



Is polychaete diversity in the deep sublittoral of an Antarctic fiord related to habitat complexity?

Krzysztof PABIS* and Jacek SICIŃSKI

Zakład Biologii Polarnej i Oceanobiologii, Uniwersytet Łódzki,
ul. Banacha 12/16, 90-237 Łódź, Poland

<sicinski@biol.uni.lodz.pl> <cataclysta@wp.pl> * corresponding author

Abstract: Seventy-six species of Polychaeta were found in 19 quantitative samples collected in the deep sublittoral (200–500 m) of Admiralty Bay (South Shetlands). Three assemblages were distinguished by similarity analysis (clustering, nMDS). The soft bottom in depths from 200 to 300m was strongly dominated by *Maldane sarsi antarctica* and had very low species richness and diversity. The second assemblage was distinguished in the areas of the sea floor in the same depth range but with aggregations of Ascidiacea and Bryozoa. It was again characterized by high abundance of *Maldane sarsi antarctica*, but showed significantly higher species richness and diversity. Diversity of polychaete feeding guilds was also high in these areas. This pattern was probably associated with an increased habitat complexity due to the presence of dense aggregations of large suspension feeders. High species richness and diversity was also noted in the third assemblage, associated with the deepest sublittoral (400–500 m) of Admiralty Bay. This is the area characterized by very stable environmental conditions, where the assemblage was dominated by *Tharyx cincinnatus*, *Sternaspis* sp., *Maldane sarsi antarctica*, and *Asychis amphiglypta*.

Key words: Antarctic, Admiralty Bay, soft bottom, Polychaeta, feeding guilds.

Introduction

Polychaetes are an important group of the Antarctic benthos in terms of species diversity, abundance and biomass. They are also a group representing a diversity of feeding guilds (Fauchald and Jumars 1979). These invertebrates are considered to be good indicators of bottom conditions (Pocklington and Wells 1992). Most of the quantitative studies on the Southern Ocean polychaete assemblages concerned shallow areas (Hardy 1972; Lowry 1975; Richardson and Hedgpeth 1977; Duchêne 1984; Gallardo *et al.* 1988; Gambi *et al.* 1997). Little research has been dedicated to studies of the deeper areas of the continental shelf (San Martín *et al.* 2000; Hilbig *et al.* 2006; Neal *et al.* 2011; Parapar *et al.* 2011). Even in Admiralty Bay,

one of the most intensively sampled areas in the Antarctic (Siciński *et al.* 2011), the polychaete fauna has been studied mainly at shallow depths, down to about 170 m (Siciński and Janowska 1993; Bromberg *et al.* 2000; Siciński 2004; Petti *et al.* 2006; Pabis and Siciński 2010a). Information on polychaetes associated with deeper parts of the bottom (150–250 m) was presented by Siciński (1986). The only study concerning the deep sublittoral of Admiralty Bay was based on trawling samples and it was focused on larger, mainly epibenthic polychaetes (Pabis and Siciński 2010b).

The shallow Antarctic shelf is affected by disturbance processes associated with mineral suspension inflow and ice scouring (Smale 2008a, b; Brown *et al.* 2004; Siciński *et al.* 2012) while the deeper sublittoral areas are considered as undisturbed. The influence of icebergs is much lower at depths between 200 and 500m and the habitats at those depths are characterized by relatively stable hydrological, physical and chemical conditions (Barnes 1999; Gutt 2001). The rate of inflow of suspended matter in those parts of the shelf is also low, and its impact on the bottom fauna is minimal (Pęcherzewski 1980; Pabis *et al.* 2011). This results in good development of suspension-feeding communities, dominated by sponges, ascidians and bryozoans. These sessile animals form biogenic structures which can increase the habitat complexity and may serve as a refuge from predators. The competition in these habitats is also lower (Sebens 1991; Tews *et al.* 2004). Macroinvertebrate assemblages associated with those aggregations of filter-feeders are often very rich and diverse (Conradi and Cervera 1995; Morgado and Tanaka 2001). Therefore the patches of these relatively large animals located on dropstones may function as small-scale biodiversity hot spots. Moreover, the patchy distribution of Antarctic epibenthic communities creates a mosaic of various habitats at different stages of succession, and contributes to an increased diversity on a larger scale (Gutt and Piepenburg 2003).

In the central basin of Admiralty Bay the suspension-feeding communities occur from 40 to about 380 m depth, ascidians and bryozoans being almost completely absent from the shallowest sublittoral (0–40 m) (Jazdzewski *et al.* 1986; Pabis *et al.* 2011). On the other hand the almost complete lack of these animals in the deepest sublittoral of the bay (400–500 m depth) may be explained by the decrease in inflow of organic suspended-matter associated with weak, near-bottom currents, and thus lower food concentration (Saiz-Salinas *et al.* 1997, 1998; Pabis *et al.* 2011). These conditions may result in a different composition of polychaete assemblages than those observed in shallower parts of the shelf.

The aim of the present study was to describe the patterns of distribution, diversity and feeding-guild structure of polychaetes in the deep areas of the Antarctic shelf, both on the bare muddy bottom and in bottom areas with ascidian and bryozoan aggregations. This study addressed the following question: Is polychaete richness and diversity of the Antarctic deep sublittoral influenced by habitat complexity?

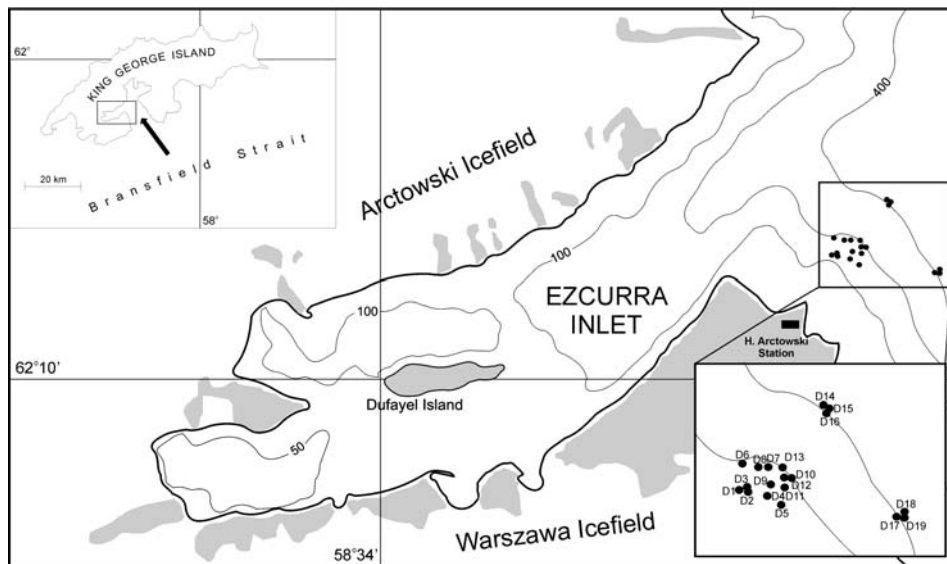


Fig. 1. Admiralty Bay with indicated sampling positions.

Study area

Admiralty Bay is a large Antarctic fiord of tectonic origin located on King George Island. It consists of three inlets (Martel, McKellar and Ezcurre) and a central basin. The central part of the bay is the deepest, reaching almost 550 m in depth, and it opens into the Bransfield Strait. It is the largest bay on the South Shetlands with a surface area of ca 120 km² (Kruszewski 2002). Glaciers are distributed mainly in the inner fiords. In the central basin they can be found almost exclusively on the eastern coast (Braun and Grossmann 2002). The central basin of the bay is characterized by a low mineral sedimentation rate (Pęcherzewski 1980) and low water turbidity (Lipski 1987) compared to the inner fiord areas. In the deepest part of the bay relatively stable environmental conditions occur (Szafranski and Lipski 1982; Siciński 2004; Siciński *et al.* 2011).

Material and methods

Sampling. — Material was collected in 1985 in the central basin of the bay (Fig. 1). Nineteen samples were taken with a van Veen grab (0.1 m²) at the depths ranging from 200 to 500 m. Samples were collected on the bare muddy bottom and in areas with ascidian and bryozan aggregations (Table 1). The material was sieved on a 0.5 mm mesh sieve. Samples were fixed in 4% formalin solution.

Table 1
 Characteristics of samples collected.

Samples	Assemblage	Depth [m]	Ascidiacea wet weight [g/0.1m ²]	Bryozoa wet weight [g/0.1m ²]	Number of polychaete individuals	Number of polychaete species	Latitude S	Longitude W
D1	B	205	288.0	29.7	83	22	62°09.154'	58°26.929'
D2	B	206	0	0.3	136	31	62°09.149'	58°26.927'
D3	A	212	0.3	1.4	34	8	62°09.149'	58°26.927'
D4	B	221	78.2	21.1	99	29	62°09.159'	58°26.857'
D5	B	240	1.3	24.5	96	24	62°09.175'	58°26.745'
D6	B	242	165.0	11.4	121	24	62°09.101'	58°26.939'
D7	B	252	13.2	10.0	214	24	62°09.106'	58°26.878'
D8	B	256	0.5	22.0	150	14	62°09.105'	58°26.897'
D9	B	263	21.0	20.5	98	20	62°09.130'	58°26.796'
D10	A	280	0.09	0.2	197	8	62°09.115'	58°26.673'
D11	B	290	0.2	23.0	112	16	62°09.150'	58°26.728'
D12	A	291	0	0.006	192	6	62°09.115'	58°26.721'
D13	B	296	0	0.8	173	16	62°09.106'	58°26.765'
D14	C	400	0	0	144	24	62°08.690'	58°26.000'
D15	C	405	0	0	187	12	62°08.728'	58°25.980'
D16	C	405	0	0	209	28	62°08.738'	58°25.990'
D17	C	492	0	0	125	14	62°09.240'	58°24.396'
D18	C	496	0	0	227	14	62°09.245'	58°24.381'
D19	C	502	0	0	151	16	62°09.250'	58°24.378'

Data analysis. — The data matrix of polychaete density values (ind./0.1 m²) was fourth-root transformed. The Bray-Curtis similarity index was used to calculate the similarities between the samples. Hierarchical agglomerative clustering was performed using the group average method. Non-metric multidimensional scaling (nMDS) was also used for sample ordination (Clarke and Warwick 1994). Indices of species richness (S – number of species), species diversity (Shannon index $H' = -\sum p_i \ln p_i$), evenness ($J' = H'/\ln S$), Hurlbert rarefaction index - $ES(n)$, (where $n = 50$) as well as density values (ind./0.1 m²) were calculated for each sample. The Shannon index was also calculated for the feeding guilds (Magurran 2004). Frequency (F) as a percentage of total occurrences was calculated for each species in each assemblage. Similarity and diversity measures were calculated using PRIMER 6 package (Clarke and Warwick 1994). Statistical differences for these indices between groups were estimated by the Mann-Whitney U test using the STATISTICA 6 package. In practice, one of three assemblages analyzed (A) was excluded from testing because only three samples were grouped in this cluster, however the mean values were calculated and presented. Each species was assigned to a feeding guild according to the classification proposed by Fauchald and Jumars (1979).

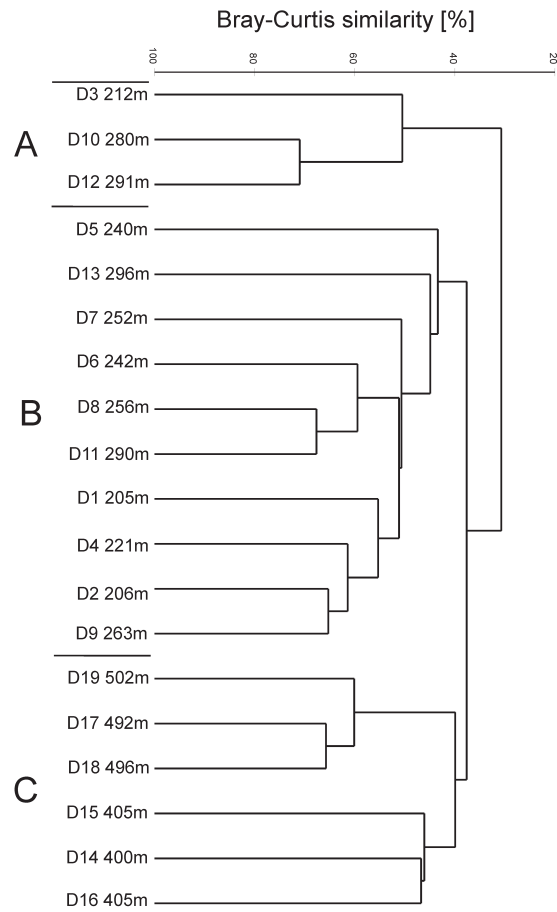


Fig. 2. Dendrogram of samples for the Bray-Curtis similarity, fourth root transformed data and group average grouping method.

Results

Characteristics of assemblages

Seventy six species (2748 individuals) were recorded in the analyzed material (Table 2). Three groups of samples (assemblages A, B and C) representing three different bottom areas were distinguished in the cluster analysis (Fig. 2). A similar trend was observed in the nMDS plot (Fig. 3). The lowest values of species richness, evenness and diversity were found in assemblage A. Although of the same depth range, this assemblage differs strongly from assemblage B in terms of species composition, diversity and richness (Fig. 4, Table 2). Significant differences between assemblages B and C were found for density values and the rarefaction index. There were no significant differences with respect to the other indices (Man-Whitney U test, $p < 0.05$).

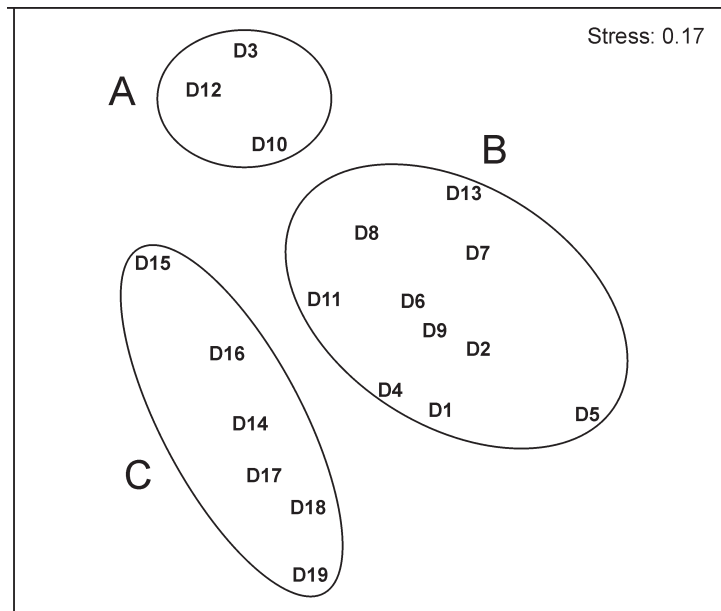


Fig. 3. nMDS plot for the Bray-Curtis similarity, fourth root transformed data.

Assemblage A. — Only 12 species were found in this group of samples from the middle sublittoral (200–300 m), in a bottom area devoid of ascidian and bryozoan aggregations. This assemblage was strongly dominated by one species, *Maldane sarsi antarctica* (120.6 ± 86.3 ind./0.1 m², F = 100%). The second important species was *Sternaspis* sp. (8.3 ± 7.2 ind./0.1 m², F = 66.6%). The species *Axionice spinifera* was found only in this group. Diversity (Rarefaction 5.3 ± 2.3 ; Shannon index 0.7 ± 0.4), species richness (7.3 ± 1.1) and evenness (0.3 ± 0.2) were very low in this assemblage compared to the other groups (Fig. 4).

Assemblage B. — This was the assemblage with the highest number of species recorded. Fifty-six species were found in the middle sublittoral in the areas with ascidian and bryozoan aggregations. The biomass of ascidians and of bryozoans was low (Tab. 1) in only two samples (D2, D13) grouped in this assemblage. Twenty-two species were found only in this assemblage. The most abundant species were: *Maldane sarsi antarctica* (61.5 ± 45.2 ind./0.1 m²; F = 90%), *Asychis amphiglypta* (6.1 ± 4.1 ind./0.1 m²; F = 80%), *Tharyx cincinnatus* (6.1 ± 3.5 ind./0.1 m²; F = 90%), *Tharyx fusiformis* (5.6 ± 3.8 ind./0.1 m²; F = 100%), *Aricidea (Aedicira) antarctica* (5.2 ± 7.8 ind./0.1 m²; F = 60%), *Notomastus latericeus* (4.1 ± 3.9 ind./0.1 m²; F = 90%), and *Cirrophorus brevicirratu*s (4.1 ± 6.3 ind./0.1 m²; F = 70%). A relatively high number of motile polychaetes was observed in this assemblage. High frequency values were found for a few motile epibenthic species, for example *Barrukia cristata* (F = 70%), *Eulalia picta* (F = 70%) and *Aglaophamus trissophyllus* (F = 80%). Assemblage B had the highest

Table 2
 Density with standard deviation [ind./0.1m²], and frequency of occurrence (F) of polychaetes in distinguished assemblages together with their feeding guild. CMJ – carnivore, motile, jawed; CDJ – carnivore, discretely motile, jawed; HMJ – herbivore, motile, jawed; SMX – surface deposit feeding, motile, non-jawed; SDT – surface deposit feeding, discretely motile, tentaculate; SMT – surface deposit feeding, motile, tentaculate; SST – surface deposit feeding, sessile, tentaculate; SDJ – surface deposit feeding, discretely motile, jawed; SMJ – surface deposit feeding, motile, jawed; BMX – burrowing, motile, non-jawed; BSX – burrowing, sessile, non-jawed; FST – filter-feeding, sessile, tentaculate. The order of species in table is based on the dendrogram of Bray-Curtis similarity between the species (fourth root transformed data and group average grouping method).

Species	A (200–300 m)		B (200–300m ascidian and bryozoan colonies)		C (400–500 m)		Feeding guild
	Density [ind./0.1m ²] ± SD	F [%]	Density [ind./0.1m ²] ± SD	F [%]	Density [ind./0.1m ²] ± SD	F [%]	
Orbiniidae gen. sp.	–	–	–	–	0.1 ± 0.4	16.6	BMX
<i>Euphrosine armadilloides</i> Ehlers, 1900	–	–	0.1 ± 0.3	10.0	–	–	CMJ
<i>Amphicteis gunneri antarctica</i> Hesse, 1917	–	–	–	–	0.3 ± 0.8	16.6	SST
<i>Exogone tridentata</i> Hartmann-Schröder et Rosenfeldt, 1993	–	–	–	–	0.3 ± 0.8	16.6	HMJ
<i>Anaitides bowersi</i> (Benham, 1927)	–	–	–	–	0.1 ± 0.4	16.6	CMJ
Rhodiniinae gen. sp.	–	–	–	–	0.1 ± 0.4	16.6	BSX
<i>Glycera kerguelensis</i> McIntosh, 1885	–	–	0.1 ± 0.3	10.0	0.3 ± 0.8	16.6	CDJ
Syllidae gen. sp. 2	–	–	–	–	0.1 ± 0.4	16.6	CMJ
Spionidae gen. sp.	–	–	–	–	0.1 ± 0.4	16.6	SDT
<i>Phyllochaetopterus</i> sp.	–	–	–	–	0.1 ± 0.4	16.6	SST
Terebellidae gen. sp.	–	–	–	–	0.1 ± 0.4	16.6	SST
<i>Syllidia</i> sp.	–	–	–	–	1.6 ± 4.0	16.6	CMJ
<i>Praxillella</i> sp.	–	–	–	–	1.3 ± 3.2	16.6	BSX
<i>Notoproctus</i> sp.	–	–	–	–	0.8 ± 1.6	33.3	BSX
Melliniinae gen. sp.	–	–	–	–	0.3 ± 0.8	16.6	SST
<i>Leitoscoloplos kerguelensis</i> (McIntosh, 1885)	–	–	–	–	0.1 ± 0.4	16.6	BMX
Ampharetinae gen. sp.	–	–	–	–	0.1 ± 0.4	16.6	SST
<i>Anobothrella antarctica</i> (Monro, 1939)	–	–	–	–	0.3 ± 0.5	33.3	SST
<i>Thelepidetes koehleri</i> Gravier, 1911	–	–	–	–	0.1 ± 0.4	16.6	SST
<i>Kinbergonuphis notialis</i> (Monro, 1930)	–	–	–	–	2.0 ± 2.2	66.6	SDJ?
<i>Streblosoma</i> sp.	–	–	–	–	0.5 ± 0.8	33.3	SST
<i>Autolytus</i> sp.	–	–	0.2 ± 0.4	20.0	–	–	CMJ
<i>Brada villosa</i> (Rathke, 1843)	–	–	0.1 ± 0.3	10.0	–	–	SDT
<i>Ephesiella</i> sp.	–	–	0.1 ± 0.3	10.0	0.1 ± 0.4	16.6	BMX
<i>Parougia furcata</i> (Hartman, 1953)	–	–	0.1 ± 0.3	10.0	–	–	SMJ?

Table 2 – continued.

Species	A (200–300 m)		B (200–300m ascidian and bryozoan colonies)		C (400–500 m)		Feeding guild
	Density [ind./0.1m ²] ± SD	F [%]	Density [ind./0.1m ²] ± SD	F [%]	Density [ind./0.1m ²] ± SD	F [%]	
<i>Pherusa</i> sp.	–	–	0.1 ± 0.3	10.0	–	–	SDT
<i>Lacydonia</i> sp.	–	–	0.1 ± 0.3	10.0	–	–	CMJ
<i>Flabelligena</i> sp.	–	–	0.1 ± 0.3	10.0	–	–	SMT
<i>Polyeunoa</i> sp.	–	–	0.3 ± 0.4	30.0	–	–	CMJ
<i>Spiophanes tcherniai</i> Fauvel, 1950	–	–	0.3 ± 0.6	20.0	–	–	SDT
<i>Axionice spinifera</i> (Ehlers, 1908)	0.3 ± 0.5	33.3	–	–	–	–	SST
<i>Praxillella kerguelensis</i> (McIntosh, 1885)	–	–	0.2 ± 0.6	10.0	–	–	BSX
Polynoidae gen. sp.	0.6 ± 0.5	66.6	0.5 ± 0.7	40.0	–	–	CMJ
<i>Neanthes kerguelensis</i> (McIntosh, 1885)	0.6 ± 0.5	66.6	0.3 ± 0.6	20.0	–	–	HMJ
<i>Tharyx</i> sp.	–	–	2.6 ± 3.3	60.0	1.8 ± 2.9	33.3	SMT
<i>Perkinsiana littoralis</i> (Hartman, 1967)	0.6 ± 0.5	66.6	2.6 ± 3.6	60.0	0.3 ± 0.8	16.6	FST
<i>Tharyx fusiformis</i> Monro, 1939	0.3 ± 0.5	33.3	5.6 ± 3.8	100.0	0.6 ± 0.8	50	SMT
<i>Notomastus latericeus</i> Sars, 1851	4.3 ± 5.1	66.6	4.1 ± 3.9	90.0	0.3 ± 0.5	33.3	BMX
<i>Thelepus cincinnatus</i> (Fabricius, 1780)	2.3 ± 0.5	100.0	1.8 ± 1.7	70.0	1.0 ± 1.6	33.3	SST
<i>Aglaophamus trissophyllus</i> (Grube, 1877)	0.3 ± 0.5	33.3	1.3 ± 1.1	80.0	0.5 ± 0.5	50	CMJ
Oweniidae gen. sp.	0.6 ± 0.5	66.6	2.1 ± 3.6	70.0	0.8 ± 0.9	50	BMX?
<i>Maldane sarsi antarctica</i> Arwidsson, 1911	120.6 ± 86.3	100.0	61.5 ± 45.2	90.0	30.5 ± 41.6	83.3	BSX
<i>Sternaspis</i> sp.	8.3 ± 7.2	66.6	1.1 ± 3.1	20.0	34.8 ± 21.2	100	BMX
<i>Cirrophorus brevicirratu</i> Strelzov, 1973	–	–	4.1 ± 6.3	70.0	7.1 ± 10.6	66.6	SMX
<i>Lumbrineris magalhaensis</i> (Kinberg, 1865)	–	–	1.8 ± 2.4	60.0	5.1 ± 2.7	100	CDJ?
<i>Tharyx cincinnatus</i> (Ehlers, 1908)	–	–	6.1 ± 3.5	90.0	43.6 ± 28.7	100	SMT
<i>Asychis amphiglypta</i> (Ehlers, 1897)	1.6 ± 2.8	33.3	6.1 ± 4.1	80.0	20.3 ± 19.2	100	BSX
<i>Sphaerodoropsis arctovskensis</i> Hartmann-Schröder et Rosenfeldt, 1988	–	–	3.3 ± 4.9	50.0	1.0 ± 2.4	16.6	BMX
<i>Ophelina cylindricaudata</i> (Hansen, 1878)	–	–	2.7 ± 3.4	60.0	0.5 ± 1.2	16.6	BMX
<i>Nicomache monroi</i> Hartman, 1967	–	–	0.7 ± 0.8	50.0	–	–	BSX
<i>Amphitrite kerguelensis</i> McIntosh, 1876	–	–	0.6 ± 0.6	50.0	–	–	SST
<i>Eulalia picta</i> (Kinberg, 1866)	–	–	1.0 ± 0.9	70.0	1.3 ± 1.6	50	CMJ

Table 2 – *continued.*

Species	A (200–300 m)		B (200–300m ascidian and bryozoan colonies)		C (400–500 m)		Feeding guild
	Density [ind./0.1m ²] ± SD	F [%]	Density [ind./0.1m ²] ± SD	F [%]	Density [ind./0.1m ²] ± SD	F [%]	
<i>Aricidea (Aedicira) antarctica</i> Hartmann-Schröder et Rosenfeldt, 1988	–	–	5.2 ± 7.8	60.0	0.8 ± 1.6	33.3	SMX
<i>Levinsenia gracilis</i> (Tauber, 1879)	–	–	1.3 ± 1.8	50.0	0.6 ± 1.6	16.6	SMX
<i>Ophelina syringopyge</i> (Ehlers, 1901)	–	–	0.3 ± 0.4	30.0	2.0 ± 4.8	16.6	BMX
Syllidae gen. sp. 1	–	–	1.3 ± 2.7	40.0	–	–	CMJ
<i>Aricidea (Acesta) strelzovi</i> Hartmann-Schröder et Rosenfeldt, 1988	–	–	0.5 ± 0.7	40.0	–	–	SMX
<i>Terebellides kerguelensis</i> (McIntosh, 1885)	–	–	0.5 ± 0.5	40.0	0.8 ± 0.9	50	SST
<i>Barrukia cristata</i> (Wiley, 1902)	–	–	0.9 ± 0.7	70.0	0.1 ± 0.4	16.6	CMJ
<i>Harmothoe</i> spp.	–	–	0.4 ± 0.5	40.0	0.1 ± 0.4	16.6	CMJ
<i>Exogone heterosetoides australis</i> Hartmann-Schröder et Rosenfeldt, 1988	–	–	0.4 ± 0.6	30.0	0.5 ± 0.8	33.3	HMJ
<i>Chaetozone</i> sp.	–	–	0.6 ± 1.0	30.0	3.5 ± 6.1	66.6	SMT
<i>Laonice</i> sp.	–	–	0.6 ± 1.2	30.0	1.1 ± 2.8	16.6	SDT
<i>Ophelina</i> cf. <i>breviata</i> (Pettibone, 1954)	–	–	0.3 ± 0.4	30.0	0.3 ± 0.5	33.3	BMX
<i>Cirriformia</i> sp.	–	–	0.6 ± 1.5	20.0	1.1 ± 2.4	33.3	SMT
<i>Sphaerodoropsis parva</i> (Ehlers, 1913)	–	–	0.6 ± 1.2	30.0	1.3 ± 1.9	16.6	BMX
<i>Rhodine intermedia</i> Arwidsson, 1911	–	–	0.3 ± 0.4	30.0	1.1 ± 1.6	50	BSX
<i>Eupraxillella antarctica</i> Hartmann-Schröder et Rosenfeldt, 1989	–	–	0.2 ± 0.6	10.0	–	–	BSX
<i>Perkinsiana</i> sp.	–	–	0.7 ± 1.2	30.0	–	–	FST
<i>Euchone pallida</i> Ehlers, 1908	–	–	0.1 ± 0.3	10.0	0.1 ± 0.4	16.6	FST
<i>Laetmonice producta</i> Grube, 1877	–	–	0.1 ± 0.3	10.0	–	–	CMJ
<i>Pista corrientis</i> McIntosh, 1885	–	–	0.1 ± 0.3	10.0	–	–	SST
<i>Austrophyllum charcoti</i> (Gravier, 1911)	–	–	0.4 ± 0.9	20.0	–	–	CMJ
<i>Typosyllis</i> sp.	–	–	0.7 ± 1.2	40.0	–	–	CMJ
<i>Anaitides patagonica</i> (Kinberg, 1866)	–	–	0.3 ± 0.4	30.0	–	–	CMJ
<i>Phyllocomus crocea</i> Grube, 1877	–	–	0.1 ± 0.3	10.0	–	–	SST

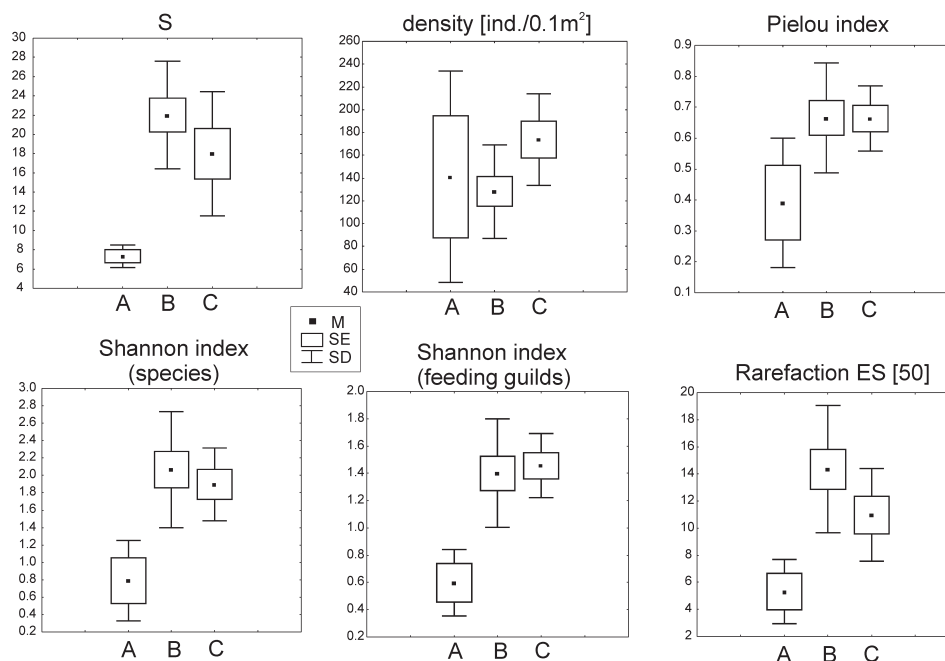


Fig. 4. Comparison of density and diversity indices in the distinguished assemblages. M – mean, SE – standard error, SD – standard deviation.

mean species richness (22.0 ± 5.5) and diversity (Rarefaction 14.3 ± 4.7 ; Shannon index 2.0 ± 0.6) (Fig. 4).

Assemblage C. — Fifty-one species were recorded in the deepest sublittoral of Admiralty Bay (400–500 m). Nineteen species were found only in this assemblage. The most abundant species were *Tharyx cincinnatus* (43.6 ± 28.7 ; $F = 100\%$), *Sternaspis* sp. (34.8 ± 21.2 ; $F = 100\%$), *Maldane sarsi antarctica* (30.5 ± 41.6 ; $F = 83.3\%$) and *Asychis amphiglypta* (20.3 ± 19.2 ; $F = 100\%$). Values of evenness (0.66 ± 0.10), diversity (Rarefaction 10.9 ± 3.4 ; Shannon index 1.8 ± 0.4) and species richness (18.0 ± 6.4) were very similar to those recorded in the assemblage B (Fig. 4).

Feeding guild structure. — The polychaete species were classified into 12 feeding guilds (Table 2). The most homogenous structure of polychaete feeding guilds was found in assemblage A (Fig. 5), which was dominated (86.8%) by burrowing, sessile non-jawed polychaetes (mostly *M. sarsi antarctica*). Members of seven guilds were found in this assemblage. The number of polychaete feeding guilds was high (11 feeding guilds) in assemblage B. Despite the strong dominance (53.8%) of burrowing, sessile non-jawed species (especially maldanids) all trophic guilds were relatively numerous in this assemblage. The percentages of filter feeders (FST – 2.7%) and motile carnivores (CMJ – 5.9%) were the highest in this group. In the last assemblage (C) members of 11 feeding guilds were also ob-

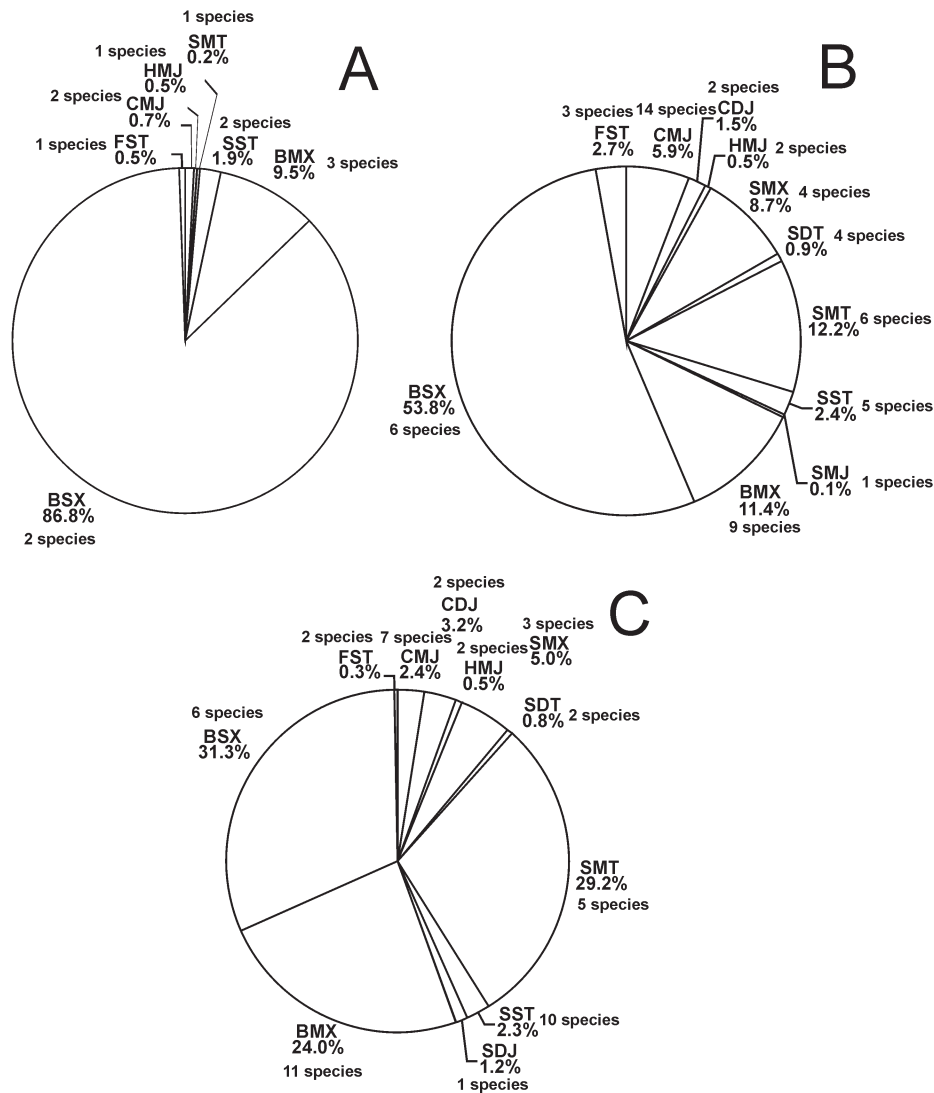


Fig. 5. Dominance structure of feeding guilds in each of the distinguished assemblages. CMJ – carnivore, motile, jawed; CDJ – carnivore, discretely motile, jawed; HMJ – herbivore, motile, jawed; SMX – surface deposit feeding, motile, non-jawed; SDT – surface deposit feeding, discretely motile, tentaculate; SMT – surface deposit feeding, motile, tentaculate; SST – surface deposit feeding, sessile, tentaculate; SDJ – surface deposit feeding, discretely motile, jawed; SMJ – surface deposit feeding, motile, jawed; BMX – burrowing, motile, non-jawed; BSX – burrowing, sessile, non-jawed; FST – filter-feeding, sessile, tentaculate.

served. Three feeding guilds (BSX – 31.3%; BMX – 24.0% and SMT – 29.2%) dominated in the polychaete fauna of the Admiralty Bay deepest sublittoral (Fig. 5). Shannon diversity calculated for feeding guilds was high for assemblages B and C and very low in assemblage A (Fig. 4).

Discussion

The present knowledge on the diversity and distribution of the deep sublittoral polychaete fauna of the Antarctic shelf is relatively scarce (San Martin *et al.* 2000; Hilbig *et al.* 2006; Neal *et al.* 2011; Parapar *et al.* 2011). The Admiralty Bay soft-bottom polychaete fauna at depths from 200 to 300 m had very low species richness and diversity and was dominated by *Maldane sarsi antarctica*. However, this result might be biased as just three samples were grouped in the assemblage A. The strong dominance of *Maldane sarsi antarctica* at a similar depth range, together with a substantial homogeneity of communities were recorded earlier on the Antarctic shelf by Gallardo and Castillo (1969), Gallardo *et al.* (1977), and by Siciński (1986). These results contrast with the present data from the same depth, but at places with aggregations of suspension-feeding organisms (assemblage B). High diversity of the polychaete fauna in this place, compared with surrounding bottom areas, could be associated with two factors. First of all the presence of three-dimensional, structurally-complex aggregations can increase the habitat complexity. In southeastern Brazil Morgado and Tanaka (2001) recorded more than 100 macroinvertebrate species associated with bryozoan colonies of *Schizoporella errata*, 70 of which were polychaetes. As expected, this complex habitat that provides a variety of ecological niches ultimately shows also a high variety of feeding guilds. The large proportion of motile epibenthic species in assemblage B, which are mainly predators (14 species), is probably a result of the importance of these structures as shelter, as well as an increased availability of prey (Tews *et al.* 2004; Le Hir and Hily 2005).

The second reason for high diversity and high density, especially of deposit feeders, could be a higher amount of organic matter (such as decaying fragments of colonies) in these areas of the sea-bed. Ascidiaceans, bryozoans and sponges are often regarded as the most important animals for energy transfer from the pelagic to the benthic zone, especially at greater depths supported by lower quantities of suspended organic matter (Gili *et al.* 2001). A high density of cirratulids, and a lower abundance of sessile, burrowing species were very characteristic features of the deepest sublittoral (assemblage C). It is worth noting that the density of the common eurytopic *Tharyx cincinnatus* was higher (43.6 ± 28.7 ind./0.1 m²) in this assemblage than in any of the previously described Admiralty Bay polychaete assemblages, including the “*Tharyx cincinnatus* assemblage” (with 30.6 ind./0.1 m²) recorded by Siciński (2004). Those tentaculate surface-deposit feeders are very selective and possibly out-compete less selective, sessile species (e.g. maldanids) in areas of lower organic matter in greater depths of the Antarctic shelf (Fauchald and Jumars 1979; Self and Jumars 1978; Saiz-Salinas *et al.* 1998; Smith *et al.* 2006). Neal *et al.* (2011) found a high abundance of *Maldane sarsi antarctica* in regions of enhanced productivity and high food availability in the sediments of the West Antarctic Peninsula shelf near Anvers Island, whereas in sites with contrasting

conditions abundance of this species decreased. Hilbig *et al.* (2006) also linked the lower abundance of infaunal burrowers with lower food supply. In addition, Kröger and Rowden (2008) mentioned that polychaete communities on the Ross Sea shelf, even at depths reaching 250 m, are influenced by primary production in the surface waters.

The diversity of two (B and C) of three distinguished assemblages was very high. The number of species recorded in both of those bottom areas was also high. In a study of the soft bottom polychaete fauna of Admiralty Bay, over a depth range from 4 to 170 m, Siciński (2004) distinguished eight assemblages. Only two of them consisted of more than 50 species. The first, with 81 species recorded, was an assemblage of the central basin (35–150 m depth) associated with heterogeneous bottom sediments. The second was associated with deeper areas of Ezcurra Inlet at the depths from 45 to 165 m. Fifty-seven species were found in this assemblage. High number of species (almost 80) was also found in the complex labyrinth of *Himantothallus grandifolius* holdfasts (Pabis and Siciński 2010a). The diversity and species richness of the present assemblage C is similar to values found in group B. Presumably it is a result of stable environmental conditions below 400 m depth. Any influence of mineral suspension or ice disturbance is absent in the deepest parts of the Admiralty Bay central basin (Pęcherzewski 1980) and stability of factors like temperature and salinity is also greater than in shallower areas of the bay (Szafranski and Lipski 1982; Siciński *et al.* 2011). The influence of icebergs at bottom areas deeper than 400 m is almost completely absent (Gutt 2001; Gerdes *et al.* 2003). The large sessile burrower *Maldane sarsi antractica* is still a very important element of assemblage C; however, this area is also characterized by abundant and/or constant presence of *Asychis amphiglypta*, *Sternaspis* sp., and *Kinbergonuphis notialis*. The last two species were found in Admiralty Bay exclusively in the deep sublittoral, and are also recorded from great depths in other Antarctic sites (Hartmann-Schröder and Rosenfeldt 1989; Orensanz 1990; San Martin *et al.* 2000; Pabis and Siciński 2010b). Węslawski *et al.* (2011) suggested that homogenization of bottom communities could occur as a consequence of climate warming. He considered deep-water fiord areas with oxygen-rich bottom water and stable temperature as potential refuges of diversity. Such areas could be especially important for Antarctic, stenothermic benthic invertebrates (Peck 2005). The deepest sublittoral areas of Antarctic fiords, including those with megabenthic fauna attached to dropstones, may serve as similar refuge.

Equally, it is difficult to define a clear boundary between the bottom communities in the deepest sublittoral of Admiralty Bay, and the relatively small differences in richness and diversity between assemblages B and C are somewhat surprising. It seems that hydrological differences between the 200–300 m and 400–500 m bottom areas are not very significant. On the other hand one might expect much higher richness and diversity in the more complex habitat. Nevertheless the species composition of those two assemblages is different. Greater habitat complexity

resulting from presence of bryozoans and ascidians may influence the diversity of carnivores and other motile epibenthic species as has been observed elsewhere (Tews *et al.* 2004; Le Hir and Hily 2005). The increased share of filter feeders is most probably associated with sites favourable for the attachment of sessile polychaetes (Pabis and Siciński 2010a). In contrast, the soft bottom is a favourable habitat for some other species, including mostly surface and subsurface deposit feeders. It seems that the complex habitat of bryozoans and ascidian colonies is not influencing all polychaete ecological groups in the same way. In consequence, the species composition is different but the richness and diversity in both communities remains similar. Unfortunately, there are no data on sediment characteristics from the samples studied. Those data could have made the possible conclusions more reliable. Sediment characteristics are an important element in the structuring of polychaete communities in Antarctic waters (Siciński 2004; Parapar *et al.* 2011). However sediment analysis based on only single samples from this area suggests a similarity in sediment characteristics at 200–300 m and at deeper parts of Admiralty Bay (Tatur and Siciński unpublished data). Gutt and Starman (1998) also pointed out the role of near-bottom currents. Furthermore, the depth itself is a very important factor that influences the character of bottom communities (Saiz-Salinas *et al.* 1997; Rehm *et al.* 2006; Pabis *et al.* 2011).

Our analysis has shown that biogenic structures may play a role in shaping the composition and diversity of polychaete communities. However, the complex habitat provided by ascidians and bryozoans may influence only some ecological groups and may not necessarily be the reason for higher richness and diversity when compared to the surrounding soft bottom. The number of factors involved in the process of structuring polychaete communities in the deeper sublittoral of Antarctic fiords is high. That is why further studies of the polychaete fauna associated with the deeper shelf areas should focus on the influence of habitat complexity on distribution, richness and diversity of their assemblages, based on a larger sampling effort, and should include a wide range of environmental factors.

Acknowledgments. — Authors would like to thank Roger Bamber for the language corrections. We also want to thank Jan Marcin Węśławski and two anonymous reviewers for the corrections that helped us to improve the manuscript. The study was supported by the grant of Polish Ministry of Science and Higher Education N°51/N-IPY/2007/0 as well as by Census of Antarctic Marine Life project.

References

- BARNES D.K.A. 1999. The influence of ice on polar nearshore benthos. *Journal of Marine Biological Association of the United Kingdom* 79: 401–407.
- BRAUN M. and GROSSMANN H. 2002. Glacial changes in the areas of Admiralty Bay and Potter Cove, King George Island, maritime Antarctica. *In*: L. Beyer and M. Bolter (eds) *Geoecology of the Antarctic Ice-Free Coastal Landscapes*. Springer Verlag, Berlin: 75–90.

- BROMBERG S., NONATO E.F., CORBISIER T.N. and PETTI M.A.V. 2000. Polychaete distribution in the near-shore zone of Martel Inlet, Admiralty Bay (King George Island, Antarctica). *Bulletin of Marine Science* 6: 175–188.
- BROWN K.M., FRASER K.P.P., BARNES D.K.A. and PECK L.S. 2004. Links between the structure of an Antarctic shallow-water community and icescour frequency. *Oecologia* 141: 121–129.
- CLARKE K.R. and WARWICK R.M. 1994. *Change in marine communities: an approach to statistical analysis and interpretation*. Natural Environment Research Council, Plymouth: 144 pp.
- CONRADI M. and CERVERA L. 1995. Variability in trophic dominance of Amphipods associated with the bryozoans *Bugula neritina* (L., 1758) in Algeciras Bay (Southern Iberian Peninsula). *Polish Archives of Hydrobiology* 42: 483–494.
- DUCHÈNE J.C. 1984. Données descriptive sur le macrobenthos annelidien dans le Golfe du Morbihan, Kerguelen. *CNFRA* 55: 75–94.
- FAUCHALD C. and JUMARS P.A. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology. An Annual Review* 17: 193–284.
- GALLARDO V.A. and CASTILLO J.C. 1969. Quantitative benthic survey of the infauna of Chile Bay (Greenwich Island, South Shetland Islands). *Gayana Zoology* 16: 3–17.
- GALLARDO V.A., CASTILLO J.G., RETAMAL M.A., YANEZ A., MOYANO H.I. and HERMOSILLA J.G. 1977. Quantitative studies on the soft-bottom macrobenthic animal communities of shallow Antarctic Bays. In: G.A. Llano (ed.) *Adaptations within Antarctic ecosystems*. Gulf, Houston: 361–387.
- GALLARDO V.A., MEDRANO S.A. and CARRASCO F.D. 1988. Taxonomic composition of the sublittoral soft-bottom Polychaeta of Chile Bay (Greenwich Island, South Shetland Islands, Antarctica). *Serie Científica Instituto Antártico Chileno* 37: 49–67.
- GAMBI M.C., CASTELLI A. and GUIZZARDI M. 1997. Polychaete populations of the shallow soft bottoms off Terra Nova Bay (Ross Sea, Antarctica): distribution, diversity and biomass. *Polar Biology* 17: 199–210.
- GERDES D., HILBIG B. and MONTIEL A. 2003. Impact of iceberg scouring on macrobenthic communities in the high-Antarctic Weddell Sea. *Polar Biology* 26: 295–301.
- GILI J.M., COMA R., OREJAS C., LOPEZ-GONZALES P.J. and ZABALA M. 2001. Are Antarctic suspension-feeding communities different from those elsewhere in the world? *Polar Biology* 24: 473–485.
- GUTT J. 2001. On the direct impact of ice on marine benthic communities, review. *Polar Biology* 24: 553–564.
- GUTT J. and PIEPENBURG D. 2003. Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Marine Ecology Progress Series* 253: 77–83.
- GUTT J. and STARMANS A. 1998. Structure and diversity of megabenthos in the Weddell and Lazarev Seas (Antarctica): ecological role of physical parameters and biological interactions. *Polar Biology* 20: 229–247.
- HARDY P. 1972. Biomass estimates for some shallow-water infaunal communities at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* 31: 93–106.
- HARTMANN-SCHRÖDER G. and ROSENFELDT P. 1989. Die Polychaeten der „Polarstern“ – Reise ANT III/2 in die Antarktis 1984. Teil 2: Cirratulidae bis Serpulidae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 86: 65–106.
- HILBIG B., GERDES D. and MONTIEL A. 2006. Distribution patterns and biodiversity in polychaete communities of the Weddell Sea and Antarctic Peninsula area (Southern Ocean) *Journal of the Marine Biological Association of the United Kingdom* 86: 711–725.
- JAŹDŹEWSKI K., JURASZ W., KITTEL W., PRESLER E., PRESLER P. and SICIŃSKI J. 1986. Abundance and biomass estimates of the benthic fauna in Admiralty Bay, King George Island, South Shetland Islands. *Polar Biology* 6: 5–16.
- KRÖGER K. and ROWDEN A.A. 2008. Polychaete assemblages of the northwestern Ross Sea shelf: worming out the environmental drivers of Antarctic macrobenthic assemblage composition. *Polar Biology* 31: 971–989.

- KRUSZEWSKI G. 2001. *Złodzenie Zatoki Admiralicji – przebieg i uwarunkowania*. Wydawnictwo Uczelniane Akademii Morskiej w Gdyni, Gdynia: 123 pp.
- LE HIR M.I. and HILY C. 2005. Macrofaunal diversity and habitat structure in intertidal boulder fields. *Biodiversity and Conservation* 14: 233–250.
- LIPSKI M. 1987. Variations of physical conditions, nutrients and chlorophyll a contents in Admiralty Bay (King George Island, South Shetland Islands, 1979). *Polish Polar Research* 8: 307–332.
- LOWRY J.K. 1975. *Soft bottom macrobenthic community of Arthur Harbour*. Antarctic Research Series. 23. American Geophysical Union, Washington DC: 1–19.
- MAGURRAN A.E. 2004. *Measuring Biological Diversity*. Blackwell Publishing, Oxford: 256 pp.
- MORGADO E.H. and TANAKA M.O. 2001. The macrofauna associated with the bryozoan *Schizoporella errata* (Walters) in southeastern Brazil. *Scientia Marina* 65: 173–181.
- NEAL L., MINCKS HARDY S.L., SMITH C.R. and GLOVER A.G. 2011. Polychaete species diversity on the West Antarctic Peninsula deep continental shelf. *Marine Ecology Progress Series* 428: 119–134.
- ORENSANZ J.M. 1990. The eunicemorph polychaete annelids from Antarctic and Subantarctic seas. In: L.S. Kornicker (ed.) *Biology of the Antarctic Seas XXI*. Antarctic Research Series 52: 1–183.
- PABIS K. and SICIŃSKI J. 2010a. Polychaete fauna associated with holdfasts of the large brown alga *Himantothallus grandifolius* in Admiralty Bay, King George Island, Antarctic. *Polar Biology* 33: 1277–1288.
- PABIS K. and SICIŃSKI J. 2010b. Distribution and diversity of polychaetes collected by trawling in Admiralty Bay – an Antarctic glacial fiord. *Polar Biology* 33: 141–151.
- PABIS K., SICIŃSKI J. and KRYMARYS M. 2011. Distribution patterns in the biomass of macrozoobenthic communities in Admiralty Bay (King George Island, South Shetlands, Antarctic). *Polar Biology* 34: 489–500.
- PARAPAR J., LOPEZ E., GAMBI M.C., NUNEZ J. and RAMOS A. 2011. Quantitative analysis of soft-bottom polychaetes of the Bellingshausen Sea and Gerlache Strait (Antarctica). *Polar Biology* 34: 715–730.
- PEÇHERZEWSKI K. 1980. Distribution and quantity of suspended matter in Admiralty Bay (King George Island, South Shetland Islands). *Polish Polar Research* 1: 75–82.
- PECK L. S. 2005. Prospects for survival in the Southern Ocean: vulnerability of benthic species to temperature change. *Antarctic Science* 17: 497–507.
- PETTI M.A.V., NONATO E.F., SKOWRONSKI R.S.P. and CORBISIER T.N. 2006. Bathymetric distribution of the meiofaunal polychaetes in the nearshore zone of Martel Inlet, King George Island, Antarctica. *Antarctic Science* 18: 163–170.
- POCKLINGTON P. and WELLS P.G. 1992. Polychaetes key taxa for marine environmental quality monitoring. *Marine Pollution Bulletin* 24: 593–598.
- REHM P., THATJE C.S., ARNTZ W.E., BRANDT A. and HEILMAYER C.O. 2006. Distribution and composition of macrozoobenthic communities along a Victoria-Land Transect (Ross Sea, Antarctica). *Polar Biology* 29: 782–790.
- RICHARDSON M.D. and HEDGPETH J.W. 1977. Antarctic soft-bottom, macrobenthic community adaptations to a cold, stable, highly productive, glacially affected environment. In: G.A. Llano (ed.) *Adaptations within Antarctic ecosystems*. Proceedings of 3rd SCAR symposium on Antarctic Biology. Smithsonian Institution, Washington: 181–196.
- SAIZ-SALINAS J.I., RAMOS A., GARCIA F.J., TRONCOSO J.S., SAN MARTIN G., SANZ C. and PALACIN C. 1997. Quantitative analysis of macrobenthic soft-bottom assemblages in South Shetland Waters (Antarctica). *Polar Biology* 17: 393–400.
- SAIZ-SALINAS J.I., RAMOS A., MUNILLA T. and RAUSCHERT M. 1998. Changes in the biomass and dominant feeding mode of benthic assemblages with depth off Livingston Island (Antarctica). *Polar Biology* 19: 424–428.

- SAN MARTIN G., PARAPAR J., GARCIA F.J. and REDONDO M.S. 2000. Quantitative analysis of soft bottoms infaunal macrobenthic polychaetes from South Shetland Islands (Antarctica). *Bulletin of Marine Sciences* 67: 83–102.
- SEBENS K.P. 1991. Habitat structure and community dynamics in marine benthic systems In: S.S. Bell, E.D. McCoy and H.R. Mushinsky (eds) *Habitat structure – the physical arrangement of objects in space*. Chapman and Hall, London: 211–234.
- SELF R.F.L. and JUMARS P.A. 1978. New resource axes for deposit feeders? *Journal of Marine Research* 36: 627–641.
- SICIŃSKI J. 1986. Benthic assemblages of Polychaeta in chosen regions of the Admiralty Bay (King George Island, South Shetland Islands). *Polish Polar Research* 7: 63–78.
- SICIŃSKI J. 2004. Polychaetes of Antarctic sublittoral in the proglacial zone (King George Island, South Shetland Islands). *Polish Polar Research* 25: 67–96.
- SICIŃSKI J. and JANOWSKA E. 1993. Polychaetes of the shallow sublittoral of Admiralty Bay, King George Island, South Shetland Islands. *Antarctic Science* 5: 161–167.
- SICIŃSKI J., JAŻDŻEWSKI K., DEBROYER C., PRESLER P., LIGOWSKI R., NONATO E.F., CORBISIER T.N., PETTI M.A.V., BRITO T.A.S., LAVRADO H.P., BŁAŻEWICZ-PASZKOWYCZ M., PABIS K., JAŻDŻEWSKA A. and CAMPOS L.S. 2011. Admiralty Bay Benthos diversity – A census of a complex polar ecosystem. *Deep-Sea Research II* 58: 30–48.
- SICIŃSKI J., PABIS K., JAŻDŻEWSKI K., KONOPACKA A. and BŁAŻEWICZ-PASZKOWYCZ M. 2012. Macrozoobenthos of two Antarctic glacial coves: a comparison with non-disturbed bottom areas. *Polar Biology* 35: 355–367.
- SMALE D.A. 2008a. Ecological traits of benthic assemblages in shallow Antarctic waters: does ice scour disturbance select for small, mobile, secondary consumers with high dispersal potential? *Polar Biology* 31: 1225–1231.
- SMALE D.A. 2008b. Continuous benthic community change along a depth gradient in Antarctic shallows: evidence of patchiness but not zonation. *Polar Biology* 31: 189–198.
- SMITH C.R., MINKS S. and DE MASTER D.J. 2006. A synthesis of benthic-pelagic coupling on the Antarctic shelf: food banks, ecosystem inertia and global climate change. *Deep Sea Research II* 53: 875–894.
- SZAFRAŃSKI J. and LIPSKI M. 1982. Characteristics of water temperature and salinity at Admiralty Bay (King George Island) during austral summer 1978–1979. *Polish Polar Research* 3: 7–24.
- TEWS J., BROSE U., GRIMM V., TIELBORGER K., WICHMANN M.C., SCHWAGER M. and JELTSCH F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of key-stones structures. *Journal of Biogeography* 31: 79–92.
- WĘSŁAWSKI J.M., KENDALL M.A., WŁODARSKA-KOWALCZUK M., IKEN K., KĘDRA M., LEGEŻYŃSKA J. and SEJR M.K. 2011. Climate change effects on Arctic fjord and coastal macrobenthic diversity – observations and predictions. *Marine Biodiversity* 41: 71–85.

Received 31 March 2012

Accepted 22 May 2012