Quantitative analysis of soft-bottom polychaetes of the Bellingshausen Sea and Gerlache Strait (Antarctica)

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Abstract

The basin off the Bellingshausen Sea, in contrast to other better known areas such as the Antarctic Peninsula and the Ross and Weddell Seas, has been little investigated due to remoteness and the prevalence of ice for most of the year. The present study focuses on an analysis of polychaetes collected from soft bottoms of this sea and off the west coast of the Antarctic Peninsula (Gerlache Strait) by means of a box-corer (25×25 cm) in two intensive surveys carried out during austral summers of 2002–2003 and 2005–2006 (BENTART-03 and BENTART-06). Three different polychaete assemblages were determined from the classification and ordination analyses of sampling stations based on the Bray-Curtis similarity index. One group of stations encompassed the deep stations from the shelf of the Bellingshausen Sea, the second one the shallower stations from the same area and the third one those stations located near the coast of Peter I Island and Gerlache Strait, off the Antarctic Peninsula. The environmental variables involved in segregating these groups were several sedimentary features (redox potential, gravel content) and depth. The present study provides further support to previous ones that considered the shelf of the Bellingshausen Sea as a differentiated region within the Southern Ocean, clearly distinct to the adjacent Weddell and Scott Seas and the Antarctic Peninsula.

Keywords

Introduction

Factors determining composition and spatial distribution of marine soft-bottom communities are numerous and acting at different spatial scales. The sediment characteristics (e.g., chlorophyll a content, sorting coefficient and organic matter content) are among those factors (Gray 1974), as the relationship between sediment and fauna constitutes a crucial aspect explaining the benthic ecology (Rhoads 1974) also in soft-bottom polar habitats (Gerdes et al. 1992). Other factors thought to be important as structuring agents of Antarctic benthic assemblages are hydrodynamics (Wu et al. 1992a, b), primary production in surface waters (Arrigo et al. 1998), flow of organic matter from the pelagic realm to the seabed (Grebmeier and Barry 1991) and iceberg scouring (Gutt and Starmans 1998, 2001; Gutt 2000, 2001; Gutt and Piepenburg 2003), the latter being particularly important in shallow water communities (Smale et al. 2007; Smale 2008a, b).

The Bellingshausen Sea represents a very interesting Antarctic area because it constitutes a natural connection between the Ross Sea and the Antarctic Peninsula; this area also has high zoogeographical importance because of its role in the dispersion of species around the waters of the Antarctic continent and South America through the Scotia Arc (Saiz et al. 2008). Due to its remoteness and the prevalence of ice during most of the year, the Bellingshausen Sea was much less visited by research vessels and less studied compared to the Weddell and Ross Seas or the Antarctic Peninsula, where many countries have carried out vast research programs in past decades (e.g., Arntz et al. 1994; Guglielmo et al. 2000; Brandt et al. 2004).

Polychaetes are one of the most relevant components of Antarctic soft-bottom macrobenthic assemblages (Arnaud 1974; Knox 2007) contributing substantially to the benthic community both in terms of abundance and biomass (e.g., Gerdes et al. 1992; Saiz-Salinas et al. 1997; Piepenburg et al. 2002). Only little and scarce information on the composition and structure of the polychaete fauna of the Bellingshausen Sea is yet available, whereas more information exists about these organisms in other parts of Antarctica (e.g., Hartmann-Schröder and Rosenfeldt 1988, 1989, 1990, 1991, 1992; Cantone et al. 2000; Cantone and di Pietro 2001; Hilbig 2001, 2004; Hilbig et al. 2006; Schüller and Ebbe 2007; Schüller and Hilbig 2007; Schüller 2008a; Schüller et al. 2009). Past data derive mainly from European cruises done in the first half of the twentieth century (Augener 1932; Fauvel 1936) and more recent US American expeditions (Hartman 1952, 1967; Maciolek and Blake 2006).

The present study draws upon the polychaete material collected in two intensive surveys conducted off the north-west coast of the Antarctic continent in the frame of the Spanish BENTART-03 and BENTART-06 cruises. The study of the polychaete collections obtained from two previous cruises to the Antarctic Peninsula, namely BENTART-94 and BENTART-95, was already published by Parapar and San Martín (1997), San Martín and Parapar (1997) and San Martín et al. (2000).

The aim of this work is to analyse the species composition, abundance and distribution of the polychaete fauna in the shelf and slope of the Bellingshausen Sea and adjacent areas in order to characterize their assemblages present on the sea floor, to identify the environmental factors that may affect and/or determine the distribution of the species and to compare our results with those available on other groups in the same area, either benthic or suprabenthic, such as molluscs (Troncoso et al. 2007; Troncoso and Aldea 2008), fishes (Matallanas and Olaso 2007) and cumaceans (Corbera et al. 2009), and with the whole collected infauna and suprabenthos studied at higher taxonomic level (Saiz et al. 2008; San Vicente et al. 2009).

Materials and methods

Study area and sample collection

The material analysed in this study was obtained during the Spanish oceanographic cruises BENTART-03 (24 January to 3 March 2003) and BENTART-06 (2 January to 17 February 2006) on board the R/V *Hespérides*. Samples were collected from 40 stations distributed along the NW sector of the Antarctic Ocean, from the Antarctic Peninsula (mainly from Gerlache Strait) (AP) to the Thurston Island in the Bellingshausen Sea (BS) and the proximity of the Peter I Island (PI) (Fig. 1). Benthic polychaetes from the soft bottoms were collected by different sampling gears (Agassiz trawl, Suprabenthic sledge and box-corer) but only the material taken with the USNEL-type box-corer (BC) with a maximum breakthrough of 60 cm and an effective surface of sampling of 25×25 cm was considered for the present work. When possible, two duplicate samples per station were collected. Each BC sample was subdivided into four equal sub-samples of 0.063 m^2. The first sub-sample was immediately used on board to measure redox (Eh) and later to analyse sediment grain size and content of carbonates and organic matter. The three remaining sub-samples (or one coming from the first BC and two equivalent sub-samples from the second BC if two samples were collected at the station) were used for quantitative assessment of the fauna. For this purpose, the collected sediment was sieved through three mesh sizes (5, 1 and 0.5 mm); the polychaetes collected in the two larger sieves were counted on board to estimate their relative abundance within the total macrobenthic fauna collected. Then, all the specimens were fixed on board in a buffered 4% formaldehyde seawater solution and afterwards preserved in 70% ethanol. More detailed description of sampling gear, sampling method and sediment abiotic variables analysis can be found in Saiz et al. (2008).

The use of the box-corer and its effectiveness in sampling were limited by weather conditions; for this reason, only 30 stations were sampled with this gear, 28 of which provided polychaete specimens. The geographical positions of the stations are reported in Fig. 1, and their location and depth (ranging from 90 to 3,304 m), as well as the studied environmental variables, are given in Table 1.

Data analysis

A species/abundance matrix was created, summarizing the actual number of individuals of each polychaete species present in each station, respectively, the sum of the three sub-samples. Statistical analysis was carried out using the PRIMER v5.0 (Plymouth Routines In Multivariate Ecological Research) software package (Clarke and Warwick 1994). Univariate measures were computed for each station: total abundance (N), number of species (S), Margalef diversity index (d), Shannon-Wiener diversity index (H' $\log_e$ based) and Pielou's evenness (J') based on Shannon-Wiener index. A second matrix was derived from the abundance matrix, showing the similarity between stations by means of the Bray-Curtis coefficient, after data have been log-transformed ($X = \log (x + 1)$) to limit the influence of the most dominant species. From this matrix, a classification of the stations was performed by cluster analysis based on the group-average sorting algorithm. A non-metric Multi-Dimensional Scaling (nMDS) ordination was also performed based on the similarity matrix. The SIMPER (similarity percentage) application was used to identify species that contributed in higher proportion to the differentiation of station groups.

The BIO-ENV procedure was used to investigate the relationship between polychaete assemblages and the measured abiotic variables, although station AP39 was excluded from this analysis because of the lack of environmental data. All environmental variables were $\log (x + 1)$ transformed previously to analysis. The variables considered were depth (m), organic matter content (%) and percentage of

each granulometric fraction (%), whereas carbonates were discarded from the analysis because of the lack of data in a large number of stations. The assessment of the importance of the redox potential at the surface of the sediment posed a problem, since in stations BS14 and AP25 such data were missing. Thus, BIO-ENV procedure was carried out in a twofold way: first the application was run considering all the stations without the redox potential, and then it was re-run considering all the variables but eliminating stations BS14 and AP25. In order to check the stability of the groups obtained from cluster and nMDS, these analyses were re-computed without considering the two rejected stations.

The statistical level of significance of differences between groups regarding to mean values of faunistic and environmental parameters was checked by means of a non-parametric test (Kruskal–Wallis), which was carried out using the SPSS v16.0 statistical package. The differences were considered significant when $P < 0.05$.
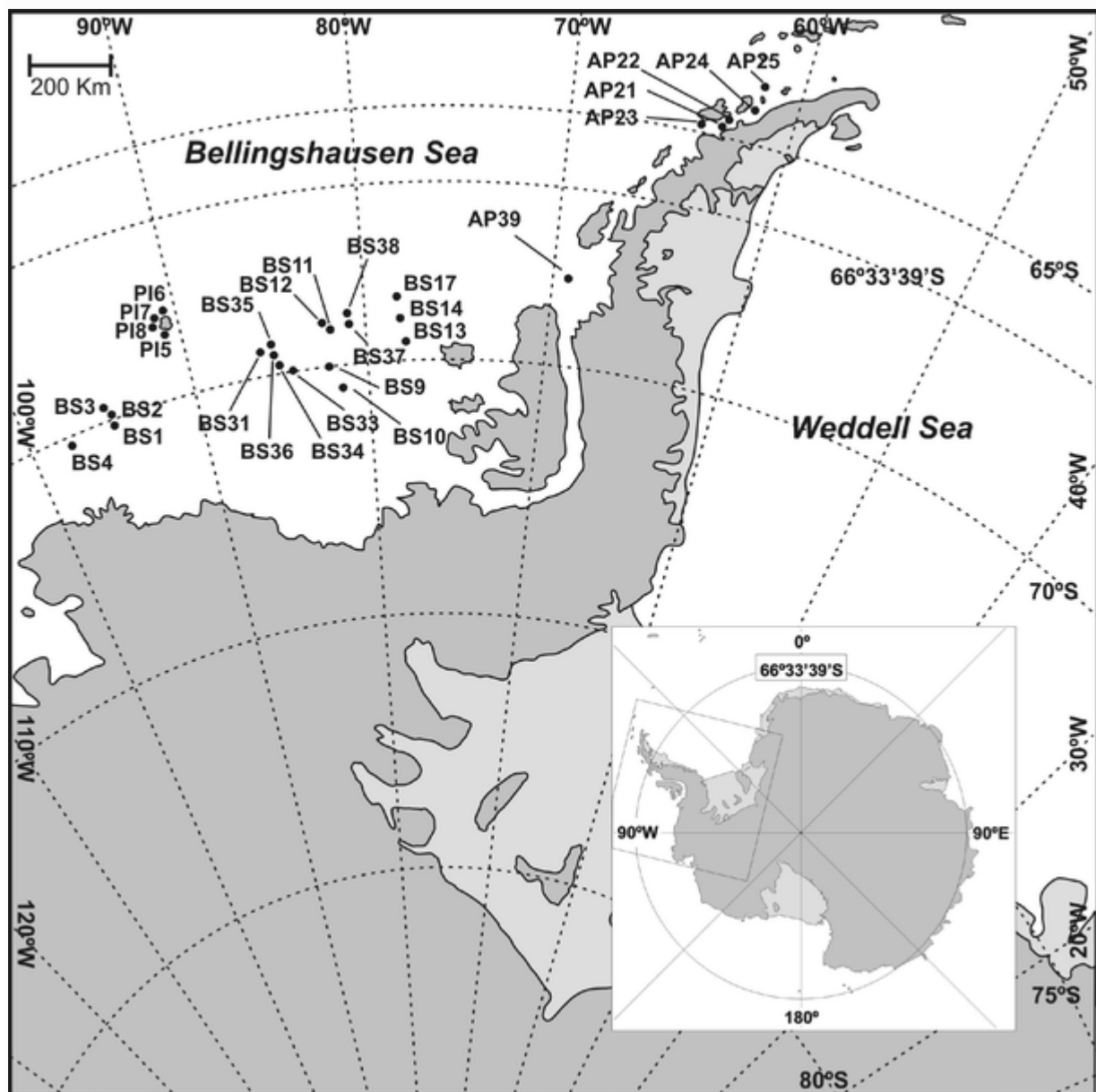

Fig. 1 Study area showing box-corer sampling stations surveyed during the BENTART-03 and BENTART-06 cruises with polychaete specimens. *AP* Antarctic Peninsula, *BS* Bellingshausen Sea, *PI* Peter I Island

Table 1 Location, depth and environmental parameters at the surface of sediment of the surveyed stations: Depth (m), redox potential (mV), organic matter (%), carbonates (%), gravel (>2 mm, %), coarse sand (>0.5 mm, %), medium sand (>0.25 mm, %), fine sand (>0.0625 mm, %) and mud (<0.0625, %)

Station	Latitude S	Longitude W	Depth	Redox	OM	Carbonates	Gravel	CS	MS	FS	S + C
BS1	70º38.22′	95º15.36′	534	252.2	4.81	n.d.	14.30	7.90	7.50	19.10	51.20
BS2	70º29.25′	95º14.83′	780	289.3	5.02	n.d.	81.40	1.80	1.10	4.20	11.50
BS3	70º17.58′	95º11.86′	1,431	259.8	5.42	n.d.	29.00	4.30	3.40	30.50	32.80
BS4	70º52.86′	98º26.12′	425	271.3	4.56	n.d.	31.00	9.60	5.40	16.40	37.60
PI5	68º56.70′	90º35.70′	126	199.3	1.43	n.d.	0.14	0.14	0.32	19.50	79.90
PI6	68º49.61′	90º48.78′	210	122.5	1.35	n.d.	0.00	0.10	0.10	21.00	78.80
PI7	68º42.20′	90º40.80′	410	174.8	1.85	n.d.	0.00	0.20	0.20	6.10	93.50
PI8	68º50.18′	90º51.08′	90	155.8	1.23	n.d.	0.10	0.80	4.90	58.90	35.30
BS9	70º14.40′	81º47.03′	532	261.8	5.96	n.d.	3.90	6.10	4.40	12.40	73.20
BS10	70º44.31′	81º27.85′	497	260.0	4.05	n.d.	15.80	5.20	7.90	16.40	54.70
BS11	69º27.07′	82º06.76′	1,289	266.0	3.81	n.d.	22.40	8.50	3.70	10.60	54.80
BS12	69º24.27′	82º11.88′	2,032	261.5	5.29	n.d.	23.00	11.10	5.80	18.06	42.04
BS13	69º49.56′	77º43.68′	605	240.5	4.64	n.d.	10.20	3.60	4.10	17.50	64.60
BS14	69º21.12′	78º04.91′	498	n.d	3.68	n.d.	34.70	5.10	3.80	11.70	44.70
BS17	68º54.88′	78º14.16′	2,044	224.7	1.98	n.d.	64.50	18.60	3.90	2.90	10.10
AP21	64º54.01′	63º01.11′	107	133.5	2.49	n.d.	4.40	14.80	17.90	34.80	28.10
AP22	64º50.58′	62º57.91′	294	137.0	6.40	n.d.	0.00	0.00	0.30	3.20	96.50
AP23	64º55.95′	63º38.40′	655	272.5	6.75	n.d.	0.00	0.50	0.50	7.10	91.90
AP24	64º20.11′	61º58.82′	1,056	170.5	8.32	n.d.	0.00	0.24	0.23	1.63	98.00
AP25	63º52.85′	61º48.52′	110	n.d.	1.16	n.d.	23.80	22.90	13.50	36.30	3.50
BS31	69º56.98′	86º19.27′	1,426	207.8	5.31	2.54	0.00	2.22	4.81	20.74	72.22
BS33	70º15.90′	84º11.45′	438	290.2	4.02	1.38	20.11	12.99	8.86	26.32	31.72
BS34	70º08.20′	84º51.68′	603	326.0	1.80	1.27	0.00	12.91	14.98	59.89	12.21
BS35	69º56.03′	85º11.30′	1,117	260.7	7.36	2.40	47.65	3.78	1.73	9.13	37.72
BS36	69º56.28′	80º24.55′	560	289.0	8.51	0.47	33.15	1.08	1.08	3.96	60.72
BS37	69º26.38′	80º51.62′	495	244.0	5.70	0.64	35.37	17.04	10.27	16.16	21.27
BS38	69º14.08′	80º61.20′	1,324	298.2	5.98	0.83	65.69	3.14	1.26	2.72	27.20
AP39	68º07.78′	69º35.31′	167	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

CS Coarse sand, *MS* Medium sand, *FS* Fine sand, *OM* Organic matter, *S + C* Silt and clay, *n.d.* Not determined

Results

A total of 1,328 polychaete specimens were collected belonging to 28 families (Appendix). Seventy-seven taxa were identified to species level; for the remaining 14 taxa, the systematic attribution was limited by the fact that the collected specimens were incomplete or badly damaged ("undet.") or belonged to poorly known genera or family that need a thorough revision to be properly classified ("sp.").

Faunistic parameters

The most diverse family in number of species was Maldanidae (7 species), followed by Spionidae and Terebellidae (6 species), while the best represented families in terms of abundance (number of individuals) were Maldanidae (344 specimens), Terebellidae (196) and Cirratulidae (162) with the maldanid *Rhodine intermedia* (182 individuals), the cirratulid *Aphelochaeta cincinnata* (120 individuals), the terebellid *Pista spinifera* (91 individuals) and the spionid *Laonice antarcticae* (86 individuals) being the most abundant species.

Number of species (S), abundance (N), diversity (H') and evenness (J') all varied widely in the studied area (Table 2). The variability among stations in terms of number of species and abundance showed strong differences according to geographical position (Fig. 2). Values of the samples from Peter I Island (PI) and Antarctic Peninsula (AP) were generally higher than those in the Bellingshausen Sea (BS), especially regarding the abundance. The number of polychaete individuals occurring in each station (Table 2) ranged from 2 (stations BS12, BS31, BS33 and BS35) to 296 (station AP21); in the same way, the species number showed its minimum (2) in the group of stations with lower abundances, whereas in station AP21, the highest number of species was achieved (44).

The values of diversity indexes (Table 2) paralleled those of species number. Both Margalef and Shannon-Wiener indexes were lowest in stations BS12, BS31, BS33 and BS35 ($d = 1.44$; $H' = 0.69$, respectively); maximum values were recorded in AP39 ($d = 5.77$; $H' = 2.89$) and AP21 ($d = 7.56$; $H' = 2.97$). Values for J' were usually higher than 0.6, except for stations PI8 (0.48) and AP23 (0.55).

Polychaete assemblages and community structure

Three major groups of stations could be identified in the plot resulting from the cluster analysis (Fig. 3), although the similarity was low (below 20%). Group A1 (similarity around 14.21%) included most of the stations located within the Bellingshausen Sea, whereas BS4, BS9 and BS33 formed the group A2 that is a smaller cluster linked to the former at a low similarity value (23.62%). Group B (similarity 17.81%) included those stations located around Peter I Island or off the Antarctic Peninsula and Gerlache Strait. These three groups were also apparent in the nMDS analysis (Fig. 4a) based on Bray-Curtis similarity. The groups A1 and A2 were well defined and occupied the left half of the plot, whereas the group B appeared clearly segregated from them in the right half. There were differences among clusters in mean abundance and number of species per station. Thus, groups A1 and A2 have similarly low average numbers of individuals (mean ± standard deviation; 7.69 ± 5.30 and 10.00 ± 7.00, respectively) and species (5.77 ± 3.27 and 7.00 ± 4.58) while the mean number of individuals (118.40 ± 5.30) and species (18.20 ± 10.54) was higher in group B; differences were statistically significant for these two parameters ($P = 0.000$ for number of individuals and $P = 0.001$ for number of species). Diversity values were consistently higher in stations of group B (average $d = 3.61 ± 1.85$, average $H' = 1.97 ± 0.61$) than those in group A1 (average $d = 2.38 ± 0.80$; average $H' = 1.51 ± 0.58$) and A2 (average $d = 2.62 ± 1.13$, average $H' = 1.67 ± 0.87$); however,

confidence levels were not enough to warrant statistical significance ($P = 0.138$ for d and $P = 0.355$ for H').

Table 2 Ecological parameters at each station

Station	S	N	d	H'	J'
BS1	5	5	2.49	1.61	1.00
BS2	3	3	1.82	1.10	1.00
BS3	9	10	3.47	2.16	0.98
BS4	7	8	2.89	1.91	0.98
PI5	15	88	3.13	2.09	0.77
PI6	14	118	2.72	1.79	0.68
PI7	18	87	3.81	2.04	0.71
PI8	22	176	4.06	1.48	0.48
BS9	5	6	2.23	1.56	0.97
BS10	7	11	2.50	1.77	0.91
BS11	8	13	2.73	1.93	0.93
BS12	2	2	1.44	0.69	1.00
BS13	6	9	2.28	1.58	0.88
BS14	13	20	4.01	2.42	0.94
BS17	4	5	1.86	1.33	0.96
AP21	44	296	7.56	2.97	0.78
AP22	9	70	1.88	1.48	0.67
AP23	14	135	2.65	1.45	0.55
AP24	7	94	1.32	1.22	0.63
AP25	14	56	3.23	2.31	0.88
BS31	2	2	1.44	0.69	1.00
BS33	2	2	1.44	0.69	1.00
BS34	11	15	3.69	2.34	0.98
BS35	2	2	1.44	0.69	1.00
BS36	8	13	2.73	1.99	0.96
BS37	8	10	3.04	2.03	0.97
BS38	6	8	2.40	1.67	0.93
AP39	25	64	5.77	2.89	0.90

S number of species, N number of specimens collected in 1,875 cm^2, d Margalef diversity index, H' Shannon-Wiener diversity index, $\log_e$ based, J' Pielou evenness index, based on H'
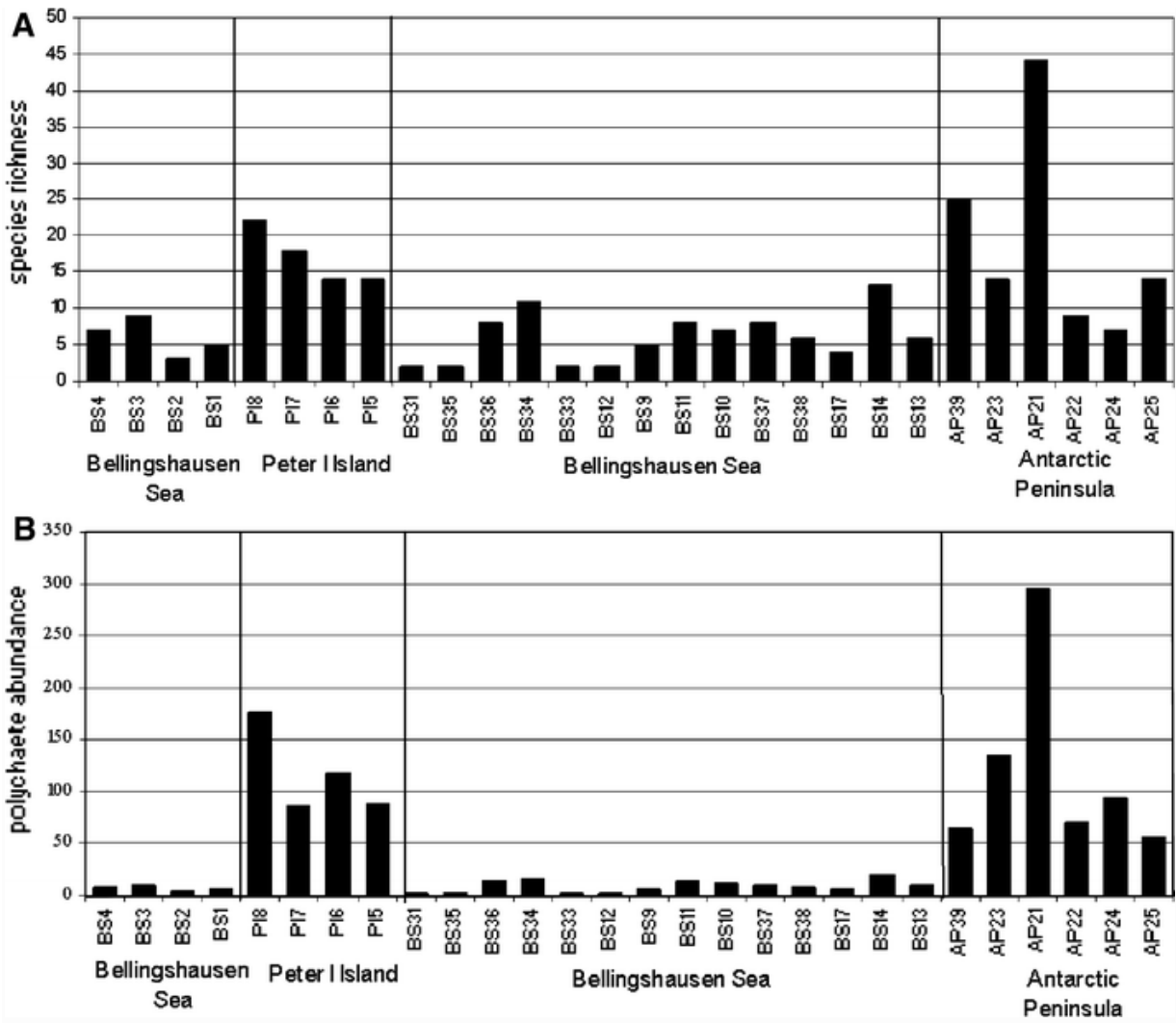
Fig. 2 Number of species (**a**) and abundance (**b**) of Polychaeta at each station; stations arranged according to geographical position from west to east
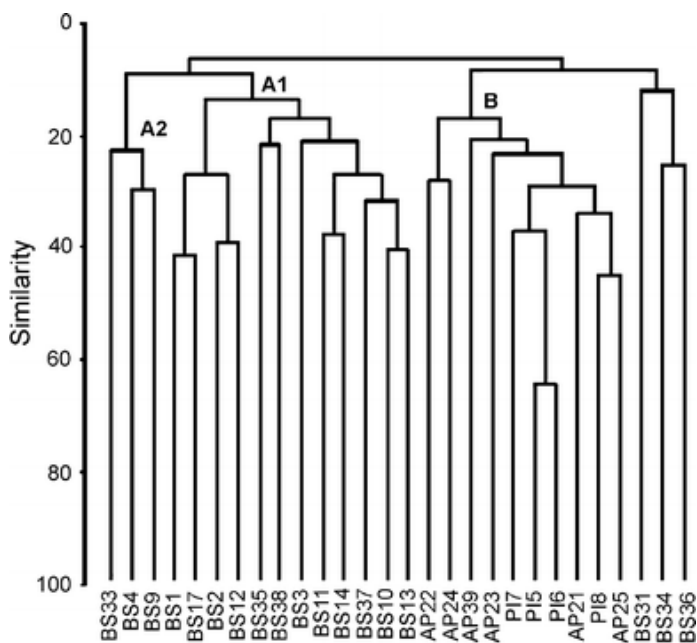

Fig. 3 Plot resulting from the cluster analysis of the similarity matrix obtained from the pairwise computing of the Bray-Curtis index

Internal similarities and differences in the faunistical composition of the defined assemblages were analysed by means of the SIMPER application (Tables 3, 4; Fig. 5). The group A1 (Bellingshausen Sea samples) was dominated by families Paraonidae, Maldanidae, Capitellidae and Opheliidae (Fig. 5) and characterized by proportionately higher abundances of the capitellid species *Notomastus latericeus* and the scalibregmatid *Travisia abyssorum*. The maldanid *Maldane sarsi antarctica*, the paraonid *Aricidea (Allia) belgicae* and the glycerid *Glycera kerguelensis* contributed to most of the cumulative similarity of the group (up to 86.67%). In turn, the families that contributed most to group A2 were Paraonidae, Cirratulidae and Nephthyidae; this group was especially characterized by the paraonid species *A. (A.) belgicae* and the nephthyid *Aglaophamus trissophyllus*, with these two species accounting for 100% of cumulative similarity. In group B, the numerically dominant taxa were Maldanidae and Terebellidae. Many species contributed to the similarity within the assemblage (Table 3). Of these, only the lumbrinerid *Lumbrineris kerguelensis* contributed to more than 10% of cumulative similarity. The maldanid *Rhodine intermedia* accounted for 9.6% of similarity, and the maldanid *M. sarsi antarctica*, the cirratulid *Aphelochaeta cincinnata*, the spionid *Laonice weddellia* and the terebellid *Pista spinifera* contributed around 5% each. However, the species more important when explaining the differences between the group B and groups A1 and A2 varied slightly from the former results (Table 4); those contributing to differentiate group B from A1 and A2 were the maldanid *R. intermedia*, the terebellid *P. spinifera* as well as the terebellid *Artacama proboscidea* and the spionid *Laonice antarcticae*.
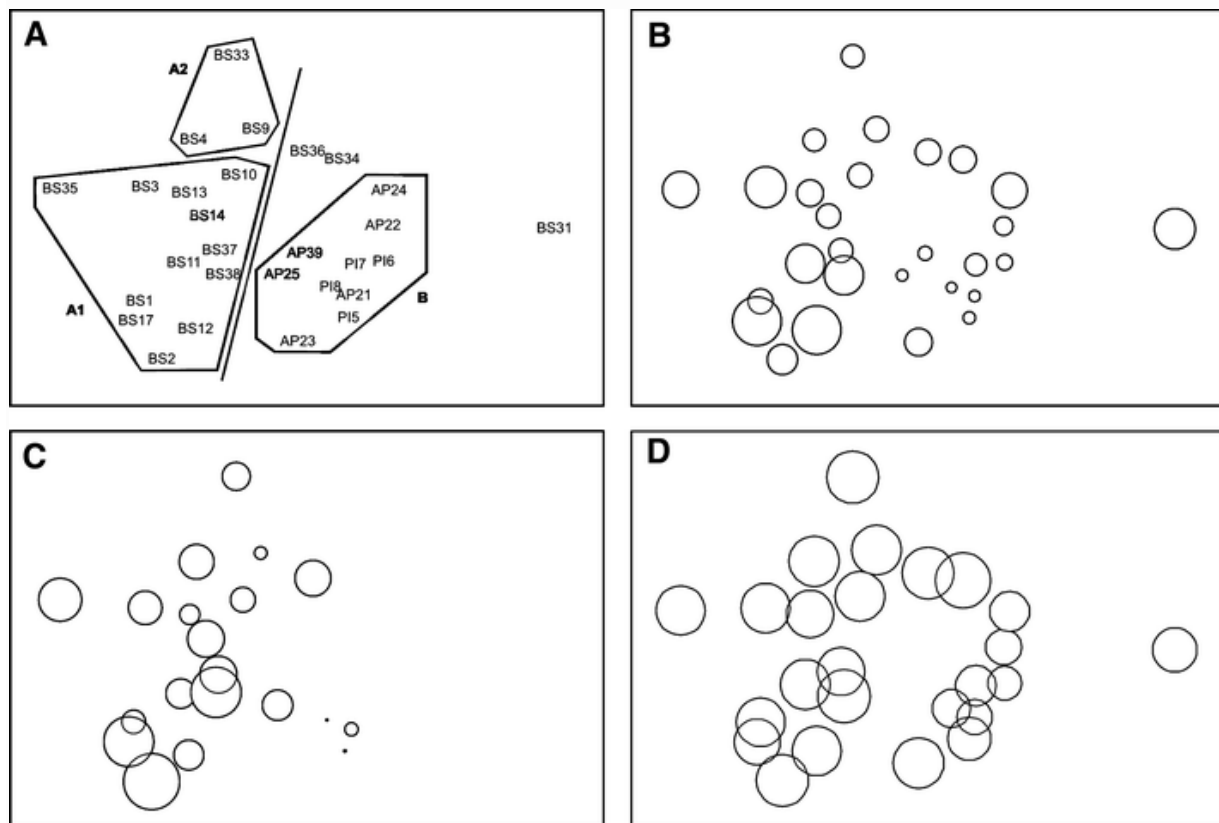

Fig. 4 a Plot resulting from the Multi-Dimensional Scaling analysis of the similarity matrix obtained from the pairwise computing of the Bray-Curtis index. The *solid line* indicates separation between the two main groups (shelf of the Bellingshausen vs. Antarctic Peninsula and Peter I Island). Stress: 0.18. **b–d** The same nMDS ordination of stations as in (**a**) showing superimposed values of variables selected by the BIO-ENV procedure. **b** depth; **c** gravel; and **d** redox potential (Eh). Values of all environmental variables are not available for AP39; redox values for BS14 and AP25 were missing

Table 3 Species contributing to the similarity of stations within the groups identified by the Bray-Curtis similarity analysis, as defined by SIMPER

Species	AvAbnd	AvSim	Sim/SD	Contrib%	Cum%
Group A1 (Average similarity = 18.38)					
Notomastus latericeus	1.18	8.01	0.83	43.58	43.58
Travisia abyssorum	1.00	4.06	0.72	22.07	65.65
Maldane sarsi antarctica	0.55	1.48	0.33	8.06	73.71
Aricidea (Allia) belgicae	0.91	1.21	0.21	6.60	80.31
Glycera kerguelensis	0.45	1.17	0.32	6.36	86.67
Phyllochaetopterus monroi	0.36	0.93	0.34	5.07	91.75
Group A2 (Average similarity = 24.52)					
Aricidea (Allia) belgicae	1.33	19.76	3.69	80.58	80.58
Aglaophamus trissophyllus	0.67	4.76	0.58	19.42	100.00
Group B (Average similarity = 13.96)					
Lumbrineris kerguelensis	6.40	3.39	1.35	24.28	24.28
Rhodine intermedia	17.80	1.35	0.42	9.65	33.92
Maldane sarsi antarctica	2.60	1.06	1.05	7.58	41.51
Aphelochaeta cincinnata	11.90	1.04	0.48	7.48	48.99
Laonice weddellia	3.00	0.92	0.45	6.62	55.61
Pista spinifera	9.10	0.86	0.18	6.17	61.78
Maldanidae gen. sp.	5.20	0.70	0.24	5.05	66.83
Amphicteis gunneri antarctica	5.20	0.51	0.25	3.62	70.45
Notomastus latericeus	2.10	0.48	0.59	3.44	73.89
Laonice antarcticae	8.60	0.46	0.72	3.31	77.20
Eulalia subulifera	1.50	0.46	0.59	3.28	80.48
Spiophanes tcherniai	1.90	0.41	0.44	2.93	83.41
Euchone pallida	1.70	0.34	0.49	2.46	85.87
Ophelina breviata	2.10	0.27	0.37	1.93	87.80
Galathowenia scotiae	1.60	0.27	0.32	1.91	89.71
Axiothella antarctica	5.00	0.26	0.20	1.85	91.56

AvAbnd Average abundance within the group, *AvSim* Average similarity groups, *Sim/SD* Ratio value of similarity within group/standard deviation of the same, *Contrib%* Contribution to similarity within the group and *Cum%* Cumulative similarity within the group

Table 4 Species contributing to the dissimilarity between the pairs of groups of stations identified by the Bray-Curtis similarity analysis, as defined by SIMPER

Species	Group A1 AvAbnd	Group A2 AvAbnd	AvDiss	Diss/SD	Contrib%	Cum%
A1 versus A2 (Average dissimilarity = 91.29)						
Aricidea (Allia) belgicae	0.91	1.33	13.44	1.80	14.72	14.72
Notomastus latericeus	1.18	0.00	8.88	1.32	9.73	24.44
Travisia abyssorum	1.00	0.00	6.63	0.91	7.27	31.71
Aglaophamus trissophyllus	0.09	0.67	4.87	1.15	5.33	37.04
Aphelochaeta undet.	0.00	0.67	4.55	0.65	4.98	42.02
Jasmineira regularis	0.00	0.33	4.34	0.58	4.75	46.78
Maldane sarsi antarctica	0.55	0.00	4.31	0.65	4.72	51.50
Glycera kerguelensis	0.45	0.33	4.09	0.83	4.48	55.98
Laonice weddellia	0.18	0.33	3.10	0.72	3.39	59.38
Galathowenia scotiae	0.18	0.33	3.09	0.66	3.38	62.76
Lumbrineris kerguelensis	0.09	0.33	2.91	0.68	3.19	65.95
Thelepus cincinnatus	0.36	0.00	2.86	0.45	3.13	69.08
Spionidae undet.	0.09	0.33	2.75	0.67	3.01	72.09

Species	Group A1 AvAbnd	Group B AvAbnd	AvDiss	Diss/SD	Contrib%	Cum%
A1 versus B (Average dissimilarity = 96.48)						
Rhodine intermedia	0.00	17.80	10.93	0.55	11.33	11.33
Pista spinifera	0.00	9.10	7.86	0.51	8.14	19.47
Artacama proboscidea	0.00	6.60	6.11	0.37	6.33	25.81
Laonice antarcticae	0.00	8.60	6.11	0.39	6.33	32.13
Lumbrineris kerguelensis	0.09	6.40	5.97	1.15	6.18	38.32
Aphelochaeta cincinnata	0.09	11.90	5.93	0.67	6.14	44.46
Axiothella antarctica	0.00	5.00	5.74	0.38	5.95	50.41
Amphicteis gunneri antarctica	0.09	5.20	5.20	0.48	5.39	55.80

Species						
Maldanidae gen. sp.	0.09	5.20	4.76	0.58	4.93	60.73
Laonice weddellia	0.18	3.00	3.19	0.71	3.30	64.04
Maldane sarsi antarctica	0.55	2.60	1.91	1.07	1.98	66.01
Terebella ehlersi	0.00	1.70	1.77	0.33	1.84	67.85
Notomastus latericeus	1.18	2.10	1.72	1.00	1.79	69.64
Spiophanes tcherniai	0.00	1.90	1.68	0.69	1.74	71.38
Species	**Group A2 AvAbnd**	**Group B AvAbnd**	**AvDiss**	**Diss/SD**	**Contrib%**	**Cum%**
A2 versus B (Average dissimilarity = 97.90)						
Rhodine intermedia	0.00	17.80	11.17	0.54	11.41	11.41
Pista spinifera	0.00	9.10	8.05	0.50	8.22	19.63
Artacama proboscidea	0.00	6.60	6.27	0.37	6.41	26.03
Laonice antarcticae	0.00	8.60	6.23	0.38	6.36	32.39
Aphelochaeta cincinnata	0.00	11.90	6.07	0.67	6.20	38.59
Lumbrineris kerguelensis	0.33	6.40	5.93	1.11	6.06	44.65
Axiothella antarctica	0.00	5.00	5.93	0.38	6.06	50.71
Amphicteis gunneri antarctica	0.00	5.20	5.33	0.47	5.44	56.15
Maldanidae gen. sp.	0.00	5.20	4.86	0.57	4.96	61.12
Laonice weddellia	0.33	3.00	3.27	0.71	3.34	64.45
Maldane sarsi antarctica	0.00	2.60	2.16	1.10	2.20	66.66
Terebella ehlersi	0.00	1.70	1.82	0.33	1.86	68.52
Galathowenia scotiae	0.33	1.60	1.74	0.60	1.77	70.29

AvAbnd Average abundance, *AvDiss* Average dissimilarity between groups, *Diss/SD* Ratio value of dissimilarity between groups/standard deviation of the same, *Contrib%* Contribution to dissimilarity between groups, *Cum%* Cumulative dissimilarity between groups

In the case of group B, although the cluster analysis brought together the two groups of geographically distant stations (AP and PI) without a clear separation between them, certain species were only present in Peter I Island, such as the terebellid *Pista spinifera* (PI5 and PI6), whereas the spionid *Laonice weddellia* (AP39) and the cirratulid *Chaetozone setosa* (AP21) were found exclusively in the Antarctic Peninsula. Only one station in Peter I Island (PI8) showed higher similarity with the Antarctic Peninsula stations (AP25 and AP21) than with the rest of the stations located in the vicinity of the island; this affinity was mainly due to the shared greater abundance of the maldanid *Rhodine intermedia*.

Three stations from west Bellingshausen Sea, BS31, BS34 and BS36, did not group into any cluster, although they were surprisingly located closer to group B (AP and PI stations) than to group A (remaining BS stations) in the plot (Fig. 4a). This fact seemed not to be related to sediment characteristics, depth or geographical position, but to the faunal composition. The few polychaete taxa identified in these samples revealed a number of species that were present only in these stations (namely *G.* cf. *capitata*, *Levinsenia antarctica* and *Scolelepis eltaninae*) as well as a number of species shared with stations of cluster B (*M. sarsi*, *R. intermedia*, *L. kerguelensis*, *Ampharete kerguelensis* and *Ophelina breviata*), while only one species, *Aricidea*(*Acmira*) *simplex*, was sheared with the samples forming the cluster A.

Depth ranges of the most abundant polychaete species are depicted in Fig. 6; most of them had a wide distribution from the upper shelf to the slope at about 2,000 m. Only four species were not found in
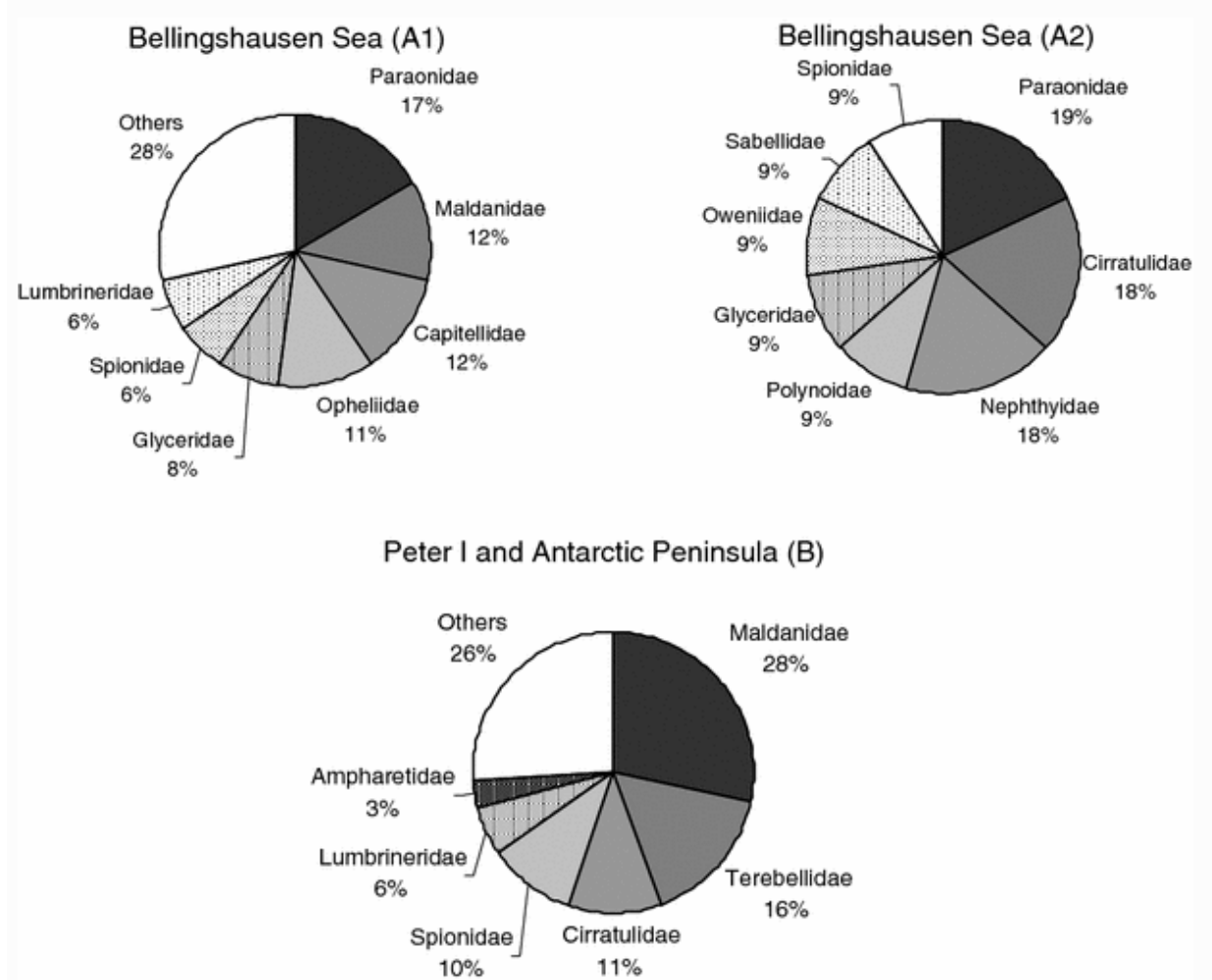

Fig. 5 Most abundant polychaete families in each group as defined by cluster analysis

shallower waters, namely *T. ehlersi*, *A. antarctica*, *P. monroi* and *A. (A.) belgicae*, while others seemed to be limited to the shelf (i.e., *P. spinifera*, *S. tcherniai*, *E. pallida*, *R. intermedia*, *E. subulifera*, *A. cincinnata* and *A. gunneri antarctica*). No species had a distribution restricted to the slope (below 1,000 m depth).

Relationship between biotic and environmental variables

The first run of the BIO-ENV procedure pointed out that depth and gravel content of the sediment showed the highest correlations with faunistical data (Table 5). Thus, the three defined groups of stations could be discriminated on the basis of their abiotic conditions (Table 6), with A1 comprising deep stations from the shelf of the Bellingshausen Sea (average depth = 1,053.83 ± 579.16 m) with relatively high content of gravel in the sediment (average = 37.00 ± 23.02%), A2 comprising relatively shallow (average depth = 465.00 ± 58.39 m) stations from the shelf of the Bellingshausen Sea with medium gravel content in the sediment (average = 18.34 ± 13.64%) and B comprising stations from the vicinity of Peter I Island and off the Antarctic Peninsula, usually shallow (average depth = 322.50 ± 326.2 m) and with a low gravel content in the sediment (average = 3.44 ± 2.86%). The differences were statistically significant for the two variables ($P = 0.003$ and $P = 0.001$, respectively).
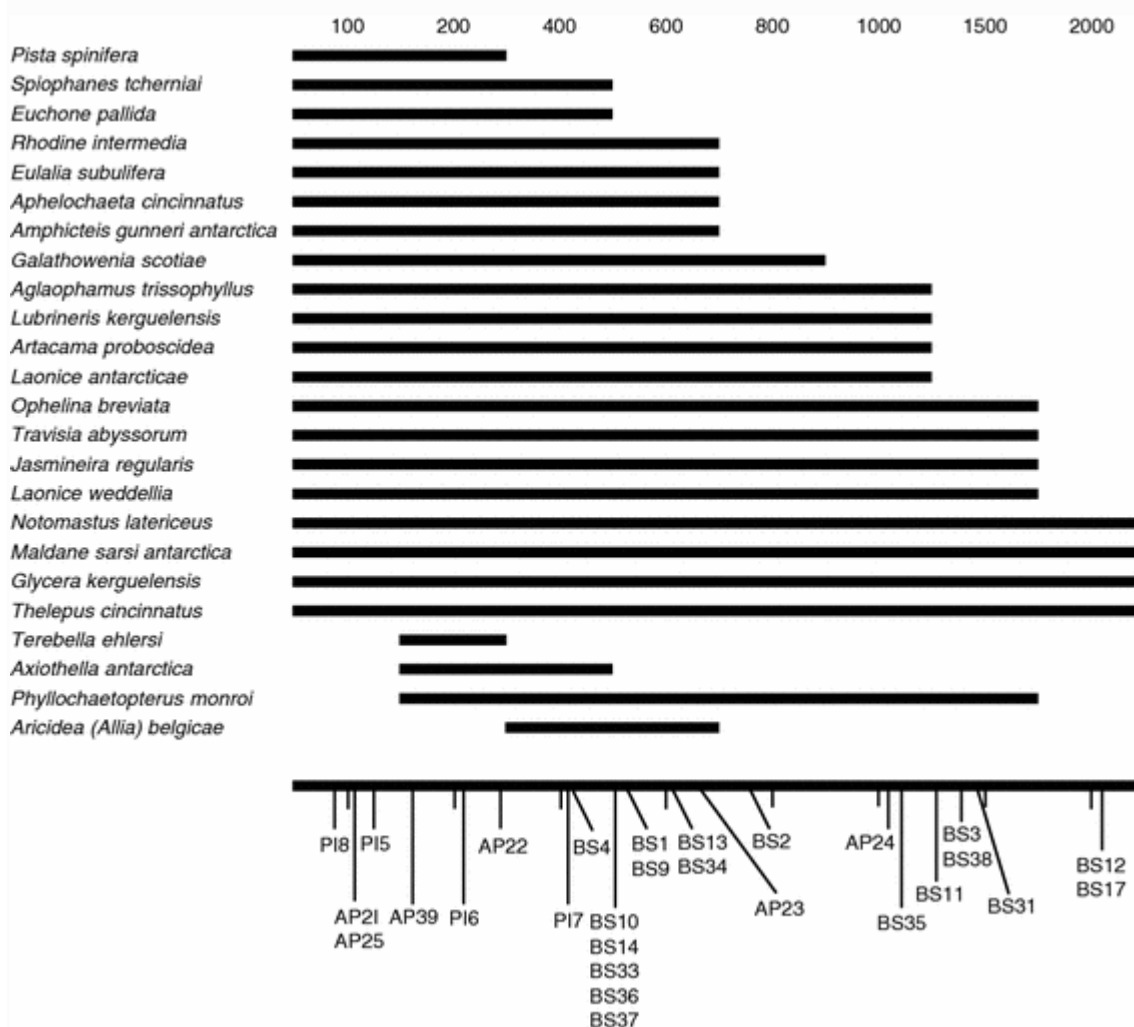

Fig. 6 Depth distribution ranges of most abundant polychaete species and position related to depth of each sampling station (*bottom*)

Prior to performing the BIO-ENV analysis again considering also the redox potential, the consistency of the clusters was tested by re-analysing the data after eliminating those stations in which this variable was not measured. These new analyses gave consistent and similar outputs, this time the three previous detected groups (A1, A2 and B) being even more clearly defined. The analysis resulted in only a slight modification of internal topography in the case of the cluster analysis and a virtually identical location of samples in the nMDS plot. In the re-run of the BIO-ENV test (Table 5), depth resulted secondarily important to discriminate the station groups, whereas the redox and gravel content in the sediment became the best variable combination. The redox potential, in particular, seemed important to discriminate the groups. Thus, the average redox potential was 259.54 ± 80.95 mV in group A1 and 274.43 ± 14.6 mV in A2, while in group B, it was clearly lower (170.74 ± 48.20 mV), being statistically significant ($P = 0.005$).

The distribution of values of the aforementioned variables superimposed on the nMDS plot suggests the presence of an environmental gradient in the studied area (Fig. 4b–d). This gradient involved gravel content, redox potential at the sediment surface and depth and it is characterized by more oxidized sediments with higher contents of gravel at the deeper stations, which are represented at the left part of the plot while the other stations are placed on the opposite side.

Table 5 Best combinations of variables obtained through BIO-ENV analysis according to the values of the Spearman rank correlation (p_w)

Correlation (p_w)	Variable combination
All stations considered; redox excluded	
0.314	Depth, gravel
0.294	Depth, gravel, fine sand
0.293	Depth, gravel, coarse sand
0.288	Depth, gravel, medium sand
0.286	Depth, organic matter, gravel
0.285	Gravel, mud
0.281	Gravel, fine sand
0.280	Gravel, coarse sand, mud
0.276	Depth, gravel, mud
0.276	Gravel, medium sand, mud
Redox considered; BS14 & AP25 excluded	
0.326	Redox, gravel
0.315	Redox, gravel, coarse sand
0.310	Depth, redox, gravel
0.307	Redox, gravel, mud
0.301	Redox, organic matter, gravel
0.300	Depth, redox, gravel, mud
0.300	Redox, gravel, medium sand
0.296	Gravel, mud
0.294	Depth, gravel
0.291	Depth, gravel, mud

Table 6 Mean values and standard deviations for environmental and ecological parameters at the stations within the groups identified by the Bray-Curtis similarity analysis

Cluster	Depth	Redox	OM	Gravel	CS	MS	FS	Mud	S	N	d	H′	J′
A1	1053.83 ± 579.16	259.54 ± 80.95	4.81 ± 1.36	37.00 ± 23.02	7.51 ± 5.48	4.54 ± 2.83	13.25 ± 8.08	37.72 ± 17.60	6.08 ± 3.20	8.17 ± 5.24	2.46 ± 0.78	1.58 ± 0.55	0.96 ± 0.04
A2	465.00 ± 58.39	274.43 ± 14.46	4.85 ± 1.00	18.34 ± 13.64	9.56 ± 3.45	6.22 ± 2.34	18.37 ± 7.17	47.51 ± 22.44	4.67 ± 2.52	5.33 ± 3.06	2.19 ± 0.73	1.39 ± 0.63	0.98 ± 0.02
B	322.50 ± 312.37	170.74 ± 48.20	3.44 ± 2.86	3.16 ± 7.87	4.41 ± 8.44	4.22 ± 6.77	20.95 ± 19.27	67.28 ± 35.37	18.20 ± 10.54	118.40 ± 72.14	3.61 ± 1.85	1.97 ± 0.61	0.71 ± 0.13

Depth (m), redox potential (mV), organic matter (%), carbonates (%), gravel (>2 mm, %), coarse sand (>0.5 mm, %), medium sand (>0.25 mm, %), fine sand (>0.0625 mm, %), and mud (<0.0625, %). *CS* Coarse sand, *d* Margalef diversity index, *H′* Shannon-Wiener diversity index, loge based, *J′* Pielou evenness index, based on *H′*, *MS* Medium sand, *FS* Fine sand, *N* Number of specimens collected in 1,890 cm^2, *S* Number of species and *OM* Organic matter

Discussion

Since Hartman's contributions to the taxonomy of Antarctic polychaetes in the fifties and sixties of twentieth century (e.g., Hartman 1952, 1953, 1964, 1966, 1967), much effort has been made by many authors to increase the knowledge of this taxon, especially in the late eighties (e.g., Hartmann-Schröder and Rosenfeldt 1988, 1989, 1990, 1991, 1992) and in more recent years (e.g., Hilbig 2004; Schüller and Ebbe 2007; Schüller and Hilbig 2007; Schüller 2008a, b; Schüller et al. 2009). Nevertheless, apart from papers by Hartman (1978) and Knox and Cameron (1998) devoted to the Weddell and Ross Seas, respectively, there are no recent monographs that compile this information and much work is still necessary to shade light in many polychaete taxa still poorly known. For example, the genus *Ampharete* Malmgren, 1866 is among the most species-rich genera in boreo-arctic waters, with eight species described or reported to date (Holthe 1986; Jirkov 2001), while in Antarctic waters is represented by just a single species: *Ampharete kerguelensis* McIntosh, 1885 (see Schüller 2008a). In addition, we agree with Gambi and Mariani (1999), who stated that many of the northern species traditionally reported in austral waters (e.g., *P. cristata, T. cincinnatus, N. latericeus and C. cirratus*) probably represent new species, as has already been reported for some taxa belonging to Scalibregmatidae (Blake 1981), Oweniidae (Blake 1984; Parapar 2003), Melinninae (Parapar and San Martín 1997), Sabellidae (Giangrande and Gambi 1997), Opheliidae (Maciolek and Blake 2006) and Trichobranchidae (Parapar and Moreira 2008). These current limitations in the knowledge of the polychaete taxonomy of the Southern Ocean limit in certain way the quality of the catalogue of species presented here, which in spite of certain lack of definition in the identification in some taxa, comes to fill anyway an important emptiness in the knowledge of the polychaete fauna in the Bellingshausen Sea.

From the analysis of the list of species obtained, two main groups of stations could be defined. On the one hand, most of the stations from the Bellingshausen Sea determined the group A, which could, in turn, be divided into groups A1 and A2; on the other hand, the stations from off the Antarctic Peninsula, Gerlache Strait and the vicinity of Peter I Island formed group B, even though geographically Peter I belongs to the Bellingshausen Sea. Groups A and B showed sharp differences in their polychaete species composition as well as in abundance and number of species which were noticeably higher in stations of group B. There were differences in the mean values of diversity indexes as well they were, however, not significant.

When environmental variables were considered, stations of group A were characterized by higher redox potential and gravel content in the sediment than those of group B. In turn, the two sub-groups within group A (A1 and A2) showed environmental differences related to depth, with group A1 representing deeper stations. The stations included within group B were usually located at relatively shallow depths.

From the present data, it can be concluded that the polychaete faunas of the Antarctic Peninsula and the Bellingshausen Sea (except for those from the vicinity of Peter I Island) are clearly different. Our results referred to the Antarctic Peninsula did not differ substantially from those previously recorded for the area (San Martín et al. 2000), reporting again Maldanidae, Terebellidae and Cirratulidae as the most abundant families. However, Hilbig et al. (2006) did not find such high abundances for Terebellidae in the Weddell Sea, while Terebellidae are among the most speciose family in the Ross Sea (Cantone et al. 2000; Cigliano and Gambi unpublished data). At the species level, all the characteristic taxa herein recorded were mentioned as such by the above-mentioned authors; this situation suggests that most of the polychaete fauna reported from the Antarctica has a wide distribution through the Southern Ocean. Hilbig (2004) noticed these patterns, suggesting that they

reflect the persistence of a pre-existing polychaete fauna around Antarctica related to the establishment of the circum-Antarctic current in the past coupled with the characteristically high physiological flexibility of these animals.

Interestingly, in spite of the remoteness of this island placed nearly in the middle of the Bellingshausen Sea, the stations located around Peter I Island harboured polychaete assemblages more similar to those found off the Antarctic Peninsula than to those typical of the shelf of Bellingshausen Sea. This parallelism might be, at least in part, due to the presence of the same kind of gravel-free sediment which revealed the absence of stones in the sediment surface. These stones are much more abundant in many of the BS stations, as already reported by Saiz et al. (2008), and are brought by icebergs on their journey from the continent, falling to the bottom as a result of the melting process of the ice. In addition, the disturbance created on the seabed by the iceberg scouring could be the cause of some environmental changes that would result in a different specific composition in the stations of cluster A. In fact, there were three stations at western central Bellingshausen Sea which were left out of the main groupings and were located closer to cluster B; this may highlight a greater stability of the sediment as suggested by the presence of maldanids, which are also typical from this group. On the contrary, group A has sediments disturbed by the action of iceberg scouring and therefore has a fauna dominated by polychaetes of short life cycle, such as capitellids and paraonids.

In contrast to the waters around the Antarctic Peninsula, the Bellingshausen Sea has been little investigated to date due to the prevalence of ice for most of the year (Clarke and Johnston 2003; Linse et al. 2006); thus, our results cannot be compared with previous quantitative studies on the area. A short list of species from Peter I island was provided by Hartman (1967), and some observations on general benthos (not including polychaetes) have been done with remote sensing ROV (Gutt et al. 1996). However, when most characteristic species are considered, differences arise not only with the Antarctic Peninsula but also with adjacent areas such as the Weddell Sea (Hilbig et al. 2006), in which the amphinomid *Paramphinome australis* and the cirratulids *Monticellina* sp. and *Chaetozone* sp. were the most characteristic species in open sea stations, or the Ross Sea, in which Terebellidae was the most species-rich family (Cantone et al. 2000; Cantone and di Pietro 2001; Cigliano and Gambi unpublished data). The noticeably low values for abundance and diversity herein found were previously reported for comparably deep stations from the Weddell Sea (Hilbig 2001), although in this region the number of species tended to be quite high.

From these results, it seems that the Bellingshausen Sea constitutes to some extent a differentiated area in the Southern Ocean, pointing to a well-defined biogeographical region, as proposed by Clarke et al. (2004). Other researches conducted with molluscs collected during the expeditions BENTART 2003 and 2006 also showed similar results (Troncoso et al. 2007; Troncoso and Aldea 2008). At higher levels of taxonomic resolution, Saiz et al. (2008) described benthic assemblages characterized by low values of abundance and diversity and constituted by impoverished faunas dominated by foraminiferans, which caused the region to be described as a "benthic desert". This paucity of species and individuals might be linked in part to the particular sediment composition of the shelf in Bellingshausen Sea, which is defined by foraminifer-bearing, opal-free sediments in the west of the region and diatom-bearing, carbonate-free in the east (Hillenbrand et al. 2003).

From our results, it could be inferred that sediment characteristics, followed by depth, were the main environmental variables determining the structure of polychaete assemblages in the Bellingshausen Sea and nearby areas of the Antarctic Peninsula. However, other studies undertook in the same area and devoted to other taxa found depth as having greater importance than sediment features

(Matallanas and Olaso 2007; Troncoso et al. 2007, 2008; Saiz et al. 2008); some of the sediment features (namely redox potential and mud content) were, however, found to act combined to depth in determining suprabenthic community structure (San Vicente et al. 2009). In fact, the identity of the most important environmental variables determining benthic communities in the Southern Ocean is still a matter of discrepancy. Apart of the above-commented iceberg scouring, which is a major source of disturbance at both shallow waters and shelf and slope depths (Gutt and Starmans 2001), depth has been traditionally considered a major factor determining the structure of these communities (Arntz et al. 1994), probably due to the limited organic input received by deeper bottoms (Smith et al. 2006). This scheme has recently been challenged (Gutt and Starmans 1998; Gutt 2000), proposing the bottom-near currents as being the main "driving force" for Antarctic benthic communities. Our results cannot directly provide support for any of the proposed models, since depth showed a less important correlation with faunal data in the two environmental analyses performed. In fact, our analyses revealed that sediment features such as redox potential or gravel content showed more relevance than depth itself. Recent studies in the Weddell Sea by Schüller et al. (2009) also point to sediment characteristics to be more important than depth in structuring soft-bottom polychaete communities. Those features might be directly linked to the current system near the bottom, thus suggesting that a process more complex than depth-related organic input is responsible for the faunistical composition of the benthic communities inhabiting the shelf of Bellingshausen Sea.

In short, the results of this quantitative study of the polychaetes of the Bellingshausen Sea, although largely limited by the sample size that makes the conclusions to be taken with caution, suggest extreme differences in the biological parameters within the area studied. Thus, the stations off the Antarctic Peninsula and Peter I Island showed much more abundant and diverse polychaete communities than those of the Bellingshausen Sea. These differences appear to be related both to depth as to the characteristics of the sediment and probably the important role played by the intense traffic of icebergs in the area, with its plowing affect on the seabed, creates significant physical disturbance in the ecosystem by limiting the establishment of stable communities over the time.

Acknowledgments

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Appendix

Table 7 Polychaete species identified from the box-corer samples in the BENTART-2003 and 2006 cruises in the Bellingshausen Sea and Gerlache Strait

Ampharetidae
 Amphicteis gunneri antarctica Hessle, 1917
 Amythas membranifera Benham, 1921
 Ampharete kerguelensis McIntosh, 1885
 Ampharete sp.
 Phyllocomus crocea Grube, 1877
 Ampharetidae gen. sp.
Amphinomidae
 Paramphinome australis Monro, 1930
Capitellidae
 Capitella perarmata (Gravier, 1911)
 Notomastus latericeus Sars, 1850
Chaetopteridae
 Phyllochaetopterus monroi Hartman, 1967
Cirratulidae
 Aphelochaeta cincinnata (Ehlers, 1908)
 Aphelochaeta epitoca (Monro, 1930)
 Aphelochaeta fusiformis (Monro, 1939)
 Aphelochaeta undet.
 Chaetozone setosa Malmgren, 1867
 Cirratulus cirratus (Müller, 1776)
 Cirratulidae undet.
Eunicidae
 Eunice antarctica Baird, 1869
Flabelligeridae

 Pherusa sp.
 Brada villosa (Rathke, 1843)
Glyceridae
 Glycera cf. capitata Ørsted, 1843
 Glycera kerguelensis McIntosh, 1885
 Glycera undet.
Lumbrineridae
 Augeneria tentaculata Monro, 1930
 Lumbrineris kerguelensis (Grube, 1878)
 Lumbrineris sp.
 Paraninoe antarctica (Monro, 1930)
Maldanidae
 Axiothella antarctica Monro, 1930
 Asychis amphiglyptus (Ehlers, 1897)
 Maldane sarsi antarctica Arwidsson, 1911
 Lumbriclymenella robusta Arwidsson, 1911
 Nicomache sp.
 Rhodine intermedia Arwidsson, 1911
 Isocyrrus yungi Gravier, 1911
Nephthyidae
 Aglaophamus trissophyllus (Grube, 1877)
Nereididae

Oweniidae
 Galathowenia scotiae (Hartman, 1978)
 Oweniidae gen. sp.
Paraonidae
 Aricidea (Acmira) simplex Day, 1963
 Levinsenia antarctica Strelzov, 1963
 Cirrophorus brevicirratus Strelzov, 1973
 Aricidea (Allia) belgicae (Fauvel, 1936)
Phyllodocidae
 Anaitides adarensis (Benham, 1927)
 Phyllodoce sp.
 Eulalia subulifera Ehlers, 1897
Polynoidae
 Barrukia cristata (Willey, 1902)
 Barrukia curviseta (Monro, 1930)
 Harmothoe cf. acuminata Willey, 1902
 Harmothoe exanthema bergstromi Monro, 1936
 Harmothoe undet.
 Harmothoe spinosa Kinberg, 1865
Sabellidae
 Demonax polarsterni Gambi et al., 2001
 Euchone pallida Ehlers, 1908
 Euchone scotiarum Hartman, 1978
 Jasmineira regularis Hartman, 1978
 Perkinsiana borsibrunoi (Giangrande and Gambi 1997)
 Sabellidae undet.
Scalibregmatidae
 Scalibregma inflatum Rathke, 1843
 Scalibregma sp.
 Sclerocheilus minutus Grube, 1863
Serpulidae
 Serpula narconensis Baird, 1865
 Vermiliopsis nigropileata (Ehlers, 1900)
 Spirorbis nordenskjoldi Ehlers, 1900
Sphaerodoridae
 Sphaerodoropsis cf. p*arva* (Ehlers, 1913)
Spionidae
 Laonice antarcticae Hartman, 1953
 Laonice weddellia Hartman, 1978
 Laonice sp.
 Scolelepis eltaninae Blake, 1983
 Spiophanes soderstromi Hartman, 1953
 Spiophanes tcherniai Fauvel, 1951
 Spionidae undet.
Sternaspidae
 Sternaspis scutata (Renier, 1807)
Syllidae

Neanthes kerguelensis (McIntosh, 1885)

Nereis eugeniae (Kinberg, 1866)

Onuphidae

Leptoecia benthaliana (McIntosh, 1885)

Opheliidae

Ophelina breviata (Ehlers, 1913)

Travisia abyssorum (Monro, 1930)

Opheliidae gen. sp.

Orbiniidae

Leitoscoloplos kerguelensis (McIntosh, 1885)

Leitoscoloplos mawsoni Benham, 1921

Scoloplos (Leodamas) marginatus (Ehlers, 1897)

Phylo minima (Hartmann-Schröder and Rosenfeldt, 1990)

Exogone heterosetosa McIntosh, 1885

Pionosyllis dionisi Núñez and San Martín, 1991

Pionosyllis kerguelensis (McIntosh, 1885)

Salvatoria rhopalophora (Ehlers, 1897)

Syllis sclerolaema Ehlers, 1901

Terebellidae

Artacama proboscidea Malmgren, 1865

Pista cristata (Müller, 1776)

Pista corrientis McIntosh, 1885

Pista spinifera (Ehlers, 1908)

Terebella ehlersi Gravier, 1907

Thelepus cincinnatus (Fabricius, 1780)

Trichobranchidae

Terebellides kerguelensis McIntosh, 1885