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Admiralty Bay Benthos Diversity—A census of a complex polar ecosystem

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ABSTRACT

A thorough census of Admiralty Bay benthic biodiversity was completed through the synthesis of data, acquired from more than 30 years of observations. Most of the available records arise from successive Polish and Brazilian Antarctic expeditions organized since 1977 and 1982, respectively, but also include new data from joint collecting efforts during the International Polar Year (2007–2009). Geological and hydrological characteristics of Admiralty Bay and a comprehensive species checklist with detailed data on the distribution and nature of the benthic communities are provided. Approximately 1300 species of benthic organisms (excluding bacteria, fungi and parasites) were recorded from the bay's entire depth range (0–500 m). Generalized classifications and the descriptions of soft-bottom and hard-bottom invertebrate communities are presented. A time-series analysis showed seasonal and interannual changes in the shallow benthic communities, likely to be related to ice formation and ice melt within the bay. As one of the best studied regions in the maritime Antarctic Admiralty Bay represents a legacy site, where continued, systematically integrated data sampling can evaluate the effects of climate change on marine life. Both high species richness and high assemblage diversity of the Admiralty Bay shelf benthic community have been documented against the background of habitat heterogeneity.

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1. Introduction

The western Antarctic Peninsula is an extremely rich and diverse part of the Southern Ocean marine ecosystem. Benthic communities of this region have been the subject of several studies (e.g. Gallardo and Castillo, 1969; Lowry, 1975; Gallardo et al., 1977; Richardson and Hedgpeth, 1977; Sáiz-Salinas et al., 1997, 1998; Arnaud et al., 1998; Barnes and Brockington, 2003; Smale, 2008). Recent analyses by Barnes et al. (2008) from Port Foster (Deception Island) have even documented the case of a seafloor destroyed by volcanic eruptions in the late 1960s. The soft bottom macroinvertebrate species richness and diversity from Arthur Harbor (Anvers Island) were investigated by Lowry (1975) and Richardson and Hedgpeth (1977). Detailed analysis of the soft-bottom polychaete diversity of Chile Bay (Greenwich Island) was performed by Gallardo et al. (1988).

The marine ecosystem of Admiralty Bay (King George Island, South Shetland Islands) has one of the most comprehensive

long-term data series of Antarctic benthic communities, along with background environmental information. Early scientific exploration dates back to 1908 with the 2nd French Antarctic Expedition on board the *Pourquoi Pas?* (1908–1910) and was followed by the *Discovery* expedition (1927).

More recently, intensive, diversified and continuous scientific activities supported by the 'Arctowski' (Poland, since 1977) and 'Comandante Ferraz' (Brazil, since 1984) stations, and by the US Antarctic Program at ASPA No. 128 ('Peter J. Lenie' field station) have accumulated extensive biological and oceanographic information from the area for more than 30 years. Research activities at the Peruvian *Machu Picchu* Station (at Crepin Point) and at the Ecuadorian refuge (at Hennequin Point) have occurred intermittently during the summers. The area has also been investigated by biologists from Belgium, Germany and the Netherlands. Some of the studies carried out in Admiralty Bay are among the longest undertaken in the Antarctic region.

Polish studies of the benthos of this area began with the establishment of the 'Henryk Arctowski' Antarctic Station, in February 1977, which allowed a systematic study of the structure of the benthic communities, especially those occurring in Ezcurra Inlet and in the central basin of the bay (e.g. Arnaud et al., 1986;

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Jażdźewski et al., 1986, 2001; Presler, 1986; Siciński, 1986, 2000, 2004; Zieliński, 1990; Błażewicz and Jażdźewski, 1995, 1996; Presler and Figielska, 1997; Ligowski, 2002; Błażewicz-Paszkowycz and Sekulska-Nalewajko, 2004; Majewski, 2005; Majewski and Olempska, 2005; Włodarska-Kowalczyk et al., 2007; Pabis and Siciński, 2010a,b). During its early years of research (1982–1988), the Brazilian Antarctic Programme was mainly exploratory, aimed at gathering oceanographic data as well as information on the diversity of benthic assemblages along the Antarctic Peninsula and Bransfield Strait (Nonato et al., 1992a). Since 1984, following the establishment of the 'Comandante Ferraz' Antarctic Station at Keller Peninsula, most of the Brazilian benthic research has been concentrated on the Martel and Mackellar Inlets. Ecological studies have been carried out describing the structure of the megafauna (Wägele and Brito, 1990; Nonato et al., 1992b, 2000; Echeverria et al., 2005), macrofauna (Bromberg et al., 2000; Echeverria and Paiva, 2006; Filgueiras et al., 2007), meiofauna (Skowronski et al., 1998; Skowronski and Corbisier, 2002; Petti et al., 2006) and micro-phytobenthos (Skowronski et al., 2009), and the trophic web within the nearshore marine community (Corbisier et al., 2004).

Along with the northwestern North American and Siberian Plateau, the western Antarctic Peninsula is one of the areas showing the fastest rate of climate change on Earth (Vaughan et al., 2003). Since the early 1950s, the Antarctic Peninsula region has shown significant climate warming (Simões et al., 1999; Clarke et al., 2007; Turner et al., 2009 and references therein). It is difficult to predict the exact oceanic temperature increase in this region (Clarke et al., 2007), but the structure and functioning of the benthic communities might be expected to respond to these major changes in the environment (e.g. Barnes, 2005; Smale and Barnes, 2008). In order to detect, predict and compare changes occurring at different spatial and temporal scales, it is important to establish baselines of the recent marine biota. Admiralty Bay can be recognized as a suitable model for such purposes, owing to the considerable amount of data collected in this area, which ranks this region among the best known Antarctic areas.

The marine diversity of the Southern Ocean was recently discussed by Gray (2001), Clarke and Johnston (2003) and Gutt et al. (2004), and updated estimates are also presented by De Broyer and Danis (this issue). This study aims at summarizing all available information about the benthos of Admiralty Bay, in order to furnish a robust benchmark against which to evaluate possible changes in its species richness, diversity and community structure.

2. Material and methods

Admiralty Bay has been intensively sampled from the intertidal to its deepest bottom areas (ca. 500 m), during the past 30 years. A variety of sampling methods and gears, such as corers, grabs, trawls, baited traps and SCUBA diving, was used, depending on the objectives of specific projects. Most quantitative sampling of macrofaunal species has been performed using Van Veen grabs (0.1 and 0.056 m²). Bottom samples were then washed through 44–62 and 300–500 µm mesh size sieves to separate meiofauna and macrofauna, respectively.

All organisms (e.g. meiofauna, macrofauna, megafauna, diatoms and macroalgae) were initially fixed in 4–10% formalin and then transferred to 70% ethanol for storage. Seafloor images were taken mostly in Ezcurra and Martel Inlets using remote cameras and during SCUBA diving. The data records of all benthic samples have been gathered and progressively digitized using the SCAR Marine Biodiversity Information Network (www.scarmarbin.be) data protocols into a dedicated database, the Admiralty Bay

Benthos Diversity Database (ABBED) (www.abbed.uni.lodz.pl). This effort was established jointly by Poland, Belgium and Brazil as a part of the International Polar Year 2007–2009 initiative related to the *Census of Antarctic Marine Life* (www.camlaq), and is freely available to the scientific community. The resulting list of species was matched against the *World Register of Marine Species* (www.marinespecies.org) and SCARMarBIN's *Register of Antarctic Marine Species*.

3. Admiralty Bay environment—physico-chemical background

3.1. General description

Admiralty Bay has an area of ca. 122 km². The bay is a large fjord of tectonic origin with a maximum depth of 535 m, three main inlets (Ezcurra, Mackellar and Martel) and a wide opening (8.25 km width) to the Bransfield Strait (Fig. 1) (Kruszewski, 2002). The Admiralty Bay seafloor has a complex bottom topography and geomorphology. The very diverse shoreline and seafloor as well as numerous glaciers, generating icebergs and outflowing streams, provide a wide variety of habitats for benthic and pelagic communities. Glaciers and ice-falls constitute about half of the 83.4 km long shoreline of the bay.

The bathymetry and geomorphology of Ezcurra Inlet were described by Marsz (1983), and those of Martel Inlet by Rodrigues (unpubl. results). Mackellar Inlet was less studied. The seafloor in Ezcurra Inlet is divided as follows: the oldest area at the eastern side is a deep trough, while the youngest in the western side is the shallowest, with an intricate bottom configuration. These two parts are separated by a sill, which has considerable consequences for the distribution of the benthos (Siciński, 2004). Martel Inlet has a variety of geomorphologic features characterized by sharp differences in small spatial scale, by extremely irregular seafloor affected by local geology and tectonics as well as by glacial erosive processes (Rodrigues, unpubl. results). The heterogeneity of the seafloor in Admiralty Bay largely determines the local hydrodynamics, in conjunction with the circulation in the Bransfield Strait (Szafranski and Lipski, 1982).

3.2. Hydrology and hydrography

King George Island is located within the maritime Antarctic region. The hydrology of Admiralty Bay is complex, as it receives different contributions from water masses originating in the Bransfield Strait, and also from ice melt within the bay (Szafranski and Lipski, 1982). Waters entering the bay from the Bransfield Strait originate from either the adjacent Weddell Sea or Bellingshausen Sea, depending on the regional water circulation, winds and seasonal regime (Gordon and Nowlin, 1978). The influence of the Bellingshausen Sea water, warmer and less saline (2.3 °C and 33.5 psu), is usually pronounced in summer, whereas in winter the Weddell Sea water, colder and more saline (−0.8 °C and 34.4 psu), prevail (Tokarczyk, 1987). The depth gradients of environmental variables are shown in Fig. 2. The average tidal range in Admiralty Bay is 1.4 m, but maximum tides can reach 2.1 m (Catewicz and Kowalik, 1983). Tidal currents may reach 50 m s^{−1}, which are caused by water exchange between the bay and the Bransfield Strait. The complete exchange of upper water layer down to the depth of 100 m takes ca. 1–2 weeks (Pruszek, 1980).

In general, Admiralty Bay surface waters are well oxygenated, with values between 7.0 and 9.2 cm³ L^{−1} in Ezcurra Inlet (Sarukhanyan and Tokarczyk, 1988). Higher values of oxygen were found in nearshore waters (9.4 cm³ L^{−1}) (Samp, 1980; Lipski, 1987).

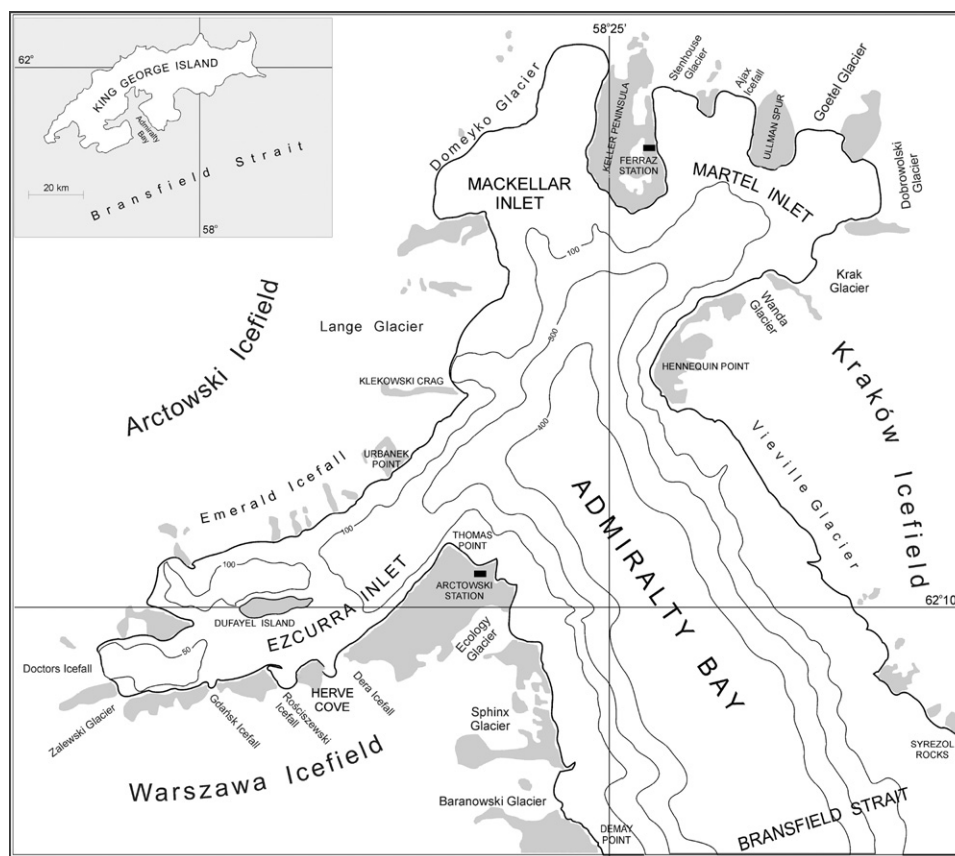


Fig. 1. Study area – Admiralty Bay.

These authors observed also that the content of inorganic phosphates was high, up to $ca. 2.6 \mu\text{mole L}^{-1}$ (even $ca. 4.8 \mu\text{mol L}^{-1}$ in areas neighbouring penguin colonies), the highest values being found in summer (Samp, 1980). High nitrate content was also found (over $30 \mu\text{mol L}^{-1}$) (Lipski, 1987). Generally, observed nutrient ranges were $0.01\text{--}0.60 \mu\text{mol kg}^{-1}$ for nitrites, 10.0 to $ca. 34.0 \mu\text{mol kg}^{-1}$ for nitrates, $73.0\text{--}90.0 \mu\text{mol kg}^{-1}$ for silicates and $1.00\text{--}2.60 \mu\text{mol kg}^{-1}$ for phosphates. The average concentrations of total nitrogen and total phosphorus in the 1 m surface layer amount to 1.054 and 0.129 mg dm^{-3} , respectively (Nędzarek, 2008). Organic nitrogen and phosphorus constituted 59% of the total nitrogen and 34% of the total phosphorus. Organic carbon in the summer of 1979 ranged from 1.62 to 3.22 mg L^{-1} for DOC and from 0.22 to 0.65 mg L^{-1} for POC with the subsurface water layers (25–100 m) showing the highest values, and the lowest values found close to glaciers (Peçherzewski, 1980a).

Admiralty Bay freezes at irregular intervals, e.g. during 11 winters in 20 years (from 1977 to 1996) as recorded by Kruszewski (1999). Recently, total freezing has occurred less frequently with gaps from 5 to 6 years.

3.3. Suspended matter

Mean values of suspended matter in the Southern Ocean range from 1 to 2 mg L^{-1} (Lisitzyn, 1969). Values in Admiralty Bay exceed by several times those found elsewhere in open Antarctic waters (Peçherzewski, 1980b). The content of suspended inorganic matter strongly fluctuates along the coastal zone of the bay, depending on season and area. Usually, the suspended matter has a prevailing inorganic fraction originated from the iceberg melt (Peçherzewski, 1980b; Jonasz, 1983), wind-transported dust, but

mostly from the melt water feeding the bay (Jonasz, 1983). The lowest values (2.8 mg L^{-1}) were observed in winter, in the central part of the bay (Peçherzewski, 1980b), and the maximum values ($ca. 270 \text{ mg L}^{-1}$) were recorded in summer in Herve Cove, a small lagoon close to the inflowing glacial stream (Piechura, unpubl. results). High amounts of mineral suspended matter ($> 100 \text{ mg L}^{-1}$) were recorded in summer in front of the glacier cliffs (Peçherzewski, 1980b).

It has been calculated that about 2000 tons of mineral suspended matter is transferred daily from land to the bay in summer (Peçherzewski, 1980b). Part of this amount is carried away by the surface current out to the Bransfield Strait and the rest is spread unevenly over the bay's seafloor. Water transparency is related to the amount of suspended matter, ranging from 2 m in the fjords, in summer, to 32 m in the central area of the bay, in winter (Lipski, 1987). This latter value is equivalent to about 2.5 mg L^{-1} of suspended matter in the water.

3.4. Bottom sediments

The Admiralty Bay seafloor consists of boulders, pebbles and gravel in the intertidal, mainly gravel and sand in the shallow subtidal and mud (silty clay sand and sandy clay silt) down to its deepest bottom areas (Gruber, unpublished; Nonato et al., 1992a,b; Rudowski and Marsz, 1996; Siciński, 2004). The bottom sediments include various fractions of randomly distributed clastic materials transported to the bay by the glaciers and subglacial streams or drifting ice. The grain size (φ scale) of the deposits studied by Siciński (2004) and by Siciński and Tatur (unpubl. results) shows the entire spectrum from medium sands to very fine silt (Fig. 3). These deposits are poorly and very poorly

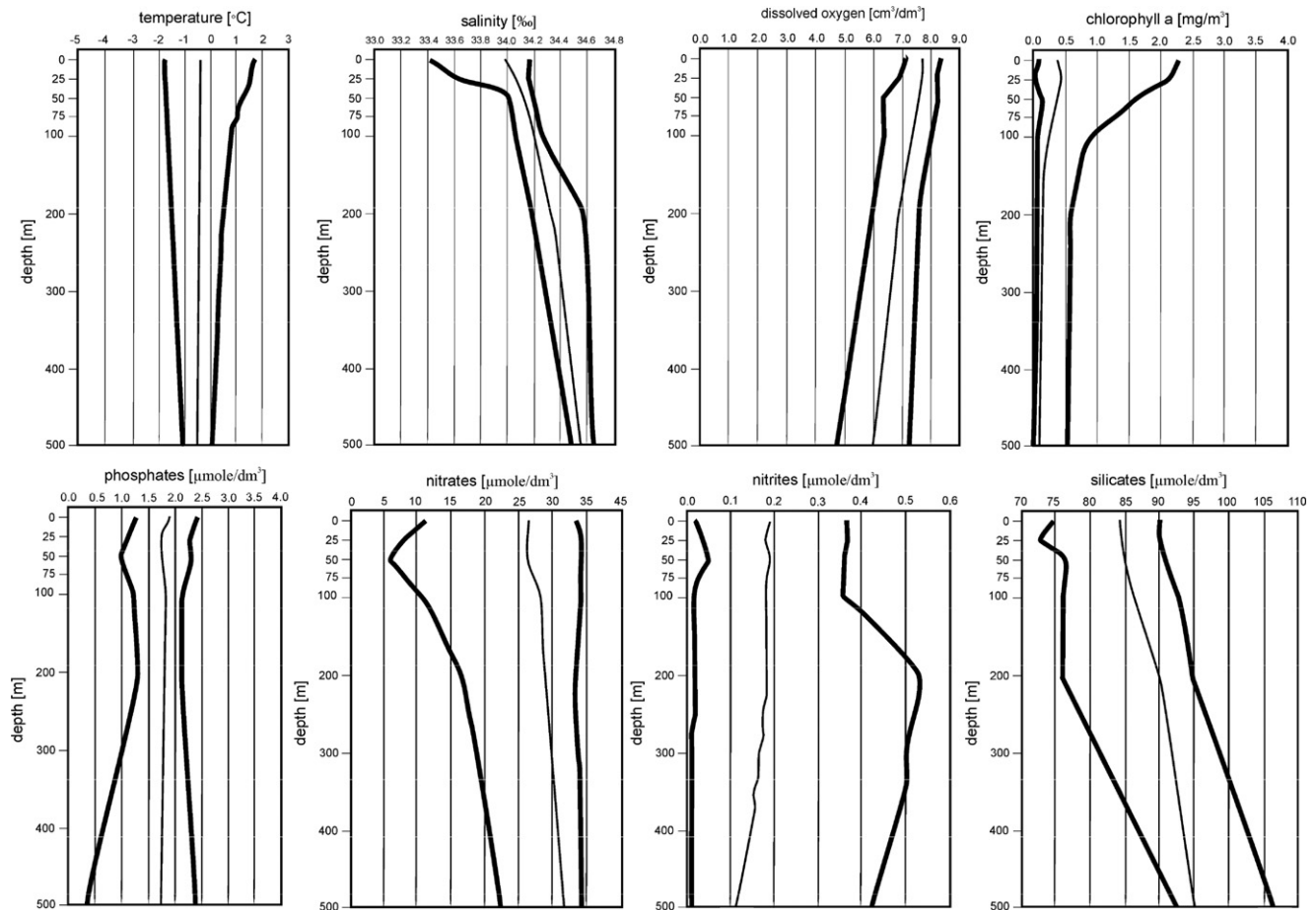


Fig. 2. Selected parameters of the water column (range and mean) in the central basin of Admiralty Bay, constructed on the basis of the data of Lipski (1987).

sorted and always contain a significant portion of very coarse sand, gravel and numerous dropstones. The thickness of the deposited layer ranges from over a dozen to several dozen meters, reaching a maximum of 150 m, as a young depositional cover most likely originating from the deglaciation of the last Holocene glaciation (Rudowski and Marsz, 1996).

The interstitial water of Admiralty Bay's sediments has rather high pH values, from 7.7 to 9.7, showing high levels of dissolved alkaline elements (Schaefer et al., 2004). Sediment interstitial water salinity shows a similarity at 20 and 60 m (35 and 34 psu, respectively), and is slightly higher at 30 m (37 psu) (Maciel, unpubl. results). Mean values of total organic matter in Martel Inlet have been estimated as $8.69 \pm 2.67\%$ (mean \pm SD) (Schaefer et al., 2004; Santos et al., 2005), with relatively low concentrations of total organic carbon (C_{org}) at 20, 30 and 60 m ($0.39 \pm 0.16\%$, $0.49 \pm 0.31\%$ and $0.41 \pm 0.15\%$, respectively), with no correlation between the C_{org} and the fractions of silt and clay in the sediment (Maciel, unpubl. results). Bio-available phosphorus content in the sediment was relatively high, between 116 and 380 mg kg⁻¹ (Schaefer et al., 2004), showing evidence of a continuity between the phosphorus-rich land sources and the phosphorus-poor marine environment. Interestingly, the phosphorus concentrations are highest in those coastal sediments that are under strong ice scour.

4. Admiralty Bay benthic species richness and diversity

The taxa inventory of Admiralty Bay revealed the presence of almost 1300 benthic species, including diatoms, foraminiferans, macroalgae, invertebrates and demersal fish but excluding

bacteria, fungi and parasites (Table 1), probably making Admiralty Bay the only place in the Antarctic with such a comprehensive list of benthic species. The most complete lists of taxa were obtained for Bacillariophyta, macroalgae, Foraminifera, Polychaeta, Cumacea, Tanaidacea, Amphipoda, Asteroidea and Bryozoa. Other taxa such as Nematoda, Porifera, Cnidaria, Echinoidea, Crinoidea and Isopoda are still not sufficiently studied in the area. Admiralty Bay is notably the type locality for several of these benthic species: 2 Foraminifera, 4 Polychaeta, 1 Bivalvia, 2 Amphipoda, 1 Cumacea, 1 Isopoda, 1 Tanaidacea and 1 Pisces (Chevreux, 1913; Hartmann-Schröder and Rosenfeldt, 1989; Teodorczyk and Wägele, 1994; Skóra, 1995; Błażewicz-Paszkowycz and Heard, 2001; Błażewicz-Paszkowycz, 2004; Passos and Domaneschi, 2006; Valério-Berardo and Piera, 2006; Sinniger et al., 2008; Majewski and Tatur, 2009).

The most important groups in terms of abundance are Polychaeta, Bivalvia and Amphipoda (Jazdzewski et al., 1986; Siciński, 2004). The bulk of macrofauna biomass consists of Ascidiacea, Bryozoa and Polychaeta but in some areas (e.g. Ezcurra Inlet and Martel Inlet) Bivalvia and/or Echinodermata also show a considerably high biomass.

5. Benthic community structure

5.1. Soft bottom communities

5.1.1. Microphytobenthos

Microphytobenthos is an important source of primary production in the Antarctic, particularly in coastal zones (Gilbert, 1991).

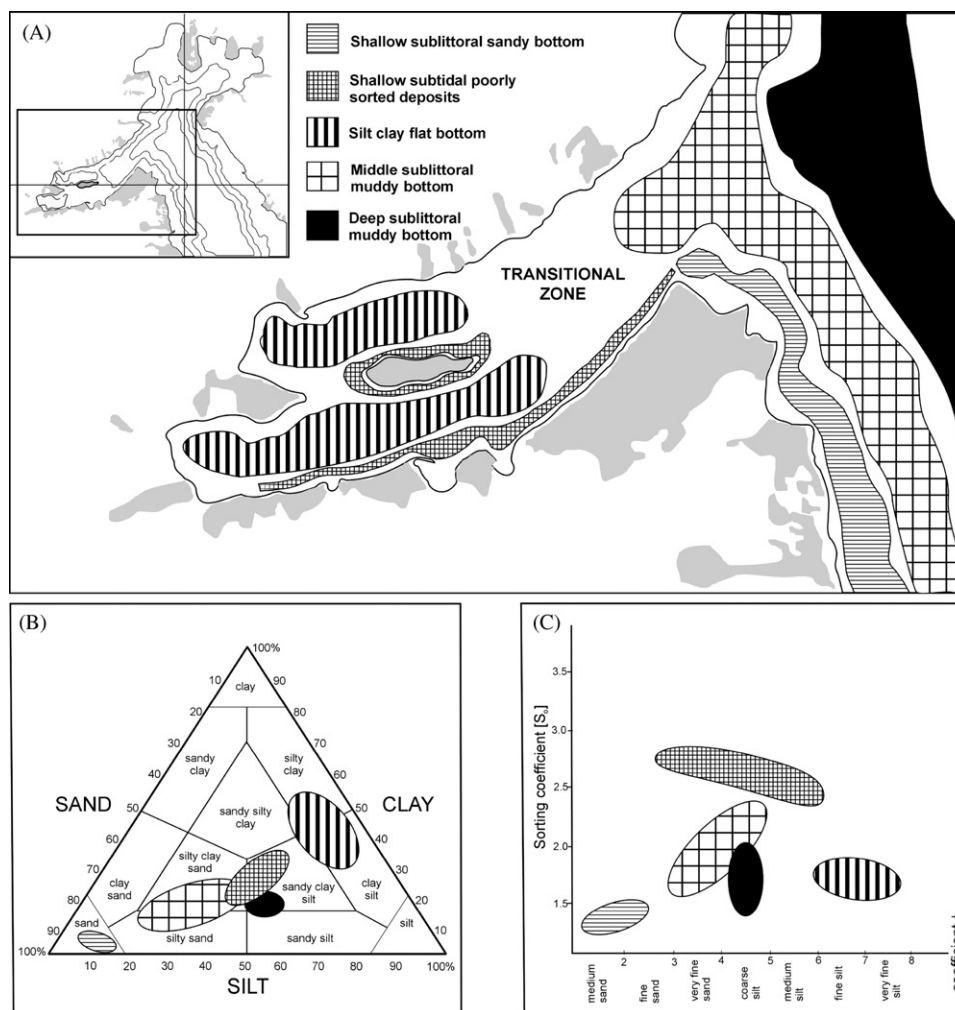


Fig. 3. Admiralty Bay soft bottom macrozoobenthic communities versus sediment diversity (sediment types distribution). (A) the distribution of communities; (B) bottom deposits typical of 5 distinguished communities (Shepard's (1954) sediment classification); (C) bottom deposits typical of 5 distinguished communities, characterized by ϕ units and sorting coefficient (S_0) (the description of communities in Table 2).

Ligowski (1993, 2002) estimated that in the stony bottom littoral zone of Admiralty Bay the average concentration of chlorophyll *a* was ca. 200 mg m^{-2} during summer. In the soft bottom sublittoral the diatom density was estimated as 6×10^2 to $6 \times 10^6 \text{ cells cm}^{-3}$. Rich diatom assemblages were found in different benthic habitats: 108 taxa of benthic diatoms were found in the stony littoral, 97 in the soft bottom sublittoral, 83 on macrophytes and 85 on various invertebrates (Ligowski, 2002). Approximate densities of diatoms per cm^2 of substratum averaged as follows: $0\text{--}1 \times 10^7$ in the littoral zone, 6×10^2 to 6×10^6 in the sublittoral, 3.5×10^5 on basal disc or rhizoids of macroalgae, $0\text{--}0.5 \times 10^6$ on branches of macroalgae, 2×10^5 on macrophyte fronds, about 10^6 on sponges, 2.7×10^4 on oral discs of anemones, 8.6×10^3 on their column wall and 10^5 on bryozoans (Ligowski, 2002).

The sublittoral microphytobenthos biomass (expressed as chlorophyll *a* and phaeopigment content) was measured in three summer periods at several sites within Martel Inlet at depths from 10 to 60 m (Skowronski and Corbisier, 2002; Skowronski et al., 2009). Mean biomass values were inversely related to the depth gradient and showed a high spatial and interannual variability. There was also a reduction in the Chl *a*/Phaeo ratio in relation to depth, from 3.2 ± 3.2 at 10–20 m to 0.7 ± 1.0 at 40–60 m.

5.1.2. Meiofauna

Studies on meiofauna in Admiralty Bay started in 1991, when samples were collected through SCUBA diving in Martel Inlet. In general, the dominant groups retained in a $44 \mu\text{m}$ mesh size screen were Nematoda and Harpacticoida, followed by nauplii and polychaetes. The density of meiofauna in Martel Inlet, excluding the ice scour affected areas, was high, and varied from 3523 ± 2117 to $7641 \pm 388 \text{ ind } 10 \text{ cm}^{-2}$ (mean \pm SD) at depths of 6–11 m, and from 3479 ± 1205 to $8216 \pm 3030 \text{ ind } 10 \text{ cm}^{-2}$ at depths of 18–25 m (Skowronski et al., 1998). Further studies at Martel Inlet during two consecutive summers revealed that high meiofaunal densities are characteristic for this whole inlet, and generally are correlated with the proportion of gravel, silt and clay (Skowronski and Corbisier, 2002). Also, a positive correlation between the biomass of the microphytobenthos and meiofaunal densities was observed during the second summer, when the biomass of the microphytobenthos was approximately 25% lower than that in the first summer (Skowronski et al., 2009).

Nematodes are the dominant meiofaunal group on Martel Inlet soft bottoms, representing more than 85% of the meiofauna in terms of abundance at depths from 6 to 60 m. So far, 98 genera belonging to 28 families have been identified (Skowronski, unpublished; Gheller, unpublished). The most frequent nematode genera recorded in Admiralty Bay belonged to non-selective

Table 1
Admiralty Bay benthos species richness, key species and ecology (a detailed checklist of benthic species is available upon request from the first author).

Taxa	Approx. no. of marine species worldwide (from different sources)	Approx. no of species in the Antarctic	No. of recognized species in Admiralty Bay	Habitat/substrate	Trophic group(s)	Most common and/or abundant species	Only the main references concerning Admiralty Bay species richness and abundance
Bacillariophyta	5000	200	157 ^a	Ubiquitous	Primary producers	Shore sea-ice: <i>Navicula glaciei</i> ; littoral: <i>Fragilaria striatula</i> , <i>Achnanthes charcoti</i> ; sublittoral: <i>Odontela weisflogii</i> , <i>Paralia sol</i> , <i>Rhabdonema arcuatum</i> ; resting spores of planktonic <i>Thalassiosira</i> sp. and <i>Chaetoceros</i> spp.; epiphytic: <i>Cocconeis costata</i> , <i>Eutopyla ocellata</i> , <i>Pseudogomphonema kantschaticum</i> ; on invertebrates: <i>Navicula directa</i> , <i>Navicula</i> sp., <i>Eutopyla</i> sp.	Ligowski (2002), Ligowski (unpubl. results)
Macroalgae	10,000	120	55	Hard substrate and epiphytes	Primary producers	Littoral: <i>Enteromorpha</i> sp., <i>Ullothrix</i> sp., <i>Urospora penicilliformis</i> , <i>Adenocystis utricularis</i> ; shallow sublittoral: <i>Monostroma harriotii</i> , <i>Protomonostroma undulatum</i> , <i>Iridaea cordata</i> , <i>Cordiaea racovitzae</i> , <i>Gigartina skottsbergii</i> , <i>Adenocystis utricularis</i> , <i>Ascoseira mirabilis</i> ; deeper sublittoral: <i>Leptosarca simplex</i> , <i>Georgiella confluens</i> , <i>Plocamium cartilagineum</i> , <i>Desmarestia</i> spp., <i>Himantothallus grandifolius</i> Eurytopic, extremely common: <i>Globocassidulina bitora</i> ; other very common: <i>Cassidulinoides parkerianus</i> , <i>Spiroplectammina biformis</i> , <i>Nodulina dentaliniformis</i> ; deepest sublittoral: <i>Astrononion echolsi</i>	Zieliński (1981, 1990), Oliveira et al. (2009)
Foraminifera	10,000	No data	135 ^b	Soft and hard bottom, epiphytic			Gaździcki and Majewski (2003), Majewski, (2005), Majewski et al. (2007), Rodrigues (unpublished), Sinniger et al. (2008)
Porifera	10,000	300	17 ^c	Soft and hard bottom	Suspension feeders	<i>Haliclona</i> sp., <i>Hymeniacidon</i> sp., <i>Iophon</i> sp., <i>Isodictya</i> sp., <i>Mycale</i> sp., <i>Phorbas domini</i> , <i>Rossella</i> sp., <i>Isosicyonis alba</i> , <i>Ascolepis</i> sp., <i>Edwardsia</i> sp.	Pisera (1997), Campos et al. (2007a,b), Hajdu (unpubl. results)
Cnidaria	10,000	400	7 ^c	Soft and hard bottom	Suspension feeders, predators		Nonato et al. (2000), Peña Cantero and Vervoort (2009), Siciński et al. (1996)
Nematoda	4000	350	98 genera ^c	Soft and hard bottom	Deposit feeders, epistrate feeders, predators/omnivores	Shallow sublittoral: <i>Sabatieria</i> sp., <i>Odontophora</i> sp., <i>Axonolaimus</i> sp., <i>Paralinhomoeus</i> sp., <i>Daptonema</i> sp., <i>Aponema</i> sp., <i>Microlaimus</i> sp., <i>Dichromadora</i> sp., <i>Prochromadorella</i> sp., <i>Acantholaimus</i> sp.	Skowronski (unpublished), Gheller (unpublished)
Polychaeta	9000	550	162	All possible substrata: soft and hard bottom, biogenic structures: macroalgae, sponges, ascidians, bryozoans	Herbivores, carnivores, suspension feeders, surface and subsurface deposit-feeders	Shallow sublittoral (5–40 m): <i>Scoloplos marginatus</i> , <i>Travisia kerguelensis</i> , <i>Apistobranchus</i> sp. and <i>Mesospio moorei</i> ; overall common: <i>Leitoscoloplos kerguelensis</i> , <i>Tauberia gracilis</i> , <i>Ophelina syringopyge</i> , <i>Rhodine intermedia</i> , <i>Tharyx cincinnatus</i> , <i>Aricidea strelzovi</i> , <i>Cirrophorus brevicirratus</i> , <i>Maldane sarsi antarctica</i> , <i>Aglaophamus trissophyllus</i> , <i>Asychis amphiglypta</i>	Siciński (1986, 2000, 2004), Siciński and Janowska (1993), Bromberg et al. (2000), Petti et al. (2006), Pabis and Siciński (2010a,b)
Nemertina	?	30	No data	Soft and hard bottom	Detritivores, scavengers	Nearshore zone (down to 20 m depth) scavenger: <i>Parborlasia corrugatus</i>	Presler (1986), Nonato et al. (2000), Jazdzewski et al. (2001)
Sipuncula	?	16	1	Soft bottom	?	<i>Golfingia (Golfingia) margaritacea margaritacea</i>	Kędra (unpubl. results)
Gastropoda	25,000	550	48 ^d	Soft and hard bottom	Detritivores, scavengers, herbivores	Uppermost sublittoral: <i>Nacella concinna</i> , <i>Laevilittorina antarctica</i> , <i>Laevilacunaria bransfieldensis</i> ; sublittoral: <i>Laevilittorina antarctica</i> , <i>Onoba turqueti</i> , <i>Amauropsis grisea</i> , <i>Skenella paludinoides</i> , <i>Margarita antarctica</i> ; scavengers: <i>Neobuccinum eatoni</i> , <i>Harpovoluta charcoti</i> , <i>Chlanidota elongata</i>	Arnaud et al. (1986), Presler (1986), Filcek (1993), Jazdzewski et al. (2001), Nonato et al. (2000), Schiaparelli (unpubl. results)
Bivalvia	6000	160	39 ^d	Soft and hard bottom, epiphytic	Filter feeders	<i>Mysella charcoti</i> , <i>Genaxinus debilis</i> , <i>Laternula elliptica</i> , <i>Yoldia eightsi</i>	Arnaud et al. (1986), Siciński et al. (1996), Absher and Feijó (1998), Nonato et al. (2000), Schiaparelli (unpubl. results)
Pycnogonida	1300	180	29 ^d	Hard bottom, kelp holdfasts, sessile animals	Carnivores, detritophages	<i>Nymphon biarticulatum</i> , <i>Austrodecus glaciale</i>	Gordon (1932), Arnaud et al. (1986), Bamber (unpubl. results)

Ostracoda	6000	240	45	Soft and mixed bottom	Filter feeders, deposit feeders, predators/scavengers	<i>Philomedes charcoti</i> ; <i>Scleroconcha gallardoi</i> ; <i>Cytheropteron acuticaudatum</i> , <i>Loxoreticulatum fallax</i>	Majewski and Olempska (2005), Białewicz and Parker (1997), Szczechura (unpubl. results)
Cumacea	1500	80	15	Soft bottom	Suspension feeders; deposit feeders; predators/scavengers	Shallow waters: <i>Eudorella splendida</i> , <i>Vauthompsonia inermis</i> , <i>Campylaspis maculata</i> ; deeper waters: <i>Ekleptostylis debroyeri</i> , <i>Leucon sagitta</i>	Białewicz and Jażdżewski (1995), Białewicz-Paszkowycz and Heard (2001), Białewicz-Paszkowycz and Ligowski (2002), Białewicz-Paszkowycz (unpubl. results)
Isopoda	5200	500	55 ^d	Soft and hard bottom and on fish	Omnivores; scavengers; detritivores; predators; filter feeders; fish parasites	Shallow sublittoral: <i>Spinoserolis beddardi</i> , <i>Paraserolis polita</i> , <i>Munna neglecta</i> , <i>M. jazdzewskii</i> , <i>Cymodocella tubicauda</i> ; deeper sublittoral: <i>Munna antarctica</i> , <i>Notopais quadrispinosa</i> , <i>Austrofilus</i> sp., <i>Joeropsis</i> sp.; common scavenger: <i>Glyptonotus antarcticus</i> s.l.	Arnaud et al. (1986), Presler (1986), Wägele and Brito (1990), Pires and Sumida (1997), Teodorczyk and Wägele (1994), Teodorczyk (unpubl. results); Malyutina (unpubl. results)
Tanaidacea	1100	130	14	Soft bottom	Deposit feeders	Shallow sublittoral: <i>Nototanais antarcticus</i> , <i>Typhlotanais grahami</i> ; deeper sublittoral: <i>Paraospinosus pushkini</i> , <i>Ekleptostylis debroyeri</i>	Białewicz-Paszkowycz and Jażdżewski (2000), Białewicz-Paszkowycz and Ligowski (2002), Białewicz-Paszkowycz (2004), Białewicz-Paszkowycz and Sekulska-Nalewajko (2004)
Amphipoda	7000	550	172	Soft and hard bottom	Omnivores; scavengers; detritivores; predators; filter feeders; herbivores	Littoral: <i>Gondogeneia antarctica</i> ; shallowest stony sublittoral (0–1 m): <i>G. antarctica</i> , <i>Paramoera edouardi</i> ; sandy sublittoral (5–30 m): <i>Prostebbingia brevicornis</i> , <i>P. gracilis</i> , <i>Schraderia gracilis</i> , <i>Hippomedon kergueleni</i> , <i>Cheirimedon femoratus</i> ; deeper muddy sublittoral: <i>Heterophoxus videns</i> , <i>Waldeckia obesa</i> , <i>Schraderia gracilis</i> ; deepest sublittoral: <i>Urothoe</i> sp., <i>Cephalophoxoides kergueleni</i> , <i>Harpiniopsis aciculum</i> ; scavengers: shallow sublittoral (5–30 m): <i>Cheirimedon femoratus</i> , <i>Hippomedon kergueleni</i> ; deeper sublittoral (60–90 m): <i>Waldeckia obesa</i> , <i>Abyssorchomene plebs</i>	Arnaud et al. (1986), Presler (1986), Wakabara et al. (1990), Jażdżewski et al. (1991a,b, 1995), Munn et al. (1999), De Broyer et al. (2007), Jażdżewska, (unpubl. results)
Asteroidea	1500	200	38	Soft and hard bottom	Predators, detritivores; scavengers	Shallow sublittoral: <i>Odontaster validus</i> , <i>Cryptasterias turqueti</i> , <i>Granaster nutrix</i> , <i>Neosmilaster georgianus</i> ; deeper sublittoral: <i>Psilaster charcoti</i>	Koehler (1912), Grieg (1929), Fisher (1940), Arnaud et al. (1986), Presler (1986), Presler and Figielska (1997)
Ophiuroidea	3000	130	27	Soft and hard bottom	Predators, planktivores, coprophages, scavengers	Scavengers: <i>Odontaster validus</i> , <i>Lysasterias hemiora</i> Upper sublittoral: <i>Ophionotus victoriae</i> , <i>Amphiplus affinis</i> , <i>Ophiomages cristatus</i> ; deep central basin: <i>Ophiuroglypha carinifera</i> , <i>Ophiolimna antarctica</i> , <i>Ophioplinthus grisea</i> ; scavenger: <i>Ophionotus victoriae</i>	Grieg (1929), Mortensen (1936), Arnaud et al. (1986), Presler (1986), Presler (1993a), Nonato et al. (2000)
Echinoidea	1000	80	5 ^c	Soft and hard bottom	Herbivores, carnivores	<i>Sterechinus neumayeri</i> , <i>Abatus</i> sp.	Grieg (1929), Arnaud et al. (1986), Nonato et al. (2000)
Holothurioidea	1400	140	10 ^d	Soft and hard and epizoic	Suspension feeders; deposit feeders	Sublittoral: <i>Cucumaria georgiana</i> , <i>Heterocucumis steineri</i> , <i>Staurocucumis turqueti</i> , <i>Trachythyone bouvetensis</i> , <i>Cucumariidae</i> sp. 1; <i>Psolidium gaini</i> , <i>Psolus charcoti</i> , <i>P. koehleri</i> , <i>Molpadia musculus</i>	Grieg (1929), Arnaud et al. (1986), Moura (unpublished)
Crinoidea	600	40	1 ^c	Hard and mixed bottom	Suspension feeders	<i>Promachocrinus kerguelensis</i>	Grieg (1929), Arnaud et al. (1986)
Bryozoa	5000	400	67 ^d	Hard and mixed bottom	Filter feeders	<i>Nematoflustra flagellata</i> , <i>Isosecuriflustra thyasica</i> , <i>I. angusta</i> , <i>I. tenuis</i> , <i>Klugeflustra antarctica</i> , <i>Cellarinella</i> sp., <i>Cellaria diversa</i> , <i>Camptoplites</i> sp., <i>Reteporella frigida</i> , <i>Antarcticaetos bubeccata</i>	Moyano (1979), Kukliński (unpubl. results)
Ascidiacea	5000	110	16 ^d	Hard and mixed bottom	Filter feeders	<i>Molgula pedunculata</i> , <i>M. enodis</i>	Oliveira (unpublished)
Demersal fish	?	200	30	Soft and hard bottom	Predators, planktivores	Shallow sublittoral: <i>Gobionotothen gibberifrons</i> , <i>Notothenia neglecta</i> , <i>N. rossi</i> , <i>Lepidonotothen nudifrons</i> ; deeper sublittoral: <i>Gobionotothen gibberifrons</i>	Skora and Neyelov (1992), Skóra (1995), Zadróžny (1996)

^a Contains also planktonic species, found living on the bottom.

^b Contains also subfossil Foraminifera.

^c Very poorly recognized group.

^d Poorly recognized group.

deposit feeders and epistrate feeders (Table 1). The diversity of genera has been associated with sediment grain size and availability of food, mainly microphytobenthos (Skowronski, unpublished; Gheller, unpublished).

A study on meiofaunal polychaetes in the nearshore zone of Martel Inlet showed that more than 70% were young individuals mainly of three species: *Apistobranchus glaciera*, *Leitoscoloplos kerguelensis* and *Ophryotrocha notialis*. However, these are considered to be temporary meiofauna, and their distribution patterns were strongly related to the distribution of macrofaunal polychaetes in the same area (Bromberg et al., 2000; Petti et al., 2006).

5.1.3. Macrofauna

Macrofauna of the soft sediments in Admiralty Bay is mostly composed of polychaetes, oligochaetes, bivalves and crustaceans such as amphipods, cumaceans and isopods (Table 2) (Jażdżewski et al., 1986, 1991a,b; Siciński, 2000, 2004; Bromberg, unpublished; Echeverria, unpublished; Filgueiras et al., 2007).

The mean density of the soft bottom macrozoobenthos of the bay was ca. 6500 ind m⁻². Maximum densities can reach over 36,000 ind m⁻² (Jażdżewski et al., 1986). The highest density values were found for bivalves, polychaetes and amphipods. Mass occurrence of Amphipoda was recorded in the shallowest sublittoral (Jażdżewski et al., 1991b). In shallow depths the most abundant species amongst the bivalves were *Mysella charcoti* and *Yoldia eightsi* (Arnaud et al., 1986; Siciński et al., 1996; Bromberg, unpublished). In the depth range 5–30 m, in the central part of the bay the most conspicuous amphipods were: *Hippomedon kergueleni*, *Prostebbingia brevicornis*, *Prostebbingia gracilis*, *Cheirimedon femoratus* and *Schraderia gracilis* (Jażdżewski et al., 1991a,b). Between 50 and 200 m *Heterophoxus videns*, *Waldeckia obesa* and *S. gracilis* were recorded in high numbers; in the deepest part of the bay (more than 200 m) *Urothoe* sp., *Cephalophoxoides kergueleni* and *Harpiniopsis aciculum* predominate (Jażdżewska, in press) (see Tables 1 and 2).

In the soft bottom, at depths below 100 m, polychaetes *L. kerguelensis* and *Levinsenia gracilis*, with density values for each species as high as 1600 ind m⁻², and the tubiculous polychaetes *Maldane sarsi antarctica* and *Asychis amphiglypta*, with densities up to 3000 ind m⁻² each, were recorded (Siciński, 1986, 2000, 2004; Wägele and Brito, 1990; Bromberg et al., 2000). These two last-mentioned subsurface deposit feeders comprised the bulk of the zoobenthic community in terms of both density and biomass.

The mean wet weight of the soft bottom zoobenthos is 700 g m⁻², with 500–900 g m⁻² falling within its 95% confidence limits (Jażdżewski et al., 1986, Jażdżewski and Siciński, 1993). Exceptionally high biomass values, reaching up to 7 kg m⁻², were recorded within the zone of high abundance of ascidians and bryozoan colonies. These animals, along with echinoderms, polychaetes and bivalves, form the bulk of the biomass of bottom assemblages in the central part of the bay. The total biomass of the benthic fauna inhabiting the entire bottom surface of Admiralty Bay was estimated to be around 67,000 tons (Jażdżewski et al., 1986). Rich aggregations of sessile suspension-feeders (Ascidacea and Bryozoa) were patchily distributed and, together with Ophiuroidea, comprised the bulk of the biomass in the central part of the bay at depths from 30 to 300 m (Jażdżewski et al., 1986; Jażdżewski and Siciński, 1993). In general a depth-related gradient in benthic biomass was observed in the central basin, from low biomass in the shallow subtidal zone down to 30–40 m depth (mean ca. 300 g m⁻²) to the highest biomass noted between 100 and 200 m (ca. 1500 g m⁻² with the range from 300 to 2300 g m⁻²). However, the macrofaunal biomass decreases again to approximately 300 g m⁻² between 300 and 500 m depth (Fig. 4). Echiura, Scaphopoda and Pycnogonida,

which are usually not abundant in the shallower sublittoral, are much more numerous in the deepest zones from 300 to 500 m. There, Echiurans comprised a very significant part (up to 60%) of the total macrozoobenthic biomass. Conversely, the maximum abundances and biomasses of Polyplacophora and Amphipoda were recorded in the shallowest nearshore zone, down to 30–40 m (Jażdżewski and Siciński, 1993; Pabis et al., in press). However, in glacially affected areas within Ezcurra Inlet the macrozoobenthic biomass distribution was unrelated to depth.

With regard to the polychaete and amphipod density (Siciński, 2004; Jażdżewska, in press; respectively) and the invertebrate biomass (Jażdżewski et al., 1986; Jażdżewski and Siciński, 1993; Pabis et al., in press) the 30–40 m isobath was the significant zoocenological boundary in the central part of the bay. Similar megafauna distribution patterns were observed in Martel Inlet, the 20–25 m depth being a boundary mostly related to ice disturbance in the shallow sublittoral (Nonato et al., 2000; Echeverria et al., 2005).

Studies on macrofauna in front of Ferraz Station during the 1989/1990, 1990/1991 and 1994/1995 austral summers were carried out using corers taken by SCUBA diving in one transect at 6, 11, 18 and 25 m. Significant differences in macrofaunal densities were observed in relation to depth and between summer seasons. Highest densities were often found in the deepest stations, which were well correlated with sediment grain size and organic matter, although ice scours reduced the densities significantly at 18 m (Bromberg et al., 2000). The dominant organisms at the shallowest stations (6 and 11 m) were the bivalves, amphipods, and the polychaetes *O. notialis* and *Mesospio* cf. *moorei*. The polychaetes *A. glaciera*, *L. kerguelensis*, *Tharyx* cf. *cincinnatus*, *Capitella perarmata* and *Ophelina* spp., as well as the amphipod *Paraperiocolodes brevisrostris*, were dominant from 18 to 25 m.

Macrofaunal communities dominated by annelids (polychaetes and oligochaetes) were studied by Echeverria (unpublished), Bromberg (unpublished) and Lavrado et al. (unpubl. results) in Martel Inlet. Seasonal and interannual fluctuations in abundance and dominance of the benthic community were observed (Figs. 5 and 6). The total density of macrofauna diminished in winter mainly because of the reduction in the number of polychaetes. Changes in macrofauna abundance observed even during short summer intervals (2–3 months) probably due to the increase in organic input from primary production throughout the season. Interannual and seasonal changes in the composition of the macrofauna (Fig. 6) possibly reflect the variation in the process of ice formation and ice melt within the bay.

Five main soft-bottom communities were distinguished in Admiralty Bay in the area from inner parts of Ezcurra Inlet to the central basin of the bay (Fig. 3; Table 2). The classification was based mainly on the polychaete distribution analysis by Siciński (2004).

An intensive deglaciation process was recently observed along the shores of Admiralty Bay. Numerous small and shallow basins and lagoons strongly influenced by glacial freshwater and mineral suspension inflow arose in these areas. The macroinvertebrate community was dominated here by some amphipod species, mostly *C. femoratus*, and polychaetes, with the most typical being *Mesospio moorei* (Siciński et al., 1996; Siciński, unpubl. results).

5.1.4. Megafauna

The megafauna of Admiralty Bay consists mainly of large vagile organisms, such as some polychaetes (e.g. *Laetmonice producta*, *Aglaothamus trissophyllus*), numerous seastars, some crustaceans

Table 2

Classification of soft bottom macrozoobenthos communities, characteristics of the main substrate types and their inhabitants (Ezcurra Inlet and central part of Admiralty Bay).

Sea bottom type	Depth range (m)	Other environmental and/or biological factors	Most common and abundant taxa	Macrozoobenthos density (ind m ⁻²)	Macrozoobenthos biomass (g m ⁻²)	References	
1. Shallow subtidal sandy bottom	0–15	Central basin of Admiralty Bay, far from glaciers	Amphipods (34 species) Serolid isopods Megaepifauna Burrowing bivalves Polychaetes (31 species)	<i>Hippomedon kergueleni</i> , <i>Monoculodes scabriculosus</i> , <i>Cardenio paurodactylus</i> , <i>Prostebbingia brevicornis</i> , <i>P. gracilis</i> , <i>Parapinia rotundifrons</i> Numerous <i>Paraserolis polita</i> , <i>Spinoserolis beddardi</i> <i>Sterechinus neumayeri</i> and <i>Abatus shackletoni</i> present in the deeper parts <i>Mysella charcoti</i> and <i>Yoldia eightsi</i> <i>Travisia kerguelensis</i> and <i>Mesospio moorei</i> (highest biomass); <i>Scoloplos marginatus</i> (highest abundance)	1900–25,000 (mean: 1000)	90–260 (mean: 200)	Jażdżewski et al. (1986, 1991a,b), Siciński and Janowska (1993), Siciński (2004), Siciński (unpubl. results)
2. Shallow subtidal, poorly sorted deposits	10–40	Ezcurra Inlet steep slope, relatively far from glaciers, highly heterogeneous sediment with sand, silt and clay mixed with granules, pebbles and cobbles	Megaepifauna Polychaetes (35 species) Amphipods (15 species)	<i>Sterechinus neumayeri</i> , ophiuroids: <i>Ophionotus victoriae</i> and <i>Amphioplus acutus</i> , seastars <i>Odontaster validus</i> and <i>Cuenotaster involutus</i> , nemertean <i>Parborlasia corrugatus</i> and giant sea anemone <i>Urticinopsis</i> sp. <i>Apistobranchus glaciera</i> (dominant) and eurytopic <i>Leitoscoloplos kerguelensis</i> and <i>Ophelina syringopyge</i> <i>Heterophoxus videns</i> , <i>H. trichosus</i> , <i>Monoculodes scabriculosus</i> Cumaceans (most abundant: <i>Eudorella splendida</i> and <i>Campylaspis maculata</i>) tanaids (most abundant: <i>Peraeospinosus</i> sp., <i>Nototanaïs dimorphus</i> and <i>N. antarcticus</i>)	1500–40,000	10–4000 (mean: 1000)	Błażewicz and Jażdżewski (1995, 1996), Błażewicz-Paszkwowicz and Sekulska-Nalewajko (2004), Siciński (2004), Jażdżewska (unpubl. results)
3. Silt clay, flat inlet seafloor	50–150	Ezcurra Inlet; activity of subglacial streams; silt and clay with extremely poor fauna; biomass increases due to the presence of single large animals (megafauna), such as ophiuroids, asteroids, echinoids, terebellid polychaetes or bivalves (mostly <i>Laternula elliptica</i> and <i>Yoldia eightsi</i>)	Polychaetes (16 species) Amphipods (17 species)	Dominants: <i>Leitoscoloplos kerguelensis</i> , <i>Tharyx cincinnatus</i> and <i>Ophelina syringopyge</i> Dominants: <i>Heterophoxus trichosus</i> , <i>H. videns</i>	1000 ± 740 (mean ± SD)	70 ± 57 (mean ± SD)	Jażdżewski et al. (1986), Siciński (2004), Jażdżewska (unpubl. results)
4. Mid-sublittoral muddy bottom	50–270	Central basin of Admiralty Bay, poorly sorted silty sand and silty clay sand bottom with high concentrations of organic matter. Occasionally abundant aggregations of ascidians and bryozoan	Polychaetes (> 90 species) Amphipods (> 90 species)	Dominants: <i>Maldane sarsi anatarctica</i> , <i>Asychis amphiglypta</i> , <i>Aricidea strelzovi</i> , <i>Cirrophorus brevicirratu</i> , <i>Tauberia gracilis</i> Dominants: <i>Heterophoxus videns</i> , Caprellidae, <i>Schraderea gracilis</i> , <i>Urothoe</i> sp., <i>Waldeckia obesa</i>	1000 ± 980 (mean ± SD)		Jażdżewski and Siciński (1993), Siciński (2004), Jażdżewska (unpubl. results)

Table 2 (continued)

Sea bottom type	Depth range (m)	Other environmental and/or biological factors	Most common and abundant taxa	Macrozoobenthos density (ind m ⁻²)	Macrozoobenthos biomass (g m ⁻²)	References
5. Deep sublittoral muddy bottom	400–530	colonies on dropstones as biogenic substrates for other epifaunal organisms. This megafauna community biomass is composed of: ascidians (63%); bryozoans (14%); polychaetes (9%); ophiuroids (7%) and echinoids (2%). Central basin of Admiralty Bay, coarse and medium poorly sorted sandy silt, and sandy clay silt, no dropstones, highly stable environmental conditions with low influence of water currents; 96% of the benthic community biomass was estimated as follows: large echinians (42%); actinarians (24%); polychaetes (17%); nemerteans (11%).	Megaepifauna Polychaetes Amphipods Echiura and Actiniaria		160–630 (mean: 440)	Lipski (1987), Pabis and Siciński (2010a), Jażdżewska (unpubl. results), Pabis et al. (in press)
			Ascidians, bryozoans, ophiuroids (mostly <i>Amphioplus</i> spp. and <i>Ophiomastus serratus</i>), occasional echinoids Dominant species: eurytopic <i>Tharyx cincinnatus</i> , <i>Sternaspis</i> sp., large maldanid <i>Asychis amphiglypta</i> and the large vagile <i>Laermonice producta</i> Rather frequent: <i>Ampelisca dallenei</i> , <i>Figorella</i> sp., <i>Byblis securiger</i> Extremely high biomass of Echiura and Actiniaria			

(isopods: *Glyptonotus antarcticus* s.l. and serolids, shrimps: *Chorismus antarcticus* and *Notocrangon antarcticus*), the nemertean *Parborlasia corrugatus*, sea urchins (*Sterechinus neumayeri* and some *Abatus* species), ophiuroids (mostly *Ophionotus victoriae*), nudibranchs, and some large sessile animals, such as sponges, large sabellid polychaetes, bryozoans, ascidians and cnidarians (Jażdżewski et al., 1986; Wägele and Brito, 1990; Nonato et al., 2000; Pabis and Siciński, 2010a). Some other large animals, such as the bivalves *Laternula elliptica* and *Y. eightsi* and some maldanid (e.g. *Isocirrus yungi*) and terebellid (e.g. *Amphitrite kerguelensis*) polychaetes, are buried in the sediment.

The megafauna is not abundant in shallow water down to 15–20 m depth. The species richness and abundance increase below 20–25 m. Ascidians, echinoderms, polychaetes and bivalves compose the bulk of biomass of megafauna in soft sediments.

SCUBA-diving observations at Martel Inlet along a transect (6–25 m) revealed that only a few species of megafauna, such as *Nacella concinna*, few amphipod species and the isopod *Frontoserolis polita* were common in the shallowest areas down to 12 m. Sessile organisms (anemones, sponges, ascidians) appeared below this depth (Fig. 7). Also below 12 m, the gastropod *Neobuccinum eatoni*, the bivalve *L. elliptica*, the nemertean *P. corrugatus* and the sea-urchin *S. neumayeri* appeared in the highest numbers (Nonato et al., 2000). At 25 m depth the bottom becomes less steep and the sediments are composed of fine sand mixed with silt and clay, with occasional dropstones. At this depth a more diverse fauna occurs. *L. elliptica*, sponges, ascidians and anemones, as well as the isopod *Glyptonotus antarcticus* s. l., the ophiuroid *O. victoriae* and different species of seastars (e.g., *Labidiaster annulatus*, *Odontaster validus*), are more abundant at this depth (Fig. 7). Between 25 and 45 m, the megabenthic community is structured additionally by high numbers of pennatulacean octocorals and the ophiuroid *Amphioplus acutus*.

5.2. Hard bottom communities

5.2.1. Intertidal

Amphipods, *Gondogeneia antarctica* and *Paramoera edouardi* (Opaliński and Siciński, 1995), and the limpet *N. concinna* are the most important components of the invertebrate assemblage on rocky and stony (boulders, cobbles and pebbles) bottom in the littoral zone. Also, several benthic diatoms (at least 15 taxa) and also marine invertebrates such as turbellarians, the nemertean *Antarctonemertes validum*, polychaetes, the gastropod *Laevilittorina caliginosa*, the bivalve *Lasaea consanguinea*, the acarid *Alaskozetes antarcticus*, some pycnogonids, amphipods and copepods were found in this zone by Campos L.S. (unpubl. results). The most abundant groups were molluscs (214 ind 0.56 m⁻²) and turbellarians (167 ind 0.56 m⁻²) followed by crustaceans (37 ind 0.56 m⁻²).

The mean density of *N. concinna* from different littoral sites in the southern shores of Admiralty Bay was estimated as 10–200 ind m⁻² (Filcek, 1993). This author has estimated the mean density and mean biomass of this gastropod to be ca. 65 ind m⁻² and ca. 130 g m⁻² (range 50–300 g m⁻²), respectively.

5.2.2. Uppermost subtidal stony sublittoral

The uppermost sublittoral stony bottom is characterized by the additional presence of gravel and sand. Macroalgal detritus occurs abundantly in spaces between the stones. This zone has a highly abundant vagile fauna, but with low species richness and diversity. It is typically dominated by seven species of amphipods (85%), five species of gastropods (11%) and some nemerteans (3%). The most common amphipods found in this zone are *G. antarctica* and *P. edouardi* (more than 90% of all amphipods). Amongst the

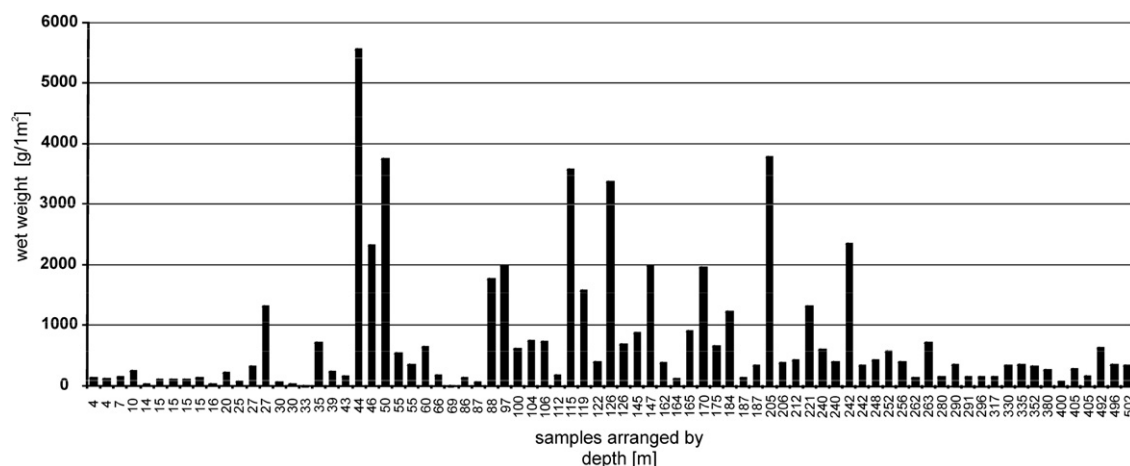


Fig. 4. Macrozoobenthos wet weight (g m^{-2}) in samples arranged according to the depth of the central part of Admiralty Bay (Pabis et al., in press).

gastropods, *Laevittorina antarctica* is dominant. Extremely high density values of macroinvertebrates have been found in this habitat. The mean density reached $13,500 \text{ ind m}^{-2}$, but in some plots it exceeded $50,000 \text{ ind m}^{-2}$, the mean wet weight was ca. 200 g m^{-2} , reaching a maximum of ca. 700 g m^{-2} (Jazdzewski et al., 2001).

5.2.3. Rocky bottom

The rocky bottom of Admiralty Bay was studied especially on Napier Rock. It is a unique rocky seafloor structure, rising from about 100 m depth at the central basin of Admiralty Bay. However, most observations were made by SCUBA diving down to 30 m (Brito, unpubl. results). Its shallowest part is densely covered by macroalgae, mainly *Desmarestia* spp., which is gradually replaced with increasing depth by *Himantothallus grandifolius* and *Cystosphaera jacquinotii*. A very rich benthic community is observed, especially in cracks whose walls are covered by abundant brachiopods and bivalves.

In the intertidal and subtidal down to 6 m depth, *N. concinna* is frequent and abundant; it was observed also on algae down to 25 m depth. In the cracks at 3 m depth, pycnogonids and also octocorals from the order Stolonifera are frequent. The bryozoans, hydroids, sponges, holothurians and the octocoral *Alcyonium* appear below 6 m. Several species, mainly sponges, solitary and colonial ascidians, holothurians, nudibranchs, isopods, pycnogonids, brachiopods, gastropods, polychaetes and octocorals, compete for space at 15 m. There is an increase in faunal coverage mainly represented by sponges and gorgonians from 15 m downwards. The highest diversity is found at this depth. Below 25 m the fauna consists mainly of dense gorgonian aggregations (Fig. 8).

5.2.4. Macroalga-associated assemblages

5.2.4.1. Phytal zone. Admiralty Bay is surrounded by a macroalgal belt (Oliveira et al., 2009). The phytal zone covers approximately 1/3rd of the total area of the bay, and three depth-related macroalgal subzones with characteristic species-compositions were described by Zieliński (1990) (Fig. 9). This author has estimated a total macroalgal biomass in the bay of ca. 74,000 tons. High macroalgal biomass indicates the ecological importance of these organisms as primary producers, a food source and a refuge for a large number of marine organisms. Fifty-five species of macroalgae were recorded in Admiralty Bay: 31 species of red algae, 15 species of brown algae,

8 species of green algae and 1 Chrysophyta species (Zieliński, 1990; Oliveira et al., 2009).

The bulk of the macroalgal biomass is made up by the predominant large brown algae, such as *H. grandifolius*, *Desmarestia* spp. and *C. jacquinotii*. The richest assemblages occur mainly at depths from 10 to 60 m. However, some brown algae (*H. grandifolius* and *Desmarestia anceps*) have been found even at 90–100 m (Fig. 9) (Zieliński, 1981, 1990). The highest biomass, density and species diversity have been recorded in the nearshore sublittoral of the central part of the bay, where macroalgae were represented by 33 species, and covered 35% of the seafloor (Zieliński, 1990). Conversely, the poorest aggregations have been found in Ezcurra Inlet, where they cover only approximately 16% of the seafloor, being represented by 12 species (Zieliński, 1981, 1990; Furmańczyk and Zieliński, 1982; Rakusa-Suszczewski and Zieliński, 1993).

5.2.4.2. Fauna of algal fronds. Morphologically distinct macroalgae were sampled between 4 and 12 m, and their associated benthic macro- and meiofauna were evaluated by Piera (unpublished) and Mieldaziz and Corbisier (unpubl. results). These algae were *Desmarestia* spp. (branched stem), *Monostroma* sp. (thin foliose thallus), *Palmaria decipiens* (unbranched foliose fronds), *Myriogramme mangini* (branched subcylindrical stem with terminal foliose fronds) and *Phaeurus antarcticus* (with branches covered with fine filaments). Density values of meiofauna found in all algal species and sites varied from 245 ± 37 to $33,830 \pm 39,820 \text{ ind } 500 \text{ mL}^{-1}$ (mean \pm SD). Copepods, generally followed by nematodes, were the most abundant group. Nematodes and filter-feeding bivalves dominated on *M. mangini* at Napier Rock. Similar meiofaunal assemblages were found in different sites within the bay on *Desmarestia* fronds. However, densities of meiofauna were considerably lower at Napier Rock than those at Martel Inlet, possibly because of the conditions of high water-dynamics in the former area.

High density values of macrofauna associated with algae fronds ranged from 159 ± 59 to $25,669 \pm 18,784 \text{ ind L}^{-1}$ (mean \pm SD). The morphology of algae fronds was the controlling factor for the dominance of particular macrofaunal groups. On algae with branching fronds, such as *Desmarestia* spp. and *P. antarcticus*, amphipods were a dominant group, whereas on algae with foliose fronds, such as *Monostroma* sp., *M. mangini* and *P. decipiens*, gastropods and spirorbid polychaetes were also dominant (Piera, unpublished). Filter-feeding bivalves were dominant on algae on rocks, in areas influenced by high

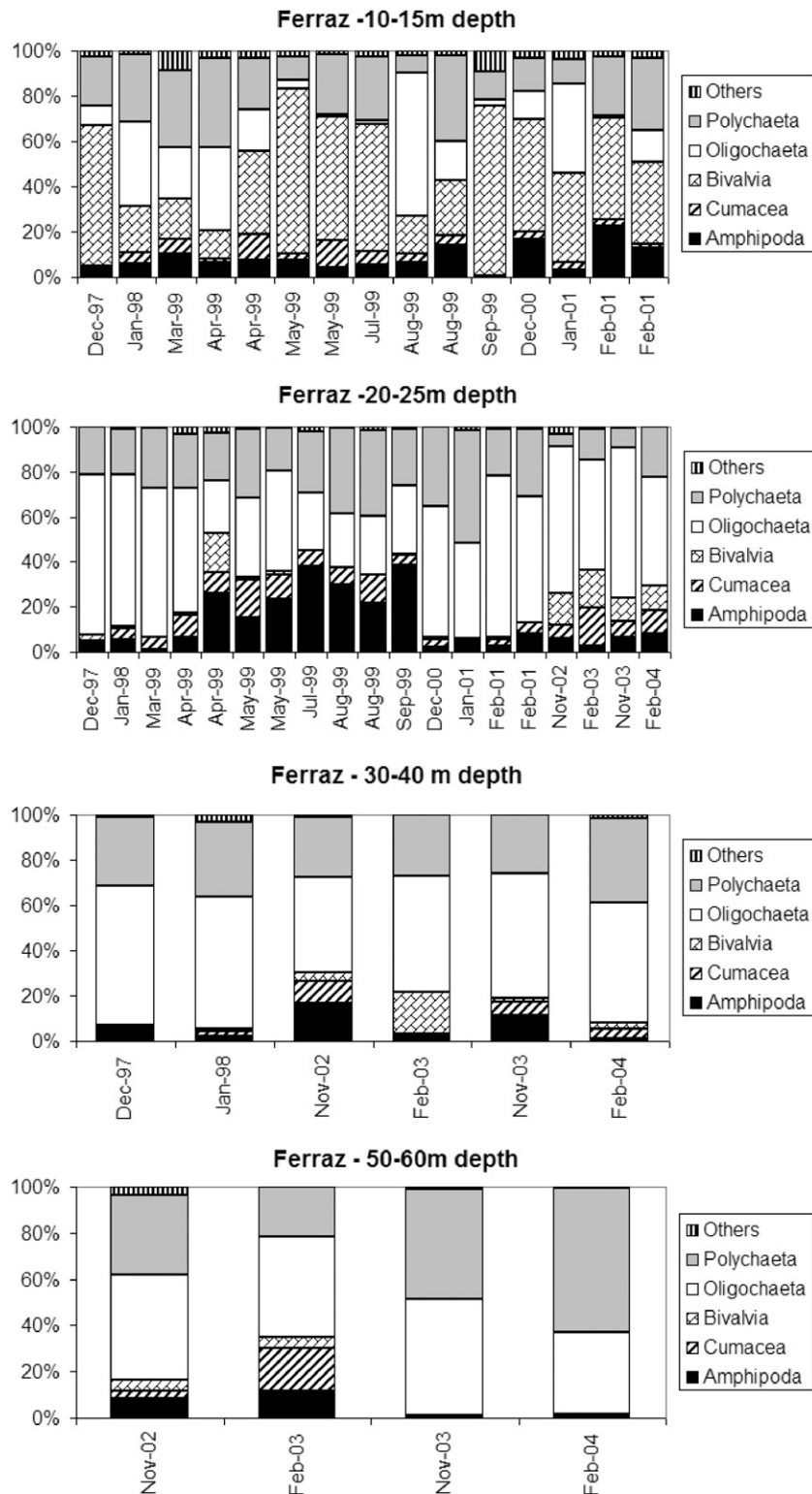


Fig. 5. Relative abundance of the main benthic macrofaunal groups in front of Ferraz from 1997 to 2004, compiled from Echeverría (unpublished), Bromberg (unpublished) and Lavrado et al. (unpublished results).

turbulence. Conversely, the highest concentration of suspended matter limited the occurrence of these suspension feeders in the inner parts of Martel Inlet.

Amphipods inhabiting algal fronds were represented by 20 species, and their composition was basically related to the algal shape. A high dominance of the largest species *G. antarctica*,

followed by *S. gracilis*, was observed on branching forms. Foliose algae were favoured by more delicate, highly mobile smaller amphipod species such as *Parhalimedes turqueti*, *Probolisca ovata* and *Prothaumatelson nasutum* (Piera, unpublished). Amphipod richness and diversity were also related to local hydrodynamics. The highest amphipod diversity occurred within the foliose algae

at sites with low turbulence and on the wrinkled macroalga *M. mangini*, in very turbulent areas (Piera, unpublished).

5.2.4.3. *Holdfast fauna*. The large brown alga *H. grandifolius* is one of the most important species in terms of density and biomass in the Admiralty Bay phytal zone (Zieliński, 1981). The three-dimensional labyrinth of its haptera forms a complex habitat,

colonized by a rich and diverse invertebrate community. Such biogenic structures attached to dropstones reach up to 15 cm in diameter and a volume from 100 to over 1000 mL. Holdfasts provide a shelter from disturbance, especially in shallow water zones (down to 40 m depth), and are functioning as small islands on the surrounding soft bottom (Pabis and Siciński, 2010b).

The *H. grandifolius* holdfast fauna is dominated by epibenthic, motile species. The most numerous groups are amphipods (35%), polychaetes (25%) and isopods (16% of all individuals). Other less numerous but very frequent groups are bivalves, nemerteans, nematods and oligochaetes (Pabis et al., in press).

The group inhabiting the holdfasts that shows the highest species richness is the polychaetes. Over 80 species have been found in this habitat. Up to 500 polychaete individuals were found on a single holdfast. Also, a high diversity of polychaete functional groups was observed by Pabis and Siciński (2010b). The most

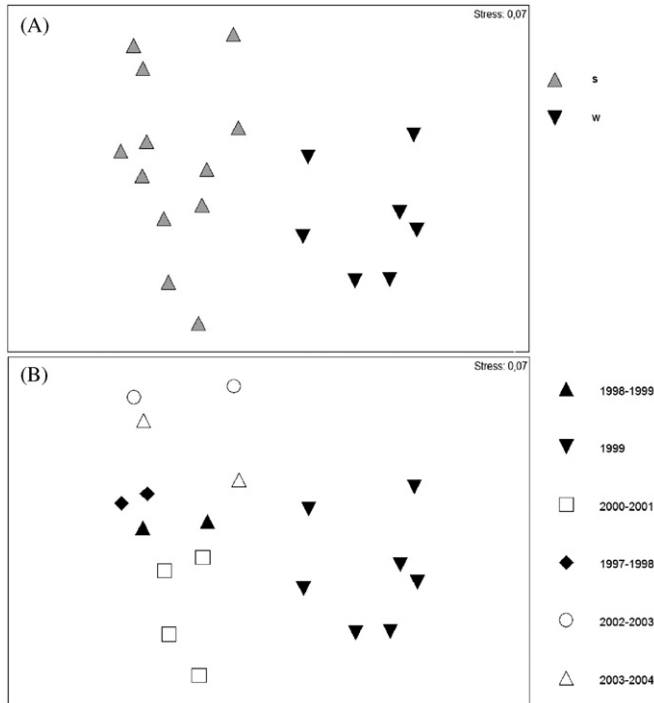


Fig. 6. MDS diagram based on macrofaunal density data sampled in front of Ferraz from 1997 to 2004. Data from Echeverria (unpublished), Bromberg (unpublished) and Lavrado (unpubl. results). (A) samples taken in the summer (s) and winter (w). (B) samples taken between 1997 and 2004.

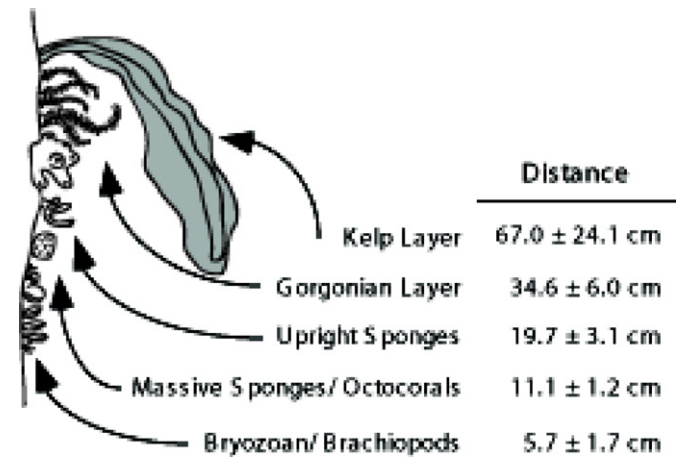


Fig. 8. Epibenthic assemblages of Napier Rock. Five distinct layers defined by kelps, gorgonians, erect and massive sponges/octocorals and bryozoans/brachiopods. Average horizontal distances (± SD) from the vertical rock wall are given (Smith, unpublished results).

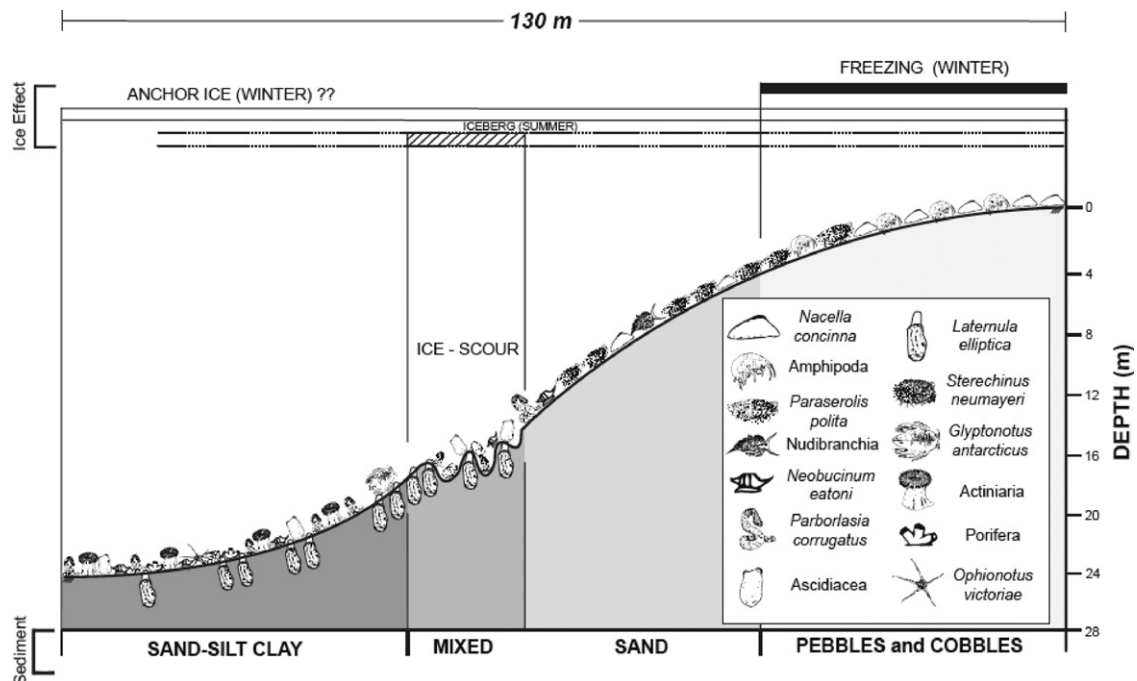


Fig. 7. Distribution of benthic megafauna in front of the Brazilian Antarctic Station (Martel Inlet) showing the depth variation and sediment characteristics (adapted from Nonato et al., 2000).

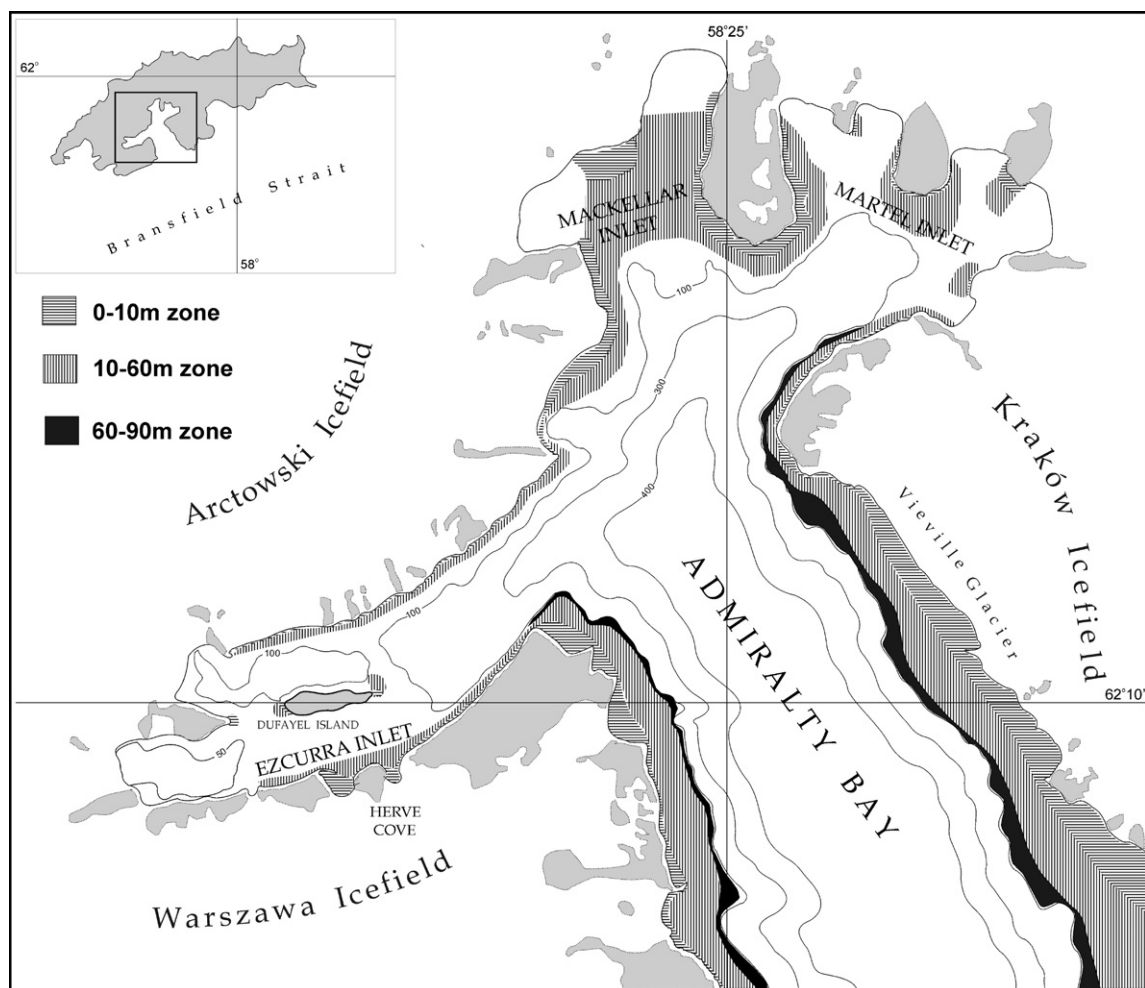


Fig. 9. Distribution and zonation of the phytal zone of Admiralty Bay (from Zieliński, 1990).

important species were the motile herbivores, *Neanthes kerguelensis* and *Brania rhopalophora*, the sessile tube dwelling bamboo worm, *Rhodine intermedia*, and the small sessile suspension feeders, the sabellid *Oriposis alata* and spirorbid *Paralaeospira antarctica*.

The amphipod holdfast fauna (25 species from 11 families) is dominated by *Ischyrocerus camptonyx*, *Schraderia cf. dubia*, *Ventojassa georgiana*, *S. gracilis* and *P. gracilis* (Jażdżewska, unpubl. results).

5.3. Nekto-benthos—demersal fishes

In Admiralty Bay 30 demersal fish species have been hitherto recorded (Skora and Neyelov, 1992; Skóra, 1995). The species richness clearly increases with depth. Quantitative data should be treated with caution, as the general proportion for any particular fish species from samples undertaken from various studies differs strongly, mainly because in each of them different types of gear were used (Skora and Neyelov, 1992; Zadróźny, 1996). Reliable data from the deep sublittoral trawl catches undertaken in the summer of 1986/87 showed the dominance of *Gobionotothen gibberifrons* (Skora and Neyelov, 1992). According to these authors the ichthyofauna of Admiralty Bay has a comparatively low fish abundance inside the fiord in relation to the shelf surrounding King George Island, where trawl catches gave a biomass 10 times as high as that inside the bay. Interestingly, immature specimens dominated the samples from the bay. Possibly, the shallowest waters from the inner parts of the bay are used as feeding grounds

for juveniles, which at a later stage of development migrate to the open and deeper waters for breeding.

6. Trophic relationships

The link between the organic matter sources and the shallow water community of Martel Inlet was evaluated during the summer of 1996/97 using the carbon isotope ratio ($\delta^{13}\text{C}$). Three primary sources have been identified: SPM (phytoplankton and suspended particulate matter), microphytobenthos and fragments of macroalgae. The soft bottom community in this shallow coastal zone had a wider range of $\delta^{13}\text{C}$ values than those from oceanic areas. Enriched values of $\delta^{13}\text{C}$ are due to the carbon contribution of the microphytobenthos and fragments of macroalgae (Corbisier et al., 2004).

There is a benthic-pelagic coupling between the plankton and suspension feeders—the bivalve *L. elliptica*, the ophiuroid *O. victoriae* and the fish *Chaenocephalus aceratus*. Based on $\delta^{13}\text{C}$ analysis the benthic grazers (the gastropod *N. concinna*), deposit feeders (the bivalve *Y. eightsi*) and the nematodes showed a close relationship with microphytobenthos (Corbisier et al., 2004). Several deposit feeders and/or omnivores (e.g., polychaetes, amphipods, holothurians, sea urchins) seem to have a mixed diet with fragments of macroalgae and organic matter from the sediment, including small quantities of microphytobenthos and/or meiobenthos. Benthic carnivores and/or scavengers, such as the isopods *F. polita* and *Glyptonotus antarcticus* s.l., the sea star

O. validus, the nemertean *P. corrugatus* and carnivorous polychaetes, generally showed a considerable isotopic carbon ratio overlap throughout the food chain without any clear coupling with the primary sources of organic material. Their diet probably consists of a wide variety of prey (Corbisier et al., 2004).

Benthic invertebrates, especially amphipods, were reported in the stomach content of different fish species (Linkowski et al., 1983). Some necrophagous amphipods were also found in the diet of pygoscelid penguins of Admiralty Bay (Jażdżewski, 1981). An interesting food link was observed by Jażdżewski and Konopacka (1999) who reported benthic necrophagous amphipods in the diet of Antarctic tern. This bird feeds on necrophages, scavenging tissues of dead animals stranded on the shore. The accessibility of such food was recently confirmed by Jażdżewska (2009) who studied a large sample of amphipods from a fur seal carcass, found in the vicinity of Admiralty Bay.

In Admiralty Bay, at depths from 5 to 90 m, 23 species of clearly necrophagous habits and 10 species that are possibly opportunistic scavengers were recognized (Table 1). Scavengers form aggregations, which differ in species composition and dominance structure depending on the site, depth, substrate quality and season. In general the species richness increases with depth. In winter the necrophagous assemblage has a very low diversity and it is dominated by amphipods: *C. femoratus* (at the depths 5–30 m), *Abyssorhynchomene plebs* and *W. obesa* (in deeper water 30–90 m). In summer, *H. kergueleni* replaces *C. femoratus* in shallow sublittoral (5–30 m); in deeper parts the same amphipod species as in winter dominate. During the summer, in deeper parts, below 30 m an important role is played by echinoderms (mostly *O. victoriae*, *O. validus* and *Lysasterias hemiora*) and by the isopod *Glyptonotus antarcticus* s.l. (Presler, 1986, 1993b).

7. Discussion and conclusions

Admiralty Bay is an area of outstanding environmental, historical, aesthetic and scientific values, characterized by remarkable glaciated mountain landscapes, varied geological features, rich sea bird and mammal breeding grounds, abundant terrestrial plant communities on the shores and highly diverse marine habitats. The comprehensive knowledge of the physical, chemical and biological processes, as well as the diversity of this area, led to the designation of this basin as an *Antarctic Specially Managed Area* (ASMA No. 1) by the Antarctic Treaty Consultative Meeting XX in Utrecht in 1996 (ATCM XXVIII document, 2005). The ASMA Management Plan was jointly prepared by the countries with active research programmes in the area: Brazil, Ecuador, Peru, Poland and USA. Before that designation, a *Site of Special Scientific Interest* (SSSI No. 8), located on the western shore of the bay, was established in 1979 and later designated as *Antarctic Specially Protected Area* (ASPA No. 128), mostly for penguin biology research performed for many years by American ornithologists. Admiralty Bay was also a reference site under the SCAR EASIZ 1994–2004 research programme.

Several authors have provided estimates of the benthic species richness for the Southern Ocean (e.g. Arntz et al., 1997; De Broyer et al., 2003; Clarke and Johnston, 2003; Gutt et al., 2004; De Broyer and Danis, this issue). The macrobenthic species richness of Admiralty Bay comprises 20% of the over 4100 known Antarctic species estimated by Clarke and Johnston (2003). On the other hand, Gutt et al. (2004), relying on quantitative records from the eastern Weddell Sea, calculated that the total number of Antarctic macrozoobenthic species might be in the range of 11,000 to 17,000. It is very likely that species estimations will increase significantly in the future, as new inventory tools

are becoming available worldwide, such as the RAMS database (www.scar.marbin.be).

The remarkably long benthic species list (~1300) provided here for Admiralty Bay is far from being complete, and may well reach over 2000 species. Several groups, such as Harpacticoida, Nematoda, Cnidaria, Echinodermata, Ascidiacea, among others, still need further detailed investigation. Based on ABED, one could estimate that Admiralty Bay comprises approximately 20% of the total species richness of Ostracoda, Cumacea, Asteroidea and Ophiuroidea and 25% of Bivalvia known from the Antarctic.

Polychaetes and amphipods are the prominent zoobenthic groups worldwide that are well-studied in Admiralty Bay. The richness in each of these groups exceed 30% of the Antarctic fauna, making them model groups for biogeographical studies in the context of global changes. A total of 161 polychaete species have been recorded from Admiralty Bay. In comparison, Lowry (1975) and Richardson and Hedgpeth (1977) recorded some 120 polychaete species from the soft bottoms of Anvers Island (Palmer Archipelago). On the Elephant Island shelf (depth range 70–552 m), Hartmann-Schröder and Rosenfeldt (1990, 1991) found 126 species. Finally, Gambi et al. (1997) published a list of 77 polychaete species collected in the Terra Nova Bay (Ross Sea) in the depth range from 23 to 194 m. These authors recognized the Admiralty Bay fauna as a rather rich one when compared with the 146 species of Polychaeta recorded to date from the whole Ross Sea.

Similarly, a total of 172 species of benthic amphipods, belonging to 42 families, have been recorded for Admiralty Bay. In the neighbouring Maxwell Bay and Fildes Strait, extensively studied by Rauschert (1991), 101 amphipod species were recorded. Other well-studied Antarctic places are much larger basins: the Davis Sea (100 species), the Ross Sea (126 species) and the Weddell Sea (> 200 species). In South Georgia – also known as a very diverse region – 193 species were recorded (De Broyer et al., 2007; d'Udekem d'Acoz, 2008, 2009; d'Udekem d'Acoz and Robert, 2008; Lörz et al., 2009). Lowry (1975) reported 23 amphipod species from Arthur Harbour on Anvers Island (Palmer Archipelago); however, his work concerned only the shallow sublittoral.

The most diverse algal group at Admiralty Bay are the benthic diatoms, whose richness represents nearly 75% of the total number of Bacillariophyceae species recorded in the Southern Ocean, and they represent key dietary elements for both errant grazers and deposit feeders (Ligowski, 1993).

Macroalgae from both the littoral and shallow sublittoral zones are also fairly well known in Admiralty Bay, encompassing 50% of the Antarctic macroalgae inventory. Extensive phytal zone in Admiralty Bay provides a complex habitat for invertebrates. Fronds and holdfasts of various algae host a great variety of animals. Besides Adelie Land (Arnaud, 1974) and Anvers Island (Huang et al., 2007), Admiralty Bay is the only site in the Antarctic, and one of the only few in the Subantarctic (Edgar, 1987; Smith and Simpson, 1998, 2002), where benthic communities associated with the complex habitat provided by macroalgal forests were studied (Piera, unpublished; Pabis and Siciński, 2010b).

One of the possible explanations for the general high diversity found in the Admiralty Bay benthos is probably the extreme heterogeneity of the bottom, which is influenced by a plethora of different factors. The shoreline of the bay is extensive and there are numerous glacier fronts. A wide connection with Bransfield Strait allows extensive exchange of oceanic waters with those, more spatially confined, of Admiralty Bay. The bottom is composed of sediments spanning all size ranges, from clay to coarse gravel, with intermixed dropstones of various sizes and shapes. Dropstones provide a substratum for large sessile suspension feeders (mostly ascidian and bryozoan colonies),

which in turn form complex habitats (biogenic structures) for other invertebrates (Pabis et al., in press). Moreover, bottom depths are variable and may reach those of the Antarctic shelf, down to 500 m. All these conditions create diverse habitats for various benthic communities related to the gradients of depth, salinity, bottom structure, sediment type and habitat stability. The Southern Ocean benthic communities have rarely been analyzed in terms of habitat structural heterogeneity and complexity (Gray, 2001). In this context, the synthesis presented here sets Admiralty Bay as an interesting, physically and biologically heterogeneous area, where specifically designed studies, which, by taking into account different spatial and temporal scales, might provide the basis for habitat modelling, and allow further comparisons with other Antarctic regions.

Although the Admiralty Bay habitat diversity may be the core factor responsible for its high benthic species richness and diversity, other factors are likely also to contribute to the observed diversity. The history of the Last Glacial Maximum (LGM) and ice retreat suggests that the Bransfield Strait could have played the role of a glacial refugium for some marine organisms and allowed shelf animals to recolonize the South Shetland Islands region very early. Ice retreat after LGM started in the North Antarctic Peninsula as early as in 18,000–14,000 yr BP (Ingólfsson et al., 1998; Heroy and Anderson, 2007). Anderson et al. (2002) suggested that the Bransfield Strait area was free of grounded ice during the LGM.

The Antarctic Peninsula is considered one of the fastest warming regions on the Earth (Clarke et al., 2007; Turner et al., 2009) with the temperature of western Antarctic Peninsula shelf waters being significantly warmer than that of other Antarctic shelves (including Bransfield Strait shelf areas) (Clarke et al., 2009). According to some predictions climate warming can cause significant changes in the structure of benthic communities, including the decrease of biodiversity, even in a relatively short period of time (Smale and Barnes, 2008). Some studies in Admiralty Bay have already focused on ice impact upon benthic communities (Nonato et al., 2000; Echeverria et al., 2005; Petti et al., 2006) and on the characterization of communities in the newly deglaciated nearshore areas (Siciński et al., 1996).

The studies on depth-related gradients as well as the research on scales of patchiness have included disturbed areas affected by mineral suspension inflow, such as Ezcurra Inlet (Jażdżewski et al., 1986; Siciński, 2004; Pabis and Siciński, 2010a). All the above mentioned studies are a suitable basis for the future research of succession in benthic communities, as well as for the assessment of possible further changes in the diversity, structure and distribution of benthic communities caused by regional climate warming.

The perceived high species richness can be partly explained by the intensive and long lasting studies carried out in this region, but such insight is absent from most other Antarctic marine habitats. The continuous development of *Admiralty Bay Benthos Diversity Database* (ABBED) will endow the Antarctic community with a valuable tool for monitoring and understanding the state and potential changes of the benthic realm in the area.

As pointed out by SCAR, Admiralty Bay is “a site of particular interest to CAML on account of almost four decades of research having been carried out in this basin and that this work can help point the way towards important area which might warrant future consideration as legacy site requiring special protection”.

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