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Distribution patterns and biodiversity in polychaete communities of the Weddell Sea and Antarctic Peninsula area (Southern Ocean)

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During the expedition EASIZ II with RV 'Polarstern' in 1998 a multibox corer yielded 151 quantitative samples from 26 stations between 120 and 2415 m water depth for benthic community analysis. From this material a total of 235 polychaete species out of 37 families was determined. Forty-seven species are new to science. The polychaete fraction contributed 41.9% to total benthic abundance and 6.5% to total benthic biomass at these stations. Overall mean polychaete abundance (ind m^{-2}) and biomass (g wet weight m^{-2}) at the stations were 1617 and 49, respectively.

Multidimensional scaling procedure clearly grouped the stations into south-eastern Weddell Sea shelf stations, deep-water stations, and stations mostly around the Antarctic Peninsula. Differences between these groups existed in terms of polychaete abundance and biomass as well as species composition, diversity, and evenness.

INTRODUCTION

In the ongoing discussions about nature conservation and faunistic changes due to alteration of environments, biodiversity studies have increased considerably in importance worldwide. For the southern hemisphere it is still an open question whether or not there exists a latitudinal cline of increasing species numbers from the poles to the tropics, but re-examination of existent data (Gray, 2001) as well as new data from recent studies (cf. Arntz & Rios, 1999 and further citations herein) questioned such general ideas. It seems that different taxa react in different directions. Sponges and bryozoans are typical examples for highest species richness in high southern latitudes (Barthel & Tendal, 1994; Moyano, 1999), decapod crustaceans may serve as one example showing the opposite trend (Gorny, 1999). However, one of the main difficulties to answer this question even today is the relatively poor knowledge of taxonomy of many invertebrate phyla worldwide and especially in the Antarctic region (Clarke & Johnston, 2003). This also holds true for polychaetes, a group that contributes substantially to Antarctic benthos. Recent studies in the Weddell Sea have shown polychaetes to make up 76.1% of overall organism abundance and 37.1% of total benthic biomass at the tip of the Antarctic Peninsula (Piepenburg et al., 2002). Comparable values from different communities living on the south-eastern Weddell Sea shelf varied between 40.9 and 52.6% in terms of abundance and 8.3 and 70.9% in terms of biomass (Gerdes et al., 1992).

The 'Polarstern' expedition ANT XV/3 in 1998 under the frame of the EASIZ programme (Ecology of the Antarctic Sea Ice Zone) provided rich material which was taken to improve our knowledge of community structure and biodiversity of the high Antarctic Weddell Sea and the Antarctic Peninsula area. With the obtained samples, we were able to provide answers to the following questions:

1. Is there a downslope transition of the faunal composition, and if so, at what depth does a faunal break occur? How high is the degree of eurybathy in the Southern Ocean compared with temperate oceans?
2. What is the role of regional distance in changes of faunal composition?
3. How do distributional patterns, both geographical and bathymetric, compare with slopes in temperate oceans of the northern hemisphere?

MATERIALS AND METHODS

The Weddell Sea with an area of 2.3×10.6 km^2 is the second largest Antarctic sea area with almost 4100 km of coast line between Atka Bay on the eastern Weddell Sea border and the tip of the Antarctic Peninsula in the west. Due to the heavy weight of the continental ice sheet, the rather narrow (10 to 100 km) south-eastern Weddell Sea shelf is depressed to depths between 200 and 800 m, whereas around the tip of the Peninsula the shelf continues directly to the ice free coastline.

During the 'Polarstern' expedition ANT XV/3 in 1998, among other gears the multibox corer (Gerdes, 1990) was deployed at 26 stations in water depths between 120 and 2415 m along the south-eastern Weddell Sea shelf and slope and in the Peninsula area (Figure 1, Table 1).

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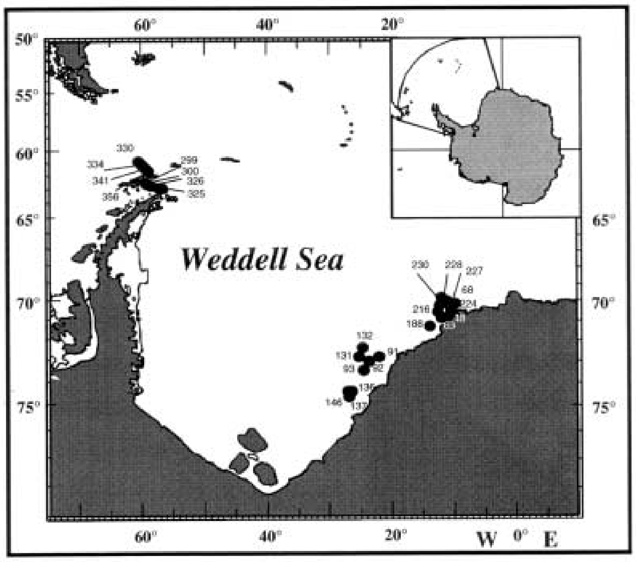

Figure 1. Study area and sampled stations.

The obtained samples—between three and seven cores per station, depending on sediment quality (Table 1)—were carefully washed onboard through 500 μm mesh size sieve and preserved in a hexamethylenetetramine buffered 10% seawater formalin solution prior to sorting and identification of specimens to species level. Abundance and biomass (wet weight) were standardized to m^{-2} from pooled cores per station.

Based on 4th-root transformed abundance, station groups were identified by multidimensional scaling (MDS) (PRIMER Vs.5, Clarke & Gorley, 2001) based on the Bray–Curtis similarity matrix. Significance of differences among station groups was tested with analysis of similarities (ANOSIM) (Clarke & Ainsworth, 1993), and the species responsible for these dissimilarities were defined with similarity percentage analysis (SIMPER). Biodiversity expressed as Shannon–Wiener index H' (Shannon & Weaver, 1949) and evenness J' (Pielou, 1969) were calculated on the basis of abundance $\log_e$.

RESULTS

The whole set of samples yielded 235 species belonging to 37 families (Appendix A), including 47 species that are new to science and will be described elsewhere. The within station variability was high (Figure 2; Table 2). The number of species per station ranged from 7 to 73. Polychaete abundance ranged from 114 to 6405 ind m^{-2}, and the biomass ranged from 0.2 to 434.4 g w.w. m^{-2}. Contribution of polychaetes to total macrofauna individual numbers at the 26 stations (mean abundance: 1617 ind m^{-2}) was 42%, for total biomass (mean: 49 g w.w. m^{-2}), the respective value was 6.5%.

Based on the abundance values of all 235 species, three main clusters resulted by nonmetric multidimensional scaling (nMDS) (Figure 3):

- Peninsula shelf station group, including Bransfield Strait, Drake Passage, and three stations on the south-eastern Weddell Sea shelf and slope (PI)

Table 1. *Sampling station data.*

Station	Location	Latitude (S) Longitude (W)	Date	No. of cores	Water depth (m)
48	north of Kapp Norvegia	70°52.15′ 10°29.26′	30 January 1998	5	245
63	north of Kapp Norvegia	70°52.10′ 10°32.40′	31 January1998	5	234
68	north of Kapp Norvegia	70°50.30′ 10°38.10′	01 February 1998	3	269
91	Kapp Norvegia	73°28.70′ 22°48.20′	04 February 1998	6	1506
92	Kapp Norvegia	73°34.06′ 22°26.50′	04 February 1998	5	993
93	Kapp Norvegia	73°28.30′ 22°53.70′	04 February 1998	7	1985
131	Kapp Norvegia 2	73°23.70′ 22°09.10′	08 February 1998	5	1944
132	Kapp Norvegia 2	73°19.80′ 22°22.50′	08 February 1998	6	2415
136	Halley Bay	74°33.00′ 27°13.10′	09 February 1998	7	2011
137	Halley Bay	74°36.20′ 27°12.70′	09 February 1998	7	1500
146	Halley Bay	74°37.80′ 27°08.00′	10 February 1998	4	1000
188	south of Kapp Norvegia	71°31.50′ 13°30.60′	15 February 1998	5	225
216	Kapp Norvegia	71°06.46′ 11°32.67′	18 February 1998	2	180
224	Kapp Norvegia	70°49.79′ 10°34.40′	19 February 1998	7	279
227	Kapp Norvegia	70°49.32′ 10°38.84′	20 February 1998	6	360
228	Kapp Norvegia	70°49.83′ 10°37.53′	20 February 1998	7	293
230	Kapp Norvegia	70°50.94′ 10°32.18′	20 February 1998	7	229
299	Bransfield Strait	62°15.88′ 58°42.61′	14 March 1998	7	212
300	Bransfield Strait	62°16.80′ 58°41.85′	14 March 1998	7	423
325	Bransfield Strait	62°22.04′ 58°42.73′	17 March 1998	7	829
326	Bransfield Strait	62°20.18′ 58°38.50′	17 March 1998	7	625
330	Bransfield Strait	61°20.65′ 58°14.78′	18 March 1998	4	2000
334	Drake Passage	61°26.55′ 58°06.49′	19 March 1998	7	1043
341	Drake Passage	61°34.55′ 58°06.73′	19 March 1998	7	428
345	Drake Passage	61°53.40′ 59°07.04′	20 March 1998	7	218
356	Drake Passage	62°00.20′ 59°15.00′	20 March 1998	7	120

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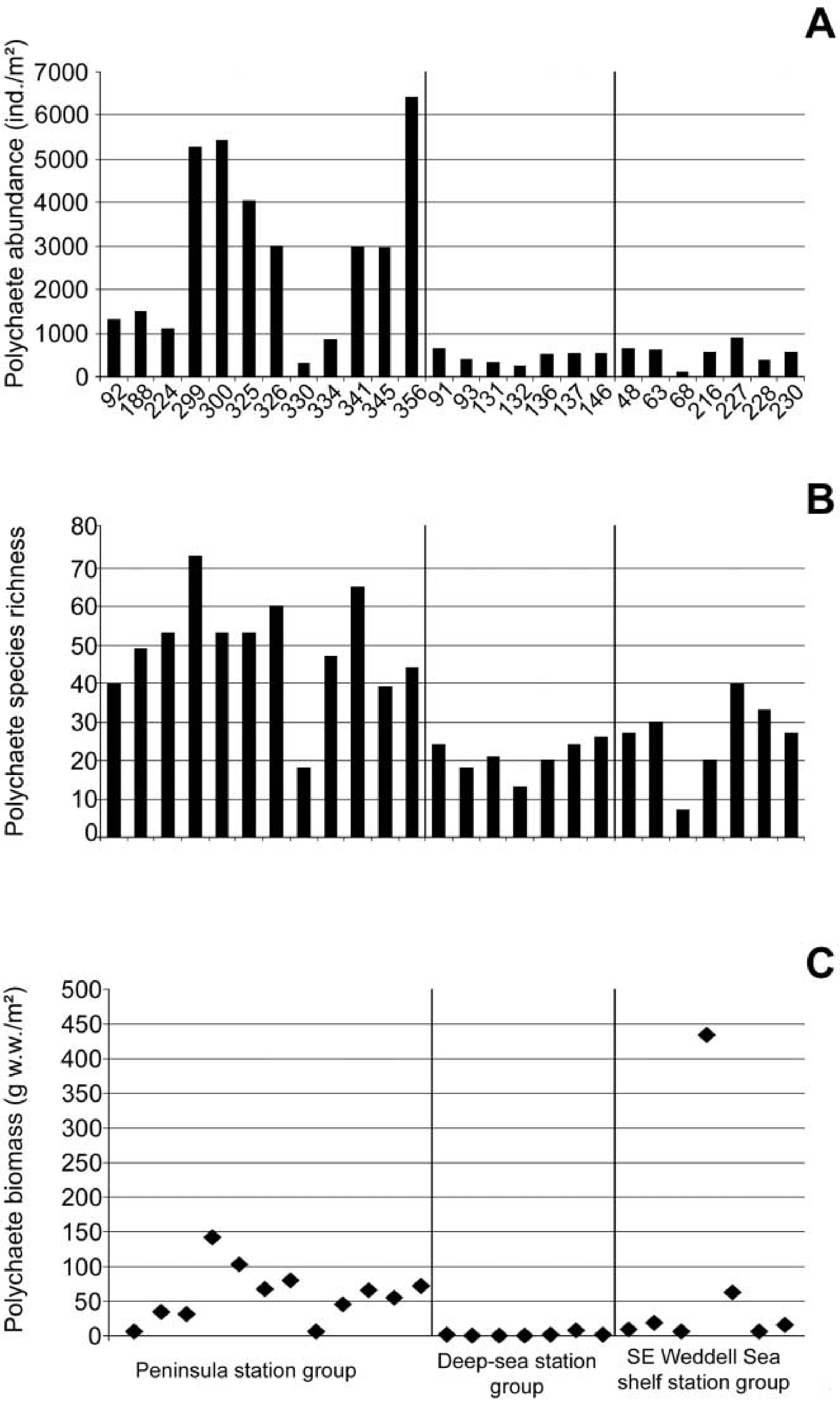

Figure 2. Polychaete species (A) abundance; (B) richness; and (C) biomass at each station, stations arranged according to cluster analysis

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Table 2. *Station parameters. Abundance is expressed as number of individuals per m^2. H′ is based on log$_e$.*

Station sampled	Area (m^2)	Species	Abundance	Diversity (H′)	Evenness (J′)
48	0.12	24	775.0	2.867	0.870
63	0.12	29	616.7	2.548	0.749
68	0.072	7	111.1	1.906	0.980
91	0.144	24	631.9	2.655	0.836
92	0.12	40	1308.3	3.062	0.830
93	0.168	18	392.9	2.520	0.872
131	0.12	21	333.3	2.752	0.904
132	0.144	13	229.2	2.194	0.855
136	0.168	20	500.0	2.470	0.825
137	0.168	24	523.8	2.553	0.803
146	0.096	26	531.3	3.108	0.954
188	0.12	49	1500.0	3.300	0.848
216	0.048	20	562.5	2.917	0.974
224	0.168	53	1107.1	3.424	0.862
227	0.144	40	881.9	3.359	0.910
228	0.168	33	386.9	3.316	0.948
230	0.168	27	488.1	2.722	0.826
299	0.168	73	5273.8	2.922	0.681
300	0.168	53	5410.7	2.307	0.581
325	0.168	53	4023.8	2.494	0.628
326	0.168	60	3000.0	2.779	0.679
330	0.096	18	291.7	2.769	0.958
334	0.168	47	857.1	3.256	0.846
341	0.168	65	2970.2	3.427	0.821
345	0.168	39	2958.3	2.760	0.753
356	0.168	44	6404.8	2.864	0.757

- Deep station group (DS)
- South-eastern Weddell Sea shelf station group (SES)

The three main groups are distinguished by the following features:

- the Peninsula station group (PI) consists of eight stations situated in 120 to 1000 m water depth in the Bransfield Strait and Drake Passage, one station from the deep Weddell Sea (1000 m) and two additional stations on the south-eastern Weddell Sea shelf (200 to 300 m). This station group is characterized by a high species richness and abundance, high biomass (Figure 2A–C), high Shannon–Wiener diversity but low evenness (Table 3). Abundance was lowest at the 1000-m stations (one from the Weddell Sea) and the Weddell Sea shelf stations grouped with the true Peninsula stations. Among the most abundant species of the station group are two species of the cirratulid genus *Aphelochaeta*, the two maldanids *Maldane sarsi antarctica* and *Rhodine intermedia*, and the onuphid *Notonuphis antarctica*, and five other species belonging to the spionids, paranoids, cirratulids, and opheliids (Figure 4A). The species responsible for 50% of the similarity among the PI stations are almost the same (Table 4).
- The deep-sea station group (DS) consists of eight stations in 1000 to 2500 m depth, located in the Weddell Sea except for one 2000-m station in the Bransfield Strait. Species richness, abundance, and biomass in this group are low (Figure 2). Diversity is also low, but the evenness is high (Table 3). Among the dominants of these stations are the amphinomid *Paramphinome australis* and two cirratulids, *Monticellina* sp. 2 and *Chaetozone* sp. 1, along with seven other species belonging to a variety of families (Figure 4B). The species responsible for 50% of the similarity among these stations are, not unexpectedly, the same (Table 4).
- The seven stations in the south-eastern Weddell Sea shelf station group (SES), spanning a depth range from 180 to 360 m, are intermediate between the other two groups. In terms of species richness and abundance they resemble the deep-sea station group, whereas in terms of biomass the group is more similar to the Peninsula group (Figure 2) but very heterogeneous. Diversity is also intermediate, with the evenness being nearly the same as in the deep-sea station group (Table 3). The species accounting for 50% of the similarity among the SES stations are the five most abundant species of the group: the spionid *Spiophanes tcherniai*, the syllids *Syllis spongiphila* and *Sphaerosyllis antarctica*, the lumbrinerid *Lumbrineris* cf. *kerguelensis*, and the orbiniid *Leodamas marginatus* (Table 4; Figure 4C).

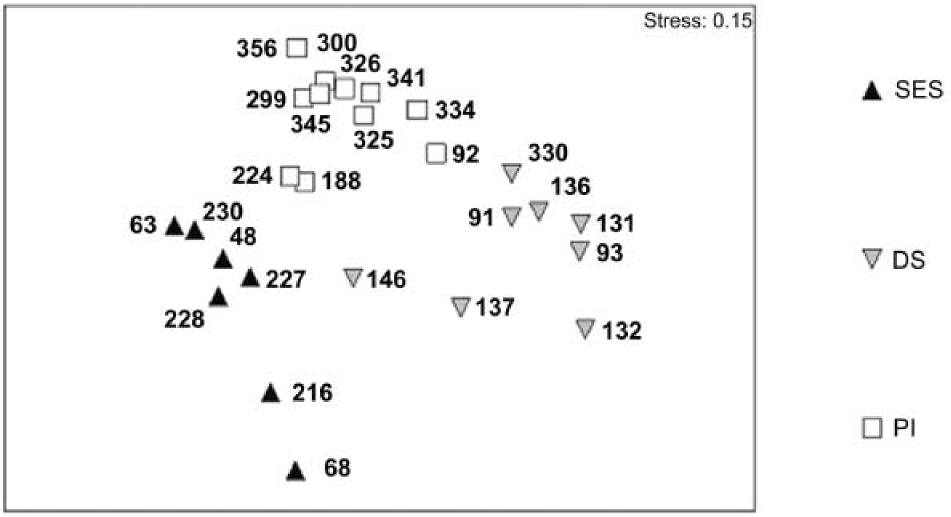

Figure 3. Nonmetric multidimensional scaling ordination based on Bray–Curtis similarity derived from 4th-root transformed abundance data.

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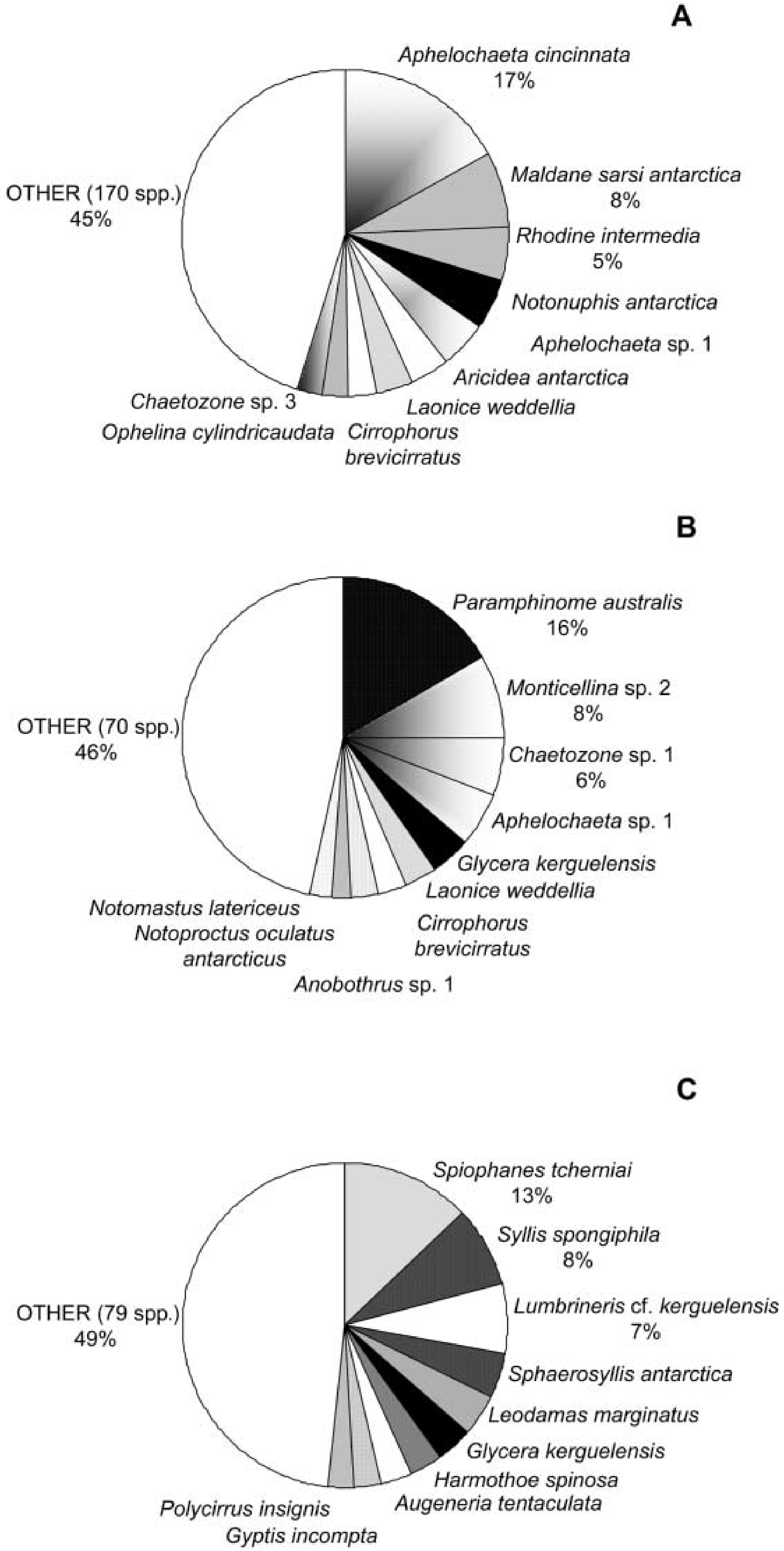

Figure 4. Most abundant polychaete species in each station group as defined by cluster analysis. (A) Peninsula group; (B) deep-sea group; and (C) south-eastern Weddell Sea shelf group.

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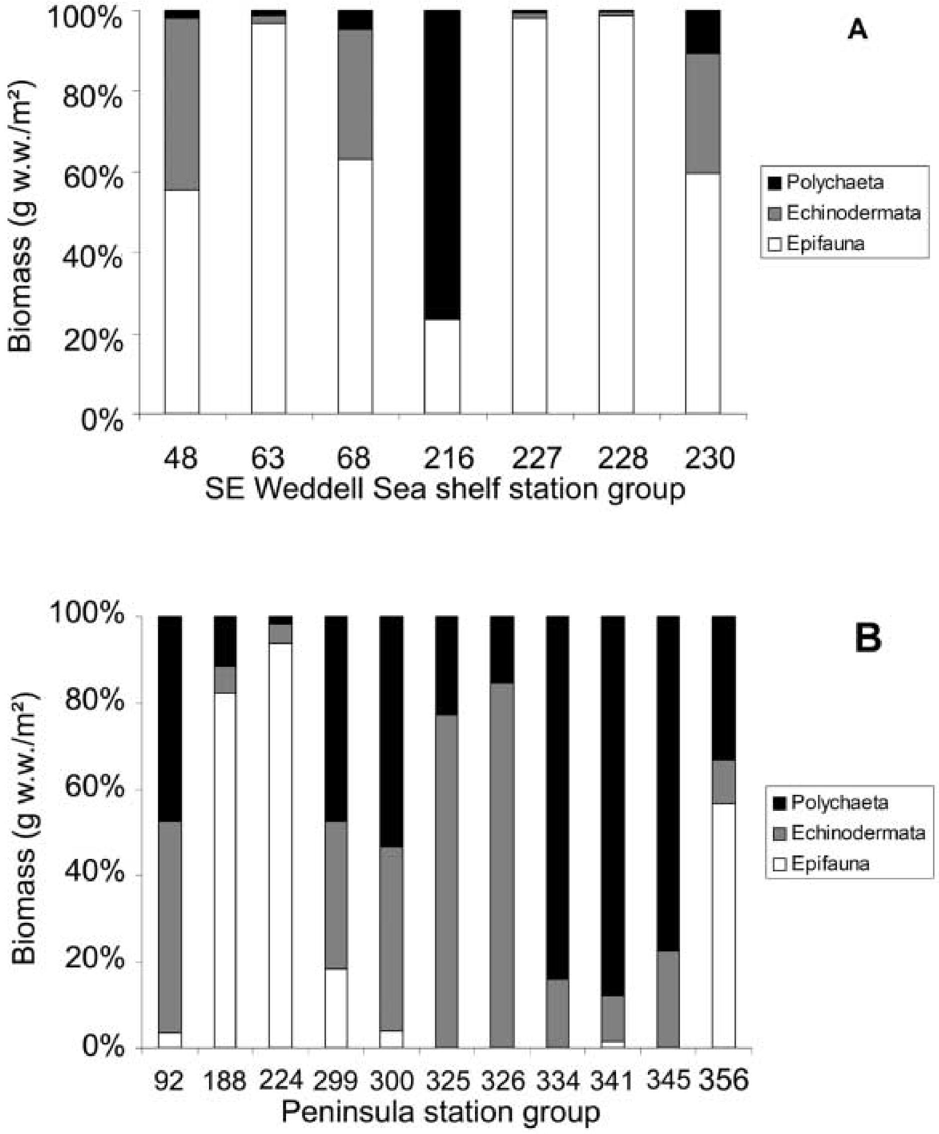

Figure 5. Biomass of major taxonomic groups at (A) Weddell Sea and (B) Peninsula stations.

Table 3. *Parameter means and standard deviations of stations grouped together by Bray–Curtis similarity. Cumulative number of species referring to pooled stations of group; mean abundance expressed as individuals per m^2, mean biomass in g wet weight per m^2. H′ based on log$_e$.*

Station group	Cumulative no. species	Mean no. species	Mean abundance (m^{-2})	Mean biomass	Mean diversity (H′)	Mean evenness (J′)
Peninsula (PI)	180	52.4 ±7.8	3164.9 ±1537.0	63.6 ±26.9	2.96 ±0.30	0.75 ±0.08
Deep (DS)	80	35.8 ±15.3	429.3 ±117.5	2.7 ±2.4	2.63 ±0.19	0.88 ±0.05
South-eastern Weddell Sea Shelf (SES)	89	26.3 ±7.3	540.8 ±165.8	79.1 ±101.5	2.81 ±0.45	0.89 ±0.07

Differences in the species composition are significant (Table 5, ANOSIM); the species contributing most substantially to the dissimilarities between pairs of station groups are listed in Table 6. The Peninsula group (PI) is dissimilar to both DS and SES mostly because of high abundances of several species that are rare or absent at both other station groups, including large cirratulids, onuphids, and maldanids. On the other hand, the shallow and deep stations on the Weddell Sea shelf and slope (DS and SES) are dissimilar because each of these groups can be characterized by species that are abundant in one group and rare or absent in the other.

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Figure 6. Depth distribution of most abundant polychaetes and less abundant species of the same families with abundances per station no less than five specimens.

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Table 4. *Species contributing to the similarity of stations in clusters identified with Bray–Curtis similarity measure, defined with SIMPER.*

Station group	Species	Average abundance	Average similarity ±SD	Per cent contribution	Cumulative per cent contribution
PI	*Aphelochaeta cincinnata*	535.71	3.55 ±0.60	16.49	16.49
	Laonice weddellia	111.69	1.96 ±1.14	9.12	25.61
	Chaetozone sp. 3	74.24	1.61 ±1.39	7.47	33.08
	Maldane sarsi antarctica	237.66	1.46 ±0.59	6.78	39.86
	Aphelochaeta sp. 1	148.38	1.09 ±0.87	5.05	44.92
	Notonuphis antarctica	154.76	1.01 ±0.34	4.71	49.63
DS	*Paramphinome australis*	71.83	6.34 ±0.81	25.77	25.77
	Monticellina sp. 2	35.97	3.69 ±0.73	15.2	40.79
	Chaetozone sp. 1	24.83	2.17 ±0.69	8.82	49.61
SES	*Spiophanes tcherniai*	72.62	2.94 ±0.50	11.63	11.63
	Syllis spongiphila	45.41	2.78 ±0.82	10.99	22.62
	Lumbrineris cf. *kerguelensis*	38.97	2.69 ±0.85	10.63	33.25
	Sphaerosyllis antarctica	25.37	2.21 ±1.40	8.37	41.98
	Leodamas marginatus	23.38	2.04 ±1.13	8.08	50.06

Table 5. *Results of one-way ANOSIM randomization test based on similarity measures derived from abundance values. Global* R*=0.839.*

Groups	*R*-statistic	Significance level (%)	Possible permutations
SES, DS	0.867	0.1	6435
SES, PI	0.854	0.1	31,824
DS, PI	0.859	0.1	75,582

There are some exceptions to the pronounced regional differences, namely the three Weddell Sea Stations 92, 188 and 224 which group with PI (Figure 3). Station 92 (1000 m) differs from DS by high abundances of *Cirrophorus brevicirratus* and *Aricidea simplex*, among others, both of which are species contributing more than 1% to the similarity of the PI stations. Stations 188 and 224 group with PI rather than SES because of high abundances of *Maldane sarsi antarctica* and *Cirrophorus brevicirratus* (Station 188) and *Laonice weddellia* and *Chaetozone* sp. 3 (Station 224), respectively. All three stations join the larger group of true Peninsula stations at a low level of similarity.

Concerning diversity, the stations in both shelf areas showed a wider range than the deep-sea stations; diversity at the deep-sea stations did not differ significantly from the shelf groups (one-way analysis of variance: F=0.178). The lower evenness in the PI group is a result of the higher dominance of a few species per station; the top dominant species contributed between 18 and 43% to the total polychaete abundance at any one station (one exception: 12% at Station 341), while at SES and DS, the same values are within a lower range of roughly 10 to 30% (only at one station each on the shelf and the slope the values are around 40%).

DISCUSSION

Most striking is the difference in abundance per station between the Peninsula station group on the one hand and the two other groups in the Weddell Sea on the other (Figure 2A). Somewhat less distinct is the difference in species richness per station (Figure 2B), but still a general trend can be seen toward higher species richness in the PI station group. These findings are also reflected in the respective mean values for the station groups (Table 3), and they suggest that depth in itself may not be as important in polar waters as in temperate areas because of the isothermic water column, at least down to the depths sampled during this study. Rather, our results indicate regional differences between the two areas. Gambi & Bussotti (1999) reported equally variable but as a whole much lower polychaete abundances from three sites between 450 and 810 m depth in the Ross Sea, closely related to sedimentary conditions. In a recent review on the diversity of Antarctic benthos, Clarke & Johnston (2003) reported a generally higher species richness in the Weddell Sea than in the Ross Sea, mostly relying on data from the shelf. San Martin et al. (2000) presented quantitative data on polychaetes off Livingston & Deception Island (South Shetlands). Their stations grouped into two clusters by depth (Livingston Island) while the samples from Deception Island were separated due to the influence of volcanic eruptions. The parameter responsible for the depth zonation pattern was organic matter content of the sediment. However, there seem to be patterns related to depth on the lower slope and abyssal plain (Brandt et al., 2004). In comparison, in Arctic waters, Schnack (1998) defined three clearly separated communities on the slope off eastern Greenland which he also interpreted as reflecting depth-related parameters such as food supply. The communities in the Peninsula and south-eastern Weddell Sea shelf areas suggest that they might be structured by food input as well, the Peninsula area being known as very productive.

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Table 6. *Polychaete species characterizing the station groups identified by clustering, determined by similarity percentage analyses (SIMPER), based on 4th-root transformed abundance data and the Bray–Curtis similarity measure.*

Group	Species	Average abundance PI	Average abundance DS	Average abundance SES	Average dissimilarity	δ/SD
SES vs DS, δ=91.32	*Spiophanes tcherniai*		0.00	72.62	6.99	0.78
	Paramphinome australis		71.83	0.00	6.97	1.03
	Syllis spongiphila		0.00	45.41	4.06	1.15
	Monticellina sp. 2		35.97	0.00	4.05	0.94
	Lumbrineris cf. *kerguelensis*		0.00	38.97	3.56	1.27
	Chaetozone sp. 1		24.83	5.95	2.59	1.09
	Leodamas marginatus		4.65	23.38	2.24	1.32
	Sphaerosyllis antarctica		2.60	25.37	2.23	1.50
	Aphelochaeta sp. 1		23.62	6.35	2.23	1.10
	Gyptis incompta		0.00	16.16	1.93	1.05
	Glycera kerguelensis		16.20	21.15	1.90	1.24
	Harmothoe spinosa		0.00	18.57	1.75	1.26
	Augeneria tentaculata		4.51	16.98	1.65	0.76
	Laonice weddellia		15.19	12.16	1.63	1.26
	Notomastus latericeus		9.24	13.01	1.53	1.05
PI vs DS, δ=91.09	*Aphelochaeta cincinnata*	535.71	2.60		11.14	0.82
	Notonuphis antarctica	154.76	0.00		5.12	0.64
	Maldane sarsi antarctica	237.66	6.94		4.89	0.85
	Rhodine intermedia	170.35	0.00		3.51	0.52
	Cirrophorus brevicirratus	94.70	11.66		3.07	0.65
	Aphelochaeta sp. 1	148.38	23.62		2.97	0.83
	Laonice weddellia	111.69	15.19		2.96	1.23
	Paramphinome australis	14.94	71.83		2.55	0.94
	Chaetozone sp. 3	74.24	1.30		2.32	1.41
	Aricidea antarctica	123.48	0.00		2.27	0.65
	Aricidea simplex	39.61	3.65		1.96	0.45
	Lumbrineris cf. *kerguelensis*	63.53	0.00		1.69	0.98
	Galathowenia wilsoni	62.23	3.57		1.65	0.51
SES vs PI, δ=91.36	*Aphelochaeta cincinnata*	535.71		1.98	10.82	0.81
	Notonuphis antarctica	154.76		0.00	4.89	0.64
	Maldane sarsi antarctica	237.66		0.00	4.73	0.83
	Rhodine intermedia	170.35		0.00	3.40	0.52
	Cirrophorus brevicirratus	94.70		2.38	2.98	0.64
	Aphelochaeta sp. 1	148.38		6.35	2.85	0.78
	Laonice weddellia	111.69		12.16	2.82	1.21
	Spiophanes tcherniai	29.65		72.62	2.67	0.76
	Aricidea antarctica	123.48		0.00	2.21	0.65
	Chaetozone sp. 3	74.24		7.60	2.05	1.35
	Aricidea simplex	39.61		0.00	1.87	0.45
	Lumbrineris cf. *kerguelensis*	63.53		38.97	1.70	1.15
	Galathowenia wilsoni	62.23		1.19	1.60	0.51
	Melinna elisabethae	53.57		0.00	1.49	0.36

δ/SD, standard deviation.

Several studies have been carried out to characterize downslope changes in benthic communities of temperate deep-sea areas, for example, off the Farallon Islands (north-east Pacific) and off the US east coast. In the Pacific, there was an abundance low at 800 m due to the OMZ, a peak at around 1900 m and a gentle decline toward the lower slope. Species richness of the total infauna and, although less pronounced, that of the polychaetes, also increased with increasing depth to about 2000 m and then gradually decreased to 3100 m. Upwelling and the downslope transport of shelf sediments may account for these gradients (Hilbig & Blake, 2006). Studies carried out in the north-west Atlantic off the United States (Grassle & Morse-Porteous, 1987) revealed a much different downslope gradient with higher abundances above 1000 m, declining rapidly with increasing depth, with an intermittent peak at 2000 m. Species richness was highest at 800 m and declined steadily to 3000 m.

Biomass

While polychaetes are an important element of the benthic infauna on the Antarctic shelves and slopes like along other coasts of the world's oceans, their contribution to biomass depends not only on sediment type, but also on features specific to the Antarctic shelf communities such as

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assemblages of large epifaunal filter feeders. The present study reveals that on the south-eastern Weddell Sea shelf, the percentage of polychaete biomass was largely corresponding to the amount of sponges, and to a lesser extent of echinoderms, in the samples; it varied greatly among stations and was highest at Station 216 (Figure 6A). At the Peninsula, sponges were much less important, resulting in a higher contribution of polychaetes to total biomass (Figure 6B). Crustaceans were not included in this comparison because their contribution to total biomass was negligible except for Station 345 (Peninsula group), where the contribution of polychaetes was in reality smaller than shown on the graph. Overall, the communities, and most likely the environmental conditions, were much more heterogeneous at the stations of the Peninsula group than at those of the shelf station group. A similarly heterogeneous distribution of biomass was reported by Piepenburg et al. (2002) who analysed macro- and megafauna from muddy bottoms around King George Island in depths between 100 and 2000 m. Polychaete biomass made up <10% to >80% of total biomass, with a mean of 37.1%, which is fairly similar to the corresponding value in the present study (29.2%). Somewhat higher values were reported by Mühlenhardt-Siegel (1988) for Elephant Island, the South Shetland Islands, South Orkney Islands, and the Antarctic Peninsula (means ranging from 9 to 116 g), with polychaetes contributing between about 20 and 75%. Gerdes et al. (1992) found that comparable values from different communities living on the south-eastern Weddell Sea shelf varied between 8.3 and 70.9%. Our findings correspond well with these results. In contrast, in sublittoral sands off King George Island (Admiralty Bay), Sicinski & Janowska (1993) found a relatively small polychaete biomass proportion of 14%, (mostly large individuals of *Aglaophamus* and *Travisia*), while the main biomass was contributed by isopods and sea urchins.

At the deep Weddell Sea stations, contributions of polychaetes to total infaunal biomass was highest at 1500 m (53%) and most variable at 2000 m where at some stations high biomass of starfish and brittle stars was encountered. Brown (1991) calculated biomass from several samples obtained off the US Atlantic coast in 2000 m water depth. She also found total biomass to be very variable at that depth because of patchy occurrences of large unidentified echinoderms (samples were destroyed as biomass was measured as wet, dry, and ash-free dry weight). The overall range of total wet weight biomass recorded by Brown (1991) was comparable to that reported for similar depths in this study, classifying the Weddell Sea slope as a highly productive deep-sea area.

The high productivity of the Antarctic has also been noted for a long time in comparison with Arctic waters. During one of the first conferences comparing the polar oceans, George (1977) stated biomass in the Arctic deep sea to be 'about 40 times lower than deep-sea biomass in the Antarctic' However, there may be more regional differences superimposed on this general pattern than noted at first sight. In the same volume, Carey & Ruff (1977) presented deep-sea biomass values from the Beaufort Sea from about 1000 to 2000 m that are quite comparable to those found in this study in the deep Weddell Sea. In general, the contribution of polychaetes to total biomass is much higher in the Arctic than in the Antarctic because of the absence of large epifauna on the shelf. Schnack (1998) reported the contribution of polychaetes to total biomass to amount to 83% at 200 m, to only 11% at 1400 m (due to the large biomass of crustaceans), and again to 82% at 2700 m.

Species composition

The presence of syllids among the dominants at shallow stations in the Weddell Sea points to a strong influence of epibenthic sponge communities on the upper shelf. Due to the presence of lumbrinerids, glycerids, and scale worms along with the syllids, the south-eastern Weddell Sea shelf is dominated by carnivores and epifaunal/interstitial forms, much like one of the sites investigated by Gambi & Bussotti (1999). The low percentage of subsurface deposit feeders is probably a result of the very short and episodic periods of high primary production in the overlying water column coupled with extensive resuspension due to strong currents (Orejas, 2000). Apparently, the suspension feeding community is much better adapted to exploit this food source than endobenthic organisms.

At the deep-water stations, the occupation of the top dominant position by *Paramphinome australis* is somewhat unusual as this species is a carnivore. Consequently, the deep stations are characterized by a mix of carnivores and surface deposit feeders, again indicating the absence of large pulses of nutrient input. The absence or paucity of opportunistic polychaete species and families exploiting episodic food inputs was already reported by Hilbig (2001). Members of the family Amphinomidae have not been reported before as dominants, even though published data demonstrate that dominant polychaete species can belong to a wide variety of families. Borowski (1995) mentioned the occurrence of amphinomids in anthropogenically disturbed areas of the Peru Basin (DISCOL experiment).

Biodiversity

As the area sampled at each station was very small (just over one-tenth of a square metre), diversity measures have to be applied with caution. Additional sampling efforts in similar areas may alter the impressions derived from this study, and larger-scale deep-sea studies currently underway, such as DIVA (Kröncke & Türkay, 2003) in the Angola Basin and ANDEEP (Fütterer et al., 2003; Brandt & Hilbig, 2004) in the Weddell and Scotia Seas may shed some more light on the diversity in the deep sea. However, comparisons with samples of a similar size ($0.1 m^2$) taken off the Farallon Islands (Hilbig & Blake, 2006) show that at depths less than 1000 m, diversity (H') is much higher in the Southern Ocean than in the northeast Pacific. Evenness is considerably higher in the Antarctic samples, and the highest values for H' calculated from samples taken off the Farallones are about the same as the lowest respective values calculated from samples taken in the Southern Ocean. Generally, the samples from the Weddell Sea slope were reminiscent more of

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samples from abyssal plains, with very low abundance and relatively high species numbers, than of samples from slopes in temperate regions.

Eurybathy

Eurybathy has generally been accepted (for example, Arntz et al., 1994) as a typical characteristic of the Antarctic fauna. However, a closer examination of available data from deep waters in non-polar areas reveals that eurybathy might be more common than originally thought. For example, on the Chatham rise (Probert et al., 1996), five of six species sampled in 1400 m had their upper distribution limit at 450 m (the shallowest station of the study was at 250 m), and nine of 11 species occurring at 1250 m were also found at 450 m. Even though the typically small deep-sea organisms may have been undersampled by Probert et al. (1996) because of the large mesh size used (1 mm), it appears that 82–83% of the fauna could be considered eurybathic.

Data compiled by Blake et al. (1987) on the US Atlantic continental slope and rise, spanning a depth range of 600 to 3500 m, show a similar trend. On the lower slope (zonation of the slope according to Hecker, 1994) in 2000–3000 m, nearly all polychaetes (90–92% of all species) belonged to eurybathic species, i.e. they were present to the upper middle slope (600–800 m). In 3500 m, still 56% of all polychaetes showed an upper distribution limit of 600–800 m. A typical lower-slope fauna contributed no more than 3–5% to total polychaete species richness in 2000–3000 m, and only at depths of 3500 m did lower-slope species constitute a significant part of the total polychaete species richness (44% of all polychaete species). While there is no information available about the transition from shelf to slope fauna from the Atlantic data, a similar study in the Pacific off the Farallon Islands (SAIC, 1992; Hilbig & Blake, 2006), including 12 stations on the shelf at 70–200 m as well as deep-sea stations in 500–3000 m, revealed that of 383 polychaete species collected in the deep sea, no more than 33 occurred also on the shelf (roughly 9%).

The above information from two large deep-sea programmes suggests that in temperate oceans, there are faunal breaks between shelf and upper slope and between lower slope and rise. These breaks are characterized by a—more or less complete—replacement of one suite of species by another, on the lower slope additionally by a pronounced decrease in species richness. In contrast, the Southern Ocean deep sea seems to be characterized by a continuous downslope decrease of species richness, with no distinct faunal elements of the slope and rise occurring that might replace the shelf fauna. The weakly pronounced dissimilarity between stations in shallow and deep water, respectively, in the Weddell Sea found in this study is in part caused by the eurybathy of most of the numerically dominant species (Table 3; Figure 5). Piepenburg et al. (2002) observed a similar decrease in the number of gross taxa constituting the mega- and macrofauna at nine stations off King George Island (all also included in this study), even though they noted an increase of megabenthic taxa from 100 to 1000 m in the Drake Passage.

One can also conclude that eurybathy as such, if defined as distribution over a wide depth range of several 100s or 1000s of metres, is not necessarily a specialty of Antarctic fauna. As far as one can tell from the sparse data available from the slopes of the Southern Ocean, the difference between Antarctic and temperate seas may be the absence of a true deep-sea community with upper distribution limits on the Antarctic slope. The low species richness observed in depths below 1000 m during our study apparently is the result of a gradual drop-out of species already present at relatively shallow depths around 100 to 200 m (Figure 5). Of the 66 species analysed, comprising the ten most abundant species of each station group and all species of the same families represented by no less than five individuals at any single station, only three had their upper distributional limits below 1000 m; all others were species occurring from the shelf down to different slope depths.

However, this statement should be made with caution as it is possible that a faunal break between slope and rise may occur at greater depths not yet sampled adequately, or that a true deep-sea fauna can only be found on the abyssal plains of the Southern Ocean. In comparison with the Arctic, Bilyard (1991) found that polychaetes as a whole have a greater depth range in the Antarctic, but there were no significant differences if different feeding types were considered. His results were based on literature data for the Antarctic (standard works by Hartman, 1964, 1966, 1967, 1978) and own data from the Beaufort Sea. The author suspected that the results might be impaired by differences in sampling intensity in both polar oceans. Brey et al. (1996) concluded from their analysis of the depth distribution of a few selected taxa-only scale worms in the case of polychaetes- that the degree of extended eurybathy in Antarctic waters is very different depending on the taxonomic group. For polychaetes, the authors found no significant difference between Antarctic and non-Antarctic species, and they concluded that taxa with such a behaviour might have developed their ability to live in a wide depth range before they colonized the Antarctic shelves and slopes.

Investigations of physiological challenges of life in the deep sea and within great depth ranges point in the same general direction as the results by Brey et al. (1996). The decreasing pressure with increasing water depth affects mainly enzyme activity and processes associated with cell membranes, including electrophysiological processes (Somero et al., 1983; Somero, 1990), while temperature may not have as strong an effect (see also Hilbig & Blake, 2006). The ability to cope with large changes in hydrostatic pressure over both ecological and evolutionary time, appears to be developed to very different degrees in different organisms (Somero et al., 1983) and may be a pre-adaptation in polychaetes to colonize the deep sea from the shelf and, in the case of the Southern Ocean, also to recolonize the shelf from the deep sea, but is obviously not limited to the Antarctic.

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Appendix A. *Polychaete species identified from 26 stations in the Weddell Sea, Bransfield Strait, and Drake Passage.*

Family Acrocirridae
- *Flabelligella* sp. 2

Family Ampharetidae
- *Amage sculpta* Ehlers, 1908
- *Ampharete kerguelensis* McIntosh, 1885
- *Amphicteis gunneri* (Sars, 1835)
- *Amphisamytha* sp. 1
- *Anobothrella antarctica* (Monro, 1939)
- *Anobothrus gracilis* (Malmgren, 1866)
- *Anobothrus* sp. 1
- *Anobothrus* sp. 2
- *Asabellides* sp. 1
- *Ecamphicteis* sp. 1
- *Eusamythella sexdentata* (Hartman, 1967)
- *Glyphanostomum pallescens* (Theel, 1878)
- *Grubianella antarctica* McIntosh, 1885
- *Melinantipoda antarctica* Hartman, 1967
- *Melinna elisabethae* McIntosh, 1914
- *Neosabellides elongatus* (Ehlers, 1908)
- *Phyllocomus crocea* Grube, 1877
- *Sosanopsis kerguelensis* Monro, 1939

Family Amphinomidae
- *Paramphinome australis* Monro, 1930

Family Aphroditidae
- *Hermionopsis levisetosa* Seidler, 1923

Family Apistobranchidae
- *Apistobranchus gudrunae* Hartmann-Schröder & Rosenfeldt, 1988

Family Capitellidae
- *Capitella capitata* complex (Fabricius, 1780)
- *Notomastus latericeus* Sars, 1850

Family Chaetopteridae
- *Phyllochaetopterus monroi* Hartman, 1967

Family Cirratulidae
- *Aphelochaeta cincinnata* (Ehlers, 1908)
- *Aphelochaeta* cf. *epitoca* (Monro, 1930)
- *Aphelochaeta* sp. 1
- *Aphelochaeta* sp. 2
- *Aphelochaeta* sp. 3
- *Caulleriella* sp. 1
- *Chaetozone andersenensis* (Augener, 1932)
- *Chaetozone* sp. 1
- *Chaetozone* sp. 2
- *Chaetozone* sp. 3
- Cirratulidae sp. 1
- *Cirratulus cirratus* (Müller, 1776)
- *Cirratulus filiformis* Keferstein, 1862
- *Cirratulus parafiliformis* Hartmann-Schröder & Rosenfeldt, 1989)
- *Monticellina* sp. 1
- *Monticellina* sp. 2
- *Protocirrineris antarctica* (Monro, 1930)
- *Tharyx* sp. 1
- *Tharyx* sp. 2

Family Dorvilleidae
- *Ophryotrocha notialis* (Ehlers, 1908)

Family Eunicidae
- *Eunice pennata* (O.F. Müller, 1776)

Family Euphrosinidae
- *Euphrosine antarctica* Hartmann-Schröder & Rosenfeldt, 1992
- *Euphrosine armadilloides* Ehlers, 1900
- *Euphrosine cirrata* Sars, 1862
- *Euphrosine cirribranchis* Hartmann-Schröder & Rosenfeldt, 1992

Family Flabelligeridae
- *Diplocirrus hirsutus* (Hansen, 1879)
- *Flabelligera mundata* Ehlers, 1908
- *Flabelligera picta* Ehlers, 1913
- *Pherusa kerguelarum* (Grube, 1878)

Family Glyceridae
- *Glycera kerguelensis* McIntosh, 1885

Family Hesionidae
- *Gyptis incompta* Ehlers, 1912
- *Kefersteinia fauveli* Averincev, 1972

Family Lacydoniidae
- *Lacydonia antarctica* Hartmann-Schröder & Rosenfeldt, 1988

Family Lumbrineridae
- *Augeneria tentaculata* Monro, 1930
- *Lumbrineris* cf. *kerguelensis* (Grube, 1878)
- *Paraninoe brevipes* (McIntosh, 1903)

Family Maldanidae
- *Asychis amphiglyptus* (Ehlers, 1897)
- *Axiothella antarctica* Monro, 1930
- *Eupraxillella antarctica* Hartmann-Schröder & Rosenfeldt, 1989
- *Isocirrus yungi* Gravier, 1911
- *Lumbriclymenella robusta* Arwidsson, 1911
- *Maldane sarsi antarctica* Arwidsson, 1911
- Maldanidae sp. 1
- *Nicomache* sp. 1
- *Notoproctus oculatus antarcticus* Arwidsson, 1911
- *Praxillella kerguelensis* (McIntosh, 1885)
- *Rhodine intermedia* Arwidsson, 1911
- *Rhodine loveni* Malmgren, 1865

Family Nephtyidae
- *Aglaophamus posterobranchus* Hartman, 1967
- *Aglaophamus trissophyllus* (Grube, 1877)
- *Micronephtys* sp. 1
- *Nephtys magellanica* Augener, 1912

Family Nereididae
- *Ceratocephale* sp. 1
- *Ceratonereis antarctica* Hartmann-Schröder & Rosenfeldt, 1988
- *Nereis eugeniae* (Kinberg, 1866)

Family Onuphidae
- *Kinbergonuphis notialis* (Monro, 1930)
- *Kinbergonuphis* nr *notialis* (Monro, 1930)
- *Kinbergonuphis* sp. 1
- *Notonuphis antarctica* (Monro, 1930)

Family Opheliidae
- *Ophelina breviata* (Ehlers, 1913)
- *Ophelina cylindricaudata* (Hansen, 1878)
- *Ophelina gymnopyge* (Ehlers, 1908)
- *Ophelina nematoides* (Ehlers, 1913)
- *Ophelina syringopyge* (Ehlers, 1901)
- *Travisia kerguelensis* McIntosh, 1885

Family Orbiniidae
- *Leitoscoloplos kerguelensis* (McIntosh, 1885)
- *Leodamas marginatus* (Ehlers, 1897)
- *Orbinia* sp. 1
- *Phylo minima* Hartmann-Schröder & Rosenfeldt, 1990

Family Oweniidae
- *Galathowenia wilsoni* Blake, 1984
- *Myriochele joinvillensis* Hartmann-Schröder & Rosenfeldt, 1989
- *Myriochele* sp. 1
- *Myrioglobula antarctica* Hartman, 1967

Family Paraonidae
- *Aricidea antarctica* Hartmann-Schröder & Rosenfeldt, 1988
- *Aricidea* cf. *antennata* Annenkova, 1934
- *Aricidea oculata* Hartmann-Schröder & Rosenfeldt, 1990
- *Aricidea simplex* Day, 1963
- *Aricidea strelzovi* Hartmann-Schröder & Rosenfeldt, 1990
- *Aricidea* nr. *trilobata* Imajima, 1973
- *Cirrophorus brevicirratus* Strelzov, 1973

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Cirrophorus brunneus Hartmann-Schröder & Rosenfeldt, 1988
Levinsenia antarctica (Strelzov, 1973)
Levinsenia gracilis (Tauber, 1879)
Family Pholoidae
Pholoe sp. 1
Family Phyllodocidae
Austrophyllum charcoti (Gravier, 1911)
Eteone sculpta Ehlers, 1897
Eulalia picta (Kinberg, 1866)
Eulalia subulifera Ehlers, 1897
Mystides borealis Théel, 1879
Nereiphylla polyphylla (Ehlers, 1897)
Phyllodoce longipes Kinberg, 1866
Protomystides cf. *occidentalis* (Ditlevsen, 1917)
Protomystides sp. 1
Sige sp. 1
Zverlinum monroi (Hartman, 1964)
Family Polygordiidae
Polygordius sp. 1
Family Polynoidae
Barrukia cristata (Willey, 1902)
Eucranta villosa notialis Monro, 1936
Eulagisca gigantea Monro, 1939
Eunoe anderssoni (Bergström, 1916)
Harmothoe crosetensis (McIntosh, 1885)
Harmothoe nr. *crosetensis* (McIntosh, 1885)
Harmothoe cf. *magellanica* McIntosh, 1885
Harmothoe monroi Ushakov, 1962
Harmothoe spinosa Kinberg, 1855
Polyeunoa laevis McIntosh, 1885
Family Sabellidae
Euchone pallida Ehlers, 1908
Euchone scotiarum Hartman, 1978
Euchone undulocincta Hartmann-Schröder & Rosenfeldt, 1989
Fabricia stellaris stellaris Blainville, 1828
Fabricinae sp. 1
Jasmineira crumenifera Hartmann-Schröder, 1986
Jasmineira sp. 1
Myxicola sulcata Ehlers, 1912
Oriopsis kocki Hartmann-Schröder & Rosenfeldt, 1989
Oriopsis longipyge Hartmann-Schröder & Rosenfeldt, 1989
Oriopsis sp. 1
Perkinsiana borsibrunoi Giangrande & Gambi, 1997
Perkinsiana littoralis Giangrande & Gambi, 1997
Sabella sp. 1
Family Scalibregmatidae
Asclerocheilus ashworthi Blake, 1981
Asclerocheilus nr *tropicus* Blake, 1981
Axiokebuita minuta (Hartman, 1967)
Hyboscolex dicranochaetus (Schmarda, 1861)
Oligobregma hartmanae Blake, 1981
Oligobregma sp. 1
Pseudoscalibregma bransfieldium (Hartman, 1967)
Scalibregma inflatum Rathke, 1843
Sclerocheilus antarcticus Ashworth, 1915
Family Serpulidae
Chitinopomoides wilsoni Benham, 1927
Serpula narconensis Baird, 1865
Family Sphaerodoridae
Clavodorum antarcticum Hartmann-Schröder & Rosenfeldt, 1990
Ephesiella antarctica (McIntosh, 1885)
Ephesiella mühlenhardtae Hartmann-Schröder & Rosenfeldt, 1988
Sphaerodoropsis arctowskyensis Hartmann-Schröder & Rosenfeldt, 1988
Sphaerodoropsis parva (Ehlers, 1913)
Sphaerodoropsis polypapillata Hartmann-Schröder & Rosenfeldt, 1988
Sphaerodoropsis sp. 1
Family Spionidae
Laonice antarcticae Hartman, 1953
Laonice cirrata (Sars, 1851)
Laonice weddellia Hartman, 1978
Microspio moorei (Gravier, 1911)
Prionospio cf. *dubia* Monro, 1930
Prionospio cf. *ehlersi* Fauvel, 1928
Scolelepis eltaninae Blake, 1983
Scolelepis sp. 1
Spiophanes sp. 1
Spiophanes tcherniai Fauvel, 1951
Family Sternaspidae
Sternaspis scutata (Renier, 1807)
Family Syllidae
Autolytus charcoti Gravier, 1906
Autolytus gibber Ehlers, 1897
Autolytus maclearanus McIntosh, 1885
Brania rhopalophora (Ehlers, 1897)
Braniella palpata Hartman, 1967
Eusyllis kerguelensis McIntosh, 1885
Exogone heterosetoides australis Hartmann-Schröder & Rosenfeldt, 1988
Exogone obtusa Hartmann-Schröder & Rosenfeldt, 1988
Exogone sp. 1
Pionosyllis maxima Monro, 1930
Pionosyllis stylifera Ehlers, 1913
Sphaerosyllis antarctica Gravier, 1807
Sphaerosyllis joinvillensis Hartmann-Schröder & Rosenfeldt, 1988
Syllides articulosus Ehlers, 1897
Syllides articulosus pumilus Hartmann-Schröder, 1983
Syllides sp. 1
Syllis spongiphila Verrill, 1885
Typosyllis armillaris (Müller, 1776)
Typosyllis pennelli Knox & Cameron, 1998
Typosyllis variegata (Grube, 1860)
Family Terebellidae
Amphitrite cirrata Müller, 1771
Amphitritides sp. 1
Artacama proboscidea Malmgren, 1865
Hauchiella tribullata (McIntosh, 1869)
Lanicides sp. 1
Laphania cf. *boecki* Malmgren, 1866
Leaena antarctica McIntosh, 1885
Leaena collaris Hessle, 1917
Leaena pseudobranchia Levenstein, 1964
Leaena sp. 1
Lysilla loveni macintoshi Hessle, 1917
Nicolea chilensis (Schmarda, 1861)
Phisidia rubrolineata Hartmann-Schröder & Rosenfeldt, 1989
Pista corrientis McIntosh, 1885
Pista mirabilis McIntosh, 1885
Pista patriciae Hartmann-Schröder & Rosenfeldt, 1989
Polycirrus insignis Gravier, 1907
Proclea cf. *glabrolimbata* Hessle, 1917
Streblosoma bairdi antarctica Monro, 1936
Streblosoma sp. 1
Streblosoma variouncinatum Hartmann-Schröder & Rosenfeldt, 1991
Terebella ehlersi Gravier, 1907
Thelepides koehleri Gravier, 1911
Thelepus cincinnatus (Fabricius, 1780)
Family Trichobranchidae
Octobranchus antarcticus Monro, 1936
Octobranchus sexlobatus Hartmann-Schröder & Rosenfeldt, 1989
Octobranchus sp. 1
Terebellides sp. 1
Terebellides stroemi kerguelensis McIntosh, 1885
Trichobranchus glacialis Malmgren, 1866
Trichobranchus glacialis antarcticus Hessle, 1917

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