was the unique area with a positive residual value (see Fig. 5b), suggesting a relatively high regional diversity for that sampling effort. There was not a significant strong relationship between numbers of samples per area and gamma diversity, which varied among areas. For example, Eights Coast, the least sampled area, had the lowest value of gamma diversity, whereas the Bellingshausen Sea, which was also poorly sampled, had the highest value.

These results suggest that variation in gamma diversity could be affected not only by different sampling coverage among areas, but also by other factors acting at large scale. In particular, factors such as speciation, evolutionary adaptation and climate are generally regarded as having primacy at large scales (Clarke & Lidgard 2000).

In general, the values of diversity found in this study agree with recent studies in the Southern Ocean that have found high species richness at both small and large scales (see review in Brandt *et al.* 2007). A large number of molluscs are also typical for other deep sea areas (e.g. Rex *et al.* 1997, Olabarria 2005). Nevertheless, it is known that processes driving patterns of diversity differ at different scales, and therefore it is difficult to compare data from different areas. Factors such as the age of the environment and the evolutionary time available for species to develop in an area have been invoked as main drivers of the high

species richness found in the Southern Ocean compared to the northern polar areas (Webb & Gaston 2000).

Another striking result in this study was the lack of correlation between alpha and gamma diversity. In this context, the regional enrichment model suggests that local diversity represents a balance between local extinction and colonization from the regional species pool (see Rex *et al.* 1997). Thus, a larger regional pool of colonists would, on average, support higher local diversity. Under an adequate sampling coverage, this lack of relationship in the study area might indicate that local assemblages are not yet saturated. Unfortunately, some areas were under-sampled and, therefore, this fact precludes any meaningful examination of this question for molluscan assemblages.

Spatial patterns

The pattern of distributions of species' range sizes are typically strongly right-skewed, agreeing with that previously reported in the Antarctic deep sea (Ellingsen *et al.* 2007). The finding that the most species-rich areas did not contain significantly more rare species does not always hold true in marine systems (Ellingsen 2001). There was a high percentage of 'rare' species measured as uniques, duplicates, singletons and doubletons. In particular, more than 21.6% of the species were represented by single individuals and more than 37% occurred in only one site. The large numbers of rare species resulted in low levels of faunal similarities between sites (i.e. high beta diversity). A great proportion of rare species is quite common in the Southern Ocean (Brandt *et al.* 2005, Ellingsen *et al.* 2007, Clarke *et al.* 2007). Acceptance of the lognormal distribution of individuals among species implies that most species are rare, occurring at low abundances per sample unit. One possible explanation is that only very few samples (i.e. low intensity of sampling) of the regional diversity are taken into account. If sampling intensity increases, more 'rare' species most likely to be found, and faunal similarity between sites will decrease (Ellingsen *et al.* 2007). In this study, there was no relationship between sampling intensity and the proportion of 'rare' species, suggesting that the number of rare species could respond to other factors apart from sampling intensity (e.g. Bellingshausen Sea or Eights Coast were poorly sampled

areas). It has been suggested for molluscs that rare species in deep sea samples is the result of source-sink dynamics, in which many abyssal populations are maintained by immigration from the bathyal zone (Rex *et al*. 2005). Isolation and scanty information for some areas (i.e. Eight Coast and Peter I Island) may also account for a great proportions of rare species.

Variation of beta diversity with vertical and horizontal distance

Studies of biodiversity have provided abundant evidence that large-scale processes strongly affect both regional, landscape and local diversity at all small scales (Ricklefs & Schluter 1993). Furthermore, different taxa are affected by different processes suggesting a causal balance between history and modern ecology.

In our study, the Bray-Curtis similarity between all combinations of sites was only related to depth, although this relationship was quite weak. While this seems to match current paradigms, conflicting patterns of variation in diversity with depth have been observed, depending on whether studies cover temperate and tropical or Antarctic areas. For example, gastropods displayed a parabolic relationship whereby diversity increased with depth until 2000–3000 m then declined at deeper sites (Rex 1981). Nematodes from temperate and tropical areas exhibited a non-linear increase in diversity with depth through the bathyal zone, with a decrease at deeper sites (Boucher & Lambshead 1995). Previous studies in the Southern Ocean have reported contrasting results regarding diversity patterns of diverse taxonomic groups (e.g. Brandt *et al*. 2005, Ellingsen *et al*. 2007). For example, isopods displayed higher species richness in the middle depth range and lower in the shallower and deeper parts of the area (Brandt *et al*. 2005). In contrast, the number of polychaete species showed a negative relationship to depth, whereas bivalves showed no clear relationship (Linse 2004, Ellingsen *et al*. 2007). None of these studies found a significant relationship between patterns of diversity and horizontal distance (i.e. latitude and/or longitude). In contrast, Linse *et al*. (2006) found that molluscs exhibited geographic variation in patterns of diversity in the Southern Ocean with large variation between distinct sub-regions (i.e. 1000 km scale).

One possible explanation for the lack of a horizontal gradient in our study might be that the scale of the study area was too small. Large-scale trends in benthic diversity may only be evident over very large latitudinal spans (Gaston 2000). Alternatively, patterns of molluscs' diversity in the Southern Ocean might be more affected by processes associated with depth rather than horizontal distance. Depth-related gradients have been attributed to differences in productivity, competition, predation (Rex 1981), sediment heterogeneity (Etter & Grassle 1992), and evolutionary factors (Gage 2004). Nevertheless, the highly inadequate sampling away from the continental shelves makes the distinguishing of any depth clines in the Southern Ocean very difficult (see Clarke *et al*. 2007). Therefore, any conclusion regarding depth clines should be interpreted with caution since the major bulk of data in this work come from the continental shelf.

Acknowledgements

References

ALDEA, C., OLABARRIA, C. & TRONCOSO, J.S. 2008. Bathymetric zonation and diversity gradient of gastropods and bivalves in West Antarctica from the South Shetland Islands to the Bellingshausen Sea. *Deep-Sea Research I*, **55**, 350–368.

ANDERSON, M.J. & LEGENDRE, P. 1999. An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *Journal of Statistical Computation and Simulation*, **62**, 271–303.

ARNAUD, P.M., TRONCOSO, J.S. & RAMOS, A. 2001. Species diversity and assemblages of macrobenthic Mollusca from the South Shetland Islands and Bransfield Strait (Antarctica). *Polar Biology*, **24**, 105–112.

BONNET, E. & VAN DE PEER, Y. 2002. Zt: a software tool for simple and partial Mantel tests. *Journal of Statistical Software*, **7**(10), 1–12.

BOUCHER, G. & LAMBSHEAD, P.J.D. 1995. Ecological diversity of marine nematodes in samples from temperate, tropical, and deep sea regions. *Conservation Biology*, **9**, 1594–1604.

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 II*, **51**, 1457–1919.

BRANDT, A., ELLINGSEN, K.E., BRIX, S., BRÖKELAND, W. & MALYUTINA, M. 2005. Southern Ocean deep-sea isopod species richness (Crustacea, Malacostraca): influences of depth, latitude and longitude. *Polar Biology*, **28**, 284–289.

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*, **B362**, 39–66.

BROWN, J.H. 1984. On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.

CATTANEO-VIETTI, R., CHIANTORE, M., SCHIAPARELLI, S. & ALBERTELLI, G. 2000. Shallow- and deep-water mollusc distribution at Terra Nova Bay (Ross Sea, Antarctica). *Polar Biology*, **23**, 173–182.

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.

CLARKE, A., GRIFFITHS, H.J., LINSE, K., BARNES, D.K.A. & CRAME, J.A. 2007. How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographic patterns in Southern Ocean gastropod and bivalve molluscs. *Diversity and Distributions*, **13**, 620–632.

CLARKE, K.R. & AINSWORTH, M. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, **92**, 205–219.

CLARKE, K.R. & GORLEY, R. 2005. *Primer-E version 6.0*. Plymouth: NERC, Plymouth Marine Laboratory, 91 pp.

CLARKE, K.R. & WARWICK, R.M. 1994. *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth: Plymouth Marine Laboratory, 144 pp.

COLWELL, R.K. 1997. *EstimateS: statistical estimation of species richness and shared species from samples*, version 5. User's Guide and Application. University of Connecticut Storrs, CT: Department of Ecology and Evolutionary Biology. http://viceroy.eeb.uconn.edu/estimates.

COLWELL, R.K. & CODDINGTON, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London*, **B345**, 101–118.

ELLINGSEN, K.E. 2001. Biodiversity of a continental shelf soft-sediment macrobenthos community. *Marine Ecology Progress Series*, **218**, 1–15.

ELLINGSEN, K.E. & GRAY, J.S. 2002. Spatial patterns of benthic diversity: is there a latitudinal gradient along the Norwegian continental shelf? *Journal of Animal Ecology*, **71**, 373–389.

ELLINGSEN, K.E., BRANDT, A., EBBE, B. & LINSE, K. 2007. Diversity and species distribution of polychaetes, isopods and bivalves in the Atlantic sector of the deep Southern Ocean. *Polar Biology*, **30**, 1265–1273.

ETTER, R.J. & GRASSLE, J.F. 1992. Patterns of species diversity in the deep sea as a function of sediment particle size. *Nature*, **360**, 576–578.

GAGE, J.D. 2004. Diversity in the deep-sea benthic macrofauna: the importance of local ecology, the large-scale, history and the Antarctic. *Deep-Sea Research II*, **51**, 1689–1709.

GASTON, K.J. 2000. Global patterns in biodiversity. *Nature*, **405**, 220–227.

GORDON, A.L. & NOWLIN, W.D. 1978. The basin waters of the Bransfield Strait. *Journal of Physical Oceanography*, **8**, 258–264.

GRASSLE, J.G. & MACIOLEK, N.J. 1992. Deep-sea species richness: regional and local diversity estimated from quantitative bottom samples. *American Naturalist*, **139**, 313–341.

GRAY, J.S. 1997. Marine biodiversity: patterns, threats and conservation needs. *Biodiversity and Conservation*, **6**, 153–175.

GRAY, J.S. 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *Journal of Experimental Marine Biology and Ecology*, **250**, 23–49.

GUTT, J. & PIEPENBURG, D. 2003. Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Marine Ecology Progress Series*, **253**, 77–83.

HARPER, J.L. & HAWKSWORTH, D.L. 1994. Biodiversity: measurement and estimation. *Philosophical Transactions of the Royal Society of London*, **B345**, 5–12.

HUSTON, M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge: Cambridge University Press, 702 pp.

LINSE, K. 2004. Scotia Arc deep-water bivalves: composition, distribution and relationship to the Antarctic shelf fauna. *Deep-Sea Research II*, **51**, 1827–1837.

LINSE, K., GRIFFITHS, H.J., BARNES, D.K.A. & CLARKE, A. 2006. Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. *Deep-Sea Research II*, **53**, 985–1008.

OLABARRIA, C. 2005. Patterns of bathymetric zonation of bivalves in the Porcupine Seabight and adjacent abyssal plain, NE Atlantic. *Deep-Sea Research I*, **52**, 15–31.

REX, M.A. 1981. Community structure in the deep-sea benthos. *Annual Review of Ecology and Systematics*, **12**, 331–353.

REX, M.A., ETTER, R.J. & STUART, C.T. 1997. Large-scale patterns of diversity in the deep-sea benthos. *In* ORMOND, R.F.G., GAGE, J.G., ANGEL, M.V., *eds. Marine biodiversity: patterns and processes*. Cambridge: Cambridge University Press, 94–121.

REX, M.A., STUART, C.T. & COYNE, G. 2000. Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proceedings of the National Academy of Sciences of the United States*, **97**, 4082–4085.

REX, M.A., McCLAIN, C.R., JOHNSON, N.A., ETTER, R.J., ALLEN, J.A., BOUCHET, P. & WARÉN, A. 2005. A source-sink hypothesis for abyssal biodiversity. *American Naturalist*, **165**, 163–178.

RICKLEFS, R.E. & SCHLUTER, D. 1993. *Species diversity in ecological communities: historical and geographical perspectives*. Chicago, IL: Chicago University Press, 414 pp.

SCHIAPARELLI, S., LÖRZ, A. & CATTANEO-VIETTI, R. 2006. Diversity and distribution of mollusc assemblages on the Victoria Land coast and the Balleny Islands, Ross Sea, Antarctica. *Antarctic Science*, **18**, 615–631.

SHIN, P.K.S. & ELLINGSEN, K.E. 2004. Spatial patterns of soft-sediment benthic diversity in subtropical Hong Kong waters. *Marine Ecology Progress Series*, **276**, 25–35.

STUART, C.T., REX, M.A. & ETTER, R.J. 2003. Large-scale spatial and temporal patterns of deep-sea benthic species diversity. *In* TYLER, P.A., *ed. Ecosystems of the deep oceans, 28. Ecosystems of the world*. Amsterdam: Elsevier, 582 pp.

TRONCOSO, J.S. & ALDEA, C. 2008. Macrobenthic mollusc assemblages and diversity in the West Antarctica from the South Shetland Islands to the Bellingshausen Sea. *Polar Biology*, **31**, 1253–1265.

UNDERWOOD, A.J., CHAPMAN, M.G. & CONNELL, S.D. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology*, **250**, 97–115.

WARWICK, R.M. & CLARKE, K.R. 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series*, **129**, 301–305.

WEBB, S.L. & GASTON, K.J. 2000. Geographic range size and evolutionary age in birds. *Proceedings of the Royal Society*, **B267**, 1843–1850.

WHITTAKER, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.