

Environmental control on the structure of echinoid assemblages in the Bellingshausen Sea (Antarctica)

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Abstract The Bellingshausen Sea is one of the most remote and least surveyed seas of the Southern Ocean, so that little was known about benthic communities and those factors that determine community structuring until recently. The present work aims at characterizing the structure and spatial distribution of echinoid assemblages in the Bellingshausen Sea, as well as identifying the environmental factors that determine assemblage structuring. Echinoids were collected at 32 stations using an Agassiz trawl, at depths of 86–3,304 m, during BENTART oceanographic expeditions led in 2003 and 2006. Sediment and bottom water properties were analysed using an USNEL-type box corer and a Neil Brown Instrument System Mark III CTD, respectively. Echinoids were found at all stations, except Peter I Island. Seventeen species were identified, representing 22 % of the echinoid species present in the Southern Ocean and increasing twofold the number of species recorded in the Bellingshausen Sea so far. The echinoid fauna is dominated by the very abundant species *Sterechinus antarcticus*. Depth is the key factor that determines the nature of echinoid assemblages, which are mainly divided into the continental shelf, the slope and the

deep-sea basin. In addition, sediment properties, namely redox values, organic matter and mud content, best match species dispersion on the shelf. Sediment properties affect echinoid distribution depending on species food range and feeding strategy. As it might be expected, sediment properties more strongly influence specialist feeders (Schizasteridae and Cidaridae) than generalists (Echinidae).

Keywords Abiotic factors · Antarctic · Bellingshausen Sea · Benthos · Diversity · Echinodermata · Echinoidea

Introduction

The echinoid fauna is an important component of Antarctic benthic communities. Sea urchins were frequently sampled from the shallows of the continental shelf to deeper waters of the break, and down to abyssal plains of the Southern Ocean (Arnaud et al. 1998; Barnes and Brockington 2003; David et al. 2005; Brandt et al. 2007; Linse et al. 2008). There are around 80 species of Antarctic echinoids, most of which are endemic to the Southern Ocean (ca. 68 % of sp.). Most species (ca. 65 %) belong to two families: the Cidaridae (20 sp.) and the Schizasteridae (30 sp.), the remaining species being distributed within seven other families (David et al. 2005).

At family level, ecological requirements seem to be essentially determined by feeding strategies, while species of the same family may be distributed with different depth ranges (Brey and Gutt 1991; De Ridder et al. 1992; Jacob et al. 2003; David et al. 2005). In such organisms, and especially those species that are deposit-feeders, we may expect an important influence of sediment granulometry and organic content on echinoid distribution and

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assemblages too (Nichols 1959; Kanazawa 1992). In addition, factors such as biotic processes of the water column (seasonality of primary and secondary productions) and physical parameters (depth and co-varying factors, currents, ice cover, iceberg scouring, sea–floor morphology and sediment characteristics) could determine the abundance, richness or diversity of echinoid assemblages. The co-varying and interrelated contributions of those parameters may differ according to the type of habitat (shallow waters, deep continental shelf or abyssal plains) and to the scale of the study (in time, space and taxonomy). Hence, Antarctic benthic communities seem to match the classic model of shallow-shelf habitats often being tightly coupled to water column processes when both intense seasonality and short pelagic food webs occur (Thrush et al. 2006).

Finally, biological specificities such as reproduction strategies (brooding or larval broadcasting), dispersal capabilities and recruitment seem to influence community structuring (Gutt and Schikan 1998; Bowden 2005; Matallanas and Olaso 2007; Aldea et al. 2008; Hétériér et al. 2008; Linse et al. 2008), especially in the deep-sea where the patchy distribution of communities shows no clear relationships with depth or any other physical factor (Linse et al. 2007; Hétériér et al. 2008).

The present study focuses on the echinoid fauna of the Bellingshausen Sea (BS). Located between Thurston Island to the west and Marguerite Bay to the east (from 70°W to 100°W), the BS is one of the least investigated Antarctic areas by marine biologists, mainly due to remoteness and ice prevalence most parts of the year (Fairbridge 1966; Turner and Owens 1995; Grotov et al. 1998; Clarke and Johnston 2003). Therefore, echinoids of the Bellingshausen Sea were only known by eight species that had been collected over 80 years during four scientific expeditions in the period between 1897 (RV *Belgica*) and 1973 (RV *Hero*). The physical environment of the BS remains poorly documented as well, thereby limiting understanding of species distribution patterns (Gutt et al. in press).

In 2003 and 2006, BENTART expeditions were devoted to sampling in the BS; they have led to a great improvement in our knowledge of the benthos, now available through many scientific publications (García Raso et al. 2005; Matallanas and Olaso 2007; Rios and Cristobo 2007; Troncoso et al. 2007; Aldea et al. 2008; Eakin et al. 2008; García Raso et al. 2008; Troncoso and Aldea 2008; Sáiz-Salinas et al. 2008; Varela and Ramos-Esplá 2008; O'Loughlin et al. 2009). The present work is an attempt to improve our knowledge of echinoid diversity in the BS by addressing the three following questions. (1) Is the Bellingshausen Sea extremely impoverished in echinoids due to unsuitable environmental conditions? (2) What is the structure of echinoid assemblages there? (3) Which are the environmental factors that influence the structure and spatial distribution of echinoid assemblages?

Materials and methods

Field sampling

Sampling was done during BENTART expeditions (Spanish Antarctic Research Program) of the RV 'Hespérides' from January to March 2003 and from January to February 2006. Samples were collected at 32 stations between 86 and 3,304 m depth (Fig. 1; Table 1), using an Agassiz trawl with horizontal and vertical openings of 2.01 and 1.12 m, respectively, and a 10-mm mesh size (Ramos 1995; Arnaud et al. 1998). A USNEL-type box corer with a maximum breakthrough of 60 cm and an effective sampling area of 0.25 m² (Sáiz-Salinas et al. 2008) was used for infaunal organisms and sediments. Hydrographic casts were made with a Neil Brown Instrument System Mark III CTD, and water sampling at different depth was done with Niskin bottles. Suprabenthic samples were collected with a modified Macer-GIRO Q sledge (Carter and Hunter 1994). This sledge was equipped with three superimposed nets (0.5 mm mesh size).

Echinoid systematics

Echinoids were sorted, identified at species level, counted and fixed in 70 % ethanol for further investigations. Taxonomy was based on morphological characters of the test, pedicellariae and spines as described in David et al. (2005).

Environmental data

Nine environmental variables were measured in order to know the water column and bottom features. Sediment redox profiles were analysed immediately after sampling. Redox values were measured with an Orion ORP 9678 electrode coupled to an Orion 3 Star Portable pH meter. A standard ORP solution (Orion 967861) was used as a reference. Analyses of sediment granulometry (gravels %, sand %, mud %) and organic deposit (OD %) were performed following the standard methods detailed in Eleftheriou and McIntyre (2005) and Bale and Kenny (2005). Three granulometric fractions were defined following Wentworth's classification (1922). The total organic deposit (OD %) was estimated from the sediment weight loss after 4 h heating in an oven at 450 °C (see Sáiz-Salinas et al. 2008 for further details).

A 24-bottle Rosette sampler system was used to collect water samples, and a Neil Brown Instrument System Mark III CTD (conductivity, temperature, depth) with additional oxygen and fluorescence sensors was attached at the bottom of the Rosette. The Rosette sampler is equipped with 10-dm³ Niskin bottles.

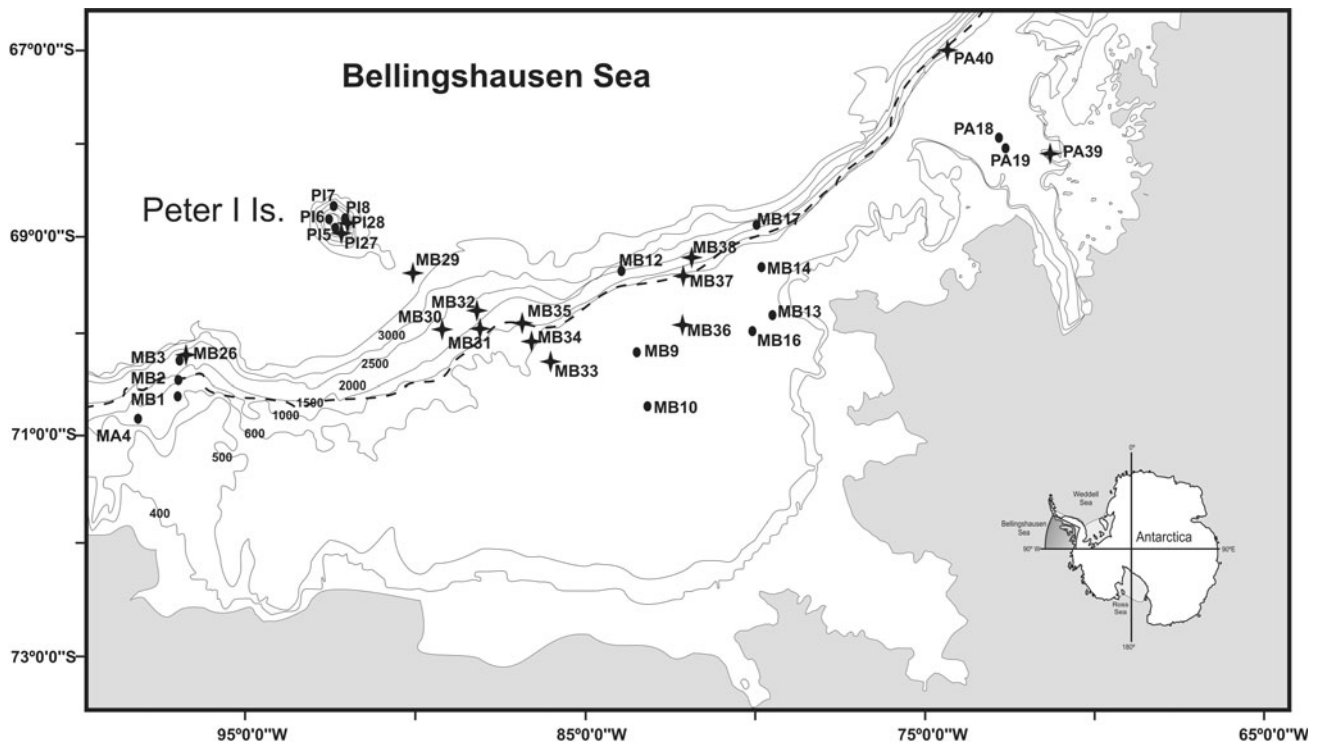


Fig. 1 Sampling area and stations of expeditions Bentart'03 (points) and Bentart'06 (crosses). Dashed line ice cover limit

The Rosette and CTD were deployed, and bottles were closed at predetermined depths. Water samples were used for inorganic nutrient analyses, for the suspended particulate matter (organic carbon and nitrogen), chlorophyll *a* (Chl *a*) and oxygen concentration determinations.

Data analyses

Echinoid species were classified according to their frequency across samples, which is a surrogate to evaluating their importance in the community. It is based on the percentage frequency of occurrence across all stations that is computed and classified into four categories: ubiquitous species (>20 % of stations), very common species (between 10 and 20 %), common species (between 5 and 10 %) and rare or accidental species (<5 %) (Mora 1980; Manjón-Cabeza and García Raso 1994; Manjón-Cabeza and Ramos 2003).

To investigate the structure of echinoid assemblages, similarities between samples were computed by a hierarchical cluster analysis using the UPGMA agglomerative algorithm (Sneath and Sokal 1973; RMACOQUI ver. 1.0 software Olivero et al. 2011).

It was made on the similarity matrix of the Baroni-Urbani coefficients calculated from presence/absence data (Baroni-Urbani and Buser 1976). The robustness of each cluster was supported by a test of biological significance of the boundaries between echinoid assemblages (McCoy

et al. 1986). Strong and weak boundaries were defined between assemblages following McCoy et al. (1986). A strong boundary separates two significantly different clusters with no species in common. A weak boundary separates two significantly different clusters that share common species. When boundaries are not significant, it means that species distribution is homogeneous in the studied area. Boundary analysis follows Olivero et al. (1998).

Stations were plotted using a correspondence analysis and a canonical correspondence analysis computed from the presence/absence matrix and based on the eigenvalues of χ^2 distances between all data points (Ter Braak and Prentice 1988; Hennebert and Lees 1991; Legendre and Legendre 1998), using PAST—paleontological statistics, ver. 1.181 computer program (Hammer et al. 2001). Once identified, the environmental variables that best matched echinoid significant assemblages were selected to run a canonical correspondence analysis (CCA). They were used to define ordination axes on which echinoid data (with both stations and specimens) were plotted. Environmental variables were plotted as well as correlations with ordination axes.

Results

A total of 1,913 specimens of echinoids were examined for this work, and 17 species representing 6 families and 5

Table 1 List of stations with species, environmental data and other data as abundance (per species and per station) (N), species richness (S) and occurrence

Abrev.	Species/stations	MB1	MB2	MB3	MB4	PI5	PI6	PI7	PI8
Order Cidaroida									
Family Cidaridae									
AE	<i>A. eltaniana</i> Mooi et al., 2000								
CP	<i>C. perrieri</i> Koehler, 1912								
CS	<i>C. speciosa</i> Mortensen, 1910								
NG	<i>N. gaussensis</i> Mortensen, 1909								
NL	<i>N. lanceolata</i> Mooi et al., 2000			1	1				
NM	<i>N. mortenseni</i> (Koehler, 1900)			1	1				
Order Echinoida									
Family Echinidae									
SA	<i>S. antarcticus</i> Koehler, 1901		105	8					
AD	<i>S. Koehler</i> , 1926	5							
Order Echinothuroidea									
Family Echinothroidae									
KA	<i>K. asteritas</i> (A. Agassiz, 1881)								
Order Holasteroidea									
Family Plexechinidae									
PP	<i>P. planus</i> (Mironov, 1978)		9						
Family Pourtalesidae									
PD	<i>P. debilis</i> (Koehler, 1926)								
Order Spatangoida									
Family Schizasteridae									
ABE	<i>A. elongatus</i> (Koehler, 1908)								
AL	<i>A. lorioli</i> Koehler, 1901								
AR	<i>A. rostratus</i> (Koehler, 1926)								
AS	<i>A. similis</i> Mortensen, 1936								
TC	<i>T. cordatus</i> (Koehler, 1912)								
TA	<i>T. abatooides</i> (H. L. Clark, 1925)								
N	Abundance (number of specimens)	5	114	10	2	0	0	0	0
N (%)	Abundance (%)	0.26	5.96	0.52	0.10	0.00	0.00	0.00	0.00
S	Species richness	1	2	3	2	0	0	0	0
Lat	Latitude (°)	70.64	70.49	70.29	70.87	68.9	68.8	68.7	68.8
Lon	Longitude (°)	95.17	95.24	95.20	98.44	90.6	90.8	90.7	90.4
D	Depth (m)	523	726	1,432	426	124	220	370	86
OD	Organic deposit (%)	4,808	5,019	5,417	4,56	1,43	1,35	1,85	1,23
G	Gravels (%)	11.15	40.3	14.03	14.18	0.25	0.65	0.08	0.13
S	Sand (%)	32.68	24.48	47.33	31.53	18.6	23.9	11.8	74.1
M	Mud (%)	56.2	35.25	38.6	54.3	81.1	75.5	88.2	25.8
R	Redox	252.2	289.3	259.8	271.3	199	123	175	156
T	Temperature (°C)	1.29	1,049	0.658	1,368	-0.4	1,49	1,87	-1
SI	Salinity (ups)	34.74	34.74	34.73	34.73	34.2	34.6	34.7	34
O ₂	Oxygen (mmol/L)	203	204.9	213.3	197.6	253	199	190	307

Table 1 continued

Abrev.	Species/stations	MB9	MB10	MB12	MB13	MB14	MB16	MB17	PA18
Order Cidaroida									
Family Cidaridae									
AE	<i>A. elatiana</i> Mooi et al., 2000								
CP	<i>C. perrieri</i> Koehler, 1912								
CS	<i>C. speciosa</i> Mortensen, 1910								1
NG	<i>N. gausseusis</i> Mortensen, 1909								
NL	<i>N. lanceolata</i> Mooi et al., 2000								
NM	<i>N. mortenseni</i> (Koehler, 1900)				2	1			2
Order Echinoida									
Family Echinidae									
SA	<i>S. antarcticus</i> Koehler, 1901	30	28	2	25	26	12		17
AD	<i>S. Koehler</i> , 1926							11	
Order Echinothuoidea									
Family Echinothriidae									
KA	<i>K. asterias</i> (A. Agassiz, 1881)								
Order Holasteroidea									
Family Plexechinidae									
PP	<i>P. planus</i> (Mironov, 1978)								1
Family Pourtalesidae									
PD	<i>P. debilis</i> (Koehler, 1926)								
Order Spatangoida									
Family Schizasteridae									
ABE	<i>A. elongatus</i> (Koehler, 1908)								
AL	<i>A. lorioli</i> Koehler, 1901	3	1						
AR	<i>A. rostratus</i> (Koehler, 1926)								
AS	<i>A. similis</i> Mortensen, 1936								
TC	<i>T. cordatus</i> (Koehler, 1912)								
TA	<i>T. abatooides</i> (H. L. Clark, 1925)								
N	Abundance (number of specimens)	33	29	2	27	27	13	11	20
N (%)	Abundance (%)	1.73	1.52	0.10	1.41	1.41	0.68	0.58	1.05
S	Species richness	2	2	1	2	2	2	1	3
Lat	Latitude (°)	70.24	70.74	69.40	69.82	69.35	69.99	68.92	67.96
Lon	Longitude (°)	81.77	81.49	82.22	77.75	78.07	78.32	78.24	71.06
D	Depth (m)	540	494	2,043	608	492	906	1,947	355
OD	Organic deposit (%)	4.05	5.957	3.811	4.639	3.678		1.979	
G	Gravels (%)	8.833	2.475	8.833	30.1	9.25	33.7	33.7	
S	Sand (%)	36.1	23.1	36.1	26.77	27.43	23.78	23.78	
M	Mud (%)	55.07	74.43	55.07	43.2	63.35	42.52	42.52	
R	Redox	260	261.8	266	240.5			224.7	
T	Temperature (°C)	1.152	1.112	0.816	1.148				
SI	Salinity (ups)	34.74	34.74	34.73	34.74				
O ₂	Oxygen (mmol/L)	197.8	197.2	215.6	187.5				

Table 1 continued

Abrev.	Species/stations	PA19	MB26	PI27	PI28	MB29	MB30	MB31	MB32	MB33
Order Cidaroida										
Family Cidaridae										
AE	<i>A. elatiana</i> Mooi et al., 2000									
CP	<i>C. perrieri</i> Koehler, 1912	3								
CS	<i>C. speciosa</i> Mortensen, 1910									
NG	<i>N. gausensis</i> Mortensen, 1909									
NL	<i>N. lanceolata</i> Mooi et al., 2000									
NM	<i>N. mortenseni</i> (Koehler, 1900)									
Order Echinoida										
Family Echinidae										
SA	<i>S. antarcticus</i> Koehler, 1901							5	31	555
AD	<i>S. Koehler</i> , 1926		4				48			
Order Echinothuoidea										
Family Echinothroidae										
KA	<i>K. asterias</i> (A. Agassiz, 1881)					1				
Order Holasteroidea										
Family Plexechinidae										
PP	<i>P. plamus</i> (Mironov, 1978)		7				8	36		
Family Pourtalesidae										
PD	<i>P. debilis</i> (Koehler, 1926)							2		
Order Spatangoida										
Family Schizasteridae										
ABE	<i>A. elongatus</i> (Koehler, 1908)									
AL	<i>A. lorioli</i> Koehler, 1901									
AR	<i>A. rostratus</i> (Koehler, 1926)									
AS	<i>A. similis</i> Mortensen, 1936	1								1
TC	<i>T. cordatus</i> (Koehler, 1912)	1								
TA	<i>T. abatooides</i> (H. L. Clark, 1925)									
N	Abundance (number of specimens)	5	11	0	0	1	56	43	31	556
N (%)	Abundance (%)	0.26	0.58	0.00	0.00	0.05	2.93	2.25	1.62	29.06
S	Species richness	3	2	0	0	1	2	3	1	2
Lat	Latitude (°)	68.07	70.24	69	68.9	69.43	69.98	69.95	69.80	70.27
Lon	Longitude (°)	70.95	95.04	90.4	90.3	88.44	87.52	86.32	86.54	84.19
D	Depth (m)	517	1,920	1,873	1,191	3,304	1,814	1,426	1,849	438
OD	Organic deposit (%)		1.991			8.916	5.31	7.005		4.017
G	Gravels (%)		1.331			1.543	0	58.38		20.11
S	Sand (%)		89.73			13.27	27.78	11.68		48.17
M	Mud (%)		8.935			85.19	72.22	29.95		31.72
R	Redox		178.9			262.1	207.8	187.7		290.2
T	Temperature (°C)		0.551			0.385	0.724	0.563		
SI	Salinity (ups)		34.7			34.7	34.71	34.7		
O ₂	Oxygen (mmol/L)		216.9			109.7	211.3	214.4		

Table 1 continued

Abrev.	Species/stations	MB34	MB35	MB36	MB37	MB38	PA39	PA40	N	N (%)	O (%)
Order Cidaroida											
Family Cidaridae											
AE	<i>A. eltaniana</i> Mooi et al., 2000						27	1	28	1.464	6.25
CP	<i>C. perrieri</i> Koehler, 1912								3	0.157	3.13
CS	<i>C. speciosa</i> Mortensen, 1910			1					1	0.052	3.13
NG	<i>N. gausseensis</i> Mortensen, 1909								1	0.052	3.13
NL	<i>N. lanceolata</i> Mooi et al., 2000			1					3	0.157	9.38
NM	<i>N. mortenseni</i> (Koehler, 1900)			1			2	2	12	0.627	25.00
Order Echinoida											
Family Echinidae											
SA	<i>S. antarcticus</i> Koehler, 1901	23	12	30	559	2	70	100	1,645	85.991	62.50
AD	<i>S.</i> Koehler, 1926								63	3.293	9.38
Order Echinothuoidea											
Family Echinothroidae											
KA	<i>K. asterias</i> (A. Agassiz, 1881)								1	0.052	3.13
Order Holasteroidea											
Family Plexechinidae											
PP	<i>P. planus</i> (Mironov, 1978)	52				4			117	6.116	21.88
Family Pourtalesidae											
PD	<i>P. debilis</i> (Koehler, 1926)								2	0.105	3.13
Order Spatangoida											
Family Schizasteridae											
ABE	<i>A. elongatus</i> (Koehler, 1908)	10							11	0.575	6.25
AL	<i>A. lorioli</i> Koehler, 1901	8		1					13	0.680	12.50
AR	<i>A. rostratus</i> (Koehler, 1926)								1	0.052	3.13
AS	<i>A. similis</i> Mortensen, 1936								1	0.052	3.13
TC	<i>T. cordatus</i> (Koehler, 1912)	1							2	0.105	6.25
TA	<i>T. abatooides</i> (H. L. Clark, 1925)	9							9	0.470	3.13
N	Abundance (number of specimens)	103	12	34	559	6	100	103	1,913	Specimens	
N (%)	Abundance (%)	5.38	0.63	1.78	29.22	0.31	5.23	5.38			
S	Species richness	6	1	5	1	2	4	3	17	Species	
Lat	Latitude (°)	70.14	69.93	69.94	69.44	69.23	68.13	66.96			
Lon	Longitude (°)	84.86	85.18	80.41	80.86	80.07	69.59	72.58			
D	Depth (m)	603	1,117	560	495	1,324	167.1	402			
OD	Organic deposit (%)	1.799	7.36	8.507	5.703	5.981					
G	Gravels (%)	0	47.65	33.15	35.37	65.69					
S	Sand (%)	87.79	14.63	6.124	43.5	7.113					
M	Mud (%)	12.21	37.72	60.72	21.2	27.2					
R	Redox	326	260.7	289	244	298.2					
T	Temperature (°C)	1.173		1.188	1.309	0.862					
SI	Salinity (ups)	34.71	34.71	34.71	34.72	34.71					
O ₂	Oxygen (mmol/L)	198.8	192.9	193.7	193.7	210.5					

orders were identified (Table 1). This is 22 % of the total number of species recorded in the Southern Ocean and only three families are absent: the Arbaciidae, Urechinidae and Temnopleuridae.

New records and distribution data

Very few specimens of *Sterechinus dentifer*, *Kamptosoma asterias* and *Plexechinus planus* were previously recorded in the Southern Ocean (David et al. 2005, Fig. 2). The present new records increase significantly the biogeographic distribution and bathymetric range known so far. *K. asterias* is a new record in the Ross quadrant, and its depth range now extends from 3,304 m to 4,200 m. *S. dentifer* is new in the Weddell and Ross quadrants, and its depth range has been increased towards deeper waters, from 1,600 to 1,920 m. *P. planus* is a new record in the Ross quadrant, and its depth range has been increased from 603 to 1,152 m. Interestingly, the two last species were sampled in relatively high abundance as compared to previous records, and *P. planus* is even classified as ubiquitous (22 %) on the continental break and deep shelf of the Bellingshausen Sea (Fig. 3).

Abundance and species richness

Overall abundance values ($N\%$) were rather low, except for high values at two stations [MB33 (29.06 %) and MB37 (29.2 %)], which are mainly due to high local abundance by specimens of *Sterechinus antarcticus* [MB33 (555 specimens) and MB37 (559 specimens)] (Figs. 3, 4). The next most abundant species were *P. planus* (117 specimens) and *S. dentifer* (63 specimens) (Fig. 3a, b, c). Highest values of species richness (S) were recorded at stations close to the ice shelf [MB34 (6 species) and MB36 (5 species)], while no echinoids were found at stations off Peter I Island during the two surveys (Fig. 4). The three most frequent families are the Echinidae, Schizasteridae and Cidaridae (Fig. 3b), for which samples are characterized either by the exclusive occurrence of a single species at almost all stations (Echinidae) or by a non-exclusive turnover among several species (Cidaridae and Schizasteridae) (Table 1).

Of the 17 species recorded, three species were classified as ubiquitous ($>20\%$): *S. antarcticus*, *Notocidaris mortenseni* and *P. planus*; three as very common (between 10 and 20 %): *Amphipneustes lorioli*, *Notocidaris lanceolata* and *S. dentifer*; three as common (between 5 and 10 %):

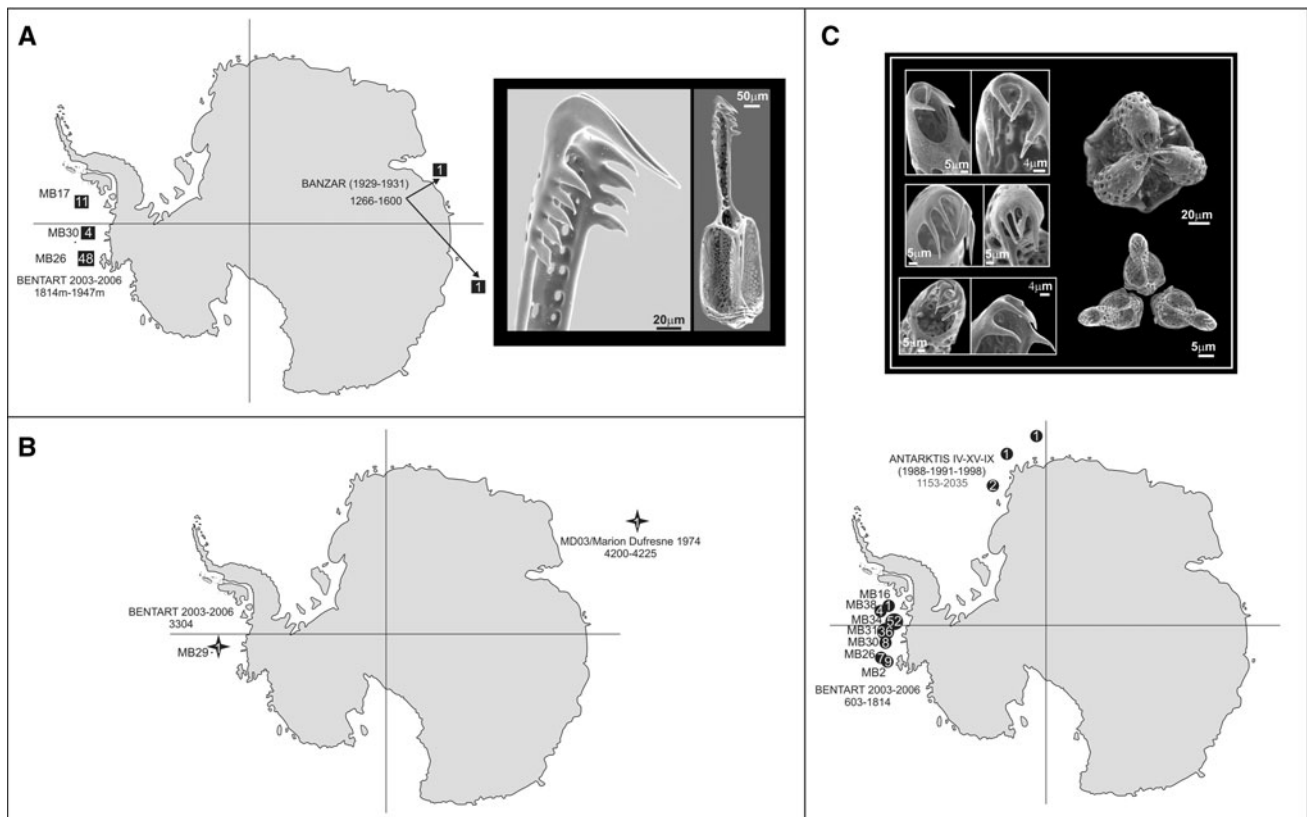


Fig. 2 Antarctic maps showing former and new records for *S. dentifer* (a), *K. asterias* (b) and *P. planus* (c) along with abundance data, BENTART stations and names of former expeditions (number

of the specimens recollected at each station). SEM pictures of pedicellariae of *S. dentifer* (bottom left) and *P. planus* (top left). See also Table 1

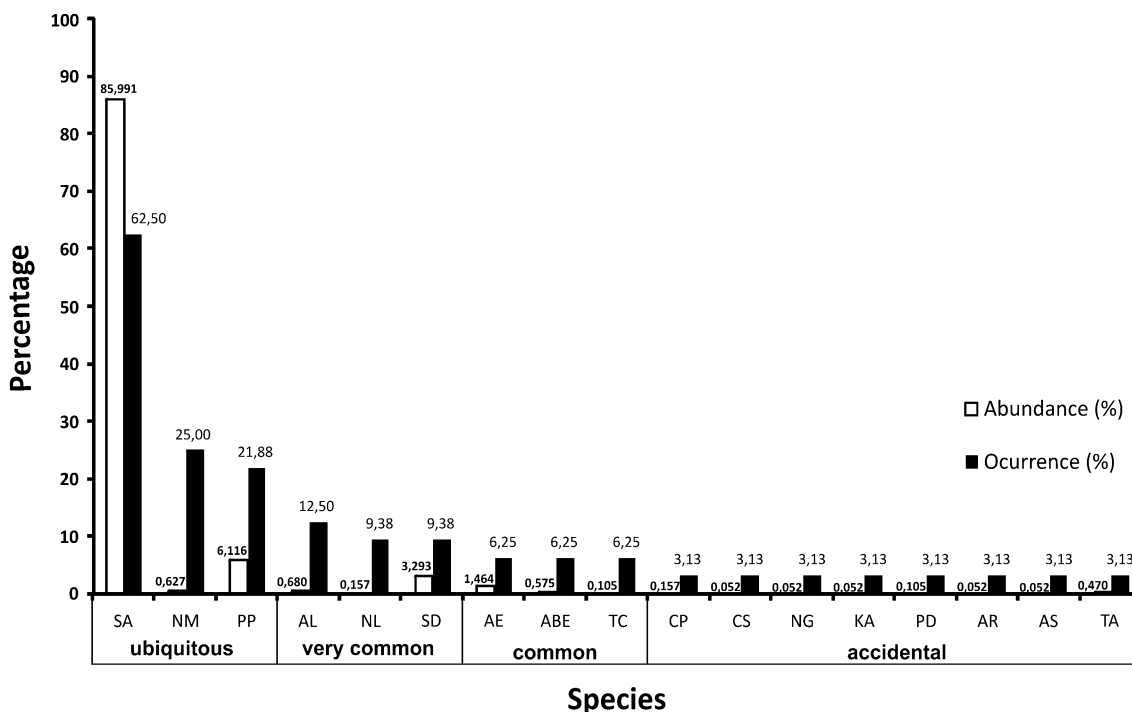


Fig. 3 Relative abundance (N %) and occurrence (%) across stations. Species ranking and classification according to the percentage frequency of occurrence (D): ubiquitous species (Ci > 20 %); very common species (10 % < Ci < 20 %); common species (5 % < Ci < 10 %);

and rare or accidental species (Ci < 5 %) (Mora 1980; Manjón-Cabeza and García Raso 1994; Manjón-Cabeza and Ramos 2003). For abbreviations, see Table 1

Aporocidaris eltaniana, *Tripylus cordatus* and *Abatus elongatus*; eight (i.e. 47 % of species) as accidental species (<5 %): *Ctenocidaris perrieri*, *Ctenocidaris speciosa*,

Notocidaris gaussonis, *Tripylus abatoides*, *Amphipneustes rostratus*, *Amphipneustes similis*, *A. lorioli* and *K. asterias*; and *Pourtalesia debilis* (Fig. 3d).

Fig. 4 Total abundance data (right) and species richness (left). Stations ordered by longitude from left (west) to right (east)

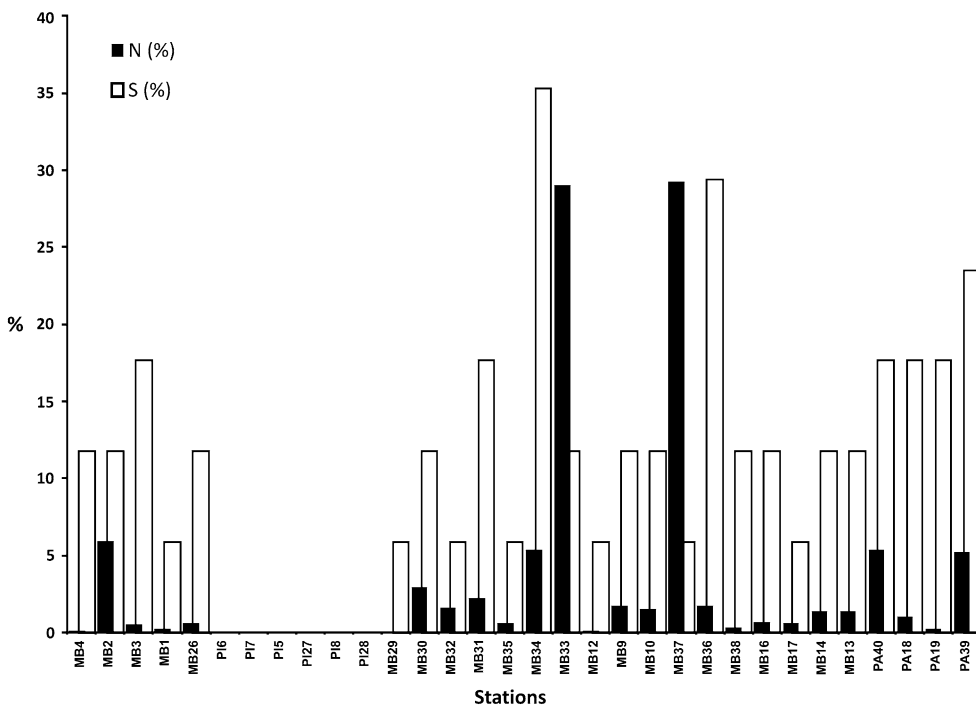
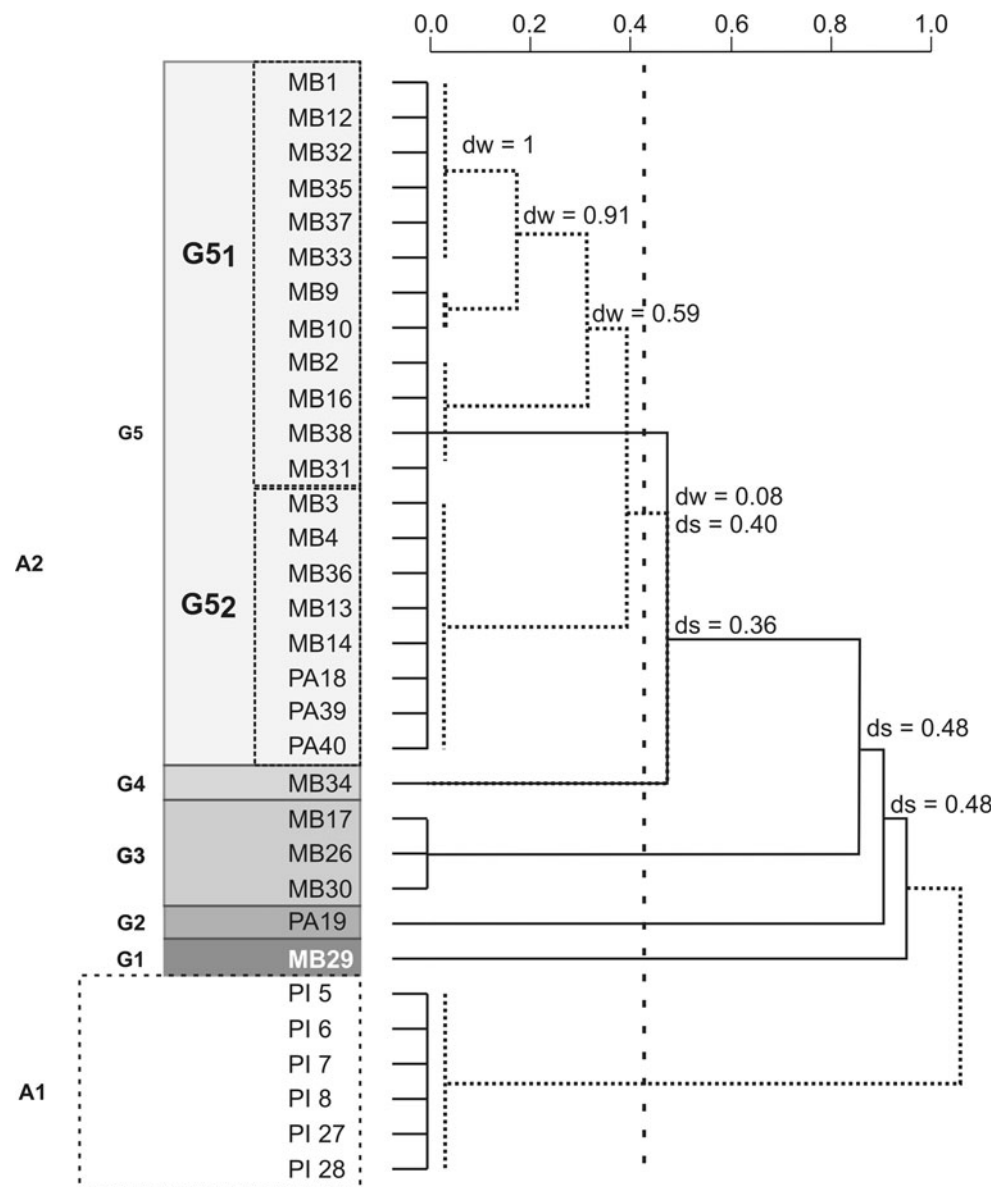


Fig. 5 Qualitative analysis of similarity (Baroni–Urbani index and UPGMA agglomeration algorithm). The segregations versus aggregations are explained in the text (“Results”). *dw* Significant weak boundary, *ds* significant soft boundary



Echinoid assemblages

The cluster analysis (Fig. 5) shows a clear partitioning between two well-defined areas: A1 (Peter I Island) and A2, stations with low values of species richness except for two of them (MB34 and MB36) (Figs. 3, 6). In the A2 grouping, cluster (Fig. 5) and correspondence (Fig. 8) analyses show the existence of five distinctive assemblages separated by strong boundaries and two subgroups by a weak boundary. Species composition of echinoid assemblages is characterized as follows.

- A1 All the stations of Peter I Island are devoid of echinoids
- A2 All the other stations of the Bellingshausen Sea are clustered into the five following assemblages:

- G1 The only true abyssal station characterized by the exclusive presence of *K. asterias*
- G2 Station characterized by two species that are absent from other stations: *A. similis* and *C. perrieri*. Echinidae (*S. antarcticus* and *S. dentifer*) are absent
- G3 Three stations characterized by low abundance and species richness values, and the presence of the deep Echinidae *S. dentifer*
- G4 Station characterized by high abundance and richness values (Figs. 4, 7). Species richness is provided by Schizasteridae and abundance values due to the Plexechinidae *P. planus* and the Echinidae *S. antarcticus*. Cidaridae are absent from the station

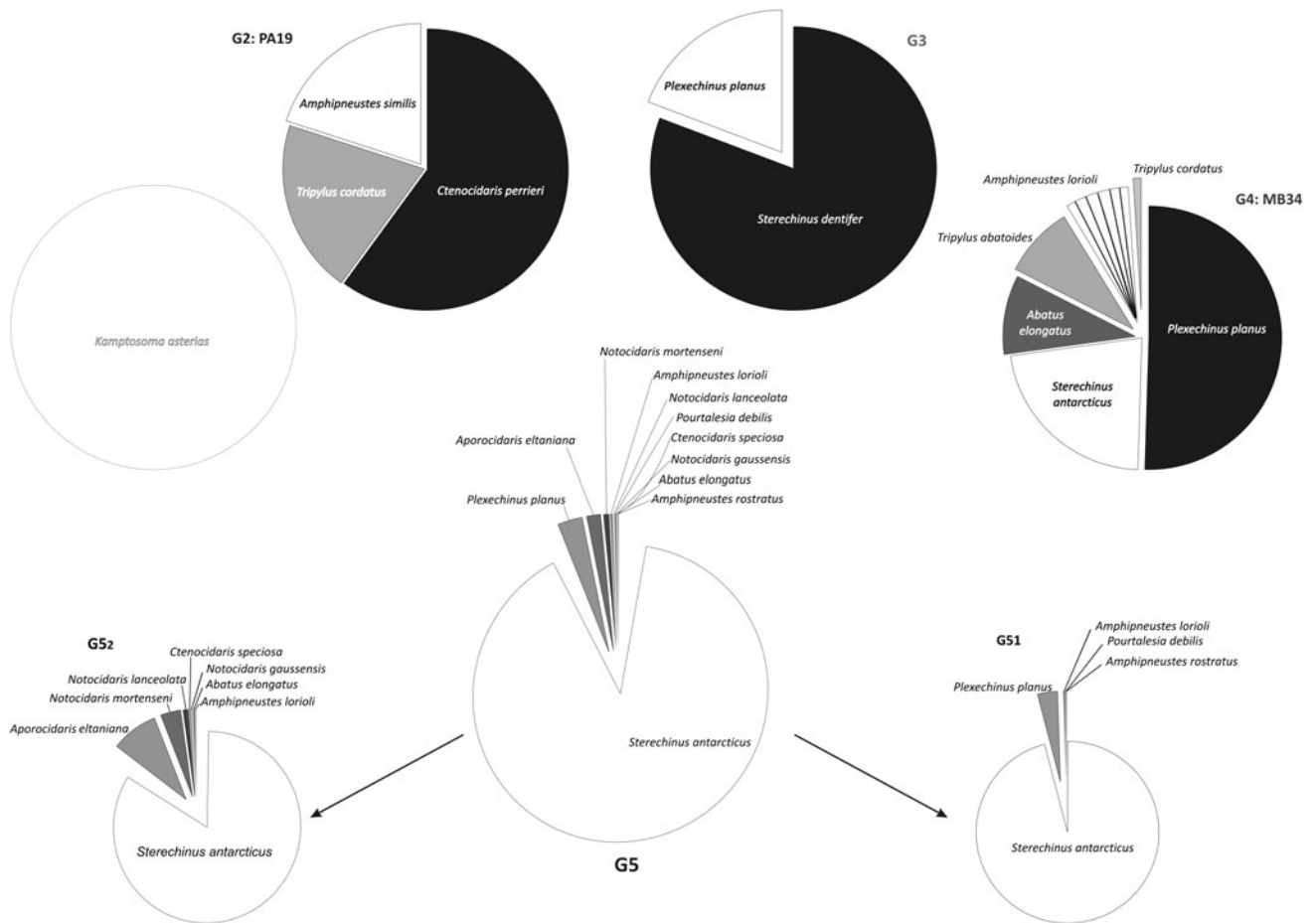


Fig. 6 Composition (abundance %) of echinoid assemblages as defined by the hierarchical cluster analysis and supported by the Baroni–Urbani coefficients

- G5 Abundance is dominated by the Echinidae *S. antarcticus*. No distinction is shown on first axes of the CA (Fig. 8), though the two following subsets are separated by a weak boundary (Fig. 5):
- G5(1) The common feature is the low species richness, only one or two species associated with the ubiquitous *S. antarcticus*, most often *P. planus* or *A. lorioli* depending on depth
- G5(2) Stations characterized by high values of species richness (Figs. 4, 7), mainly due to Cidaridae

The environmental control of echinoid assemblages

Depth, sediment redox values, mud and OD % contents were retained as explanatory variables, and a CCA analysis was carried out to project biotic data in the space of the four environmental variables herein (Fig. 8). Stations from Peter I Island were excluded from the analysis as the CCA does not support that all variable values equal ‘0’.

The two first axes (eigenvalues: $\lambda_1 = 0.60$; $p < 0.001$ and $\lambda_2 = 0.36$; $p = 0.006$ with 10,000 replicate permutation test) clearly show a good match between the four selected environmental variables and echinoid assemblages (Fig. 8). Depth appears as the main factor that controls the dividing of echinoid assemblages into the deep-sea (G1), the slope (G3) and the continental shelf (G4 + G5). Redox values, mud and OD % contents seem to control the partitioning of assemblages on the continental shelf (between G4 and G5, and within G5). Echinoid species were plotted on the two first axes of the CCA to visualize their respective environmental preferences. The main distinction can be made between species exclusive of the deep basin (*K. asterias*), those of the continental slope (*S. dentifer*), the deep species present both on the slope and the shelf (*P. planus*) and species exclusive of the shelf (*S. antarcticus*, Schizasteridae and Cidaridae). Cidaridae are mainly distinguished by their preference for sediments rich in mud and organic matter whereas Schizasteridae are more frequent in low-organic sandy sediments.

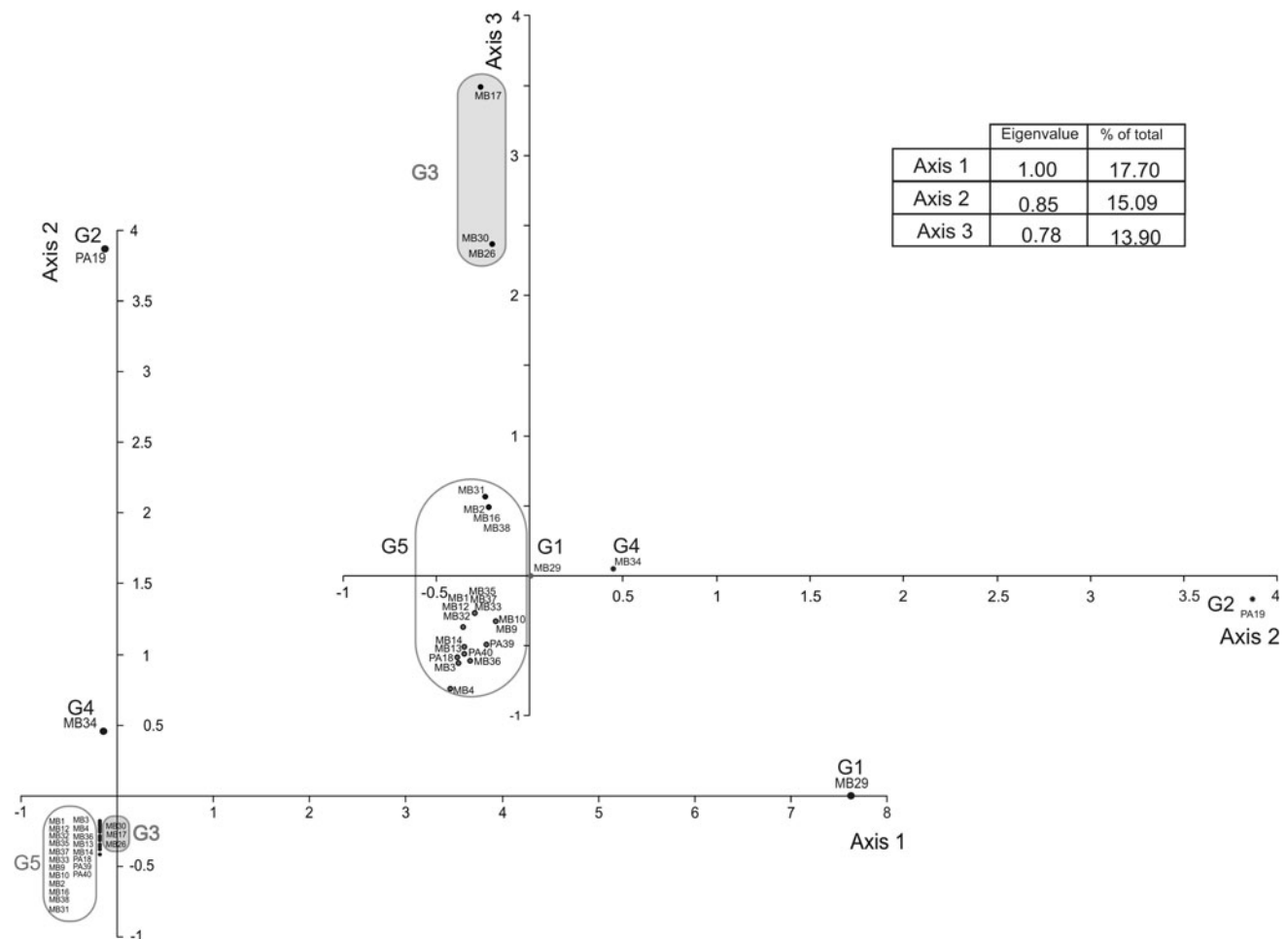


Fig. 7 Correspondence analysis. Groups were defined by the hierarchical cluster analysis and supported by the Baroni–Urbani coefficients

Discussion

Is the Bellingshausen Sea really impoverished in echinoids?

The BS is sometimes considered as a vast ‘benthic desert’ controlled by oligotrophic conditions (Sáiz-Salinas et al. 2008; San Vicente et al. 2009) and intense iceberg traffic (Peck et al. 1999; Gutt 2000). In the Weddell and Ross Seas, dense 3-D communities of filter feeders have been reported, while such a spatial complexity and diversity of habitats seem to be absent from the BS (San Vicente et al. 2009). During BENTART expeditions, eleven new records were added to the catalogue of echinoid species present in the BS. The total number of echinoid species now recorded in the BS is nineteen that is almost 25 % of Antarctic echinoid species. At least for echinoids, the BS is not particularly impoverished compared with previous considerations.

The absence of echinoids off Peter I Island is remarkable and contrasts with other taxa that were sampled there: fish (Matallanas and Olosó 2007), suprabenthic fauna (San

Vicente et al. 2009), decapods (García Raso et al. 2005) gastropods and bivalves (Aldea et al. 2008; Troncoso and Aldea 2008). However, the low values of benthic species richness and of diversity reported (Matallanas and Olosó 2007; San Vicente et al. 2009) along with high local abundance of a few species (Troncoso and Aldea 2008) suggest the prevalence of peculiar ecological conditions. The absence of echinoids could be explained either by unsuitable physical or unfavourable biological conditions, or both. The importance of passive dispersal of larvae by currents to colonization processes were emphasized by Matallanas and Olosó (2007). Brooding is a common feature of many Antarctic echinoids, but frequent species such as *S. antarcticus*, *S. dentifer* and *P. planus* are indirect developers with mobile larvae (Brey and Gutt 1991; David et al. 2005), and recent investigations showed that non-brooders (echinoids) can disperse and colonize shallow waters of remote areas after ice-shelf collapse and intense ice disturbance (Saucède 2008). Peter I Island is a volcanic island that acts as a topographic barrier to currents and shifts the course of the westward-flowing bottom current in

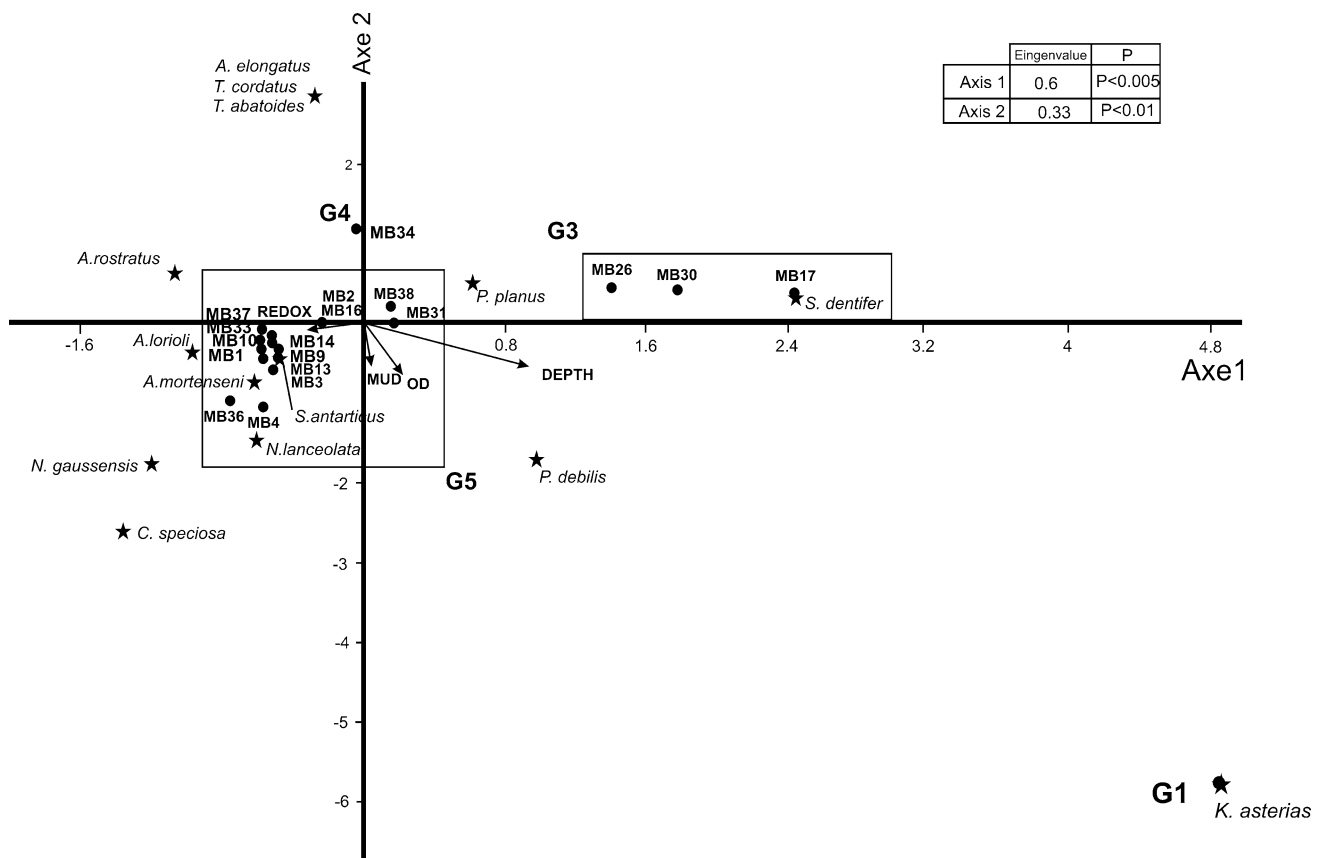


Fig. 8 Canonical correspondence analysis (CCA). Eigenvalues are $\lambda_1 = 0.60$ ($p = 0.0016$) and $\lambda_2 = 0.33$ ($p = 0.0075$) for the two first axes (significance tested by 10,000 replicate permutations). Groups

were defined by the hierarchical cluster analysis and supported by the Baroni–Urbani coefficients

the BS (Scheuer et al. 2006). Current conditions are unlikely to affect dispersal of echinoid larvae to Peter I, as it does not seem to impede dispersal of other taxa. The prevalence of low-organic sediments, low salinity and redox values in Peter I island might reduce the survival of settling echinoid larvae, although echinoids occur under comparable conditions elsewhere.

At the moment, the absence of echinoids is best explained by local benthic conditions, characterized by low-organic sediments along with low salinity and redox values, which might impede echinoid settlement and survival off Peter I Island.

What is the structure of echinoid assemblages?

The structure of echinoid assemblages is essentially related to the distribution and abundance of Echinidae: *S. dentifer* on the continental break and *S. antarcticus* on the continental shelf. The abyssal echinoid *K. asterias* characterizes the deep-sea basin. On the continental shelf, assemblages are determined by cidarid distribution. Schizasteridae and Cidaridae are by far the most diversified echinoid families in the Southern Ocean (David et al. 2005). Schizasteridae

were collected at all stations of the continental shelf, whereas Cidaridae were sometimes missing. Interestingly, Schizasteridae and Cidaridae were not collected outside the shelf, though both families are represented by deep-sea species in the Southern Ocean (David et al. 2005).

Abundance, species richness and diversity values are low in the deep-sea basin and on the continental break (Figs. 3, 7), but there is no significant trend of decreasing values with depth on the continental shelf. This is consistent with previous results on bivalves and gastropods (Aldea et al. 2008).

Which are the environmental factors that best match the structure and spatial distribution of echinoid community?

Depth and sediment characteristics, mainly redox values, organic and mud contents have been reported to be controlling benthic assemblages on the continental shelf of the BS (Sáiz-Salinas et al. 2008; Troncoso and Aldea 2008; San Vicente et al. 2009). Current intensity, bottom morphology and ice disturbance (iceberg scouring) have been pointed out too (Starmans et al. 1999; Gutt 2000; Barry

et al. 2003; Sáiz-Salinas et al. 2008), while others noticed the importance of life strategies and dispersal capabilities (Aldea et al. 2008; Matallanas and Olaso 2007).

Depth is the factor that best discriminates among main echinoid assemblages, which are divided into the deep-sea basin, the continental slope and the shelf. On the shelf, sediment characteristics—redox values, organic and mud contents—best explain the distribution patterns of Schizasteridae and Cidaridae. The significant contribution of sediment characteristics on echinoid distribution can be explained by differences in food ranges and feeding strategies among echinoid families that feed and live on the sediment. This is also explained by a stronger control of sediment characteristics on the distribution of specialist feeders (Schizasteridae and Cidaridae) than on that one of generalists (Echinidae) (Jacob et al. 2003; David et al. 2005). Schizasteridae are deposit-feeders that are able to plough and burrow into the sediment, and some can tolerate relatively low-organic sandy substrates. In contrast, Cidaridae are epibenthic echinoids and mostly scavengers that are more dependent on the biomass and type of organic deposits (animal matter or organic detritus) present on the sea floor (De Ridder and Lawrence 1982; David et al. 2005).

In the present work, depth just discriminates between the two species of Echinidae, *S. antarcticus* and *S. dentifer* but not among species of Cidaridae nor Schizasteridae. The genus *Sterechinus* is the only Antarctic representative of the family Echinidae and is represented by three species—*Sterechinus neumayeri*, *S. antarcticus* and *S. dentifer*—which occupy different depth ranges (Brey and Gutt 1991; David et al. 2005). Patterns of distribution among species of Schizasteridae and Cidaridae are much less clear (David et al. 2005).

Conclusion

This study shows how complex it can be to interpret distribution patterns when different factors—herein, depth and sediment characteristics—interfere at different scales (geographic and taxonomic) to control biotic assemblages.

On a large scale, the impact of environmental parameters such as depth and sediment characteristics on benthic assemblages has been questioned (Gutt 2000). In the BS, echinoid assemblages were partly explained by those parameters. However, complementary studies of other parameters might help understand more clearly the relationship between those patterns and environmental parameters.

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