

Polychaete fauna associated with holdfasts of the large brown alga *Himantothallus grandifolius* in Admiralty Bay, King George Island, Antarctic

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Abstract The polychaete community associated with holdfasts of the brown alga *Himantothallus grandifolius* in Admiralty Bay has been studied. It is the first study of its kind in this area and only the second in the Antarctic. Samples were collected in the summer season of 1979/1980 from a depth range of 10–75 m. Seventy-eight species were found on 19 holdfasts. The community was dominated by *Brania rhopalophora* and *Neanthes kerguelensis*. Analysis of similarity showed that polychaete fauna associated with this habitat did not show any partitioning related to depth. Regression analysis showed that densities of both species and individuals decreased with increased holdfast volume. A positive correlation was found between the number of individuals and holdfast volume. Polychaetes from 10 feeding guilds were found with dominance of macrophagous motile herbivores and sessile filter feeders. The complex habitat provided by holdfasts is a shelter for a rich polychaete fauna and may function as important protection from disturbance in the shallow areas of Admiralty Bay.

Keywords West Antarctic · Holdfast fauna · Habitat heterogeneity · Habitat complexity · Polychaete

Introduction

Thalli and holdfasts of large brown algae are considered to be structurally complex habitats (Steneck et al. 2002). The degree of habitat complexity is an effect of increasing effective surface area or volume available for various organisms (Le Hir and Hily 2005). It has already been pointed out that complex habitats support a more diverse fauna and species richness in those habitats is high (Kohn and Leviten 1976; Smith 2000; Norderhaug et al. 2002; Anderson et al. 2005; Eriksson et al. 2006; Coleman et al. 2007). There are a few reasons for increased diversity in these habitats. These, mostly biogenic, structures can provide a shelter for invertebrates and decrease the influence of mechanical stress (Koehl 1999; Smith 2000). Competition and the influence of predators could be lower in these habitats (Almany 2004; Corkum and Cronin 2004; Hereu et al. 2005). Also, the number of potential ecological niches and diverse ways of exploiting the environmental resources could be higher in these habitats (Tews et al. 2004). It was recently emphasized that Southern Ocean benthic communities have as yet rarely been analysed in the context of structural heterogeneity of habitats. This lack of such research is particularly distinct in macroalgal forests, which are the most important complex biodiversity hot spots in the Antarctic (Gray 2001).

There are only scarce data reported on Antarctic and Subantarctic invertebrate faunas associated with holdfasts of various macroalgae and most of these contain only species lists with minor ecological interpretation or are based on the composition of higher taxa. Arnaud (1974) presented some information on the invertebrate fauna of *Macrocystis pyrifera* (L.) C. Agardh and *Durvillea antarctica* (Chamisso) Hariot holdfasts from Morbihan Bay on the Kerguelen Islands and of *Himantothallus grandifolius* (A. Gepp & E.S.

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Gepp) Zinova holdfasts from Adélie Land. A short list of species found on floating *Macrocystis pyrifera* rhizoids from the Subantarctic and the Patagonian shelf was presented by Smirnov (1982). Invertebrate communities associated with *Durvillea antarctica* holdfasts from the Subantarctic Macquarie Island were also recently described by Smith and Simpson (1998, 2002). Benthic macroinvertebrate communities associated with *Macrocystis pyrifera* have also been analysed in Southern Chile (Ojeda and Santelices 1984), the Strait of Magellan (Rios et al. 2007) and in the Beagle Channel (Adami and Gordillo 1999).

Current knowledge on holdfast macroinvertebrate faunas in Antarctica is poor. Recognition of holdfast fauna can be also a first step in understanding the patterns of distribution of some species in the Antarctic. Detached thalli and holdfasts drifting with Antarctic Circumpolar Current may be an important vector for dispersion and the reason for the circumpolar distribution of many invertebrates including polychaetes (Edgar 1987; Helmuth et al. 1994; Smith 2002).

Polychaete diversity and distribution have been intensively studied in Admiralty Bay, but all the studies were focused on the soft-bottom fauna (Sicinski 1986; Sicinski and Janowska 1993; Bromberg et al. 2000; Sicinski 2004; Petti et al. 2006; Pabis and Sicinski 2010). In Admiralty Bay, the phytal zone covers about 30% of the bottom surface and until now there are no data on macroinvertebrate communities associated with this habitat. The most dense and diverse algal communities are located in the central basin. Among 42 taxa of seaweeds recorded from this basin *H. grandifolius* and *Desmarestia anceps* Montagne are among the most common species and have the highest range of vertical distribution. Both species can be found from 10 to 90 m depth (Furmanczyk and Zielinski 1982; Zielinski 1990; Oliveira et al. 2009). Holdfasts of the large brown alga *H. grandifolius* are attached to dropstones, which are the only hard substratum on the soft bottom and can be treated as small islands on the surrounding soft bottom. As a result, *H. grandifolius* differs from most of the other species of large Antarctic brown algae, which are associated with typical hard bottoms. The three-dimensional labyrinth of holdfasts (Fig. 1) forms a very peculiar, complex habitat compared to compacted, shallow sublittoral bottom sediments. The aim of the present study was to describe the polychaete community associated with holdfasts of *H. grandifolius* in Admiralty Bay.

Materials and methods

Study area

Admiralty Bay is a fjord-like embayment, which consists of a central basin and three inlets: Ezcurra Inlet, Martel



Fig. 1 Holdfast of *Himantothallus grandifolius*

Inlet and MacKellar Inlet. The central basin is the deepest part of the bay, reaching 550 m, and it is open to the Bransfield Strait. Almost half of the Admiralty Bay shoreline is covered by glaciers and icefalls especially on the eastern coast of the central basin and in the inner fjords (Braun and Grossmann 2002). It is the largest bay on the South Shetland Islands with surface area of approximately 120 km².

A large part of the Admiralty Bay coastline has a surrounding macroalgal zone (Oliveira et al. 2009). The most dense macroalgal populations are distributed in the central basin of the bay and the poorest in the Ezcurra Inlet. The total macroalgal biomass of Admiralty Bay was estimated to be around 74,000 tonnes (Furmanczyk and Zielinski 1982; Zielinski 1990).

Sampling

Material was collected in the central basin of Admiralty Bay close to the “H. Arctowski” Polish Station (Fig. 2). Nineteen *H. grandifolius* holdfasts from a depth range of 10–75 m were collected in the summer season of 1979/1980. The volume of each holdfast was measured by placing it in a beaker and measuring the volume of displaced water. Holdfasts were pulled off the bottom together with whole thalli that were attached to various sampling gears such as bottom nets, fish pots or dredges (net mesh size from 0.1 to 0.5 cm). In the laboratory, the holdfasts were washed over a 0.5 mm sieve. On board the ship, each holdfast was carefully put into a separate container immediately after the sample was brought on board. Only the holdfasts that were still partially filled with sediment and still attached to a dropstone, and thus in which the invertebrates had not been washed out by water, were used. Thus, possible underestimations, which may result from invertebrates that could actively escape were minimized and may concern rather amphipods than (even motile) polychaetes.

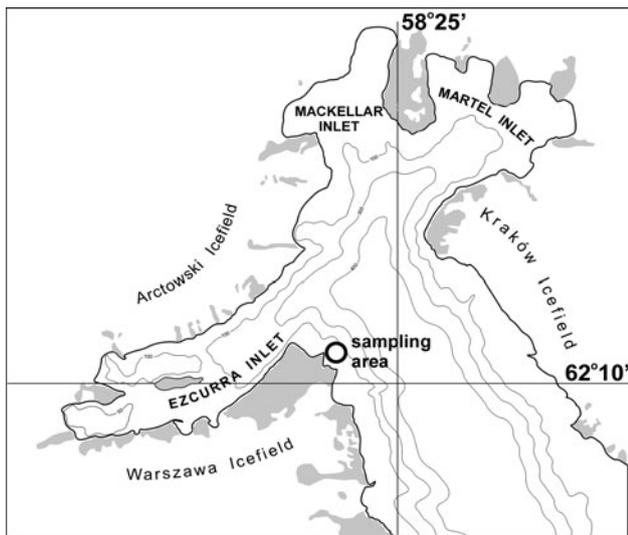


Fig. 2 Admiralty Bay with the indicated sampling area

In the polar conditions, it is very difficult to collect such material from the deeper sublittoral by SCUBA diving. This is why previous similar analyses were restricted to very shallow (several meters) depths (Arnaud 1974; Dunton et al. 1982; Włodarska-Kowalczyk et al. 2009). The present study involves sampling from depths that are out of the range of SCUBA diving in the Antarctic (up to 75 m depth).

Data analysis

Similarity analyses between samples based on the Bray-Curtis similarity coefficient were performed using the PRIMER Package (Clarke and Warwick 1994). As non-comparable samples (holdfasts of different volume) were used in the analysis, standardization of data was applied. In each sample, the number of individuals of each species was divided by the total abundance (number of individuals) of all species in a given sample, the procedure recommended for samples of different volume or surface area by Clarke and Warwick (1994). Sample counts were then square root transformed. Hierarchical agglomerative clustering was performed using the group average method.

Number of species, species density [spec./100 ml] and total density of individuals [ind./100 ml] were measured for each sample. The relationships between the holdfast volume and density of individuals, species density and number of species of polychaetes, as well as between holdfast volume and number of individuals, were examined using regression analyses. Regression analysis was also used to examine the relationship between the sample depth and the density of individuals. The frequency of occurrence, dominance and density [ind./100 ml] of each species

Table 1 Holdfast samples list together with information on volume of each holdfast, depth and number of species and number of individuals

Sample	Depth [m]	Holdfast volume (ml)	Number of species	Number of individuals
A1	10	500	16	440
A2	11	720	17	497
A3	11	940	19	567
A4	13	590	13	93
A5	15	190	22	161
A6	15	100	28	133
A7	15	220	21	73
A8	20	60	14	158
A9	23	310	13	137
A10	30	100	11	58
A11	30	290	23	205
A12	30	140	26	101
A13	30	380	23	198
A14	30	640	24	252
A15	45	360	19	109
A16	45	350	19	110
A17	75	500	35	132
A18	75	680	11	144
A19	75	360	27	133

was calculated. Each species was also assigned to a feeding guild according to the classification proposed by Fauchald and Jumars (1979).

Results

Seventy-eight species of polychaetes were found on 19 *H. grandifolius* holdfasts (3701 individuals). The volume of the holdfasts varied between 60 and 940 ml. The number of species found on a single holdfast ranged between 11 and 35 (Table 1). Some Spirorbidae other than *Paralaeospira antarctica* and Spirorbidae gen sp. was not identified to the species level owing to the poor condition of the material (Table 2). In the cluster analysis, the polychaete fauna constituted one group at 40% similarity, and there was no depth or holdfast-volume partitioning observed (Fig. 3). This polychaete community seems to be very uniform in its nature at least in the composition of its dominant species and in the dominance structure. The most frequent and dominant species were *Brania rhopalophora* ($D = 23.3\%$, $F = 94.7\%$) and *Neanthes kerguelensis* ($D = 21.3\%$, $F = 100.0\%$). Other important species were *Rhodine intermedia* ($D = 6.9\%$, $F = 89.5\%$), *Oriopsis alata* ($D = 4.7\%$, $F = 68.4\%$), *Exogone heterosetosa* ($D = 4.5\%$, $F = 84.2\%$), *Scoloplos*

Table 2 Dominance (*D*), frequency of occurrence (*F*) and density [ind./100 ml] of polychaetes together with its feeding guild (Fauchald and Jumars 1979)

Species	Feeding guild	<i>D</i> [%]	<i>F</i> [%]	Mean density [ind./100 ml] with SD	
<i>Barrukia cristata</i> (Willey, 1902)	CMJ	0.05	10.5	0.02	0.09
<i>Harmothoe</i> sp.	CMJ	0.5	52.6	0.5	0.7
<i>Pholoe</i> sp.	CMJ	0.02	5.3	0.01	0.04
<i>Sigalionidae</i> gen. sp.	CMJ	0.08	15.8	0.06	0.2
<i>Euphosine armadilloides</i> Ehlers, 1900	CMJ	0.02	5.3	0.01	0.04
<i>Anaitides patagonica</i> (Kinberg, 1866)	CMJ	0.05	5.3	0.02	0.1
<i>Eteone sculpta</i> Ehlers, 1897	CMJ	0.08	10.5	0.04	0.1
<i>Genetyllis polyphylla</i> (Ehlers, 1897)	CMJ	0.9	26.3	0.5	1.4
<i>Eulalia picta</i> (Kinberg, 1866)	CMJ	0.4	31.6	0.4	0.8
Phyllodocidae gen. sp. 1	CMJ	0.2	15.8	0.1	0.4
Phyllodocidae gen. sp. 2	CMJ	0.6	42.1	0.3	0.4
Phyllodocidae gen. sp. 3	CMJ	0.1	15.8	0.05	0.1
<i>Brania rhopalophora</i> (Ehlers, 1897)	HMJ	23.3	94.7	16.8	29.4
<i>Exogone heterosetoides australis</i> Hartmann-Schröder & Rosenfeldt, 1988	HMJ	1.0	42.1	0.9	2.2
<i>Exogone heterosetosa</i> McIntosh, 1885	HMJ	4.5	84.2	3.7	4.9
<i>Exogone tridentata</i> Hartmann-Schröder and Rosenfeldt, 1993	HMJ	0.05	5.3	0.1	0.4
<i>Eusyllis maxima</i> (Monro, 1930)	CMJ	0.02	5.3	0.005	0.02
<i>Syllides articulatus</i> Ehlers, 1897	CMJ	0.05	10.5	0.03	0.1
<i>Typosyllis</i> sp.	CMJ	0.02	5.3	0.01	0.04
Exogoninae gen. sp.	HMJ	0.9	42.1	0.8	1.5
Syllidae gen. sp. 1	CMJ	0.02	5.3	0.005	0.02
Syllidae gen. sp. 2	CMJ	0.05	5.3	0.02	0.1
Hesionidae gen. sp.	CMJ	0.2	21.0	0.08	0.2
<i>Neanthes kerguelensis</i> (McIntosh, 1885)	HMJ	21.3	100.0	11.0	11.2
<i>Micronereis</i> sp.	HMJ	0.02	5.3	0.02	0.09
<i>Aglaophamus trissophyllus</i> (Grube, 1877)	CMJ	0.05	10.5	0.03	0.1
<i>Sphaerodoropsis parva</i> (Ehlers, 1913)	BMX	0.3	42.1	0.1	0.3
<i>Glycera kerguelensis</i> McIntosh, 1885	CDJ	0.02	5.3	0.01	0.04
<i>Lumbrineris magalhaensis</i> (Kinberg, 1865)	CDJ	3.3	78.9	3.0	5.9
Dorvilleidae gen. sp.	HMJ	0.02	5.3	0.05	0.2
<i>Ophryotrocha notialis</i> (Ehlers, 1908)	HMJ	0.4	26.3	0.3	0.9
<i>Leitoscoloplos kerguelensis</i> (McIntosh, 1885)	BMX	1.6	57.9	1.3	2.3
<i>Orbinia</i> (<i>P.</i>) <i>minima</i> Hartmann-Schröder & Rosenfeldt, 1990	BMX	0.02	5.3	0.01	0.07
<i>Scoloplos</i> (<i>L.</i>) <i>marginatus</i> (Ehlers, 1897)	BMX	3.4	84.2	1.4	1.1
<i>Scoloplos</i> (<i>S.</i>) sp.	BMX	0.1	5.3	0.04	0.2
<i>Aricidea</i> (<i>A.</i>) <i>antarctica</i> Hartmann-Schröder and Rosenfeldt, 1988	SMX	0.08	5.3	0.02	0.1
<i>Cirrophorus brevicirratu</i> s Strelzov, 1973	SMX	0.4	21.0	0.2	0.8
<i>Microspio moorei</i> (Gravier, 1911)	SDT	0.02	5.3	0.01	0.07
<i>Spiophanes tcherniai</i> Fauvel, 1950	SDT	0.7	42.1	0.5	1.1
<i>Apistobranchus glaciera</i> e Hartman, 1978	SDT	0.4	31.6	0.3	0.5
<i>Caulleriella</i> sp.	SMT	0.08	10.5	0.1	0.4
<i>Cirriformia</i> sp.	SMT	0.6	15.8	0.4	1.09
<i>Tharyx cincinnatus</i> (Ehlers, 1908)	SMT	1.2	31.6	0.3	1.0
<i>Tharyx epitoca</i> Monro, 1930	SMT	2.0	21.0	1.3	4.2
<i>Tharyx</i> sp.	SMT	0.1	15.8	0.06	0.1

Table 2 continued

Species	Feeding guild	<i>D</i> [%]	<i>F</i> [%]	Mean density [ind./100 ml] with SD	
Cirratulidae gen. sp. 1	SMT	2.1	52.6	1.2	1.8
Cirratulidae gen. sp. 2	SMT	0.02	5.3	0.01	0.07
<i>Flabelligera mundata</i> Gravier, 1907	SDT	0.08	5.3	0.03	0.1
<i>Flabelligera</i> sp.	SDT	0.02	5.3	0.01	0.07
<i>Sclerocheilus antarcticus</i> Ashworth, 1915	BMX	0.05	10.5	0.02	0.08
<i>Ophelina syringopyge</i> (Ehlers, 1901)	BMX	0.1	15.8	0.05	0.1
<i>Capitella</i> sp.	BMX	1.9	89.5	1.7	3.4
<i>Eupraxillella antarctica</i> Hartmann-Schröder and Rosenfeldt, 1989	BSX	0.3	31.6	0.2	0.5
<i>Lumbriclymenella robusta</i> Arwidsson, 1911	BSX	0.7	21.0	0.7	2.9
<i>Rhodine intermedia</i> Arwidsson, 1911	BSX	6.9	89.5	3.5	2.2
<i>Ampharete kerguelensis</i> McIntosh, 1885	SST	0.02	5.3	0.03	0.1
Ampharetinae gen. sp.	SST	0.02	5.3	0.03	0.1
<i>Amphitrite kerguelensis</i> McIntosh, 1876	SST	0.05	10.5	0.04	0.1
<i>Nicolea</i> sp.	SDT	0.02	5.3	0.02	0.1
<i>Pista patriciae</i> Hartmann-Schröder and Rosenfeldt, 1989	SST	0.02	5.3	0.01	0.04
<i>Polycirrus kerguelensis</i> (McIntosh, 1885)	SDT	2.0	78.9	1.5	2.2
<i>Polycirrus insignis</i> Gravier, 1907	SDT	2.0	57.9	1.2	2.2
<i>Proclea</i> sp.	SST	0.05	10.5	0.09	0.3
<i>Thelepus cincinnatus</i> (Fabricius, 1780)	SST	0.1	10.5	0.06	0.2
Amphitritinae gen. sp.	SST	0.08	10.5	0.1	0.4
<i>Terebellides kerguelensis</i> (McIntosh, 1885)	SST	0.02	5.3	0.01	0.04
<i>Trichobranchus glacialis antarcticus</i> Hesse, 1917	SST	0.4	36.8	0.3	0.5
<i>Trichobranchus</i> sp.	SST	0.2	5.3	0.2	0.9
<i>Euchone pallida</i> Ehlers, 1908	FST	0.01	5.3	0.01	0.06
<i>Oriopsis alata</i> (Ehlers, 1897)	FST	4.7	68.4	1.7	2.4
<i>Oriopsis kocki</i> Hartmann-Schröder and Rosenfeldt, 1989	FST	0.5	10.5	1.0	4.1
<i>Oriopsis longipyge</i> Hartmann-Schröder and Rosenfeldt, 1989	FST	0.3	26.3	0.3	0.8
<i>Oriopsis</i> sp.	FST	0.5	36.8	0.5	1.4
<i>Perkinsiana littoralis</i> (Hartman, 1967)	FST	0.05	5.3	0.02	0.09
Sabellinae gen. sp. 1	FST	0.02	5.3	0.01	0.04
Sabellinae gen. sp. 2	FST	0.02	5.3	0.01	0.04
<i>Paralaeospira antarctica</i> (Pixell, 1913)	FST	5.3	15.8	2.0	7.0
Spirorbidae gen. sp.	FST	0.1	5.3	0.05	0.2
Spirorbidae non det.	FST	1.5	63.1	1.8	3.4

CMJ carnivore, motile, jawed; *HMJ* herbivore, motile, jawed; *BMX* burrowing, motile, non-jawed; *CDJ* carnivore, discretely motile, jawed; *SMX* surface deposit feeding, motile, non-jawed; *SDT* surface deposit feeding, discretely motile, tentaculate; *SMT* surface deposit feeding, motile, tentaculate; *BSX* burrowing, sessile, non-jawed; *SST* surface deposit feeding, sessile, tentaculate; *FST* filter feeding, sessile, tentaculate

marginatus ($D = 3.4\%$, $F = 84.2\%$) and *Lumbrineris magalhaensis* ($D = 3.3\%$, $F = 78.9\%$). Other less numerous but still quite frequent species were *Capitella* sp. ($D = 1.9\%$, $F = 89.5\%$), *Polycirrus kerguelensis* ($D = 2.0\%$, $F = 78.9\%$), *Polycirrus insignis* ($D = 2.0\%$, $F = 57.9\%$) and Cirratulidae gen. sp. 1 ($D = 2.1\%$, $F = 52.6\%$). A further dominant species was *Paralaeospira*

antarctica, but the frequency value for this species was low ($D = 5.3\%$, $F = 15.8\%$).

The highest mean densities were found for *B. rhopalophora* (16.9 ind./100 ml) and *N. kerguelensis* (11.0 ind./100 ml). For other species, mean densities were low and did not exceed 4 ind./100 ml, for most of the species being much lower than 1 ind./100 ml (Table 2).

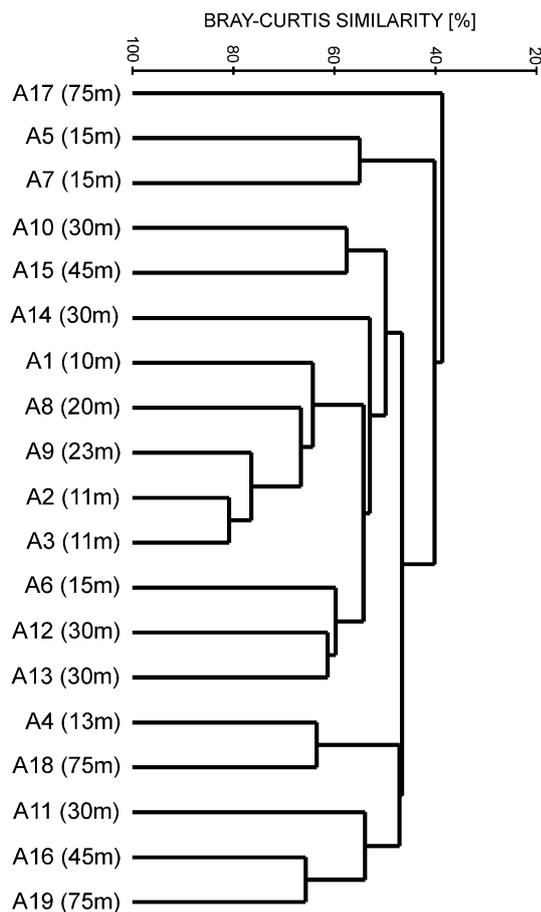


Fig. 3 Dendrogram of samples for the Bray-Curtis similarity, standardized, square root transformed data and group average grouping method

A high diversity of polychaete feeding guilds was observed. The holdfast fauna was strongly dominated by motile macrophagous herbivores but it also has a very high percentage of filter feeders. Polychaetes from ten feeding guilds were found and besides motile, non-jawed surface deposit feeders and sessile, tentaculate surface deposit feeders, all groups were quite numerous in this habitat (Fig. 4).

Regression analyses showed a correlation between the holdfast volume and densities of species and individuals. Both values decrease with increased holdfast volume. There was also a positive correlation between the number of individuals and the holdfast volume. There was no relationship between the number of species and holdfast volume, nor between density and depth (Fig. 5).

Discussion

There is a relatively small number of studies focused on the fauna of Antarctic and Subantarctic macroinvertebrates

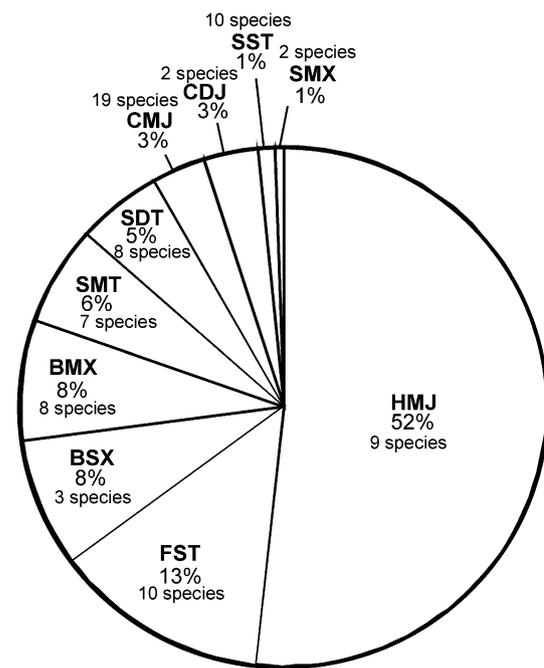


Fig. 4 Dominance structure of feeding guilds on *H. grandifolius* holdfasts according to Fauchald and Jumars (1979) classification. *CMJ* carnivore, motile, jawed; *HMJ* herbivore, motile, jawed; *BMX* burrowing, motile, non-jawed; *CDJ* carnivore, discretely motile, jawed; *SMX* surface deposit feeding, motile, non-jawed; *SDT* surface deposit feeding, discretely motile, tentaculate; *SMT* surface deposit feeding, motile, tentaculate; *BSX* burrowing, sessile, non-jawed; *SST* surface deposit feeding, sessile, tentaculate; *FST* filter feeding, sessile, tentaculate

associated with holdfasts of various macroalgae. Arnaud (1974) found 34 species of polychaetes on 20 holdfasts of *H. grandifolius* from Adélie Land, a relatively small number compared to the results of the present study (78 species). The most frequent and dominant species on Adélie Land was *Harmothoe* sp. followed by *Brania rhopalophora*, *Typosyllis brachychaeta* and *Kefersteinia fauveli*. Another 30 species were found in very small numbers and mostly in single holdfasts. Also, *Macrocystis pyrifer* holdfasts from Kerguelen Islands were dominated by macrophagous, motile species (Arnaud 1974). Twenty-seven species were found on 10 holdfasts. The most numerous and frequent species was *Platynereis magalhaensis*. Other dominant but less frequent species were *Brania rhopalophora* and *Exogone heterosetosa*. Rios et al. (2007) found 43 species of Polychaeta on *Macrocystis pyrifer* holdfasts from the Straits of Magellan. The most abundant species were *Platynereis australis* and *Hermodion magalhaensis*.

Both Arnaud (1974) and Rios et al. (2007) found some polychaetes that were present also on *H. grandifolius* holdfasts in Admiralty Bay (Table 3). The distribution of

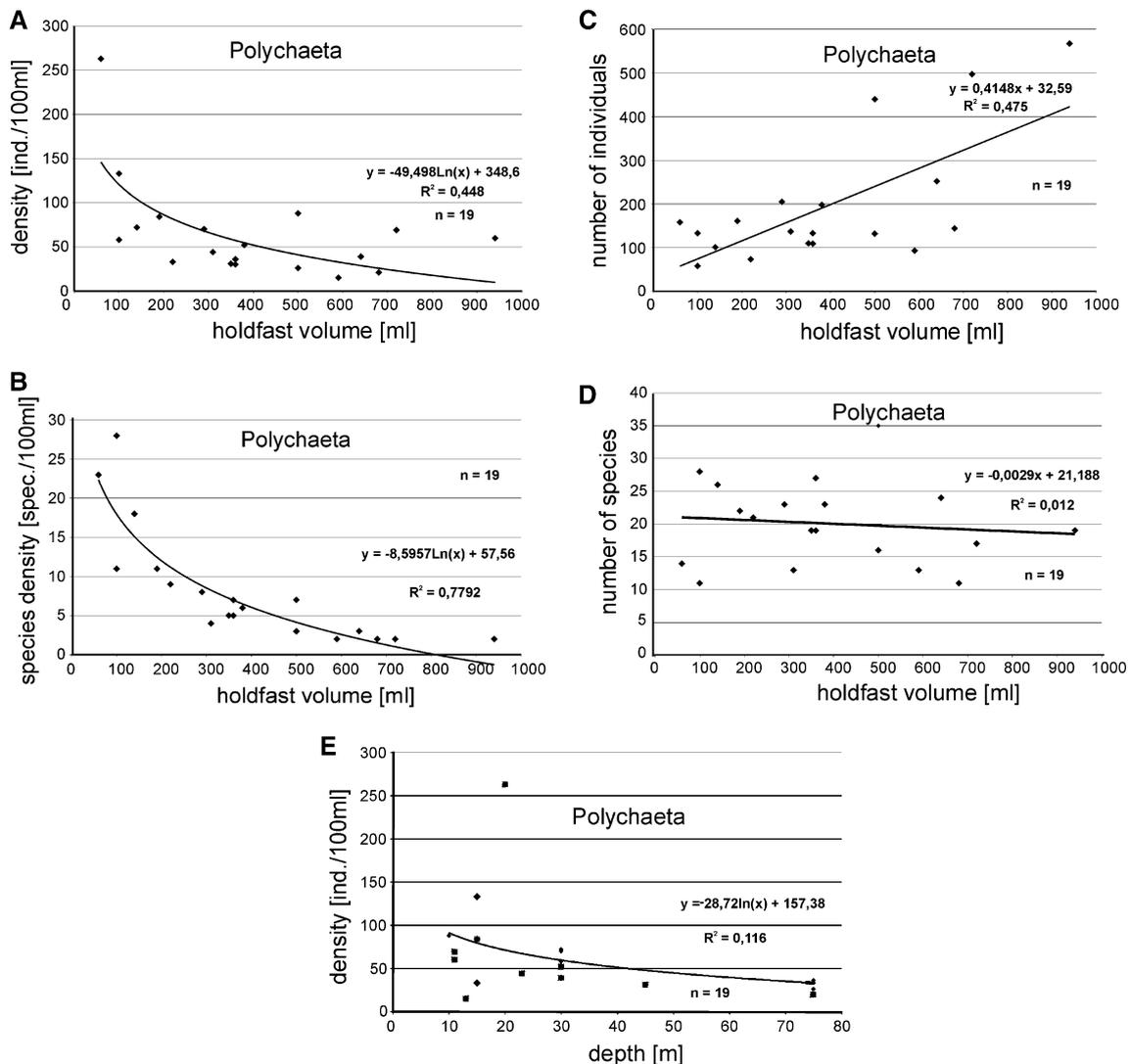


Fig. 5 Relationship between holdfast volume and: individuals density (a), species density (b), number of individuals (c) number of species (d) and relationship between depth and individuals density (e)

some of those species could be associated with drifting thalli and holdfasts of various algae. Smirnov (1982) found 30 polychaete species on floating holdfasts of *M. pyrifera*. The list includes species that were found also on *H. grandifolius* holdfasts in Admiralty Bay and on holdfasts from other Antarctic and Subantarctic locations (Table 3). *Macrocyctis pyrifera* is considered as the main kelp vector of marine benthic faunal dispersion in the Southern Ocean, followed by *Durvillea antarctica* (Edgar 1987; Smith 2002). Polychaetes from the genera *Exogone*, *Typosyllis* and *Nereis* were able to drift on those holdfasts for almost 200 days (Edgar 1987). It was also found that some invertebrates, such as the bivalve *Gaimardia trapesina*, can drift for over 2000 km (Helmuth et al. 1994). However, some other species of macroalgae may also be an important

element of this process. Floating thalli and holdfasts of *H. grandifolius* have been observed (Sicinski J., personal observation) but there are no data on their rafting fauna. The first step in understanding the dispersal processes of fauna associated with rafting holdfasts is the recognition of faunal communities associated with different macroalgae, from different Antarctic sites.

Most of the species that were found in *H. grandifolius* holdfasts were previously reported from Admiralty Bay. However, species that dominated on holdfasts, such as *Brania rhopalophora* and *Neanthes kerguelensis*, were found only in small numbers on soft-bottom habitats and were quite frequent only in shallow-water assemblages mostly in the phytal zone (Sicinski 1986; Sicinski and Janowska 1993; Bromberg et al. 2000; Sicinski 2004). It

Table 3 List of species that were found on *H. grandifolius* holdfasts in Admiralty Bay and on holdfasts of various macroalgae from other Antarctic and Subantarctic areas

	<i>Himantothallus grandifolius</i> Adélie Land	<i>Macrocystis pyrifera</i> Strait of Magellan	<i>Macrocystis pyrifera</i> Macquaire Island	<i>Macrocystis pyrifera</i> Antarctic and Patagonian shelf (floating holdfasts)	<i>Macrocystis pyrifera</i> Morbihan Bay, Kerguelen Islands	<i>Durvillea antarctica</i> Morbihan Bay, Kerguelen Islands
	Arnaud (1974)	Rios et al. (2007)	Edgar (1987)	Smirnov (1982)	Arnaud (1974)	Arnaud (1974)
<i>Neanthes kerguelensis</i>		+		+		
<i>Brania rhopalophora</i>	+		+	+	+	
<i>Exogone heterosetosa</i>	+		+	+	+	
<i>Genetyllis polyphylla</i>				+	+	
<i>Eteone sculpia</i>		+		+		
<i>Eulalia picta</i>				+		
<i>Lumbrineris magalhaensis</i>		+		+		
<i>Leitoscoloplos kerguelensis</i>		+			+	
<i>Scoloplos marginatus</i>	+			+		
<i>Spiopchanes tcherniai</i>	+					
<i>Polycirrus insignis</i>	+			+		
<i>Thelepus cincinnatus</i>	+					
<i>Oriopsis alata</i>					+	+

seems that these species are strongly associated with holdfast and are present also on soft bottom in the Admiralty Bay phytal zone. On the other hand, some species like *Oriopsis alata* and *Polycirrus insignis*, previously not reported from Admiralty Bay (Sicinski 2000, 2004; Petti et al. 2006; Pabis and Sicinski 2010), were found in this habitat in relatively large numbers. Both species were already reported from holdfasts (Table 3) but only single individuals had been found (Arnaud 1974). Another three species: *Euphrosine armadilloides*, *Sclerocheilus antarcticus* and *Oriopsis kocki* were also recorded in Admiralty Bay for the first time.

The species composition and dominance structure of the holdfast polychaete community were completely different from Admiralty Bay soft-bottom communities that had been analysed in earlier studies, including those from a similar depth range (Sicinski and Janowska 1993; Sicinski 2004; Petti et al. 2006; Pabis and Sicinski 2010). Those differences were especially distinct on the sandy bottom of the central basin in the phytal zone (the same bottom area as for the holdfasts) (Sicinski and Janowska 1993). Only one species—*Rhodine intermedia*—was an important component of both communities. The most common and abundant infaunal species in Admiralty Bay are the *Leitoscoloplos kerguelensis*, *Levinsenia gracilis*, *Ophelina syringopyge*, *Rhodine intermedia* and *Tharyx cincinnatus* (Sicinski 1986, 2004; Petti et al. 2006). These species are also common and abundant, especially in the shallow areas, at other Antarctic sites such as Arthur Harbour (Lowry

1975), Signy Island (Hardy 1972), the Davis Sea (Gruzov et al. 1967), Anvers Island (Richardson and Hedgpeth 1977) and Terra Nova Bay (Gambi et al. 1994). Also, the most important epibenthic polychaete species found on soft bottoms in Admiralty Bay are completely different from those on holdfasts (Pabis and Sicinski 2010).

Another important feature is that the polychaete species richness and diversity at those sites were low in shallow areas. These patterns observed in Antarctic waters may be due to ice disturbance, which is stronger in the shallow water (Smale 2008). However, there was a clear difference in the species richness between the holdfast assemblages and soft-bottom infaunal communities in Admiralty Bay. On the soft bottom in the phytal zone of Admiralty Bay central basin (4–30 m), only 25 species were found (Sicinski and Janowska 1993). In most other infaunal polychaete assemblages distinguished in Admiralty Bay, the number of species was much lower, varying from 9 to 35. Only in two assemblages it was higher: fifty-six species were found in the “*Tharyx cincinnatus* assemblage” (Ezcurra Inlet at 45–165 m), while eighty-one were found in the “*Tauberia gracilis* assemblage” (Central basin at 35–150 m), which is associated with heterogenous sediments that can also be treated as a comparatively more complex habitat (Sicinski 2004). It is also notable that the total number of polychaete species found in all earlier studies from Admiralty Bay, in different habitats, is 162 (in samples taken with different sampling gears—Van Veen grab, Kangas sampler, trawls, dredges, epibenthic sledge,

various corers) while in the holdfast habitat alone nearly 80 species were found. This is even more striking when the scale of the holdfast sampling area is considered in relation to surface of the whole bay (Fig. 2).

It has been pointed out that depth of 35–40 m delimits a significant zoocenological boundary for benthos in the central part of the Bay (Jazdzewski et al. 1986; Jazdzewski and Sicinski 1993). Similar observations have been made in Martel Inlet with 20–25 m depth as a limit associated with stronger ice disturbance in the shallows (Nonato et al. 2000). This boundary seems to be absent in the *H. grandifolius* holdfast polychaete community. Holdfasts constituted one group in the cluster analysis. No partitioning related to depth was observed for holdfasts compared with earlier studies on soft-bottom faunas. Holdfasts provide a shelter for invertebrates especially in shallow water, which may be why there was no depth-partitioning of the holdfast polychaete assemblage. Holdfasts may also be partially filled with sediment, providing a habitat for infauna. This ability for accumulation of sediment and detritus is a result of the complexity of holdfast labyrinths and can increase the species richness of fauna associated with this habitat (Smith 1996). It was observed that *H. grandifolius* can grow in the ice-disturbed areas. It grows on relatively small stones and can be pushed aside and thus avoids destruction (Klöser et al. 1994). Holdfasts in polar regions can provide a shelter and are probably less susceptible to destruction than other parts of the kelp (Włodarska-Kowalczyk et al. 2009). It has been observed that diversity on holdfasts can be higher when kelp is exposed to strong mechanical stresses such as wave action (Schultze et al. 1990).

In a study from temperate Australia, depth was an important factor influencing the distribution and composition of kelp-associated fauna (Coleman et al. 2007). However, most of the Antarctic polychaetes are eurybathic so factors other than depth (habitat type, habitat complexity, organic matter content, sediment type, iceberg scour) are the most important influences on the vertical distribution. While depth-partitioning has been observed in soft-bottom communities, no partitioning was found in the specific habitat of holdfasts (not dependent on the sediment type and protected from ice disturbance) and with a eurybathic group of invertebrates as the subject of study. Coleman et al. (2007) stressed also that contrary patterns may occur as a result of biogeographic variation between studies.

It has been pointed out that complex habitats are characterized by many rare species and few dominants (Hughes 1984; Morgado and Tanaka 2001), including on kelp holdfasts (Rios et al. 2007). This may be a result of recruitment patterns (Hughes 1984). Holdfasts can be treated as islands. Invertebrates can immigrate to or

emigrate from these islands. They may also demonstrate the founder effect, as has already observed for peracarid crustaceans (Thiel and Vasquez 2000). Some species can be very abundant in some holdfasts and absent in others. It was further suggested for peracarids that reproduction rates may sometimes exceed the rate of migration between the holdfasts (Thiel and Vasquez 2000). A similar situation was observed for polychaetes on *H. grandifolius* holdfasts in Admiralty Bay. Some species like *Paralaeospira antarctica*, *Tharyx epitoca*, *Tharyx cincinnatus*, *Genetyllis polyphylla* or *Lumbriclymenella robusta* show relatively high dominance and low or very low frequency.

Migrations and the island character of holdfasts might also explain why no correlation was found between the number of species and holdfast volume. Some holdfasts may receive only single colonizers while other may completely lack some species, and this accidental process is not related to factors such as depth or holdfast volume. This process is also similar to island colonization. For the animals that colonize a holdfast, it may be more favourable to remain on the “island” than to move to another one (Thiel and Vasquez 2000). However, on *Lessonia trabeculata* Villouta et Santelices, *Lessonia nigrescens* Bory de Saint-Vincent and *Macrocystis integrifolia* Bory de Saint-Vincent holdfasts in Chile, the number of invertebrate species was strongly positively correlated with increasing holdfast volume (Thiel and Vasquez 2000). The same situation was observed on *Macrocystis pyrifera* holdfasts from southern Chile (Ojeda and Santelices 1984). The number of individuals in this study increased with increasing holdfast volume (Fig. 5), confirming earlier observations of this pattern (Ojeda and Santelices 1984; Thiel and Vasquez 2000; Anderson et al. 2005). Equally, different and even contrary results can be found depending on the taxonomic group (Anderson et al. 2005).

A further feature of the polychaete community associated with holdfasts in Admiralty Bay is the decrease in the density of individuals and of species with increasing holdfast volume. This may result from recruitment and colonization processes. Holdfast colonization rate is probably high in its initial stage and decreases with time. It was observed that artificial kelp holdfasts are colonized by the typical fauna within only few days (Norderhaug et al. 2002). Small holdfasts can be effectively colonized in a relatively short time. Thus, density of polychaetes may be higher in smaller holdfasts than in larger ones. However, the number of individuals is higher in the larger holdfasts (Fig. 5). Probably, their immigration or/and reproduction cannot compensate for the larger holdfast volume. In consequence, the density remains lower than in smaller holdfasts.

It was observed that the migration between holdfasts may be restricted, and most of the species that colonized the holdfast do not migrate to another one (Thiel and

Vasquez 2000). If the number of species inhabiting holdfast is not related to the holdfast volume or depth, then the species number on each holdfast may be more or less similar. That would explain why the species density (number of species/100 ml) is negatively correlated to holdfast volume.

A difference in functional-group composition was observed between the polychaete fauna associated with holdfast and that associated with soft bottoms. The presence of microphagous detritus feeders: burrowers and surface deposit feeders is typical for the soft bottom (Gallardo et al. 1988; Gambi and Busotti 1999; San Martin et al. 2000; Sicinski 2004). A dominance of macrophagous motile polychaetes, herbivores or predators had already been observed on macroalgal holdfasts and thalli in the Antarctic as well as in other regions of the world (Arnaud 1974; Rios et al. 2007; Fraschetti et al. 2002). In the present study, a high number of filter feeders were also observed. Holdfasts are good substratum for attachment for these polychaetes. On various algae, Antoniadou and Chintiroglou (2006) found carnivorous and herbivorous species together with filter feeders as dominating groups. The important feature is that, on the soft bottom, simplification of functional-group composition was observed with a high dominance of microphagous species, mostly from four guilds of burrowing (BMX, BSX) and motile surface deposit feeding (SMT or SMX) polychaetes (Sicinski 2004). It was especially apparent in shallow areas, while on holdfasts, despite the high dominance of motile herbivores, almost all other feeding guilds were represented in significant proportions. This constitution could be directly and indirectly due to the complexity of this habitat, including the ability for accumulation of sediment in the branches of holdfasts. The number and diversity of ways of exploiting environmental resources is believed to be higher in more complex habitats (Tews et al. 2004).

Conclusions

1. The number of species on *H. grandifolius* holdfasts is much higher than that in infaunal shallow sublittoral polychaete communities. It is probable that the complex structure of holdfasts provides good shelter and protection from disturbance, especially in shallow-water bottom areas.
2. The polychaete community associated with *H. grandifolius* holdfasts is uniform in terms of its composition of dominant species and dominance structure over the whole depth range investigated.
3. The holdfast polychaete community differs strongly from previously studied polychaete communities associated with soft bottoms, mainly in terms of species

composition and feeding-guild structure. It is dominated by jawed motile herbivores and sessile tentaculate filter feeders.

4. The diversity of polychaete feeding guilds in the holdfast community was higher than that found in soft-bottom communities.

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