



Bathymetric zonation and diversity gradient of gastropods and bivalves in West Antarctica from the South Shetland Islands to the Bellingshausen Sea

Cristian Aldea^{a,b,*}, Celia Olabarria^a, Jesús S. Troncoso^a

^a*Departamento de Ecología y Biología Animal, Facultad de Ciencias del Mar, Universidad de Vigo, Campus Lagoas Marcosende, 36310, Spain*

^b*Fundación Centro de Estudios del Cuaternario de Fuego-Patagonia y Antártica (CEQUA), Punta Arenas, Chile*

Received 25 June 2007; received in revised form 30 November 2007; accepted 12 December 2007

Abstract

Depth-related zonation and diversity patterns are important topics in the study of deep-sea fauna, at both species and assemblage levels. These patterns may be attributed to complex and combined physical and/or biological factors. The lack of information about the West Antarctic deep sea is an important handicap to understanding the global-scale benthic diversity patterns. Detailed studies of the bathymetric distributions and diversity of deep-sea species in the Antarctic are needed to elucidate the factors contributing to global-scale benthic patterns. This study, based on a large data set, examined the bathymetric distribution, patterns of zonation and diversity–depth trends of gastropods and bivalves in West Antarctica, from the South Shetland Islands to the Bellingshausen Sea, a very poorly known area. A total of 647 individuals of gastropods belonging to 82 species and a total of 2934 individuals of bivalves belonging to 52 species were collected. Most gastropods showed discrete depth distributions, whereas most bivalves showed broader depth ranges. Replacement of species with depth was more gradual for bivalves than gastropods. Nevertheless, three bathymetric boundaries could be recognized: (1) a continental shelf zone from 0 to 400 m with a gradual rate of succession, (2) an upper slope zone from 400 to 800 m and (3) a lower slope zone from 800 to 2000 m, extending to 3300 m for bivalves. Diversity patterns were complex for both groups with no significant trends with depth.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Bivalves; Gastropods; Zonation patterns; Diversity; Deep sea; West Antarctica; South Shetland Islands; Bellingshausen Sea

1. Introduction

Faunal depth zonation and the factors driving the distribution and diversity of species along environmental gradients are topics of a number of studies in aquatic systems. Depth-related patterns (e.g., depth–diversity relationships, faunal replacement with depth) are an important topics in deep-sea faunal studies, at both species and assemblages

*Corresponding author at: Departamento de Ecología y Biología Animal, Facultad de Ciencias del Mar, Universidad de Vigo, Campus Lagoas Marcosende, 36310, Spain.
Tel.: +34 986 812621; fax: +34 986 812556.

E-mail addresses: cristian-aldea@uvigo.es (C. Aldea), colabarria@uvigo.es (C. Olabarria), troncoso@uvigo.es (J.S. Troncoso).

levels (e.g., Rex, 1973; Gage et al., 1985; Howell et al., 2002). Different faunal zones, defined as regions of lesser faunal change bounded by regions of greater faunal changes, have been proposed in the deep sea (e.g., Vinogradova et al., 1959; Rex, 1973; Gage et al., 1985). The causes of zonation have been related primarily to physical changes or biological interactions. For example, the tolerance to temperature or pressure (e.g., Haedrich et al., 1975; Young et al., 1996; Tyler et al., 2000; Carney, 2005), sediment type (Haedrich et al., 1975), or nutrient input (Rex, 1981; Carney, 2005) are some of the physical factors proposed to explain such patterns. Biological factors, such as larval dispersal, competition, predation and trophic level, may also play an important role (e.g., Rex, 1976; Cartes and Sardà, 1993; Young et al., 1997). For example, zonation appears to be more apparent at higher trophic levels, represented by taxa such as fish (Cartes and Carrassón, 2004) and crustaceans (Cartes et al., 2003), than at lower trophic levels, represented by taxa such as gastropods, polychaetes or bivalves (Rex, 1977; Paterson and Lamshead, 1995; Olabarria, 2005). In the deep sea, and within broad depth ranges, species may occur over wide or narrow depth bands. In both cases species show density peaks along their bathymetric distribution. Often, there are no clear reasons for these patterns (and the role of controlling factors is complex).

Depth–diversity relationships have been addressed by many studies in the deep sea (e.g., Rex, 1981; Grassle, 1989; Rex et al., 1997, 2006; Gage, 2004; McClain and Etter, 2005). Despite the plethora of studies, patterns of diversity and the causes determining such patterns remain unclear. Most studies show that local ecology is insufficient to explain the local coexistence of species (see Gage, 2004). Historical accumulation of species over time influenced by basin age, deep currents that form zoographic barriers, topographic boundaries, and water–mass structure are some of the possible causes of global diversity patterns in the deep sea (e.g., Menzies et al., 1973; Clarke and Crame, 1992; Allen and Sanders, 1996; Rex et al., 2005). In this context, the lack of data from the Antarctic deep sea is particularly an important limitation to understanding global-scale patterns of benthic diversity (Gage, 2004). Therefore, detailed studies of the bathymetric distribution and diversity of deep-sea species in the Antarctic region may help to elucidate the important factors contributing to global patterns (Brandt et al., 2007). The study of benthic

marine Antarctic fauna also provides a unique opportunity to distinguish the various factors that influence their evolutionary history (Hedgpeth, 1969).

Molluscs, particularly gastropods and bivalves, were among the earliest taxa used to investigate patterns of diversity. They provide an ideal test assemblage for testing many hypotheses about replacement of species with depth, gradients of diversity and correlated factors because they are one of the more diverse and abundant groups of macrobenthos in the deep sea (Gage and Tyler, 1991) and encompass a wide range of phylogenetic and trophic levels.

The early studies of the Southern Ocean marine faunas defined different subregions. A common feature is a latitudinal division into an Antarctic/high Antarctic zone, a subantarctic/low Antarctic zone, and a longitude division into East and West Antarctica (Powell, 1951; Hedgpeth, 1969, 1970). Although the West Antarctic region has been extensively sampled, the coverage is extremely patchy. Areas such as the South Shetland Islands and the western Antarctic Peninsula have been well sampled, whereas the Bellingshausen Sea still remains poorly sampled (Clarke et al., 2004b, 2007). Apart from many faunistic studies of benthic molluscs in West Antarctica (Gallardo, 1969, 1992; Lowry, 1975; Gallardo et al., 1977; Jażdżewski et al., 1986) and some studies on zonation patterns of diverse taxonomical groups (i.e., polychaetes, crustaceans, molluscs) in shallow waters (Zamorano, 1983; Nonato et al., 2000), few studies have dealt with molluscan assemblages in this area (e.g., Arnaud et al., 2001; Troncoso et al., 2007). On the other hand, several studies have been conducted in parts of the Weddell and Ross seas (e.g., Mühlenthal-Siegel, 1989; Hain, 1990; Arnaud and Hain, 1992; Russo and Gambi, 1994; Cattaneo-Vietti et al., 2000; Schiaparelli et al., 2006), while patterns of bivalves diversity in extensive Antarctic areas, such as the Scotia Arc, were reported (Linse, 2004). The present study, however, is the first to deal specifically with the bathymetric distribution and trends in the diversity of molluscs (gastropods and bivalves), from the shelf to lower slope, in an extensive area from the South Shetland Islands to the Bellingshausen Sea in West Antarctica. The particular hypotheses tested were that: (1) bivalve species are replaced at a more gradual rate with depth than gastropod species and (2) there is a parabolic pattern of diversity, as previously shown

for deep-sea molluscs and invertebrates elsewhere (e.g., Rex, 1981; Etter and Rex, 1990; Etter and Grassle, 1992). In addition, possible causes of these trends are considered.

2. Material and methods

2.1. Study area

The study area covers an extensive region about 2200 km long and 500 km wide from the South Shetland Islands to the Bellingshausen Sea and Thurston Island 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 towards the southwest for approximately 460 km to Low

Island. The Strait is occupied by the Bransfield trough, whose axial depth varies between 1100 m at the southwest margin and 2800 m just south of Elephant Island (Gordon and 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. Although the sea-floor topography of this region has not been described in great detail, there are indications that this area has an abrupt slope and maximum depths of about 4500 m (Nitsche et al., 2000). The region is characterized by a rough sea-floor morphology caused mainly by tectonic activity, as reflected in gravity and seismic data (Scheuer et al., 2006).

2.2. Sample collection

A total of 174 samples was collected at depths ranging from 45 to 3304 m during the BENTART

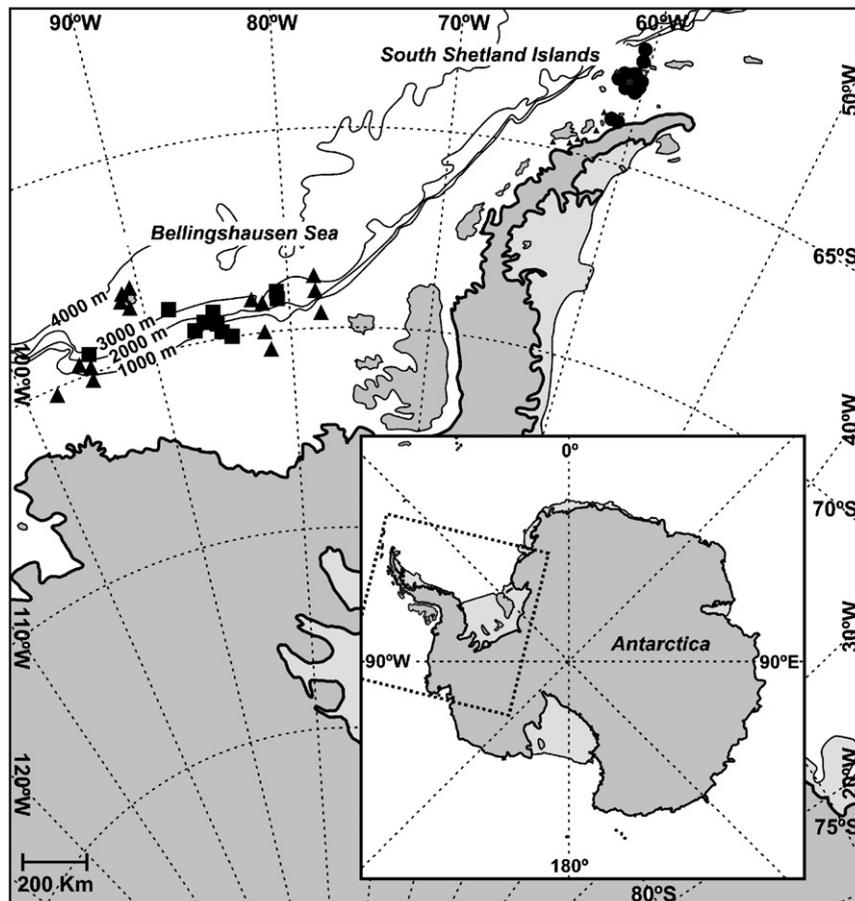


Fig. 1. Study area and location of stations of benthic samples from BENTART 1995 (black dots), 2003 (triangles) and 2006 (squares) cruises.

95, 03 and 06 cruises aboard RV *Hespérides* (Figs. 1 and 2). Samples were collected using different sampling gears, including box-corer (93 samples), Agassiz trawl (60 samples), epibenthic sledge (12 samples), rock dredge (6 samples) and Nassa trap (3 samples).

During the BENTART 95 cruise, from 16 January to 4 February 1995, comprehensive sampling was carried out on board RV *Hespérides*, extending the search and analysis of benthic assemblages to the South Shetland Islands/Bransfield Strait area. During the BENTART 03 (24 January to 3 March 2003) and BENTART 06 (2 January to 16 February 2006) cruises, intensive sampling was conducted from the West Antarctic Peninsula to the Bellingshausen Sea.

The BENTART box-corer is a quantitative gear with a maximum penetration of 60-cm and an

effective sampling area of 30×20 cm. It is designed to take undisturbed samples from the top of the seabed, and is suitable for almost every type of sediment. The Agassiz trawl, 2.01 m width, 1.12 m height and with a mesh size of 10.0 mm, does not provide an accurate measure of density although the collection of organisms of different size, particularly macrofauna. The epibenthic sledge is a semiquantitative gear having an opening-closing system, which is activated by contact with the sea-floor (preventing contamination by pelagic organisms from the water column), and with superimposed nets (0.5-mm mesh size; rectangular opening, 40×80 cm), which allow quantitative sampling of the motile fauna in three water layers, i.e., 10–50 cm (net 1), 55–95 cm (net 2) and 100–140 cm (net 3) above the sea-floor. The rock dredge is a robust gear, 0.8 m width and 0.3 m height, with a mesh size of 10.0 mm, designed to collect organisms from hard bottoms. The Nassa trap is designed to catch scavenger organisms.

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, a few were identified to genus or family level. Except for *Adamussium colbecki*, only individuals that were alive when collected were used in this study.

2.3. Data analysis

Gastropods and bivalves were treated separately, in order to compare their bathymetric and diversity patterns. To investigate the bathymetric distributions of species, all samples were grouped into 100-m depth bands. Mean abundance in each depth band was calculated for each species and then converted to percentage abundance, in order to facilitate quantitative data analysis. The range of a species was considered to be continuous between the depths of first and last occurrence.

For analysis of assemblage change with depth, data from all gears were used to give the minimum and maximum depth occurrence of each species. In order to identify possible boundaries where faunal turnover occurs, occurrences were then used to generate plots of species addition, loss and turnover with increasing depth.

To identify the main assemblages, multivariate analyses were performed using the PRIMER (Plymouth Routines in Multivariate Ecological Research) version 6.0 programme (Clarke and Gorley,

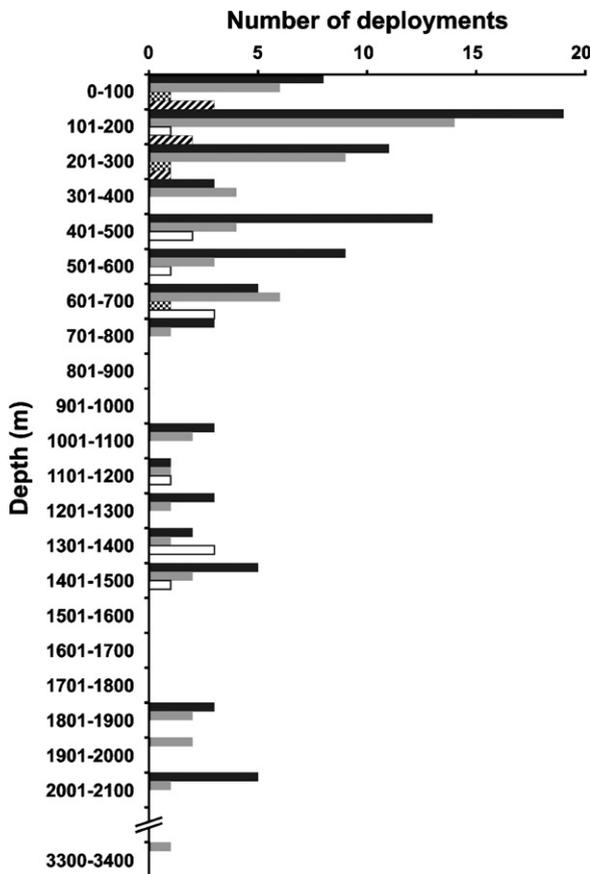


Fig. 2. Distribution of sampling effort in 100-m depth bands. Black bars: total number of box-cores; grey bars: total number of Agassiz trawls; dotted bars: total numbers of Nassa traps; white bars: total number of epibenthic sledges; banded bars: total number of rock dredges.

2005). The data were transformed into presence/absence in order to avoid the bias introduced by the use of different samplers. Samples were then grouped into 200-m depth bands and labelled A–H for gastropods and A–J for bivalves. This grouping was arbitrary but allowed data to be analysed in terms of depth rather than species change (see Bett, 2001). The Bray–Curtis similarity coefficient (Clarke and Warwick, 1994) was applied to the transformed grouped data to obtain a similarity matrix. Hierarchical clustering with group-averaged linking and non-metric multidimensional scaling (MDS) was then performed using the similarity matrix. The groupings identified by both cluster analysis and the MDS plot were investigated in PRIMER.

Diversity was analysed by means of taxonomic diversity (Δ), following Warwick and Clarke (1995). This approach gives a weight to the path length linking species in a taxonomic classification and calculates the average path length between randomly chosen individuals from the sample. Four taxonomic levels (species, genus, family and order) were included in the analyses, and weights used were 1 (for different species), 2 (for different genera), 3 (for different families) and 4 (for different orders). Taxonomic levels were allocated according to the classifications of Ponder and Lindberg (1997) and Rosenberg (2005) for Gastropoda, and Giribet and Wheeler (2002) and Rosenberg (2005) for Bivalvia. In addition, the Shannon–Wiener \log_2 -based index was used. Diversity indices obtained were plotted against water depth and best fit regression lines calculated to estimate bathymetric gradients.

3. Results

During the three BENTART cruises, we collected a total of 647 gastropod individuals belonging to 82 species, 50 genera and 28 families, and a total of 2934 bivalve individuals belonging to 52 species, 32 genera and 21 families. The most abundant species of gastropod was the buccinid *Neobuccinum eatoni* with a total of 94 individuals. The most diverse family was the Buccinidae with 15 species. Among bivalves, the cyamiid *Cyamiocardium denticulatum* was the most abundant species with 654 individuals, and the Yoldiidae was the most diverse family with seven morphospecies. Despite the extensive sampling programmes, there were several gaps in the data set that might affect the outcome of this study (Fig. 2). Nevertheless, many depth bands

were represented by more than three deployments or runs, so data were reliable and provided a fairly comprehensive representation of species distributions.

3.1. Bathymetric distribution

3.1.1. Gastropods

Gastropods showed a discrete distribution, with 49 species (60%) distributed within a narrow depth range of 100 m (Table 1, Fig. 3). Most species occurred shallower than 500 m. Those species that lived deeper than 600 m had a narrow depth range of 100 m (e.g., *Conorbela antarctica*, Emarginulinae sp., *Brookula* sp. 2, *Liotella endeavourensis*, *Lorabellula* sp. 2, *Lusitromina abyssorum*). Twenty-five species (30%) were distributed between 200 and 900 m (e.g., *Onoba gelida*, *Probuccinum tenerum*, *Amauropsis anderssoni*, *Leucosyrinx paratenoceras*), and only eight species (10%) had a broad depth range between 1000 and 1400 m (*Typhlomangelia principalis*, *Aforia multispiralis*, *Torellia planispira*, *Anatoma euglypta*, *Chlanidota signeyana*, *Melanella antarctica*, *Amauropsis aureolutea* and *Calliotropis pelseneeri*). There was a gradual replacement of species with depth down to 800 m, and many species overlapped in their ranges; about 40% of species coexisted in the 400–800 m depth range (Fig. 3).

Most species had a patchy bathymetric distribution and were abundant only over a narrow depth range of 100 m. These narrow zones of greater abundance generally occurred towards the bottom of their depth ranges (Table 1, Fig. 3), rather than in the middle or upper parts (e.g., *C. signeyana*, Buccinidae sp. 2, *M. antarctica*, *A. aureolutea*, *C. pelseneeri*, *Antimargarita dulcis*, *Trophon drygalskii*).

Zones of enhanced species turnover were identified at 300–400, 800–1000 and 1500–1800 m (Fig. 4), although the depth ranges of 800–1000 and 1500–1800 m corresponded to gaps in the data set (Fig. 2). Below this depth, very few species were present and none occurred in large numbers, except for *A. dulcis* and *M. antarctica*. Only four species lived below 1500 m (*C. pelseneeri*, *T. drygalskii*, *Calliotropis* sp. and *L. abyssorum*).

3.1.2. Bivalves

The depth ranges of bivalves were broader than those of gastropods (Table 1, Fig. 5). Only 17 species (33%) were confined to a very narrow depth range (~100 m), 22 species (42%) had an intermediate depth range between 200 and 900 m (e.g.,

Table 1

The depth distribution of gastropods and bivalves from the South Shetland Islands to the Bellingshausen Sea. Depth ranges in Southern Ocean are indicated mainly according to Dell (1990) and Hain (1990). Unknown distributions are marked with (–) symbol

Family	Species	Depth range in Southern Ocean (m)	Depth range in this study (m)	Depth of maximum abundance in this study (m)
Nacellidae	<i>Nacella polaris concinna</i> (Strebel, 1908)	10–695	100–200	100–200
Lepetidae	<i>Iothia coppingeri</i> (Smith, 1881)	5–1108	200–300	200–300
Anatomidae	<i>Anatoma euglypta</i> (Pelseneer, 1903)	18–4420	400–1500	1300–1400
Fisurellidae	<i>Cornisepta antarctica</i> (Egorova, 1972)	280–700	400–500	400–500
	Emarginulinae sp.	–	600–700	600–700
Trochidae	Trochidae sp. 1	–	400–500	400–500
	Trochidae sp. 2	–	600–1400	600–700
	<i>Antimargarita smithiana</i> (Hedley, 1916)	30–439	1100–1200	1100–1200
	<i>Antimargarita dulcis</i> (Smith, 1907)	22–731	700–1500	1400–1500
	<i>Calliotropis antarctica</i> (Dell, 1990)	247–2818	400–800	600–700
	<i>Calliotropis pelseneeri</i> (Cernohorsky, 1977)	371–796	400–1900	1800–1900
	<i>Calliotropis</i> sp.	–	1800–1900	1800–1900
	<i>Margarella refulgens</i> (Smith, 1907)	0–1108	0–300	0–100
	<i>Margarella</i> sp.	–	100–200	100–200
	<i>Solariella antarctica</i> (Powell, 1958)	455–603	1200–1300	1200–1300
	<i>Submargarita</i> sp.	–	100–700	100–700
Skeneidae	<i>Brookula</i> sp. 2	–	600–700	600–700
	<i>Liotella endeavourensis</i> (Dell, 1990)	362	1300–1400	1300–1400
	<i>Lissotesta</i> sp.	–	500–600	500–600
Turbinidae	<i>Leptocollonia innocens</i> (Thiele, 1912)	193–673	400–500	400–500
Littorinidae	<i>Pellilitorina pellita</i> (Martens, 1885)	0–238	200–300	200–300
Zerotulidae	<i>Dickdellia labioflecta</i> (Dell, 1990)	220–891	200–300	200–300
Eatoniellidae	<i>Eatoniella</i> cf. <i>keruelenensis keruelenensis</i> (Smith, 1875)	0–100	0–100	0–100
	<i>Eatoniella glacialis</i> (Smith, 1907)	6–870	100–200	100–200
Rissoidae	<i>Onoba gelida</i> (Smith, 1907)	4–870	0–700	100–200
	<i>Onoba kerueleni</i> (Smith, 1875)	0–870	0–100	0–100
	<i>Onoba turqueti</i> (Lamy, 1905)	2–385	100–200	100–200
Capulidae	<i>Torellia antarctica</i> (Thiele, 1912)	289–752	200–300	200–300
	<i>Torellia mirabilis</i> (Smith, 1907)	70–1120	200–300	200–300
	<i>Torellia planispira</i> (Smith, 1915)	107–1056	100–1100	100–200
Velutinidae	<i>Marseniopsis conica</i> (Smith, 1902)	41–860	100–200	100–200
	<i>Marseniopsis mollis</i> (Smith, 1902)	1–800	0–200	0–100
	<i>Marseniopsis syowaensis</i> (Numanami and Okutani, 1991)	5–30	100–200	100–200
Naticidae	<i>Amauropsis anderssoni</i> (Strebel, 1906)	12–578	100–500	100–200
	<i>Amauropsis aureolutea</i> (Strebel, 1908)	6–1120	0–1400	0–100
	<i>Amauropsis rossiana</i> (Smith, 1907)	9–1335	100–300	100–200
	<i>Amauropsis</i> sp.	–	0–400	0–100
	<i>Falsihunatia delicatula</i> (Smith, 1902)	40–1890	0–500	0–100
Eulimidae	<i>Melanella antarctica</i> (Strebel, 1908)	102–5194	0–1400	1300–1400
Cerithiopsidae	<i>Cerithiopsilla antarctica</i> (Smith, 1907)	45–500	200–300	200–300
Muricidae	<i>Trophon coulmanensis</i> (Smith, 1907)	183–1674	200–300	200–300
	<i>Trophon cuspidarioides</i> (Powell, 1951)	120–204	400–500	400–500
	<i>Trophon drygalskii</i> (Thiele, 1912)	193–588	1400–1900	1800–1900
	<i>Trophon echinolamellatus</i> (Powell, 1951)	342	200–300	200–300
	<i>Trophon longstaffi</i> (Smith, 1907)	5–1080	0–200	0–200
	<i>Trophon</i> sp.	–	0–100	0–100
Buccinidae	Buccinidae sp. 1	–	600–700	600–700
	Buccinidae sp. 2	–	0–500	400–500
	<i>Chlanidota signeyana</i> (Powell, 1951)	10–1116	0–1100	600–700
	<i>Lusitromina abyssorum</i> (Lus, 1993)	2380–5480	1900–2000	1900–2000
	<i>Neobuccinum eatoni</i> (Smith, 1875)	4–2350	0–700	0–100
	<i>Pareuthria</i> cf. <i>innocens</i> (Smith, 1907)	12–549	100–200	100–200
	<i>Pareuthria regulus</i> (Watson, 1882)	0–527	100–200	100–200

Table 1 (continued)

Family	Species	Depth range in Southern Ocean (m)	Depth range in this study (m)	Depth of maximum abundance in this study (m)
	<i>Probuccinum tenerum</i> (Smith, 1907)	30–673	100–300	100–300
	<i>Prosipho cancellatus</i> (Smith, 1915)	47–870	100–200	100–200
	<i>Prosipho chordatus</i> (Strebel, 1908)	94–600	0–100	0–100
	<i>Prosipho</i> cf. <i>elongatus</i> (Thiele, 1912)	193–433	100–200	100–200
	<i>Prosipho hedleyi</i> (Powell, 1958)	64–472	0–100	0–100
	<i>Prosipho pellitus</i> (Thiele, 1912)	94–150	0–100	0–100
	<i>Prosipho pusillus</i> (Thiele, 1912)	110–563	0–100	0–100
	<i>Prosipho</i> sp.	–	100–200	100–200
Volutidae	<i>Harpovoluta charcoti</i> (Lamy, 1910)	0–1469	0–700	100–200
Cancellariidae	<i>Admete</i> sp.	–	200–300	200–300
Volutomitridae	<i>Paradmete curta</i> (Strebel, 1908)	64–650	200–300	200–300
Conidae	<i>Belaturricula ergata</i> (Hedley, 1916)	100–695	500–600	500–600
	<i>Belaturricula gaini</i> (Lamy, 1910)	142–759	600–700	600–700
Turridae	<i>Aforia magnifica</i> (Strebel, 1908)	73–1890	100–400	200–300
	<i>Aforia multispiralis</i> (Dell, 1990)	265–1455	100–1100	100–1100
	<i>Conorbela antarctica</i> (Strebel, 1908)	18–1437	600–700	600–700
	<i>Leucosyrinx paratenoceras</i> (Powell, 1951)	200–810	0–600	200–500
	<i>Lorabela</i> sp. 1	–	0–200	0–100
	<i>Lorabela</i> sp. 2	–	1300–1400	1300–1400
	<i>Typhlodaphne innocentia</i> (Dell, 1990)	530–549	0–200	0–100
	<i>Typhlomangelia principalis</i> (Thiele, 1912)	310–460	400–1400	1100–1200
Acteonidae	<i>Acteon antarcticus</i> (Thiele, 1912)	101–380	1400–1500	1400–1500
	<i>Neactaeonina</i> cf. <i>edentula</i> (Watson, 1883)	5–1116	100–700	100–200
Philinidae	<i>Philine alata</i> (Thiele, 1912)	4–640	100–300	100–200
Pleurobranchidae	<i>Bathyberthella antarctica</i> (Willan and Bertsch, 1987)	66–2012	600–700	600–700
Dorididae	<i>Austrodoris georgiensis</i> (García, Troncoso, García-Gómez and Cervera, 1993)	133–138	100–200	100–200
	<i>Austrodoris kerguelenensis</i> (Bergh, 1884)	37–471	100–700	100–200
Tritoniidae	<i>Tritonia antarctica</i> (Pfeffer in Martens and Pfeffer, 1886)	98–481	0–200	0–200
	<i>Tritoniella belli</i> (Eliot, 1907)	10–732	100–200	100–200
Nuculidae	<i>Nucula austrobenthalis</i> (Dell, 1990)	3519–4209	3300–3400	3300–3400
Nuculanidae	<i>Nuculana inaequisculpta</i> (Lamy, 1906)	75–810	0–400	0–100
	<i>Propeleda longicaudata</i> (Thiele, 1912)	43–2100	100–700	400–500
Yoldiidae	<i>Yoldia eightsi</i> (Couthouy, 1839)	1–824	0–700	200–300
	<i>Yoldiella antarctica</i> (Thiele, 1912)	193–801	400–1900	400–1900
	<i>Yoldiella ecaudata</i> (Pelseneer, 1903)	265–2525	400–1500	500–600
	<i>Yoldiella oblonga</i> (Pelseneer, 1903)	459–2800	400–600	400–600
	<i>Yoldiella profundorum</i> (Melvill and Standen, 1912)	228–4758	200–2000	400–500
	<i>Yoldiella sabrina</i> (Hedley, 1916)	12–1437	1800–1900	1800–1900
	<i>Yoldiella valettei</i> (Lamy, 1906)	15–1263	0–300	0–100
Malletiidae	<i>Malletia</i> sp.	–	500–1500	1400–1500
Siliculidae	<i>Silicula rouchi</i> (Lamy, 1910)	160–1153	240–500	200–400
Arcidae	<i>Bathyarca sinuata</i> (Pelseneer, 1903)	400–2013	600–2100	2000–2100
Limopsidae	<i>Limopsis knudseni</i> (Dell, 1990)	1043–3693	400–3400	400–500
	<i>Limopsis lilliei</i> (Smith, 1915)	20–2100	0–400	0–100
	<i>Limopsis longipilosa</i> (Pelseneer, 1903)	90–2579	400–600	400–500
	<i>Limopsis marionensis</i> (Smith, 1885)	27–2804	300–500	400–500
	<i>Limopsis scotiana</i> (Dell, 1964)	97–342	0–300	100–200
Philobryidae	<i>Adacnarca limopsoides</i> (Thiele, 1912)	110–523	100–200	100–200
	<i>Adacnarca nitens</i> (Pelseneer, 1903)	8–2350	0–1400	100–200
	<i>Lissarca notorcadensis</i> (Melvill and Standen, 1907)	0–1890	0–400	200–300
	<i>Philobrya sublaevis</i> (Pelseneer, 1903)	1–923	0–300	200–300
	<i>Philobrya wandelensis</i> (Lamy, 1906)	5–870	0–100	0–100
Mytilidae	<i>Dacrydium albidum</i> (Pelseneer, 1903)	122–4636	600–1900	1800–1900
Limidae	<i>Limatula hodgsoni</i> (Smith, 1907)	6–1180	0–1900	1400–1500

Table 1 (continued)

Family	Species	Depth range in Southern Ocean (m)	Depth range in this study (m)	Depth of maximum abundance in this study (m)
Pectinidae	<i>Limatula simillima</i> (Thiele, 1912)	64–786	400–1500	1400–1500
	<i>Pectinidae</i> sp.	–	600–1500	1400–1500
	<i>Adamussium colbecki</i> (Smith, 1902)	2–4545	100–2000	1800–1900
Propeamussiidae	<i>Hyalopecten pudicus</i> (Smith, 1885)	400–5453	1300–1400	1300–1400
	<i>Cyclochlamys pteriola</i> (Melvill and Standen, 1907)	16–202	500–600	500–600
	<i>Cyclochlamys cf. notalis</i> (Thiele, 1912)	3423	1300–1400	1300–1400
Thyasiridae	<i>Thyasira bongraini</i> (Lamy, 1910)	39–1180	200–300	200–300
	<i>Thyasira cf. dearborni</i> (Nicol, 1965)	351–836	0–500	400–500
	<i>Thyasira debilis</i> (Thiele, 1912)	9–1674	0–1400	200–300
	<i>Thyasira falklandica</i> (Smith, 1885)	5–18	0–300	200–300
Carditidae	<i>Cyclocardia astartoides</i> (Martens, 1878)	2–3248	0–500	100–200
Galeommatoidae	<i>Galeommatoida</i> sp.	–	500–1400	1300–1400
	<i>Waldo parasiticus</i> (Dall, 1876)	50–470	200–300	200–300
Galeommatidae	<i>Montacuta ? nimrodiana</i> (Hedley, 1911)	6–362	100–200	100–200
	<i>Mysella antarctica</i> (Smith, 1907)	29–923	0–500	100–200
	<i>Mysella gibbosa</i> (Thiele, 1912)	64–752	500–600	500–600
	<i>Mysella</i> sp.	–	200–300	200–300
	<i>Pseudokellya cardiformis</i> (Smith, 1885)	20–710	0–200	0–100
Cyamiidae	<i>Cyamiocardium crassilabrum</i> (Dell, 1964)	161–271	0–100	0–100
	<i>Cyamiocardium denticulatum</i> (Smith, 1907)	5–1180	0–500	100–200
	<i>Cyamiomactra laminifera</i> (Lamy, 1906)	15–1281	0–100	0–100
Lyonsiidae	<i>Lyonsia arcaeorformis</i> (Martens, 1885)	12–1812	0–100	0–100
Laternulidae	<i>Laternula elliptica</i> (King and Broderip, 1831)	1–508	0–300	100–200
Thraciidae	<i>Thracia meridionalis</i> (Smith, 1885)	4–836	100–400	100–400
Cuspidariidae	<i>Cuspidaria infelix</i> (Thiele, 1912)	60–752	0–1500	100–200
	<i>Cuspidaria minima</i> (Egorova, 1993)	115–1272	100–200	100–200
	<i>Myonera fragilissima</i> (Smith, 1885)	549–550	400–500	400–500

Yoldiella oblonga, *Philobrya sublaevis*, *Cyclocardia astartoides*, *Galeommatoida* sp.) and 13 species (25%) had a broad depth range of 1000–3000 m (e.g., *Malletia* sp., *Dacrydium albidum*, *Yoldiella profundorum*, *Limopsis knudseni*). Most bivalves that were distributed deeper than 600 m had broad depth ranges (e.g., *Thyasira debilis*, *Limatula hodgsoni*, *Limatula simillima*, *Bathyarca sinuata*), and only four species had narrow depth ranges of 100 m (*Cyclochlamys cf. notalis*, *H. pudicus*, *Yoldiella sabrina* and *Nucula austrobenthalis*). There was a gradual replacement of species with depth down to 700 m (Fig. 6), and most species overlapped in their ranges, i.e., ca. 55% of species coexisted in the 400–700 m depth range. As a result, the turnover of bivalve species with depth was less than that of gastropods.

Many bivalve species were patchily distributed, with maximum abundances in narrow depth ranges. However, unlike gastropods, which tended to be the most abundant at the bottom of their ranges,

bivalves reached their highest abundances at different points along their bathymetric distribution (Table 1, Fig. 5). For example, some species exhibited a maximum at the top (e.g., *C. denticulatum*, *Adacnarca nitens*), others in the middle (e.g., *T. debilis*, *Cuspidaria infelix*) and others at the lower end of their total depth ranges (e.g., *A. colbecki*, *L. knudseni*).

Zones of species turnover and faunal discontinuities were similar to those for gastropods (Fig. 6). Between 1800 and 2100 m only seven species occurred, and only three species (*A. colbecki*, *D. albidum* and *B. sinuata*) showed a peak of abundance in this depth range. Between 3300 and 3400 m only two species occurred in very small numbers (*L. knudseni* and *N. austrobenthalis*).

3.2. Assemblages and boundaries

Both Hierarchical Cluster Analysis and MDS showed stations clustering by depth and suggested

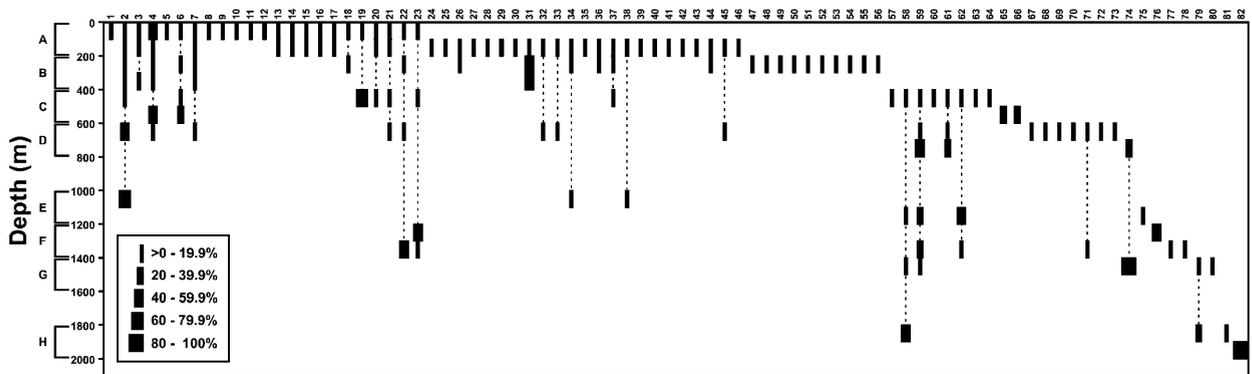


Fig. 3. Bathymetric distribution and relative abundance of gastropods from South Shetland Islands to Bellingshausen Sea, showing the total range and the relative abundance of the species found in this study. Stations were grouped into 200 m depth bands and labelled by letters: (A) 0–199, (B) 200–399, (C) 400–599, (D) 600–799, (E) 1000–1199, (F) 1200–1399, (G) 1400–1599, (H) 1800–1999. Species are: (1) *Eatoniella* cf. *kerquelenensis*, (2) *Chlanidota signeyana*, (3) *Amauropsis* sp., (4) *Neobuccinum eatoni*, (5) *Trophon* sp., (6) *Leucosyrinx paratenoceras*, (7) *Harporvoluta charcoti*, (8) *Prosipho hedleyi*, (9) *Onoba kergueleni*, (10) *Prosipho chordatus*, (11) *Prosipho pellitus*, (12) *Prosipho pusillus*, (13) *Lorabela* sp. 1, (14) *Typhlodaphne innocentia*, (15) *Marseniopsis mollis*, (16) *Trophon longstaffi*, (17) *Tritonia antarctica*, (18) *Margarella refulgens*, (19) *Buccinidae* sp. 2, (20) *Falsilunatia delicatula*, (21) *Onoba gelida*, (22) *Melanella antarctica*, (23) *Amauropsis aureolutea*, (24) *Pareuthria* cf. *innocens*, (25) *Prosipho cancellatus*, (26) *Amauropsis rossiana*, (27) *Nacella polaris concinna*, (28) *Eatoniella glacialis*, (29) *Marseniopsis conica*, (30) *Austrodoris georgiensis*, (31) *Aforia magnifica*, (32) *Submargarita* sp., (33) *Austrodoris kerguelensis*, (34) *Torellia planispira*, (35) *Tritoniella belli*, (36) *Probuccinum tenerum*, (37) *Amauropsis anderssoni*, (38) *Aforia multispiralis*, (39) *Prosipho* cf. *elongatus*, (40) *Prosipho* sp., (41) *Marseniopsis syowaensis*, (42) *Onoba turqueti*, (43) *Pareuthria regulus*, (44) *Philine alata*, (45) *Neactaeonina* cf. *edentula*, (46) *Margarella* sp., (47) *Admete* sp., (48) *Paradmete curta*, (49) *Trophon coulmanensis*, (50) *Torellia antarctica*, (51) *Torellia mirabilis*, (52) *Pellilitorina pellita*, (53) *Trophon echinolamellatus*, (54) *Dickdellia labioflecta*, (55) *Iothia coppingeri*, (56) *Cerithiopsis antarctica*, (57) *Trophon cuspidarioides*, (58) *Calliotropis pelseneeri*, (59) *Anatoma euglypta*, (60) *Leptocollonia innocens*, (61) *Calliotropis antarctica*, (62) *Typhlomangelia principalis*, (63) *Cornisepta antarctica*, (64) *Trochidae* sp. 1, (65) *Belaterricula ergata*, (66) *Lissotesta* sp., (67) *Conorbela antarctica*, (68) *Emarginulinae* sp., (69) *Brookula* sp. 2, (70) *Buccinidae* sp. 1, (71) *Trochidae* sp. 2, (72) *Bathyberthella antarctica*, (73) *Belaterricula gaini*, (74) *Antimargarita dulcis*, (75) *Antimargarita smithiana*, (76) *Solariella antarctica*, (77) *Liotella endeavourensis*, (78) *Lorabela* sp. 2, (79) *Trophon drygalskii*, (80) *Acteon antarcticus*, (81) *Calliotropis* sp., (82) *Lusitromina abyssorum*.

an arrangement of stations in four different groups for gastropods (Figs. 7a and b) and in five different groups for bivalves (Figs. 8a and b). In addition to the ordination of stations along a depth gradient, there was an arrangement of samples by geographic position within the area of study. Most stations from the South Shetlands, Peninsula and Peter I Island areas tended to cluster together, as did those from the Bellingshausen Sea (see assemblages; Figs. 7 and 8). Nevertheless, the most abundant species were widely distributed across the whole area of study.

3.2.1. Gastropods

Stations clustered into four groups (1–4; Fig. 7a) which were very dissimilar to each other (similarity close to 10%). Three of them delimited bathymetric boundaries more or less clearly. A continental shelf zone from 0 to 400 m, represented by depth bands A and B grouped together in clusters 3 and 4, could be found (Figs. 7a and b). The rate of species succession was gradual, and the 400-m boundary

marked a change in the rate at which species were added (Fig. 4). Fifty-six species occurred between 0 and 400 m; 41 of these were restricted to this zone (e.g., *Typhlodaphne innocentia*, *Amauropsis rossiana*, *P. tenerum*, *Philine alata*; Fig. 3) while the other 15 species extended deeper (e.g., *C. signeyana*, *Harporvoluta charcoti*, *M. antarctica*, *A. aureolutea*, *T. planispira*, *A. multispiralis*, *Neactaeonina* cf. *edentula*). Species that typified this zone were *Amauropsis* sp. and *Aforia magnifica*.

An upper slope zone extending from 400 to 800 m was represented by depth bands C and D. Cluster 1 (Figs. 7a and b) included only depth band C. On the other hand, band D was not grouped in a single cluster because it included a large number of widespread species that were present in several bathymetric zones (e.g., *M. antarctica*, *C. pelseneeri*, *A. euglypta*; Fig. 3). However, *Calliotropis antarctica* defined the upper slope zone, and some other species were restricted to this zone (e.g., *Trophon cuspidarioides*, *Trochidae* sp. 1, *Belaterricula gaini*). Eighteen species first appeared between 400 and

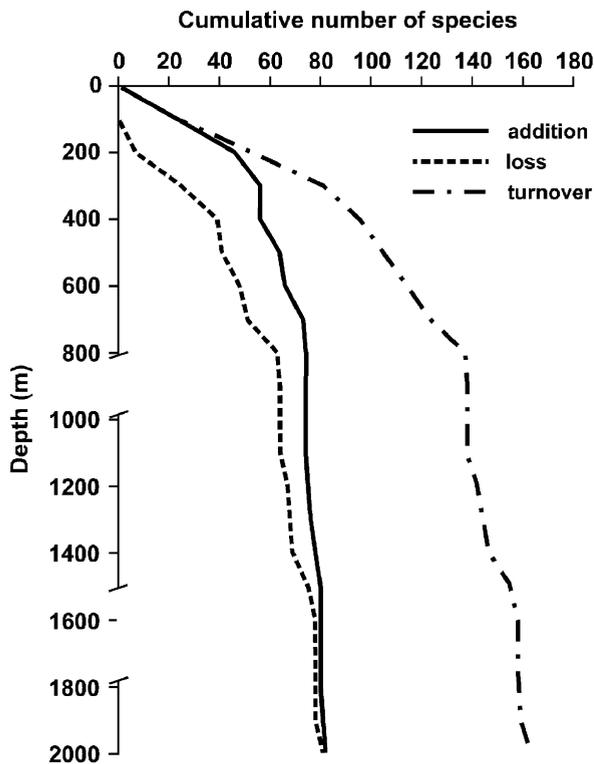


Fig. 4. Cumulative addition and loss of gastropod species with depth from full data set. Turnover (addition plus loss) of species is also plotted. Gaps along the depth axis indicate gaps in sampling.

800 m (e.g., *T. cuspidarioides*, *C. pelseneeri*) and 41 species were lost (e.g., *Amauropsis* sp. *A. magnifica*, *Iothia coppingeri*, *Cerithiopsis antarctica*). Species succession in this zone was gradual and more rapid than on the continental shelf to the depth of the boundary at 800 m, where again there was a change in the rate of species succession (Fig. 4). Nevertheless, the existence of the lower boundary at 800 m should be interpreted with caution given the incomplete sampling of deeper stations (see sampling effort; Fig. 2).

A lower slope zone from 800 to 2000 m, represented by depth bands E–H, grouped in cluster 2 (Figs. 7a and b). Eight species were added and restricted to this zone (*Antimargarita smithiana*, *Solariella antarctica*, *L. endeavourensis*, *Lorabela* sp. 2, *T. drygalskii*, *Acteon antarcticus*, *Calliotropis* sp. and *L. abyssorum*; Fig. 3). Species succession was more rapid than in both continental shelf and upper slope, with fewer species being added, but a higher loss of species, i.e., 23 species (e.g., *Neactaeonina* cf. *edentula*, *C. antarctica*, *Bathyberthella antarctica*, *B. gaini*) (Fig. 4).

3.2.2. Bivalves

Groups of stations (1–5; Fig. 8a) were more similar to each other than in the case of gastropods (similarity >20%). Four more or less clearly delimited bathymetric boundaries were recognized.

A continental shelf zone from 0 to 400 m depth represented by depth bands A and B, grouped together in clusters 4 and 5 (Figs. 8a and b). The rate of species turnover was gradual down to approximately 300–400 m, where there was a change in species addition (Fig. 6). Thirty-four species were added to this zone, of which 20 were restricted to it (e.g., *Cyamiocardium crassilabrum*, *Laternula elliptica*, *Cyamiomacra laminifera*, *Adacnarca limopsoides*, *Waldo parasiticus*; Fig. 5) and 14 extended deeper (e.g., *Yoldia eightsi*, *T. debilis*, *A. nitens*, *L. hodgsoni*, *A. colbecki*). Species that typified this zone were *Nuculana inaequisculpta*, *Limopsis lillie* and *Lissarca notorcadensis*.

An upper slope zone from 400 to 800 m was represented by depth bands C and D. These bands were grouped mainly in clusters 1–3, although cluster 3 grouped only depth band C (Figs. 8a and b). Fourteen species were added in this zone (e.g., *Yoldiella antarctica*, *Yoldiella ecaudata*, *L. simillima*), but only five species were restricted to it (*Myonera fragilissima*, *Mysella gibbosa*, *Cyclochlamys pteriola*, *Limopsis longipilosa* and *Y. oblonga*; Fig. 5). Twenty species were lost (e.g., *C. crassilabrum*, *Thyasira falklandica*, *N. inaequisculpta*). Species turnover was gradual up to 700 m, which was a depth boundary characterized by a change in the turnover of species (Fig. 6).

A lower slope zone from 800 to 3400 m, comprising depth bands E–J, grouped in clusters 1 and 2 (Figs. 8a and b). Although 19 species occurred in this zone, only four species were added and confined to these depths (*Cyclochlamys* cf. *notalis*, *Hyalopecten pudicus*, *Y. sabrina* and *N. austrobenthalis*; Fig. 5). Thirteen species were lost (e.g., *Y. oblonga*, *M. gibbosa*, *C. pteriola*). Species turnover was rapid with a low addition of species due to gaps in the data set at 800–1000, 1500–1800 and 2100–3300 m (see sampling effort in Fig. 2). Thus, this zone was poorly sampled and difficult to characterize.

3.3. Diversity gradient

3.3.1. Gastropods

Taxonomic diversity showed no clear pattern with widely scattered data (Fig. 9a). The Shannon–Wiener index showed a stronger pattern that

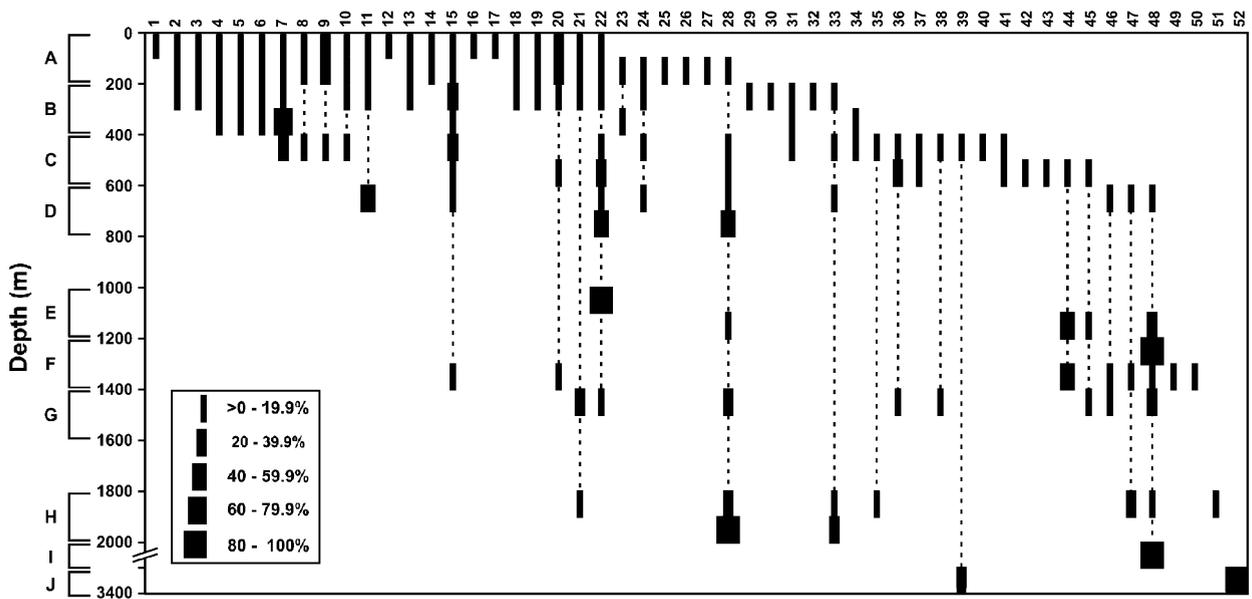


Fig. 5. Bathymetric distribution and relative abundance of bivalves from South Shetland Islands to Bellingshausen Sea, showing the total range and the relative abundance of the species found in this study. Stations were grouped into 200 m depth bands and labelled by letters: (A) 0–199, (B) 200–399, (C) 400–599, (D) 600–799, (E) 1000–1199, (F) 1200–1399, (G) 1400–1599, (H) 1800–1999, (I) 2000–2199, (J) 3200–3399. Species are: (1) *Cyamiocardium crassilabrum*, (2) *Thyasira falklandica*, (3) *Yoldiella valettei*, (4) *Nuculana inaequisculpta*, (5) *Limopsis lilliei*, (6) *Lissarca notorcadensis*, (7) *Thyasira cf. dearborni*, (8) *Mysella antarctica*, (9) *Cyamiocardium denticulatum*, (10) *Cyclocardia astartoides*, (11) *Yoldia eightsi*, (12) *Lyonsia arcaeformis*, (13) *Laternula elliptica*, (14) *Pseudokellya cardiformis*, (15) *Thyasira debilis*, (16) *Philobrya wandelensis*, (17) *Cyamiomacra laminifera*, (18) *Limopsis scotiana*, (19) *Philobrya sublaevis*, (20) *Adacnarca nitens*, (21) *Limatula hodgsoni*, (22) *Cuspidaria infelix*, (23) *Thracia meridionalis*, (24) *Propeleda longicaudata*, (25) *Adacnarca limposoides*, (26) *Montacuta ? nimrodiana*, (27) *Cuspidaria minima*, (28) *Adamussium colbecki*, (29) *Thyasira bongraini*, (30) *Waldo parasiticus*, (31) *Silicula rouchi*, (32) *Mysella* sp., (33) *Yoldiella profundorum*, (34) *Limopsis marionensis*, (35) *Yoldiella antarctica*, (36) *Yoldiella ecaudata*, (37) *Limopsis longipilosa*, (38) *Limatula simillima*, (39) *Limopsis knudseni*, (40) *Myonera fragilissima*, (41) *Yoldiella oblonga*, (42) *Mysella gibbosa*, (43) *Cycloclamys pteriola*, (44) *Galeomatoidea* sp., (45) *Malletia* sp., (46) *Pectinidae* sp., (47) *Dacrydium albidum*, (48) *Bathyarca sinuata*, (49) *Cycloclamys cf. notalis*, (50) *Hyalopecten pudicus*, (51) *Yoldiella sabrina*, (52) *Nucula austroenthalis*.

suggested a decrease of diversity with increasing depth (Fig. 9b). Neither the taxonomic diversity index nor Shannon–Wiener index showed any significant polynomial or linear correlation with depth.

3.3.2. Bivalves

Taxonomic diversity showed a weak peak above 1000 m, followed by a decreasing pattern downslope to ~2100 m (Fig. 10a). However, this trend was not significant ($r^2 = 0.047$; $p = 0.53$). The Shannon–Wiener index showed a quite different trend, with highest values down to 500 m, followed by a decreasing pattern downslope to ~1200 m (Fig. 10b). Although this trend was significant, depth explained only about 22% of variance of diversity ($r^2 = 0.221$; $p < 0.05$).

4. Discussion

The species identified in the study area matched those found in other Antarctic areas. The main molluscan species of the Ross Sea and Weddell Sea were present in the South Shetland Islands and in the Bellingshausen Sea (Arnaud et al., 2001; Troncoso et al., 2007). For example, the buccinid *N. eatoni* is a widespread species in Antarctic waters, with high abundances due to its scavenger diet, mainly at shallow depths (e.g., Cattaneo-Vietti et al., 2000). The family Buccinidae, and particularly the genus *Prosipho*, has a high diversity in Antarctic waters (Dell, 1990). Among bivalves, *C. denticulatum* is a common species in the South Shetland Islands (e.g., Arnaud et al., 2001) and the Yoldiidae is the most diverse family in the Scotia Arc Islands (Linse, 2004). Gastropods occurred in

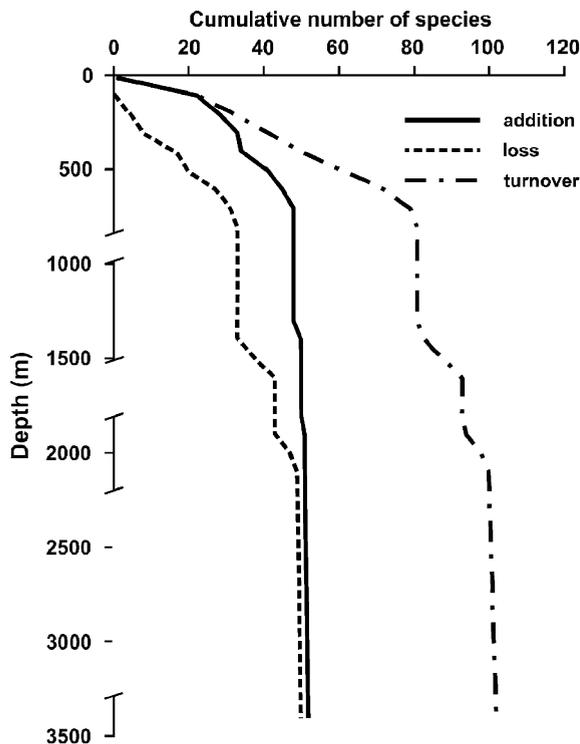


Fig. 6. Cumulative addition and loss of bivalve species with depth from full data set. Turnover (addition plus loss) of species is also plotted. Gaps along the depth axis indicate gaps in sampling.

smaller numbers than bivalves, but they had higher species richness. This agrees with other studies in neighbouring areas (Arnaud and Hain, 1992; Arnaud et al., 2001).

4.1. Bathymetric distribution

The faunal composition of gastropods and bivalves from the South Shetland Islands to the Bellingshausen Sea varied with depth, but this change was quite gradual. There were, however, some differences between the two groups. Gastropods showed higher rates of zonation than bivalves. Most of the gastropods that exhibited the deepest distributions occurred in a very narrow depth range. In contrast, most bivalves that were distributed deeper than 600 m had a broad depth range. There was also a clear difference between gastropod and bivalve species. Many gastropods showed peaks in abundance at the ends of their depth ranges, whereas the maximum abundances of bivalves occurred at the beginning, middle or the end of their depth ranges depending on the species. These

results agree with earlier findings on the bathymetric distribution of molluscs in the Northern Hemisphere (e.g., Sanders and Grassle, 1971; Rex, 1976, 1981; Grassle and Maciolek, 1992; Allen and Sanders, 1996; Olabarria, 2005, 2006).

Most species reached their greatest abundances over a narrow depth range of 100–300 m. Patchy distributions in molluscs have been reported previously for several deep-sea taxa in both the Northern (e.g., Howell et al., 2002; Olabarria 2005, 2006) and Southern Hemispheres (e.g., Linse and Brandt, 1998; Linse, 2004). This may be related in part to variations in physical factors at small scales, i.e., 10s to 100s of meters. For example, sediment characteristics in the South Shetlands area appear to vary at small spatial scales, mostly due to the irregular input and deposition of terrigenous muds, ice-rafted gravels and volcanic ash (Yoon et al., 1992). Furthermore, variations in hydrodynamic conditions from place to place (Huntley et al., 1991) may create heterogeneity in the distribution of soft sediments and hard substrates. All of these factors may account for quantitative changes in the abundances of species at small spatial scales (Arnaud et al., 2001). In addition, biological interactions have been reported to play an important role in governing the distribution of many taxa (Rex, 1977; Cartes et al., 2003). The degree of zonation increases with trophic level or size, so faunal replacement with depth is more rapid among predators (i.e., many species of gastropods in this study) than among infaunal or epifaunal deposit- or suspension-feeders, such as polychaetes or bivalves (see Rex, 1977).

The distribution patterns of some species, such as *Adasmussium colbeki* and *Y. eightsi*, differed from those exhibited by the same species in adjacent areas. In this study, both species extended their ranges to deeper waters (down to 2000 m), whereas living specimens occurred at shallower depths in the Ross Sea (e.g., Dell, 1990; Cattaneo-Vietti et al., 2000).

4.2. Patterns of zonation, assemblages and possible causes

Both gastropod and bivalve assemblages exhibited three main bathymetric discontinuities at ~400, 800 and 1500 m (see Figs. 6 and 7). These boundaries delimit three faunistic zones: (1) A zone above ~400 m marked strongly by shelf species and with few species extending deeper. More species of

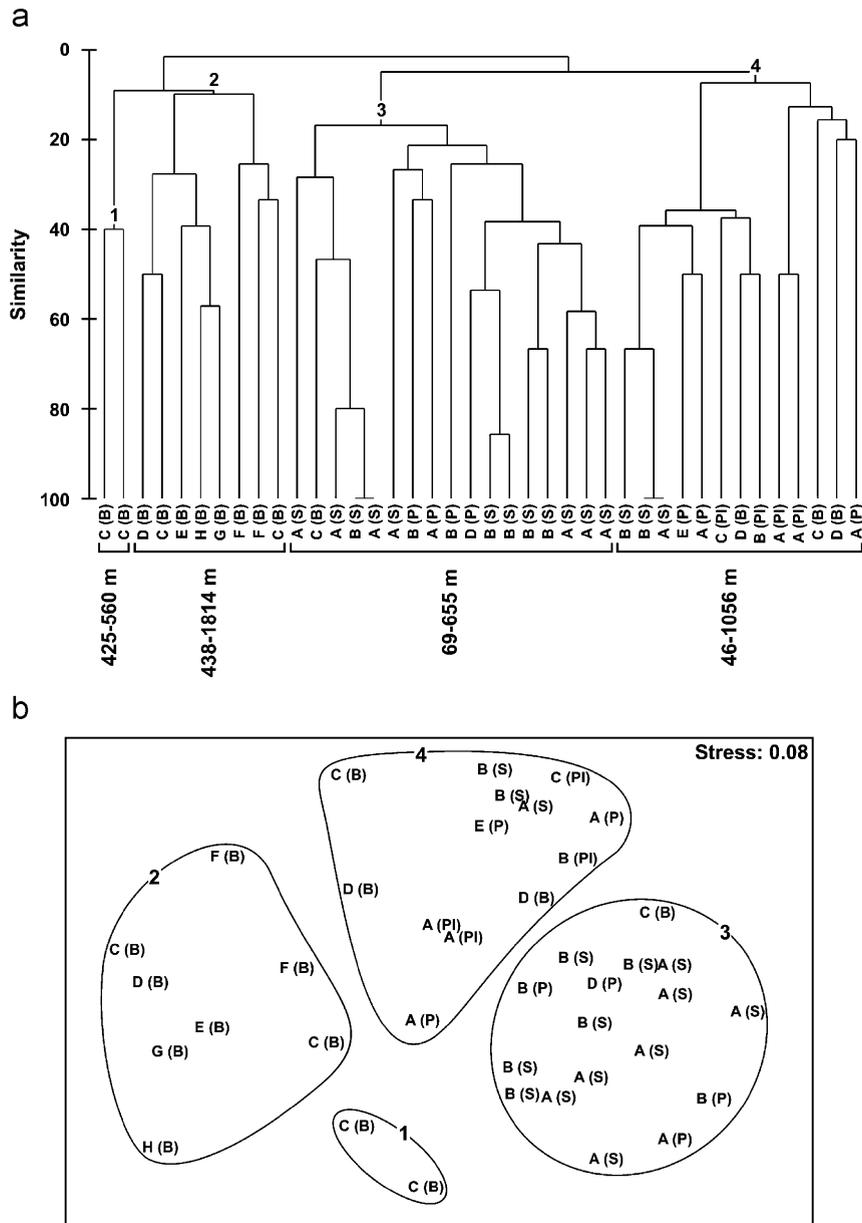


Fig. 7. Main assemblages based on combined presence-absence data (all gears) for gastropods. Stations of South Shetland Islands (S), Antarctic Peninsula (P), Bellingshausen Sea (B) and Peter I Island (PI) were grouped into 200 m depth bands labelled by letters: (A) 0–199, (B) 200–399, (C) 400–599, (D) 600–799, (E) 1000–1199, (F) 1200–1399, (G) 1400–1599, (H) 1800–1999. (a) Hierarchical cluster analysis, based on Bray Curtis similarity coefficient. Clusters 1–4 are shown. (b) Non-metric multi-dimensional scaling plot. Clusters 1–4 are shown.

bivalves than gastropods extended into deeper waters. (2) A zone from ~400 to ~800 m, which corresponds to the upper slope. This zone was less well characterized than other zones because of the large number of species with very broad distributions and very few exclusive species. In this region there was a gap in the data set (~800 m) that could account for the lack of species (Fig. 2). (3) A lower

slope zone from ~800 to ~2000 m that extended to ~3400 m for bivalves. This was marked by the presence of several species that had very broad depth ranges (1000–2500 m) and by typical species of deeper waters. The characterization of this zone, however, was quite difficult since it was poorly sampled (Fig. 2). These patterns of zonation are similar to those exhibited by other invertebrates in

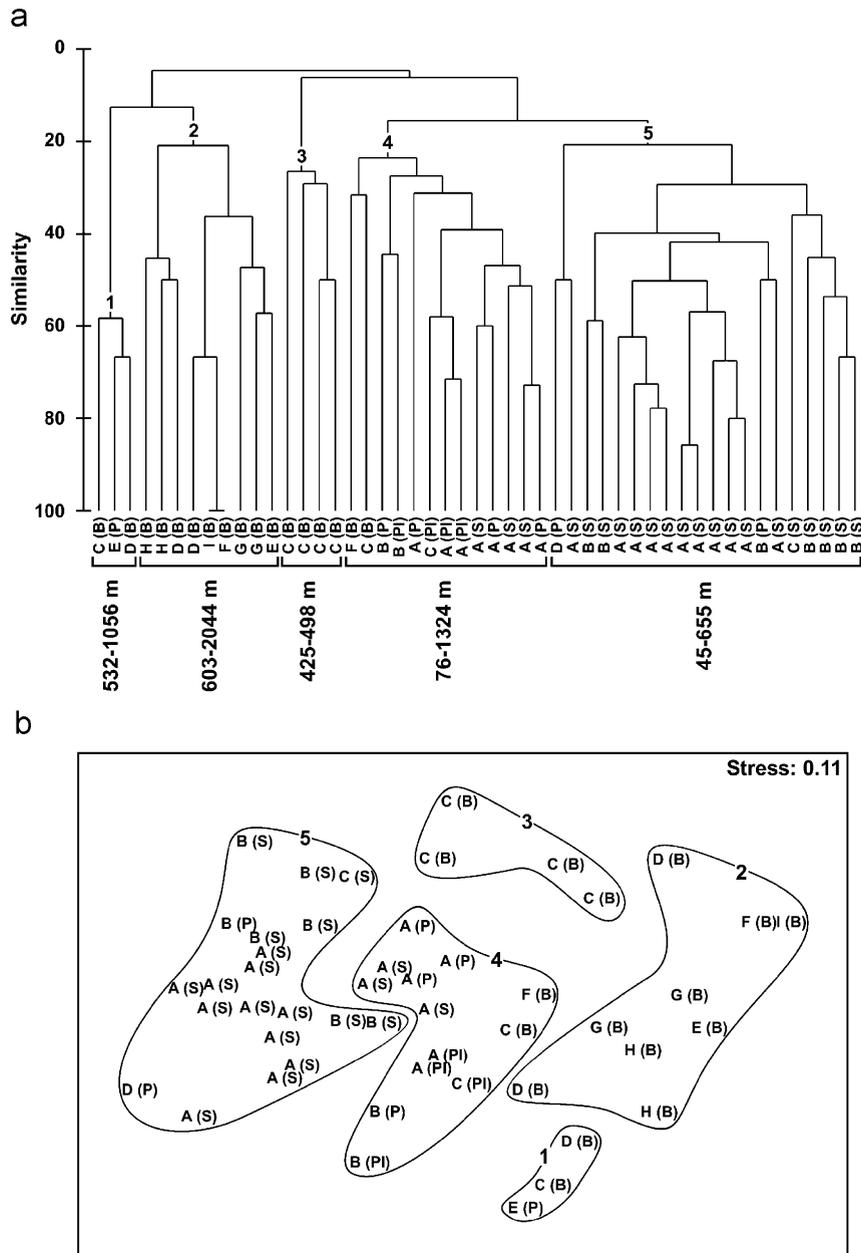


Fig. 8. Main assemblages based on combined presence–absence data (all gears) for bivalves. Stations of South Shetland Islands (S), Antarctic Peninsula (P), Bellingshausen Sea (B) and Peter I Island (PI) were grouped into 200 m depth bands labelled by letters: (A) 0–199, (B) 200–399, (C) 400–599, (D) 600–799, (E) 1000–1199, (F) 1200–1399, (G) 1400–1599, (H) 1800–1999, (I) 2000–2199, (J) 3200–3399. (a) Hierarchical cluster analysis, based on Bray-Curtis similarity coefficient. Clusters 1–5 are shown. (b) Non-metric multi-dimensional scaling plot. Clusters 1–5 are shown.

Antarctic waters (e.g., Gerdes et al., 1992; Vanhove et al., 1999; Piepenburg et al., 2002). Nevertheless, the results must be interpreted with caution because sampling artefacts, including gaps and heavy sampling in a few depth bands, may create false boundaries (see Carney, 2005).

The causes of bathymetric zonation in the deep sea are complex, and several physical and biological factors may act together to produce the observed patterns. Previous studies have pointed out that Antarctic benthic assemblages are controlled by three major factors: food supply, temperature and

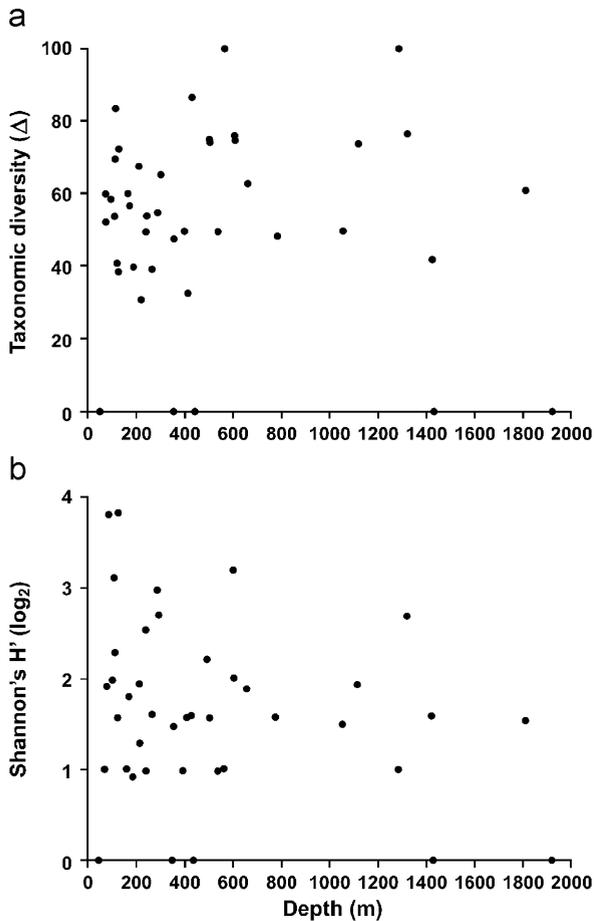


Fig. 9. Bathymetric variation of gastropods diversity measured as (a) taxonomic diversity, $y = 41.085 + 0.43x - 8.5E-006x^2 - 1.1E-008x^3$ ($r^2 = 0.124$; $F = 1.848$, $p = 0.16$) and as (b) H' , $y = 1.786 - 0.001x + 1.16E-006x^2 - 5.9E-01x^3$ ($r^2 = 0.06$; $F = 0.830$, $p = 0.49$).

sediment regime (Mühlenhardt-Siegel, 1988, 1989; Clarke, 1991; Brey and Clarke, 1993; Knox, 1994; Sáiz-Salinas et al., 1997; Piepenburg et al., 2002; Skowronski and Corbisier, 2002; Lovell and Trego, 2003). For example, temperature and food and their seasonal oscillations, influence metabolism and growth of Antarctic marine invertebrates and hence are important factors structuring benthic assemblages (Clarke, 1988, 1991; Brey and Clarke, 1993; Brêthes et al., 1994; Clarke et al., 2004a). High rates of sedimentation may inhibit suspension-feeding organisms (Lovell and Trego, 2003) or enhance phytoplankton sedimentation (Skowronski and Corbisier, 2002). Ice or iceberg impacts can also have a very considerable influence on the structure of benthic assemblages (e.g., Peck et al., 1999;

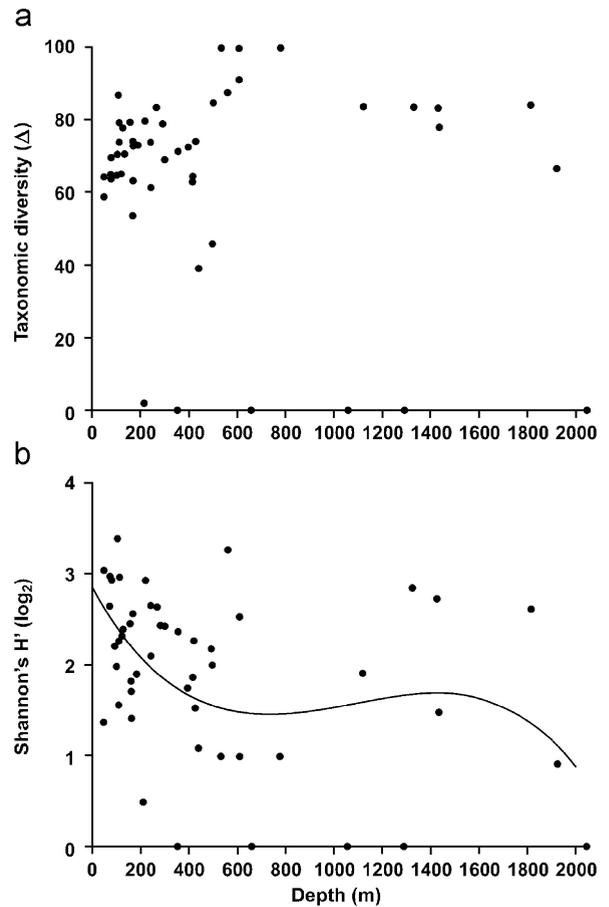


Fig. 10. Bathymetric variation of bivalves diversity measured as (a) taxonomic diversity, $y = 71.669 - 0.035x + 4.9E-005x^2 - 2.0E-008x^3$ ($r^2 = 0.047$; $F = 0.750$, $p = 0.53$) and as (b) H' , the solid line is the regression line, $y = 2.844 - 0.005x + 4.8E-006x^2 - 1.5E-009x^3$ ($r^2 = 0.221$; $F = 4.344$, $p < 0.05$). Only significant fitted relationship is shown.

Bromberg et al., 2000; Vanhove et al., 2000; Gutt, 2001). Disturbance from ice in Antarctic benthic marine systems varies at different spatial and temporal scales (Peck et al., 1999; Gerdes et al., 2003). This heterogeneity may enhance the diversity of benthic assemblages (Kvitek et al., 1998; Gutt et al., 1999; Peck et al., 1999; Gutt, 2001; Gerdes et al., 2003). For example, icebergs seem to increase the between-habitat diversity (β -diversity) and probably the overall γ -diversity in different Antarctic areas (e.g., Gutt, 2000; Gerdes et al., 2003).

In addition, biological factors may also play an important role in shaping patterns of species and assemblage distributions. It has been suggested previously that physiological factors impose lethal limits and that these set broad depth ranges.

Eurytopy, i.e., plasticity in the choice of biotopes, and eurybathy, i.e., large vertical distribution, have been considered particularly frequent among Antarctic molluscs (Cantera and Arnaud, 1985). Biological interactions between species may also help to explain their rates of zonation and distribution (see Section 4.1; Rex, 1977; Cartes et al., 2003). Life-history traits, such as developmental mode, fecundity, egg size or mobility factors, also have to be considered in order to explain the distribution and intensity of zonation in deep-sea species (e.g., Allen and Sanders, 1996).

Although the stations were arranged along a depth gradient, they also clustered together according to their geographical position. Multivariate analyses distinguished between the mollusc assemblages from the South Shetland Islands, Peninsula and Peter I Island area and the Bellingshausen Sea area. These results agree in part with a recent study based on mollusc data sets that subdivide the Western Antarctic Peninsula subprovince into three different regions: the Bellingshausen Sea, the main Antarctic Peninsula, and the South Shetland Islands (see Clarke et al., 2007). Variations in physical factors such as sediment type, topography, hydrodynamic conditions, food supply or sea-ice cover may cause differences in the composition of mollusc assemblages from place to place (see Yoon et al., 1992; Arnaud et al., 2001; Carney, 2005).

4.3. Diversity gradient

Diversity followed a complex pattern with depth for gastropods and bivalves. These patterns did not match those exhibited by these taxa in some Northern Hemisphere basins (e.g., Rex, 1973, 1981, 1983; Etter and Grassle, 1992; Allen and Sanders, 1996; Olabarria, 2005, 2006). However, these studies cannot be fully compared with the present investigation because of the different depth ranges sampled. For example, in the western Atlantic, gastropods and protobranchs showed parabolic trends, with peaks at upper rise depths (2000–3000 m) (Rex, 1973, 1983). In contrast, Allen and Sanders (1996) reported different patterns in the diversity of protobranchs from the Atlantic basins, with diversity peaks in deeper waters (3000–4000 m).

In general, diversity was high in the continental shelf and upper slope zones with peaks at ~100–500 m and then decreased down slope. This pattern has been tentatively explained by incom-

plete recolonization or poor food supply downslope (Arnaud and Hain, 1992). Disturbance from ice could also be a major factor affecting patterns of diversity in benthic assemblages (Arntz et al., 1994; Dayton et al., 1994; Gutt, 2000). In this context, the intermediate disturbance hypothesis (Connell, 1978) needs to be considered. It predicts that species diversity declines under very frequent or intense disturbance regimes, because few species are able to survive or settle successfully. In the absence of disturbance, species diversity is depressed because of competitive exclusion of inferior competitors. At intermediate levels of disturbance, maximal diversity is sustained via compensatory mortality. The range of disturbance in Antarctic benthic systems is extreme, from continual abrasion and ice encapsulation to minor effects that only occur with a very low frequency, i.e., hundreds of years. Between ~100 and 500 m the levels of disturbance are intermediate between highly impacted shallow sites (e.g., Peck et al., 1999; Gerdes et al., 2003) and infrequently disturbed deep water, i.e., below 1000–1300 m (Dayton et al., 1994; Gutt et al., 1996).

In summary, the overall species composition of gastropod and bivalve assemblages was similar to found in other Antarctic areas. Replacement of species with depth was more gradual for bivalves than for gastropods. Bivalves showed broader depth ranges, whereas gastropods showed more discrete distributions with depth. Three bathymetric boundaries, common to gastropods and bivalves, could be recognized: (1) a continental shelf zone from 0 to 400 m with a gradual rate of succession; (2) an upper slope zone from 400 to 800 m with a more rapid succession and widespread species; (3) a lower slope zone from 800 to 2000 m (3300 m for bivalves) with a rapid succession caused by a low rate of species addition and high loss of species. Patterns of diversity were complex, and, in general, there were no significant depth-diversity trends.

Acknowledgements

We would like to thank the officers and crews of *Hespérides*, as well as the colleagues who have been supportive in collecting the samples used in this study. This research has been supported by the Spanish Government through the Ministry of Education and Science (MEC). We also thank the three anonymous referees, and Prof. Gooday and Bacon, whose comments improved considerably the original manuscript.

References

- Allen, J.A., Sanders, H.L., 1996. The zoogeography, diversity and origin of the deep-sea protobranch bivalves of the Atlantic: the epilogue. *Progress in Oceanography* 38, 95–153.
- Arnaud, P.M., Hain, S., 1992. Quantitative distribution of the shelf and slope molluscan fauna (Gastropoda, Bivalvia) of the Eastern Weddell Sea (Antarctica). *Polar Biology* 12, 103–109.
- 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.
- Arntz, W.E., Brey, T., Gallardo, V.A., 1994. Antarctic zoobenthos. *Advances in Marine Biology* 32, 241–304.
- Bett, B.J., 2001. UK Atlantic margin environmental survey: introduction and overview of bathyal benthic ecology. *Continental Shelf Research* 21 (8–10), 917–956.
- 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 B* 362, 39–66.
- Br ethes, J.C., Ferreyra, G., De la Vega, S., 1994. Distribution, growth and reproduction of the limpet *Nacella (Patinigera) concinna* (Strebel 1908) in relation to potential food availability in Esperanza Bay (Antarctic Peninsula). *Polar Biology* 14, 161–170.
- Brey, T., Clarke, A., 1993. Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations? *Antarctic Science* 5 (3), 253–266.
- Bromberg, S., Nonato, E.F., Corbisier, T.N., Petti, M.A.V., 2000. Polychaete distribution in the nearshore zone of the Martel Inlet, Admiralty Bay (King George Island, Antarctica). *Bulletin of Marine Science* 67, 175–188.
- Cantera, J.R., Arnaud, P.M., 1985. Les gast eropodes proso-branches des iles Kerguelen et Crozet (Sud de l'Oc ean Indien). Comparaison  cologique et particularit es biologiques. *Comit  National Fran ais des Recherches Antarctiques* 56, 1–170.
- Carney, R.S., 2005. Zonation of deep biota on continental margins. *Oceanography and Marine Biology: An Annual Review* 43, 211–278.
- Cartes, J.E., Carrass n, M., 2004. Influence of trophic variables on the depth-range distributions and zonation rates of deep sea megafauna: the case of the Western Mediterranean assemblages. *Deep-Sea Research I* 51, 263–279.
- Cartes, J.E., Sard , F., 1993. Zonation of deep-sea decapod fauna in the Catalan Sea (western Mediterranean). *Marine Ecology-Progress Series* 94, 27–34.
- Cartes, J.E., Jaume, D., Madurell, T., 2003. Local changes in the composition and community structure of suprabenthic peracarid crustaceans on the bathyal Mediterranean: influence of environmental factors. *Marine Biology* 143, 74–758.
- 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., 1988. Seasonality in the Antarctic marine environment. *Comparative Biochemistry and Physiology* 90B, 461–473.
- Clarke, A., 1991. What is cold adaptation and how should we measure it? *American Zoologist* 31, 81–92.
- Clarke, A., Crame, J.A., 1992. The Southern Ocean benthic fauna and climate change: a historical perspective. *Philosophical Transactions of the Royal Society of London: Biological Sciences* 338 (1285), 299–309.
- Clarke, A., Prothero-Thomas, E., Beaumont, J.C., Chapman, A.L., Brey, T., 2004a. Growth in the limpet *Nacella concinna* from contrasting sites in Antarctica. *Polar Biology* 28, 62–71.
- Clarke, A., Aronson, R.B., Crame, J.A., Gili, J.M., Blake, D.B., 2004b. Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf. *Antarctic Science* 16 (4), 559–568.
- Clarke, A., Griffiths, H.J., Linse, K., Barnes, D.K.A., Crame, A.J., 2007. How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. *Diversity and Distributions* 13, 620–632.
- Clarke, K.R., Gorley, R., 2005. Primer-E version 6.0. Natural Environmental Research Council. Plymouth Marine Laboratory, Plymouth, UK, 91pp.
- Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Plymouth Marine Laboratory, Plymouth, UK, 144pp.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1309.
- Dayton, P.K., Mordida, B.J., Bacon, F., 1994. Polar marine communities. *American Zoologist* 34, 90–99.
- Dell, R.K., 1990. Antarctic mollusca with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand* 27, 1–311.
- 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.
- Etter, R.J., Rex, M.A., 1990. Population differentiation decreases with depth in deep-sea gastropods. *Deep-Sea Research* 37, 1251–1261.
- Gage, J.D., 2004. Diversity in deep-sea benthic macrofauna: the important of local ecology, the larger scale, history and the Antarctic. *Deep-Sea Research II* 51, 1689–1708.
- Gage, J.D., Tyler, P.A., 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge, 492pp.
- Gage, J.D., Pearson, M., Billett, D.S.M., Clark, A.M., Jensen, M., Paterson, G.J.L., Tyler, P.A., 1985. Echinoderm zonation in the Rockall Trough (NE Atlantic). In: Keegan, B.F., O'Connor, B.D.S. (Eds.), *Proceedings of the Fifth International Echinoderm Conference*, Galway, Balkema, Rotterdam, pp. 31–36.
- Gallardo, V.A., 1969. Quantitative benthic survey of the infauna of Chile Bay (Greenwich Island, South Shetland Islands). *Gayana (Zoolog a)* 16, 3–18.
- Gallardo, V.A., 1992. Benthic studies in shallow Antarctic of the South Shetland Island Archipelago. In: Gallardo, V.A., Ferretti, O., Moyano, H.I. (Eds.), *Oceanograf a en Ant rtica-Italia*. Centro Eula, University Concepci n, Concepci n, Chile, pp. 383–393.
- Gallardo, V.A., Castillo, J.G., Retamal, M.A., Ya ez, A., Moyano, H.I., Hermosilla, I.G., 1977. Quantitative studies on the soft-bottom macrobenthic animal communities of shallow Antarctic bays. In: Llano, G.A. (Ed.), *Adaptations within Antarctic Ecosystems*. Proceedings of the Third SCAR Symposium on Antarctic Biology. Smithsonian Institution, Washington, DC, pp. 361–387.

- Gerdes, D., Klages, M., Arntz, W.E., Herman, R.L., Galeron, J., Hain, S., 1992. Quantitative investigations on macrobenthos communities of the southeastern Weddell Sea shelf based on multibox corer samples. *Polar Biology* 12, 291–301.
- Gerdes, D., Hilbig, B., Montiel, A., 2003. Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea. *Polar Biology* 26, 295–301.
- Giribet, G., Wheeler, W.C., 2002. On bivalve phylogeny: a high-level analysis of the Bivalvia (mollusca) based on combined morphology and DNA sequence data. *Invertebrate Biology* 121 (4), 271–324.
- Gordon, A.L., Nowlin, W.D., 1978. The basin waters of the Bransfield Strait. *Journal of Physical Oceanography* 8 (2), 258–264.
- Grassle, J.F., 1989. Species diversity in deep-sea communities. *Trends in Ecology and Evolution* 4, 12–15.
- Grassle, J.F., Maciolek, N.J., 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139, 313–341.
- Gutt, J., 2000. Some “driving forces” structuring communities of the sublittoral Antarctic macrobenthos. *Antarctic Science* 12, 297–313.
- Gutt, J., 2001. On the direct impact of ice on benthic communities: a review. *Polar Biology* 24, 553–564.
- Gutt, J., Starmans, A., Dieckmann, G., 1996. Impact of iceberg scouring on polar benthic habitats. *Marine Ecology Progress Series* 137, 311–316.
- Gutt, J., Buschmann, A., Dijkstra, J., Dimmler, W., Piepenburg, D., Teixidó, N., 1999. Study on benthic resilience of the macro- and megabenthos by imaging methods. *Berichte zur Polarforschung* 301, 17–22.
- Haedrich, R.L., Rowe, G.T., Polloni, P.T., 1975. Zonation and faunal composition of epibenthic populations on the continental slope south of New England. *Journal of Marine Research* 33, 191–212.
- Hain, S., 1990. Die beschalteten Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. *Berichte zur Polarforschung* 70, 1–181.
- Hedgpeth, J.W., 1969. Introduction to Antarctic Zoogeography. Antarctic Map Folio Series, New York.
- Hedgpeth, J.W., 1970. Marine biogeography of the Antarctic regions. In: Holdgate, M.W. (Ed.), *Antarctic Ecology*. Academic Press, London, pp. 97–104.
- Howell, K.L., Billett, D.S.M., Tyler, P.A., 2002. Depth-related distribution and abundance of seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N.E. Atlantic. *Deep-Sea Research I* 49, 1901–1920.
- Huntley, M., Karl, D.V., Niiler, P., Holm-Hansen, O., 1991. Research on Antarctic Coastal Systems Rates (RACER): an interdisciplinary field experiment. *Deep-Sea Research* 38, 911–941.
- Jażdżewski, K., Jurasz, W., Kittel, W., Presler, E., Presler, P., Siciński, J., 1986. Abundance and biomass estimates of the benthic fauna in Admiralty, King George Island, South Shetland Islands. *Polar Biology* 6, 5–16.
- Knox, G.A., 1994. *Benthic Communities. The Biology of the Southern Ocean*. Cambridge University Press, London, pp. 193–220.
- Kvitek, R.G., Conlan, K.E., Iampietro, P.J., 1998. Black pools of death: hypoxic, brine-filled ice gouge depressions become lethal traps for benthic organisms in a shallow Arctic embayment. *Marine Ecology Progress Series* 162, 1–10.
- 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., Brandt, A., 1998. Distribution of epibenthic mollusca on a transect through the Beagle Channel (Southern Chile). *Journal of the Marine Biological Association of the United Kingdom* 78, 875–889.
- Lovell, L.L., Trego, K.D., 2003. The epibenthic megafaunal and benthic infaunal invertebrates of Port Foster, Deception Island (South Shetland Islands, Antarctica). *Deep-Sea Research II* 50, 1799–1819.
- Lowry, J.K., 1975. Soft bottom macrobenthic community of Arthur Harbour. Antarctica. *Antarctic Research Series* 23, 1–19.
- McClain, C.R., Etter, R.J., 2005. Mid-domain models as predictors of species diversity patterns: bathymetric diversity gradients in deep sea. *Oikos* 109, 555–566.
- Menzies, R.J., George, R.Y., Rowe, G.T., 1973. *Abyssal Environment and Ecology of the World Oceans*. Wiley, New York, 488pp.
- Mühlenhardt-Siegel, U., 1988. Some results on quantitative investigations on macrozoobenthos in the Scotia Arct (Antarctica). *Polar Biology* 8, 241–248.
- Mühlenhardt-Siegel, U., 1989. Quantitative investigations of Antarctic zoobenthos communities in winter (May/June) 1986 with special reference to the sediment structure. *Archiv für Fischereiwissenschaft* 39, 123–141.
- Nitsche, F.O., Cunningham, A.P., Larter, R.D., Gohl, K., 2000. Geometry and development of glacial continental margin depositional systems in the Bellingshausen Sea. *Marine Geology* 162, 277–302.
- Nonato, E.F., Brito, T.A.S., De Paiva, P.C., Petti, M.A.V., Corbisier, T.N., 2000. Benthic megafauna of the nearshore zone of Martel Inlet (King George Island, Antarctica) depth zonation and underwater observations. *Polar Biology* 23, 580–588.
- 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.
- Olabarria, C., 2006. Faunal change and bathymetric diversity gradient in deep-sea protobranchs from North-eastern Atlantic. *Biodiversity and Conservation* 15, 3685–3702.
- Paterson, G.L.J., Lambshead, P.J.D., 1995. Bathymetric patterns of polychaete diversity in the Rockall Trough, northeast Atlantic. *Deep-Sea Research I* 42, 1199–1214.
- Peck, L.S., Brockington, S., Vanhove, S., Beghyn, M., 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Marine Ecology Progress Series* 186, 1–8.
- Piepenburg, D., Schmid, M.K., Gerdes, D., 2002. The benthos off King George Island (South Shetland Islands, Antarctica): further evidence for a lack of latitudinal biomass cline in the southern ocean. *Polar Biology* 25, 146–158.
- Ponder, W.F., Lindberg, D.R., 1997. Towards a phylogeny of gastropod molluscs; an analysis using morphological characters. *Zoological Journal of the Linnean Society* 119, 83–265.
- Powell, A.W.B., 1951. Antarctic & Subantarctic Mollusca: Pelecypoda & Gastropoda. *Discovery Reports* 26, 47–196.
- Rex, M.A., 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science* 181, 1051–1053.

- Rex, M.A., 1976. Biological accommodation in the deep-sea benthos: comparative evidence on the importance of predation and productivity. *Deep-Sea Research* 23, 975–987.
- Rex, M.A., 1977. Zonation in deep-sea gastropods: the importance of biological interactions to rates of zonation. In: Keegan, B.F., Ceidigh, P.O., Boaden, P.J.S. (Eds.), *Biology of Benthic Organisms*. Pergamon Press, New York, pp. 521–530.
- Rex, M.A., 1981. Community structure in the deep-sea benthos. *Annual Review of Ecology and Systematics* 12, 331–353.
- Rex, M.A., 1983. Geographic patterns of species diversity in the deep-sea benthos. In: Rowe, G.T. (Ed.), *The Sea*, vol. 8. Wiley, New York, pp. 453–472.
- 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 University Press, Cambridge, pp. 94–121.
- 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. *The American Naturalist* 165 (2), 163–178.
- Rex, M.A., Etter, R.J., Morris, J.S., Crouse, J., McClain, C.R., Johnson, N.A., Stuart, C.T., Deming, J.W., Thies, R., Avery, R., 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology Progress Series* 317, 1–8.
- Rosenberg, G., 2005. Malacolog 4.1: a database of western Atlantic marine mollusca [WWW database (version 4.1.0)] <<http://www.malacolog.org/>>.
- Russo, G.F., Gambi, M.C., 1994. First quantitative data on coastal soft bottoms populations off Terra Nova Bay (Ross Sea, Antarctica): bivalve molluscs. National Scientific Committee, Antarctic Oceanographic Campaign 1989–90, Data Report (1994) II, Ministry of the University and Scientific and Technological Research, Genova.
- Sáiz-Salinas, J.I., Ramos, A., García, F.J., Troncoso, J.S., San Martín, G., Sanz, C., Palacin, C., 1997. Quantitative analysis of macrobenthic soft-bottom assemblages in South Shetland waters (Antarctica). *Polar Biology* 17, 393–400.
- Sanders, H.L., Grassle, J.F., 1971. The interactions of diversity, distribution and mode of reproduction among major groupings of the deep-sea benthos. In: Uda, M. (Ed.), *The Ocean World: Proceedings of Joint Oceanographic Assembly*. Japan Society for the Promotion of Science, Tokyo, pp. 260–262.
- Scheuer, C., Gohl, K., Udintsev, G., 2006. Bottom-current control on sedimentation in the western Bellingshausen Sea, West Antarctica. *Geo-marine Letters* 26, 90–101.
- 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 (4), 615–631.
- Skowronski, R.S.P., Corbisier, T.N., 2002. Meiofauna distribution in Martel Inlet, King George Island (Antarctica): sediment features versus food availability. *Polar Biology* 25 (2), 126–134.
- Troncoso, J.S., Aldea, C., García, F.J., Arnaud, P.M., Ramos, A., 2007. Quantitative analysis of soft bottom molluscs in Bellingshausen Sea and Peter I Island. *Polar Research* 26 (2), 126–134.
- Tyler, P.A., Young, C.M., Clarke, A., 2000. Temperature and pressure tolerances of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri* (Echinodermata: Echinoidea): potential for deep-sea invasion from high latitudes. *Marine Ecology Progress Series* 192, 173–180.
- Vanhove, S., Arntz, W., Vincx, M., 1999. Comparative study of the nematode communities on the southeastern Weddell Sea shelf and slope (Antarctica). *Marine Ecology Progress Series* 181, 237–256.
- Vanhove, S., Beghyn, M., Van Gansbeke, D., Bullough, L.W., Vincx, M., 2000. A seasonally varying biotope at Signy Island, Antarctic: implications for meiofaunal structure. *Marine Ecology Progress Series* 202, 13–25.
- Vinogradova, N.G., Birshteyn, Ya.A., Vinogradov, M.Ye., 1959. Vertical zonality in the distribution of deep-sea fauna. In: Zenkevitch, L.A. (Ed.), *Progress in the Study of the Depths of the Oceans*, pp. 32–74.
- 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.
- Yoon, H.I., Han, M.W., Park, B.K., Han, S.J., Oh, J.K., 1992. Distribution, provenance and dispersal pattern of clay minerals in surface sediments, Bransfield Strait, Antarctica. *Geo-Marine Letters* 12, 223–227.
- Young, C.M., Tyler, P.A., Gage, G.D., 1996. Vertical distribution correlates with pressure tolerance of early embryos in the deep-sea asteroid *Plutonaster bifrons*. *Journal of the Marine Biological Association of the United Kingdom* 76, 749–757.
- Young, C.M., Sewell, M.A., Tyler, P.A., Metaxas, A., 1997. Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal. *Biodiversity and Conservation* 6, 1507–1522.
- Zamorano, J., 1983. Zonación y biomasa de la macrofauna bentónica en bahía South, Archipiélago de Palmer, Antártica. *Serie Científica (INACH)* 30, 27–38.