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Necrophagous invertebrates of the Admiralty Bay of King George Island (South Shetland Islands, Antarctica)*

ABSTRACT: In 1977 and 1980 rich materials of necrophagous invertebrates were collected in the Admiralty Bay of King George Island. The collecting was carried out in 9 stations differing with respect to their habitat conditions. The stations were established at depths ranging from 5 to 90 m. In baited traps placed in the stations 295074 specimens of various animals belonging to almost 100 taxa were caught. It was found that 23 species out of the above mentioned taxa were necrophagous, and 10 further species were suspected of necrophagy. On the basis of their specific composition and domination structure the summer and winter assemblages of necrophagous invertebrates were described and compared with each other. An analysis of spatial and seasonal changes in the structure and abundance of these assemblages was carried out, and the habitat preferences of particular species as well as a list of species displaying permanent or seasonal necrophagy were determinted. Three forms of the competitive community of necrophagous invertebrates were distinguished.

Key words: Antarctica, benthos, necrophagous invertebrates.

1. Introduction

It is commonly accepted that the ecosystem of the ocean surrounding Antarctica is less complex, than the ecosystems of other oceanic areas. The number of trophic levels is lower and food chains are shorter. In

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Antarctic waters a patchy distribution of organisms is very pronounced. The areas with considerable density of biomass occur in the zones of upwellings, cyclonic whirling of water and shelves; in comparison with the coastal zone open oceanic areas situated far from the continent and islands are deserts. Rakusa-Suszczewski (1980a) is of the opinion that this zone is the main centre of the circulation of matter and energy flow in the ecosystem. Here not only the biogenic compounds are upwelled from the depths of the ocean, but also the organic matter is carried away from the sea onto the shore and it is also washed from the land to the sea. These processes determine the primary and secondary production of the ocean.

From the conceptual model of Rakusa-Suszczewski (1980b) presenting main trophic relations conditioning the circulation of matter and energy flow in the coastal part of the Antarctic ecosystem it follows that benthic organisms also play a significant role in the system. Particularly strong development of benthos takes place in the continental shelf. The abundance and growth rate of bottom communities are mainly determined by the amount of the inflowing organic matter. In cold waters, where temperature fluctuations are minimal, food is the main limiting factor for the development of benthos. Necrophagous animals, which are adapted to feed on carrion, have the possibility to use a rich source of food present in the sea bottom in every season. So far only few complex studies were devoted to the Antarctic necrophagous animals. They have been carried out only at the coast of Adelie Land and in the vicinity of the Japanese station Syowa (East Antarctica) and in the region of Kerguelen Islands (Arnaud 1964, 1970, 1974; Hoshiai 1968). Certain species of Antarctic necrophagous invertebrates have been more extensively treated in autecological works of Dearborn (1967), Pearse (1969), Bregazzi (1972a), Dearborn (1977), Rakusa-Suszczewski (1982) and Fratt and Dearborn (1984). So far, however, the interrelations between necrophagous species which occur in common, forming specific structures and functional systems, have been usually ignored.

It is often suggested (e.g. by Rakusa-Suszczewski 1980a, 1980b, 1980c) that the extinction of whales has caused the overproduction of krill (*Euphausia superba*). Part of the overproduction is consumed by rapidly reproducing seals and penguins, but it seems that the amount of krill which dies in a natural way and drops dead to the sea bottom has also increased. Taking into account the fact that the processes of decomposition in cold Antarctic water are slow (Rakusa-Suszczewski and Zdanowski 1980), it is feasible to presume that the excess of organic matter is used as food by benthic animals. As a result, the abundance and biomass of their communities may increase. To answer the question how this would affect the overall circulation of matter and energy in the

Antarctic ecosystem, the specific composition and structure of necrophagous assemblages as well as their seasonal variability and differentiation influenced by abiotic factors have first to be determined and this was the aim of the present study on the necrophagous invertebrates inhabiting the bottom of the Admiralty Bay.

2. Study area

The Admiralty Bay, from where the samples of necrophagous animals were collected, is the largest bay of the King George Island, and, also, the largest one in the South Shetland archipelago. It has the character of a fiord with a ramified system of bays (Fig. 1). The surface area of the Admiralty Bay is 120 km^2 (Jażdżewski et. al. in 1986 and the length of its varied shoreline amounts to 85 km (Rakusa-Suszczewski 1980c). The maximum depth of the bay is abt. 600 m (Furmańczyk and Marsz 1980). Characteristic sills and walls which occur in the bottom

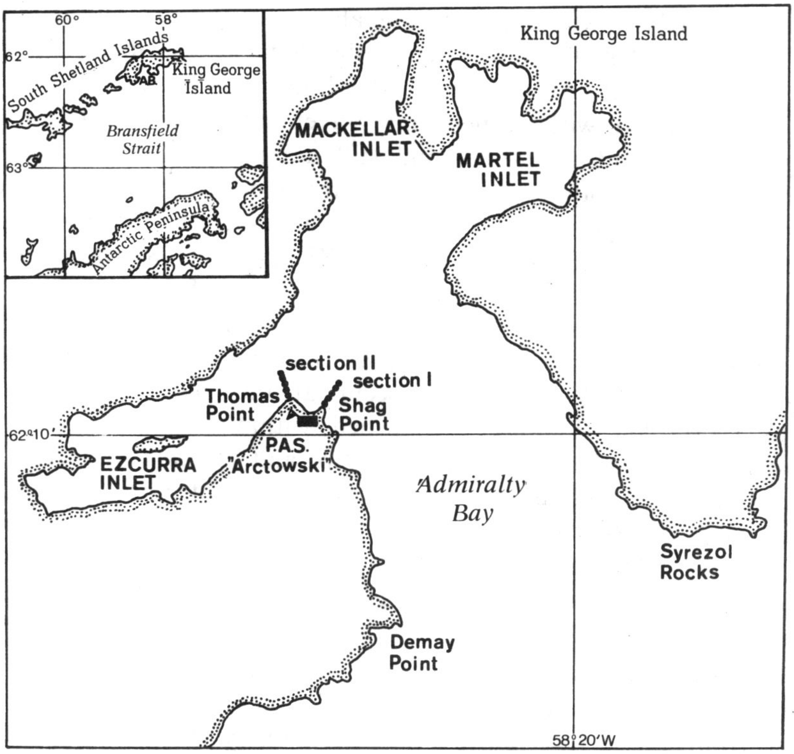

Fig. 1. Study area.

cause whirling of cold, highly saline water masses flowing into the bay from the Bransfield Strait (Rakusa-Suszczewski 1980c). Detailed information on climatic conditions of the region of the "H. Arctowski" Station and extensive hydrological characteristics of the Admiralty Bay are to be found in the papers by Dera (1979), Nowosielski (1980), Presler (1980), Pruszak (1980), Pęcherzewski (1980a, 1980b), Rakusa-Suszczewski (1980c), Samp (1980), Zubek (1980) and Szafrański and Lipski (1982).

For the study of the necrophagous invertebrates two regions of the Admiralty Bay were chosen (Fig. 1): one of them at the Shag Point, the other at Thomas Point. They strongly differ from each other with respect to bottom structure, sediments, influence of tidal currents, waves and other environmental factors. Within the boundaries of each investigated region, sampling stations were situated at depths of 5, 15, 30, 60 and 90 m on a section established along a straight line.

At the Shag Point, region, where section I was established, the bottom slopes moderately down to a depth of about 60 m and only at a distance of about 400—500 m from the shore falls down to the main, deep trough of the bay (Fig. 2a). At the shore, the bottom is rocky. At a depth of 15 m it is covered with stones and gravel, and deeper (30 and 60 m) with gravel and mud. At 90 m mud still dominates and single stones are scattered over the bottom. At Shag Pt. there occur abundant populations of algae, whose specific composition changes with increase in depth. Zieliński (1981) and Furmańczyk and Zieliński (1982) have found four algal communities. Stations A and B of section I are adjacent to the community of *Leptosomia simplex, Ascoseira mirabilis, Hildebrandia lecannellieri, Phycodrys antarctica, Desmarestia menziesii, Desmarestia* sp. and *Himantothallus grandifolius*, which occur at the depths down to 15 m. Stations C, D and E were estabilished within an algal community of *Himantothallus grandifolius, Desmarestia* sp. and *Plocamium coccineum*, and station E was situated at the limit of the range of this community. The coastal zone of the Shag Point region is exposed to the influence of strong waving and the abrasive action of the pack-ice. In stations D and E pronounced influence of vertical tidal currents and sporadic furrowing of the bottom by icebergs occurred.

Section II was established at the opening of the Ezcurra Inlet at Thomas Point. The bottom slopes sharply there: at a distance of about 300 m from the coast the depth was already 100 m (Fig. 2b). The coastal areas of the bottom were covered with stones. At a depth of 15 m the bottom is covered with stones, gravel and some mud; at a depth of 30 m it changes into gravel and mud. Still deeper the sediments are dominated by mud, with scattered pieces of rock. In the tidal zone and slightly deeper, algal community occurs, composed of *Monostroma hariotti*,

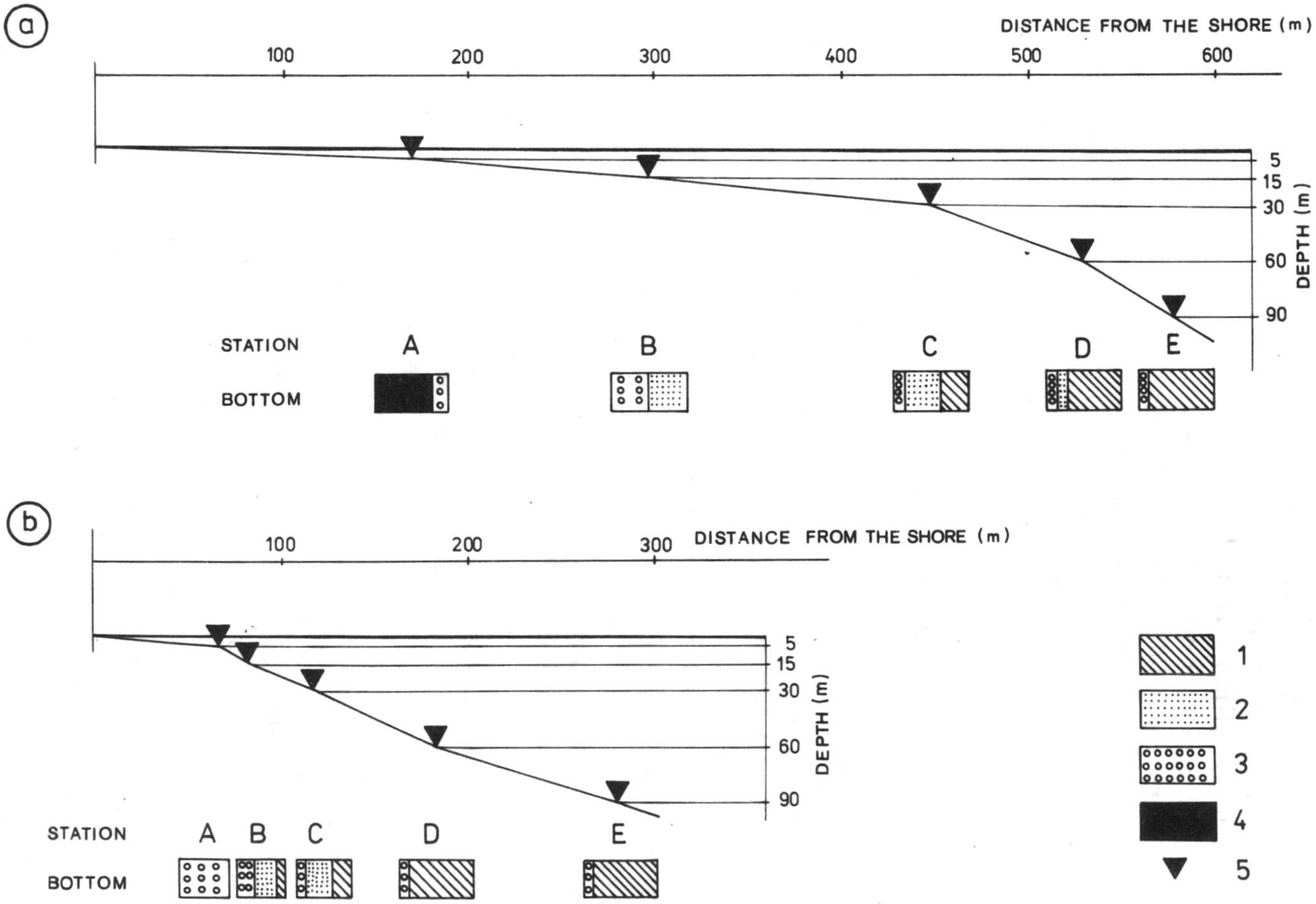

Fig. 2. Profiles of bottom in the chosen sections; a — section I at Shag Point; b — section II at Thomas Point; kind of bottom: 1 — mud, 2 — gravel, 3 — stones, 4 — rocks; 5 — sampling stations.

Adenocystis utricularis, Iridaea obovata and *Leptosomia simplex*. Still deeper, down to 90 m, in much lower density than in section I, algae from the community of *Himantothallus grandifolius, Desmarestia* sp., *Plocamium coccineum* occur (Zieliński 1981, Furmańczyk and Zieliński 1982, own data). In the region of section II (especially in stations D and E) very strong influence of tidal currents and wave action in the coastal zone was noted. In summer pack-ice frequently concentrates and moves at the coast, whereas in winter the freezing of the sea is accompanied by the appearance of characteristic hummocked ice.

3. Materials and methods

The materials were collected in 1977 and 1980, during the I-st and IV-th Polish Antarctic Expeditions to the "Arctowski" Station. In 1977 the samples were taken in September and October from under a compact ice-cover 0.5 m thick, i.e. in conditions typical of winter and that is why this sampling period was termed a winter one. In 1980 the necrophagous animals were collected in January and February and, consequently, the period was named a summer one.

Animals were caught using traps which were put on the selected stations (Fig. 2). The character of the bottom in these places was determined with the Van Veen bottom sampler.

In 1977 samplings were conducted simultaneously first in all stations of section I, and then, also simultaneously, in all stations of section II, whereas in 1980 they were carried out simultaneously in all stations of both sections. Traps used in 19777 had the form of a cylinder. They were 100 cm in length, and 50 cm in diameter. Both ends of the cylinder were truncated cones whose narrower ends were inside the cylinder. The diameter of interior, narrower ends of the cones was 15 cm. One of the cones was movable that enabled the removing of animals collected in the trap. The mesh diameter of the net covering traps was 4 mm. Traps used in 1980 (Fig. 3) were cubicoids. Their length was 100 cm, and their width and height 40 cm each. The internal opening of each of two truncated pyramids that were directed to the inside of the cubicoid had 13 cm in diameter. The mesh diameter of the net of these traps was 2 mm. In 1977 the materials were collected through the holes done in the ice-cover. In the summer of 1980 they were collected from the fishing-boat "Dziunia". To avoid changes of the position of traps (being precisely the same as those in 1977) they were connected with a rope the length of which was adjusted in the way ensuring that the traps were put on the desired depths. The set of the traps was fixed at one end to the shore, and to a rope joining a heavy anchor to a buoy floating on the sea surface. The meat of fishes from the genus *Notothenia* or of seals was used as a bait to attract necrophagous animals. A single portion of meat for each trap weighed about 0.5—1.0 kg. Traps were pulled up and lowered usually every second day. They were repeatedly lowered with a new bait immediately after removing of captured animals. In this way 162 samples were collected from all stations of section I and II (Tab. I). Due to technical difficulties, in winter of 1977 no samples were collected from the station E of section I (depth 90 m) and from the station A of section II (depth 5 m), whereas in summer 1980 from station A of section II. In 1980, before the proper sampling of necrophagous animals, the same traps were put in all of the investigated stations (including station IIA) but the bait was not put into the traps. In this way, in the course of 9 days of fishing 25 samples containing animals were obtained; the animals were trapped accidentally without being attracted by carrion. The above preliminary fishing was aimed at supplying the author with comparative material, which was used to exclude accidental species from the list of necrophagous animals.

Fig. 3. The author with a trap used to collect necrophagous animals in summer of 1980.

All captured animals were preserved in a 4% buffered formalin solution. After segregation the animals were put into a 75% ethanol. Part of the material was determined owing to the kind help of Polish and foreign specialists. The following animal groups were determined by: Prof. K. Jażdżewski and E. Presler, M.Sc. (University of Łódź — UŁ) — *Amphipoda*; T. Orman-Krynicka, M.Sc. and A. Szymczak, M.Sc. (UŁ) — *Isopoda*; Dr. P. M. Arnaud (Station marine d'Endoume, Marseille, France) — *Mollusca*. The remaining animals were determined by the author himself and the correctness of the determination of *Pycnogonida* was verified by Dr. F. Arnaud (Station marine d'Endoume, Marseille, France), whereas the verification of *Echinodermata* determinations was due to the scientists of Museum National d'Historie Naturelle in Paris — Prof. G. Cherbonnier and Dr. A. Guille, who have kindly put at author's disposal typical materials for comparative purposes.

A preliminary analysis of the specific composition of animals caught in baited traps showed that not all of them may be included among necrophagous animals. The traps were not sufficiently selective devices of sampling, because part of organisms happened to be trapped accidentally, either due to passive displacement — e.g. as a result of being carried to the trap by water currents or of being torn away from the bottom while the trap was pulled up from the bottom, or due to active movement — e.g. as a result of active moving in pursuit of prey or searching for a hiding place, etc. Proper necrophagous animals were separated from all species caught using the following criteria:

1. Direct observation of animals' feeding on carrion (in the laboratory and in natural environment) or of its feeding on other food types.
2. Literature data which specify the way of feeding and the food type.
3. Analysis of stomach contents of animals caught in traps.
4. Analysis of data obtained from the series of catches using traps without baits ("blank test"). Material obtained in this way from the same stations sampled later with baited traps was used for comparison.

The abundance of particular species caught during 24 hours (WL_0) in the non-baited trap was compared with the abundance of this species collected in the same time (WL) in the baited trap. If the latter value was higher at any of the investigated stations it was assumed that the attractive influence of the bait did occur.

5. Estimation of the frequency of species. Since the frequency of a species in samples is influenced by its abundance in the biocenosis and by the low selectivity of the traps, this criterion cannot be considered as a decisive one. Analogically to the scale of the species stability in the biocenosis which was based on frequency (Tichler 1949, after Trojan 1975), the species whose frequency (F) was less than 25% were considered as possibly accidentally caught in the baited traps.

Having selected from the materials a group of species of necrophagous invertebrates (see chapter 4.1), their biomass was measured. The wet alcoholic

Table I

Number of samples and time of sampling of necrophagous invertebrates collected in chosen sections of the Admiralty Bay in 1977 and 1980

Station Number of samples and time of sampling	SECTION I					SECTION II				
	A	B	C	D	E	A	B	C	D	E
WINTER 1977										
Number of samples	8	13	12	14		0	2	6	8	8
Total sampling time in days (24 h)	21	40	41	49	0	0	4	17	20	16
Mean time of one sampling in days (24h)	2.63	3.08	3.42	3.50	0	0	2.00	2.83	2.50	2.00
SUMMER 1980										
Number of samples	11	8	11	11	11	0	9	10	10	10
Total sampling time in days (24h)	29	22	29	29	29	0	22	24	24	24
Mean time of one sampling in days (24h)	2.64	2.75	2.64	2.64	2.64	0	2.44	2.40	2.40	2.40

weight of animals collected in 1980 was estimated by weighing all individuals from a given species present in single samples. The measurements were done to the nearest 0.1 g for small animals (*Amphipoda* and *Cirolana* cf. *oculata*) and to the nearest 0.5 g for all the others. Before weighing, the animals were dried on blotting paper until wet spots were not recorded. Estimation of the biomass of necrophagous animals collected in winter of 1977 was impossible, because a large part of the material after determination was left in cooperating laboratories and some animals were damaged or dried during the determination procedure. To be sure that the collected material was a representative one curves were drawn, which illustrate the relation between the number of collected species and time of catching with the trap. These curves proved that the total time of sampling at each station was long enough to regard the material as a representative one.

To characterize the assemblages of necrophagous invertebrates and to make proper comparisons the following indices and calculations were applied:

1. Frequency (F)

It was calculated from the ratio $F = \frac{n_a}{N} \cdot 100$, where "n" — number of samples with species "a", "N" — number of samples in a given series. The frequency was expressed in percentages.

2. Daily abundance index (WL)

It was calculated by dividing the number of all specimens of particular species caught in a given station by the total time of catching. The chosen unit of time was a 24 hours period. To avoid values below 1 the quotient was multiplied by 100.

3. Daily biomass index (WM)

It was calculated by dividing the wet weight of all specimens of particular species caught at a given station by the total time of catching expressed in days (24 h) and then multiplying the quotient by 100.

4. Index of the dominance in abundance (D_{WL})

It was calculated from the equation $D_{WL_i} = \frac{WL_i}{\sum\limits_{1\to i} WL} \cdot 100$; this index expresses the percentage share of the abundance of a given species "i" (expressed as daily abundance index — WL_i) in the total abundance of the assemblage expressed as a sum of daily abundance indices of all species of the assemblage — $\sum\limits_{1\to i} WL$.

5. Index of the dominance in biomass (D_{WM})

It was calculated quite similarly to the previous index from the equation

$$D_{WM_i} = \frac{WM_i}{\sum\limits_{1\to i} WM} \cdot 100.$$

6. Index of species' role in the structure of an assemblage (WZD)

The range of the biomass of specimens of various species is enormous hence the dominance structures of assemblages based on biomass significantly differ from the dominance structures of assemblages based on abundance. One should consider that despite very low abundance large animals may be more important in an assemblage than very abundant but small animals of other species because those of the former species may consume more carrion than the animals of the latter species. Considering this relation an index of species' role is proposed which is calculated from the equation

$$WZD = 4 + \log (D_{WL} \cdot D_{WM})$$

where "D_{WL}" and "D_{WM}" are the above explained indices, both calculated for the same species and for the same assemblages.

In order to avoid the enormously wide range of the values obtained there were taken the common logarithms of these products. Because the indices D_{WL} and D_{WM} were calculated up to the second place following the decimal point, their product, in the extreme case, may amount to 0.0001; since the common logarithm of this value is -4, to avoid further calculations on negative numbers, all values were "shifted" by adding 4 to them.

The calculation of such indices of species' role in assemblages allowed to determine the dominance structure of particular assemblage based on this index. It was assumed in this case that term "dominant" refers to those species of an assemblage for which the value of $\log(D_{WL} \cdot D_{WM})$ amounted to zero or more.

7. Assemblage diversity index (d) according to Margalef (1958) after Odum (1982) calculated from the equation

$$d = \frac{s-1}{\ln \Sigma WL}$$

where "s" is the number of necrophagous species in an assemblage. This diversity is related to the sum of daily abundance indices of all species of the assemblage; in this way it is related to a time unit.

8. Shannon-Weaver's diversity index (H')

The values of this index were calculated for particular assemblages from the equation

$$H' = -\sum \frac{n_i}{N} \cdot \ln \cdot \left(\frac{n_i}{N}\right) \quad \text{(Odum 1982)}$$

where "n_i", as a coefficient of significance of species in an assemblage, corresponds in our calculations to "WL_i" and "N" corresponds to the sum of these coefficients of significance of all species in the assemblage ($N = \sum_{1 \to i} WL_i$).

9. To determine similarities between particular assemblages of necrophagous invertebrates (or between stations) and also cenological similarities between species composing these assemblages, the dendrite method of the collection ordering and natural dividing of the dendrites was used (Florek et al. 1951) and finally a synthetic diagram was made according to the method proposed by Romaniszyn (1970). The similarities and distances between the compared elements of the collection were calculated from the equations given by Marczewski and Steinhaus (1959) and discussed by Romaniszyn (1970).
The equation for similarity is

$$s = \frac{w}{a + b - w}$$

where "a" and "b" stand for elements of compared collections and "w" for elements common for both collections.
The equation for distance was

$$r = 1 - s$$

and this value was expressed in per cent.

4. Results

4.1. List of necrophagous invertebrates of the Admiralty Bay

The total number of animals collected in baited traps amounted to 295074 specimens. Moreover in the traps devoid of bait 6008 specimens of various animals were caught. The criteria discussed in the previous chapter allowed to select from nearly 100 taxa the list of the following 23 necrophagous invertebrate species:

Nemertini
1. *Parborlasia corrugatus* (McIntosh, 1887)

Gastropoda

2. *Chlanidota elongata* (Lamy, 1910)
3. *Harpovoluta charcoti* (Lamy, 1910)
4. *Neobuccinum eatoni* (Smith, 1875)

Isopoda

5. *Cirolana* cf. *oculata* Vanhöffen, 1914
6. *Glyptonotus antarcticus* Eights, 1833

Amphipoda

7. *Cheirimedon femoratus* (Pfeffer, 1888)
8. *Hippomedon kergueleni* (Miers, 1875)
9. *Orchomene plebs* (Hurley, 1965)
10. *Orchomene rotundifrons* (K. H. Barnard, 1932)
11. *Waldeckia obesa* (Chevreux, 1905)

Asteroidea

12. *Cuenotaster involutus* (Koehler, 1912)
13. *Diplasterias brucei* (Koehler, 1908)
14. *Labidiaster annulatus* Sladen, 1889
15. *Lysasterias digitata* Clark, 1962
16. *Lysasterias hemiora* Fisher, 1940
17. *Lysasterias perrieri* (Studer, 1885)
18. *Neosmilaster georgianus* (Studer, 1885)
19. *Odontaster validus* Koehler, 1906
20. *Perknaster antarcticus* (Koehler, 1906)
21. *Porania antarctica glabra* Sladen, 1889
22. *Psilaster charcoti* (Koehler, 1906)

Ophiuroidea

23. *Ophionotus victoriae* Bell, 1902

Since in the case of some other species the result of the analysis based on the criteria mentioned in the preceding chapter was not univocal, or differed from the literature data, it was decided to distinguish an additional group of species suspected of necrophagy. The group included: *Gastropoda* — *Marseniopsis mollis* (Smith, 1902); *Isopoda* — *Cirolana* cf. *albinota* Vanhöffen, 1914; *Serolis polita* Pfeffer, 1887; *Spinoserolis beddardi* (Calman, 1920); *Amphipoda* — *Bovallia gigantea* Pfeffer, 1888; *Eurymera monticulosa* Pfeffer, 1888; *Asteroidea* — *Cryptasterias turqueti* (Koehler, 1906); *Granaster nutrix* (Studer, 1885); *Ophiuroidea* — *Amphiophiura gibbosa* Mortensen, 1936; *Ophiurolepis martensi* (Studer, 1885).

The remaining species belonging to 74 taxa caught with traps were excluded from further analysis since it was assumed that their presence in the samples was accidental.

4.2. Necrophagous invertebrates as a competitive community

4.2.1. Characteristics and comparison of the investigated assemblages of necrophagous invertebrates

Necrophagous invertebrates living in the Admiralty Bay swarm at carrion lying on the bottom and form characteristic assemblages. Depending on the place of their occurrence and on the season of the year these assemblages differ in their species composition and their dominance structure. This follows from Figs. 4, 5, 6 and 7, in which there are presented data concerning the participation of particular species in dominance structures of abundance, biomass and species' role in an assemblage structure. Due to the lack of data concerning the biomass of invertebrates collected in winter, winter assemblages (Figs. 5 and 7) were characterized only on the basis of the D_{WL} value, whereas summer assemblages (Figs. 4 and 6) on the basis of the D_{WL}, D_{WM} and WZD values. For the sake of clarity the sequence of species in the diagrams corresponds to their cenological similarities obtained by the dendrite ordering method.

Along within characteristic composition and dominance structure, particular assemblages of necrophagous invertebrates are characterized by their abundance and biomass. Considering the abundance values of assemblages of necrophagous invertebrates in stations of section I (Fig. 8a) one can see that in winter the abundance was highest at a depth of 5 m and decreased down to 30 m, and then increased in the next station D. This trend was observed also in summer, except for the fact that the lowest abundance value was recorded then at a depth of 60 m. From the comparison of the curves of summer and winter variability of the abundance it follows that the abundances in shallower stations, i.e. 5, 15 and 30 m were higher in summer, whereas in station D (60 m) it was higher in winter.

The biomass variability curve for summer assemblages of the section I (Fig. 8a) lowers from station A down to station B (depth 15 m), reaching there its lowest value, and then raises to stabilize at a level similar for stations D and E.

The biomass variability curve differs from the abundance variability curve; it is obvious bearing in mind the changes in the composition and dominance structure of assemblages of necrophagous invertebrates. Shallow stations (5 and 15 m) are dominated by small-sized animals (*Amphipoda*) whose total biomass is small despite their great abundance. At deeper stations large animals like the snails *Chlanidota elongata*, *Harpovoluta charcoti* and *Neobuccinum eatoni*, the isopod *Glyptonotus antarcticus*, the nemertean *Parborlasia corrugatus* and several species of starfishes, play an important role in the dominance structure and the decrease in the assemblage abundance

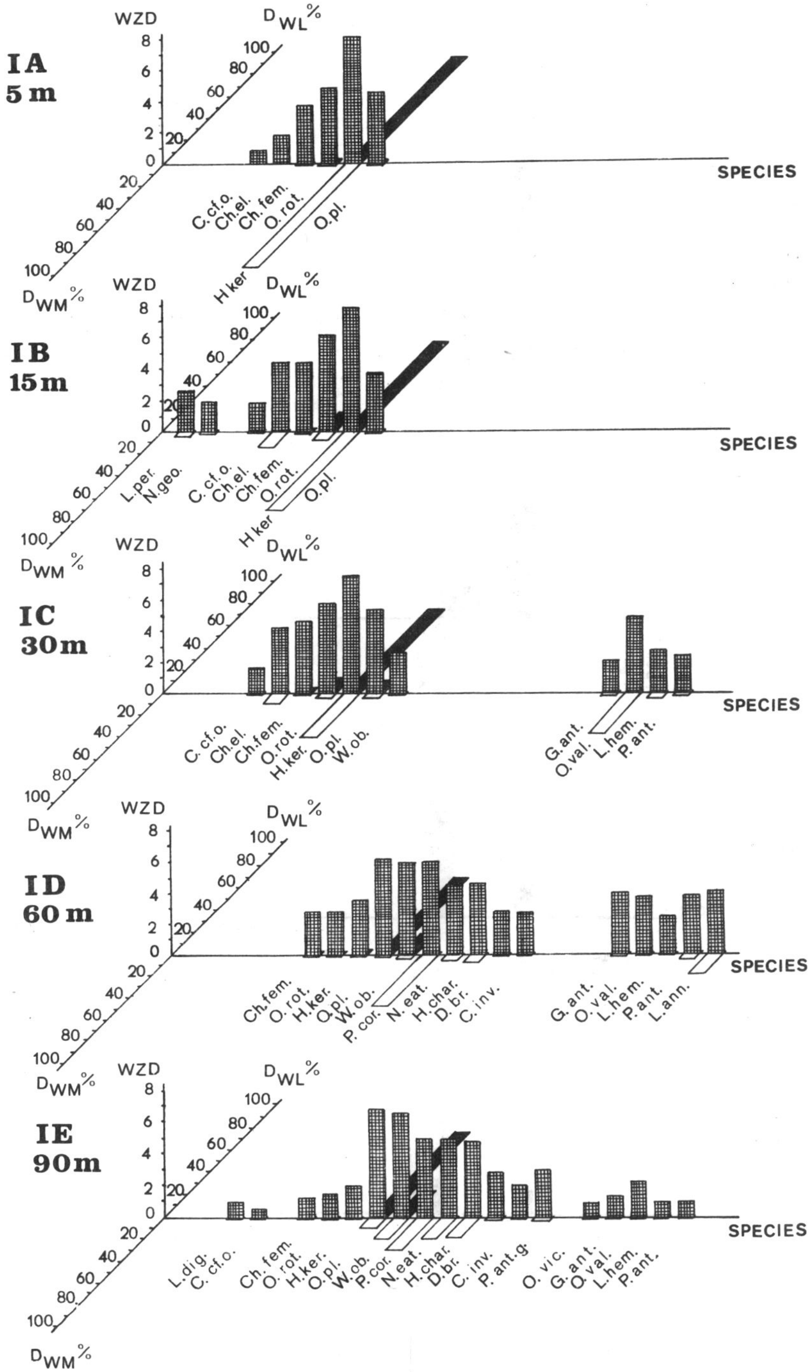

Fig. 4. Structures of the dominance in abundance (D_{WL}), in biomass (D_{WM}) and in the role of species (WZD) in the assemblages of necrophagous invertebrates collected in summer 1980 in sations of section I (Shag Pt)

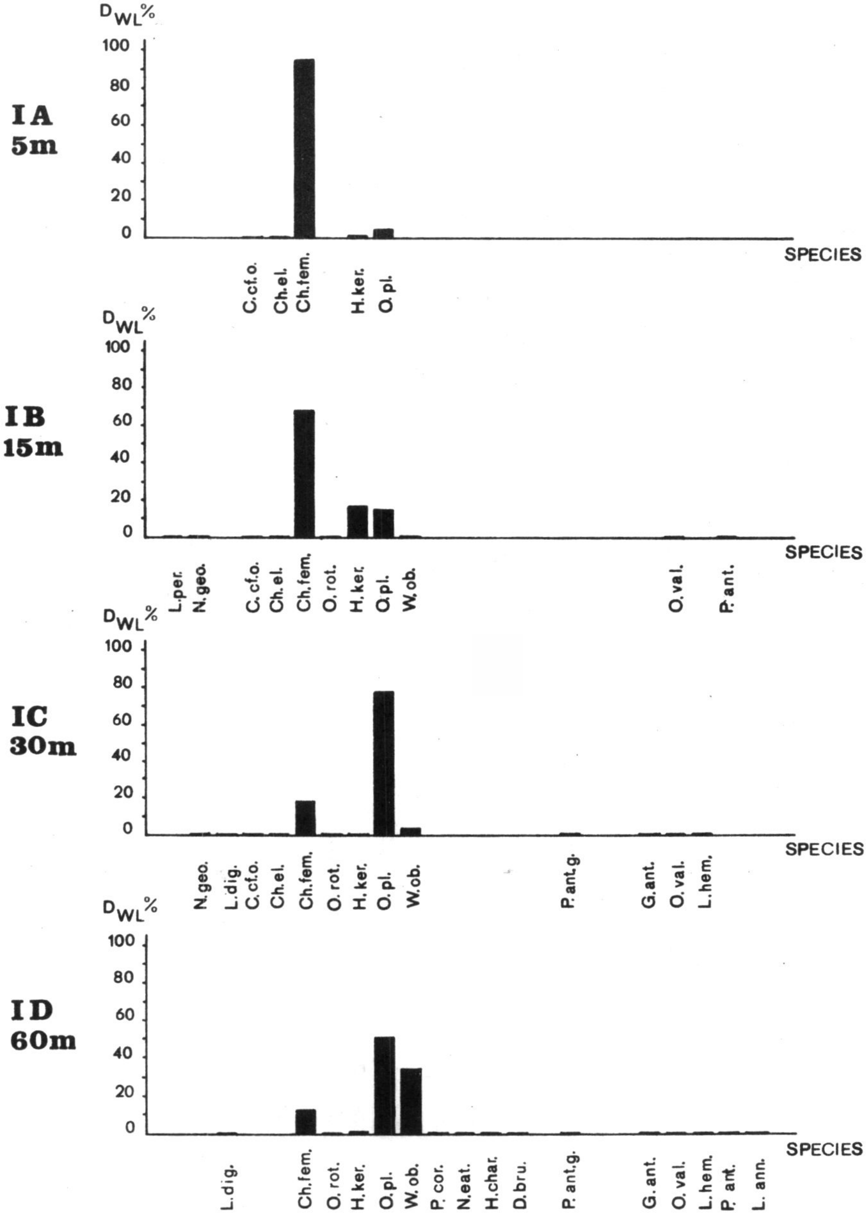

Fig. 5. Structures of the dominance in abundance (D_{WL}) in the assemblages of necrophagous invertebrates collected in winter of 1977 in stations of section I (Shag Pt.).

is accompanied by an increase in their total biomass that is caused by the large individual weight of the above-mentioned animals. In station E the

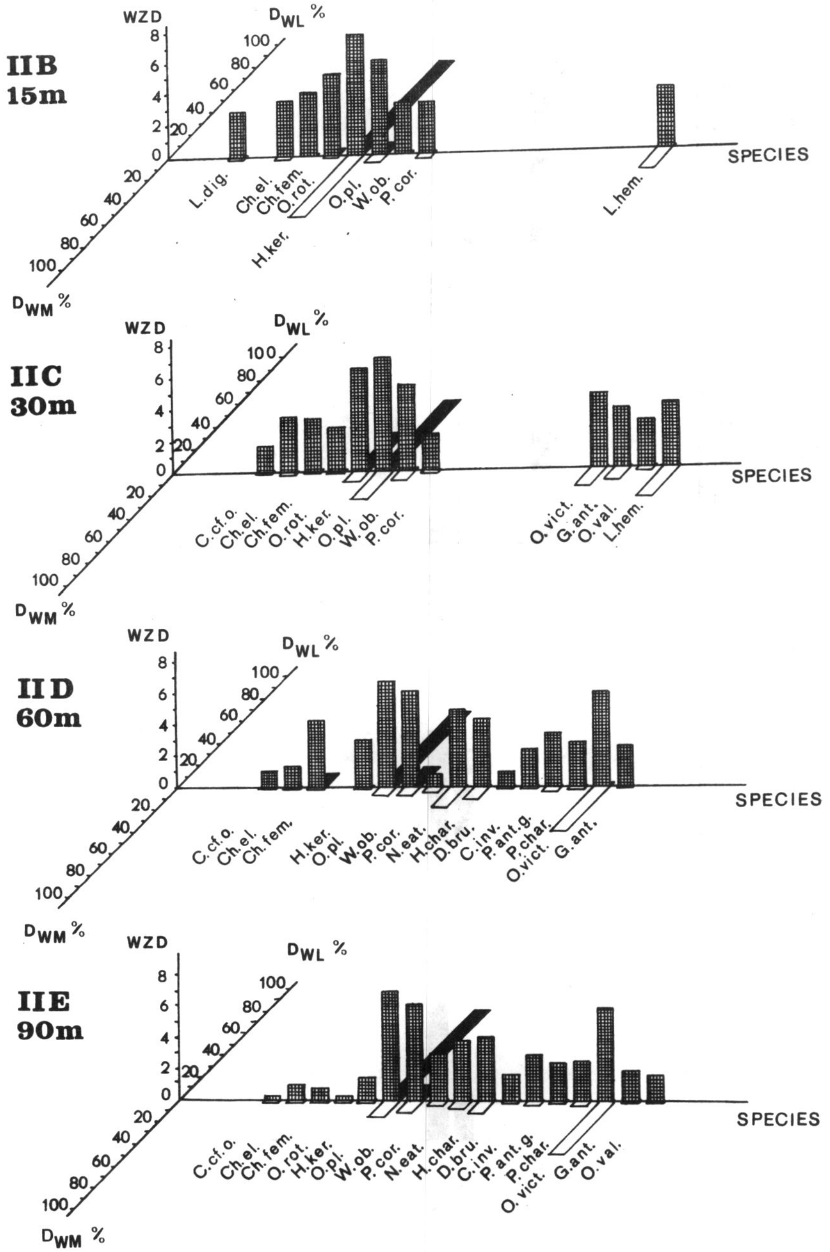

Fig. 6. Structures of the dominance in abundance (D_{WL}), in biomass (D_{WM}) and in the role of species (WZD) in the assemblages of necrophagous invertebrates collected in summer 1980 in stations of section II (Thomas Pt.).

share of *Amphipoda* again increases and this is reflected by the divergence of the curves.

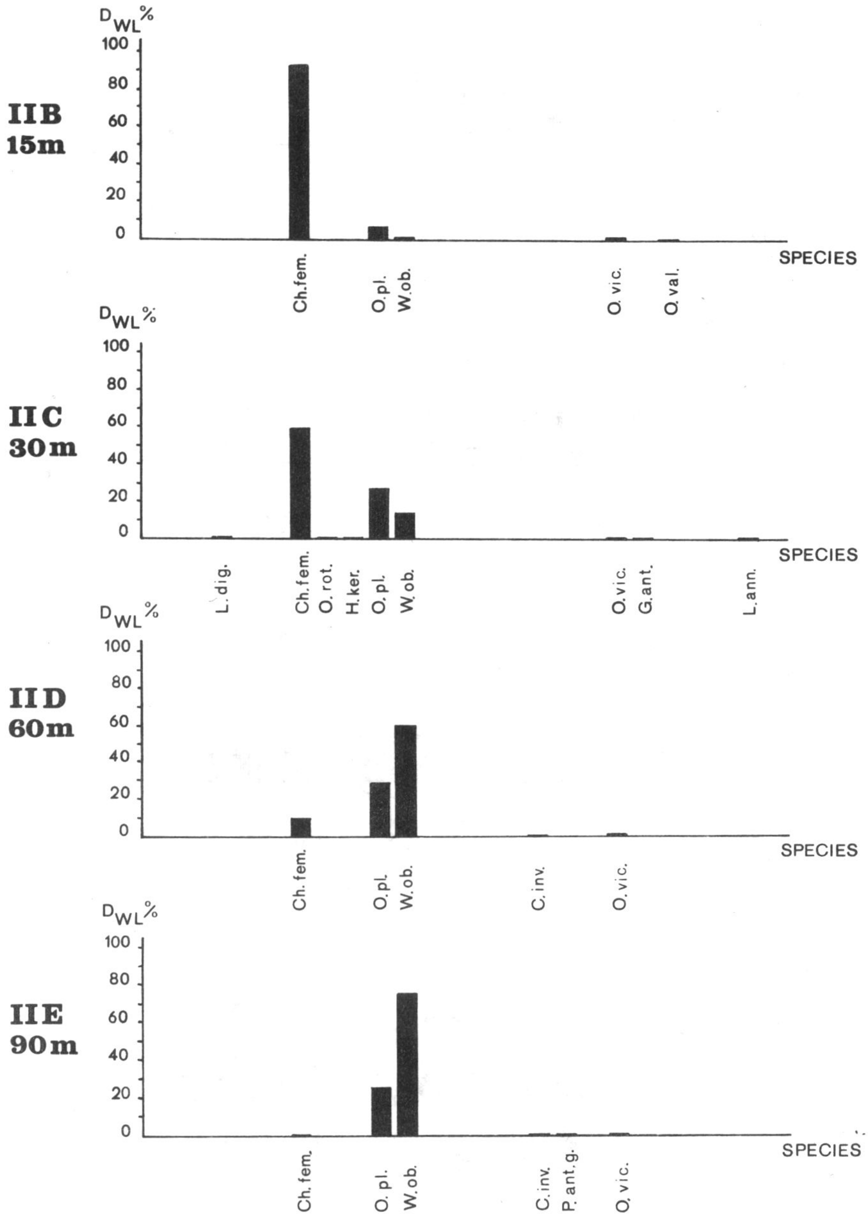

Fig. 7. Structures of the dominance in abundance (D_{WL}) in the assemblages of necrophagous invertebrates collected in winter of 1977 in stations of section II (Thomas Pt.).

The curves showing the variability of assemblage abundance in the stations of section II (Fig. 8b) are very similar to those for section I. The most important differences consist in the fact that abundances of winter

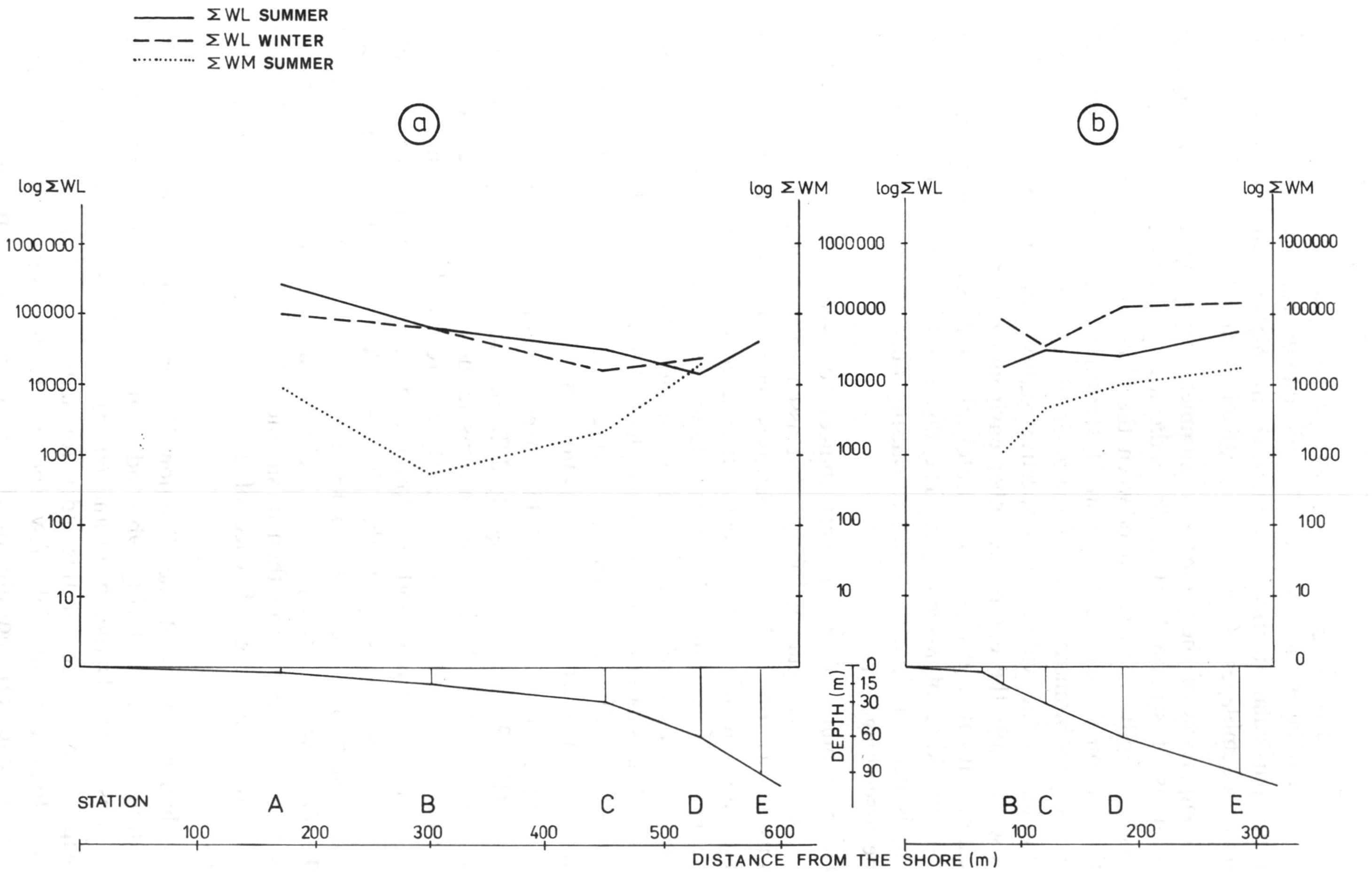

Fig. 8. Abundance and biomass of the assemblages of necrophagous invertebrates collected in winter of 1977 and in summer of 1980 in stations of section I (a) and in stations of section II (b).

necrophagous assemblages are distinctly greater than the abundances of summer assemblages and in the fact that the abundances of winter assemblages from the particular depths of section II are higher than the abundances of winter assemblages of the same depth of section I.

A comparison of the biomass of summer necrophagous assemblages of the stations of section II (Fig. 8b) indicates its continuous growth with increase in depth. The relation between the biomass and abundance curves for this section is analogous to that of section I and can be also similarly explained. The biomass values of the assemblages from section I in general are similar to the values for respective stations of section II. One can suppose that just the depth and other environmental parameters which are correlated with it (e.g. type of substrate), play a decisive role in determination of the kind of assemblages. The distance between stations (Fig. 8a and b) is here of little importance, causing only faster or slower changes of the assemblage structure.

The variability of the diversity indices "d" and "H′" is presented in Fig. 9. From this figure it follows that assemblage diversity index "d" for stations of section I (Fig. 9a) increases with increasing depth both in summer and in winter. In general the diversity was higher in winter. An exception was station A (5 m). Low values of "d" index for this station both in summer and in winter suggest the instability of this assemblage. This is natural considering the physical conditions of the environment such as strong influence of surging, strong abrasive activity of floating and coastal ice and relatively high fluctuations of temperature.

A comparison of values of this diversity index "d" for stations of section II (Fig. 9c) revealed a slightly different picture. Although in summer the diversity increased also with increasing depth, yet this relation was disturbed in winter. The highest diversity was recorded in station C (30 m) while in the remaining, both shallower and deeper stations the diversity was much lower. This suggests that the assemblages occurring in particular stations of section II are in winter less stable. This suggestion is supported by the fact that all winter values of the index "d" for all stations of this section are much lower than in summer. Probably, we have to do here with a strong, limiting influence of not yet determined physio-chemical factors.

The highest values of the Shannon-Weaver's diversity index both for the stations of section I (Fig. 9b) and section II (Fig. 9d) were obtained for stations C and D (depth 30 and 60 m). This applies both for summer and winter. Low values of this index for stations A, B and E reflect the decisive dominance of only few species. Higher values of this index (stations C and D) indicate to the more even participation of many species in the structure of assemblages.

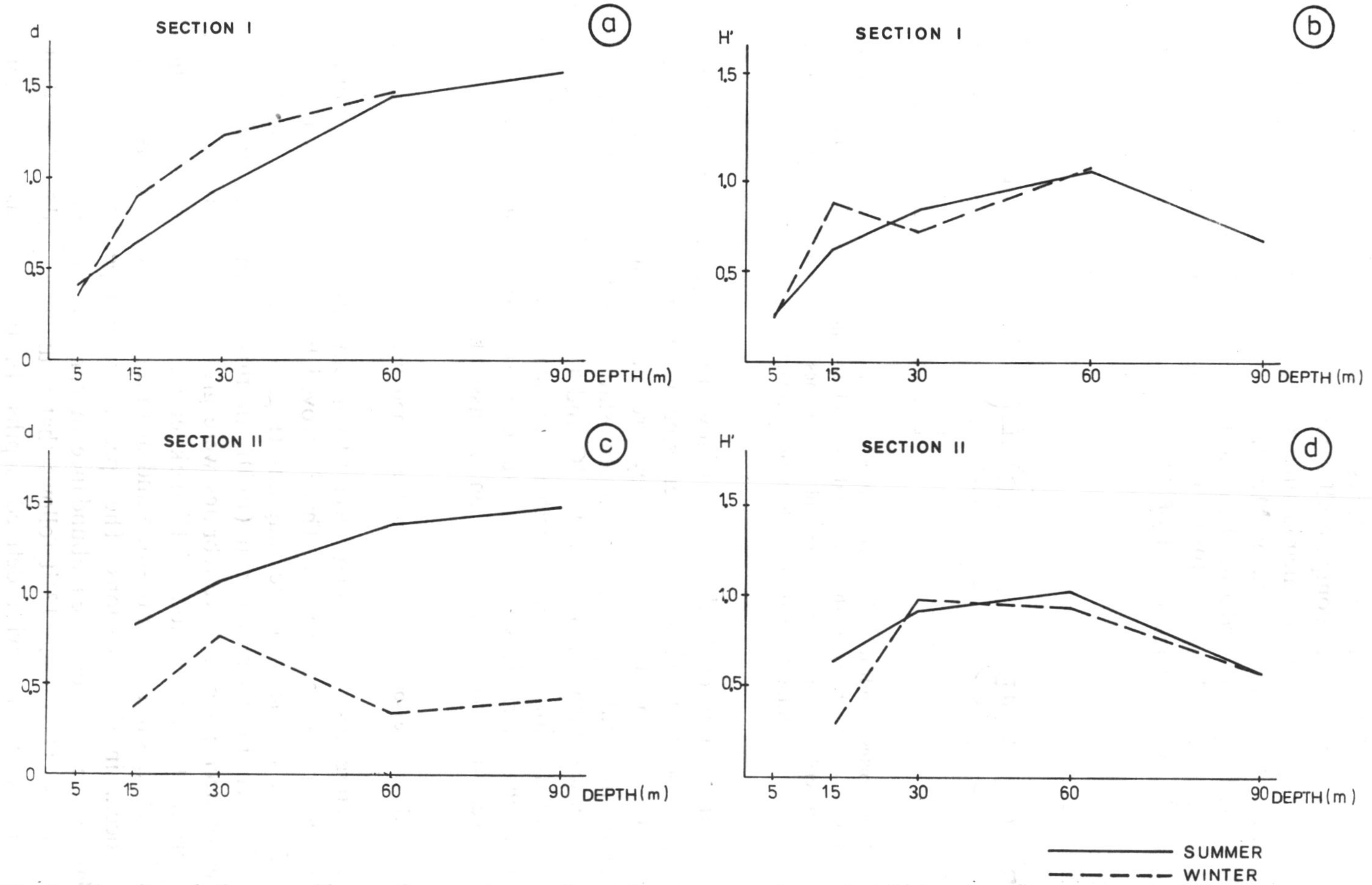

Fig. 9. Diversity of the assemblages of necrophagous invertebrates: a — values of the diversity index "d" in stations of section I; b — values of Shannon-Weaver's index of diversity "H" in stations of section I; c — values of the diversity index "d" in stations of section II; d — values of Shannon-Weaver's index of diversity "H" in the stations of section II.

On the basis of the index of species' role in the structure of assemblages (WZD) it was possible to compare all summer assemblages of necrophagous invertebrates with regard to their dominance structure in this respect. Using the equation of similarity given by Marczewski and Steinhaus (1959) and the dendrite method of ordering the collections and making natural divisions of dendrites (Florek et al. 1951), the shortest dendrite of the distances of 9 stations on the background of 23 species was drawn (Fig. 10). From the natural divisions of the dendrite it follows that as regards the domination structure of species' role in their summer assemblages in stations IID and IIE as well as in stations IA and IB they are most similar to each other. A significant similarity occurs between stations ID, IE, IID, IIE and a slightly lower between stations IIB, IC and IIC. This is the case because the natural divisions grouped together these stations of similar depths and substrate character. This, in turn, suggests that these highly correlated factors exert dominating influence on the assemblage structure.

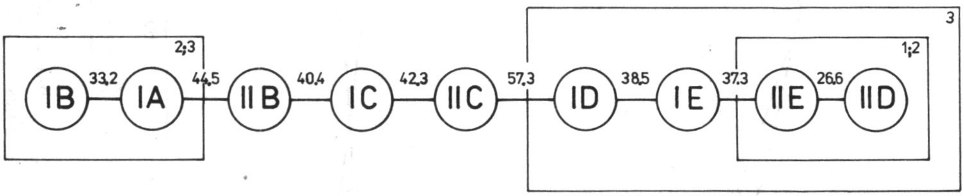

Fig. 10. The shortest dendrite of distances between 9 stations on the background of 23 species (made on the basis of the WZD values) and its three strongest natural divisions. Numbers in the upper corners of the frames stand for the sequence of the divisions resulting from their mathematical strength.

4.2.2. Spatial and seasonal variability in the composition and structure of assemblages

The preferences of particular species to specific environmental conditions cause their spatial replacement. This is proved by data included in fig. 11 and 12, and in the synthetic diagram (Fig. 13), made according to the method given by Romaniszyn (1970). In this diagram all stations and species of necrophagous invertebrates were grouped in a natural way, that is according to the method of Florek et al. (1951). Groups of stations show similarities in the composition and quantitative structure of assemblages which occur in these stations. The species are grouped on the basis of similarities arising from their abundance in particular stations.

From figs. 11, 12 and 13 it follows that abundance peaks of particular species are connected with defined depths. In the stations of section I (Fig. 11 and 13) *Cheirimedon femoratus* and *Hippomedon kergueleni* were

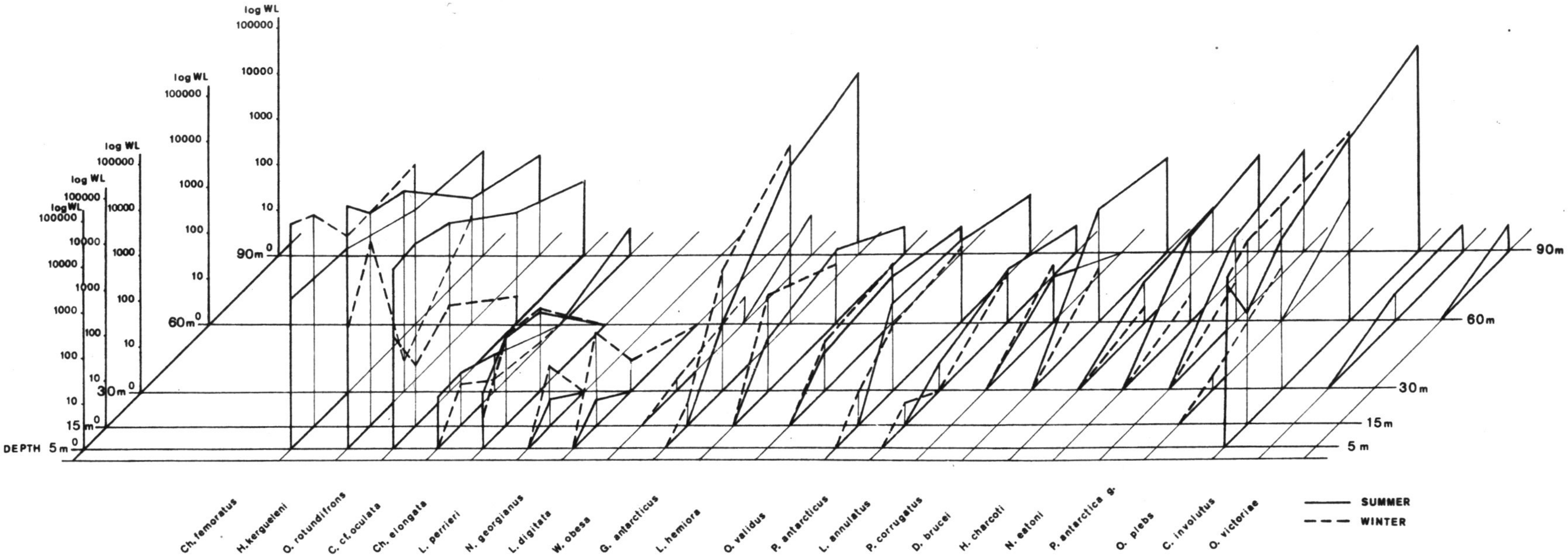

Fig. 11. Spatial and seasonal changes in the abundance of necrophagous invertebrate species collected in stations of section I.

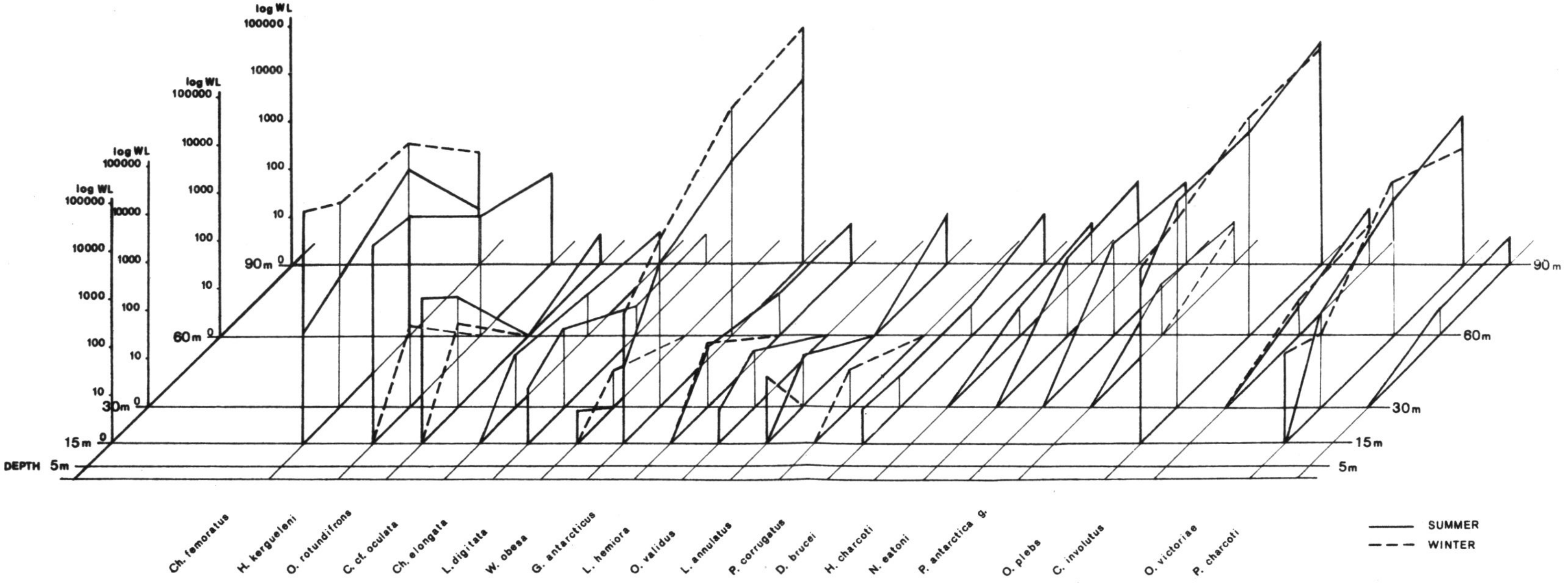

Fig. 12. Spatial and seasonal changes in the abundance of necrophagous invertebrate species collected in stations of section II.

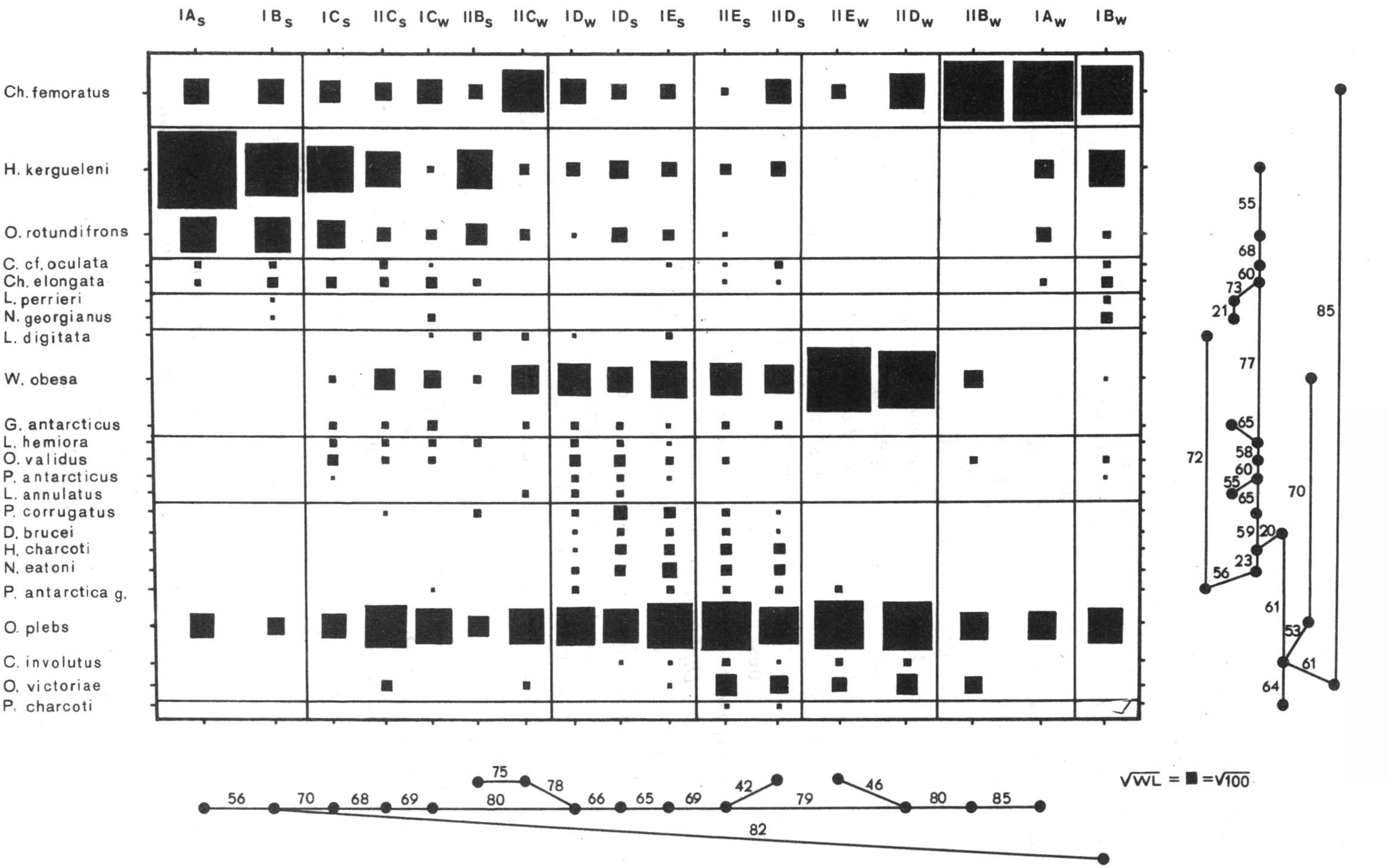

Fig. 13. Synthetic diagram of the relations of 23 species of necrophagous invertebrates and 17 stations (8 stations in winter with symbol "w" and 9 stations in summer with symbol "s"). Horizontal and vertical lines distinguish groups of stations and groups of species on the basis of three strongest natural divisions of the shortest dendrites of distances between stations and distances between species. Square areas are square roots of the values of the daily abundance indices (WL) of species. For the sake of clarity the lengths of sections in the dendrite standing for distances are distorted.

most abundant at a depth of 5 m. *Chlanidota elongata, Cirolana* cf. *oculata, Orchomene rotundifrons, Lysasterias perrieri* and *Neosmilaster georgianus* were most abundant at a depth of 15 m. *Glyptonotus antarcticus* and *Odontaster validus* had their highest abundance values at a depth of 30 m, while *Parborlasia corrugatus, Labidiaster annulatus, Lysasterias hemiora, Perknaster antarcticus* and *Porania antarctica glabra* at a depth of 60 m. At a depth of 90 m, that was investigated only in summer, *Harpovoluta charcoti, Neobuccinum eatoni, Orchomene plebs, Waldeckia obesa, Cuenotaster involutus, Diplasterias brucei, Lysasterias digitata* and *Ophionotus victoriae* attained their highest abundance values. For most species changes in the abundance connected with changes in depth are lenient.

A similar situation occurs in section II (Fig. 12 and 13). *Cheirimedon femoratus, Hippomedon kergueleni, Orchomene rotundifrons* and *Odontaster validus* occurred most abundantly at a depth of 15 m. *Chlanidota elongata, Cirolana* cf. *oculata, Glyptonotus antarcticus, Labidiaster annulatus, Lysasterias digitata* and *Lysasterias hemiora* were most abundant at a depth of 30 m. *Neobuccinum eatoni, Porania antarctica glabra* and *Ophionotus victoriae* had highest abundance values at a depth of 60 m, while the species: *Parborlasia corrugatus, Harpovoluta charcoti, Orchomene plebs, Waldeckia obesa, Cuenotaster involutus, Diplasterias brucei* and *Psilaster charcoti* at a depth of 90 m. It is interesting that in the stations of section II the highest abundance values of *Neobuccinum eatoni, Labidiaster annulatus, Lysasterias digitata, Lysasterias hemiora, Odontaster validus* and *Ophionotus victoriae* were recorded at shallower depths than in those of section I. This phenomenon suggests a closer relation between the occurrence of these species and the kind of substrate, because in section II zones in which stony bottom changes into bottom of gravel, of sand and of mud are narrower and occurring at shallower depths. Homogenous mud appears in this section at much shallower depths. Probably, this was in fact the cause of higher abundance and a larger bathymetric range of the ophiuroid *Ophionotus victoriae* in section II than in section I, as well as the cause of total lack, in section II, of the starfishes *Lysasterias perrieri, Neosmilaster georgianus* and *Perknaster antarcticus* and the cause of the presence of *Psilaster charcoti.*

Worth mentioning is also the occurrence of *Cheirimedon femoratus* and *Orchomene plebs* in all, and of *Hippomedon kergueleni, Orchomene rotundifrons* and *Waldeckia obesa,* in almost all assemblages of necrophagous invertebrates. This fact evidences for their eurytopy and eurybathy (of course taken in the scale of investigated habitats and depths). The differences in abundance of the above mentioned species indicate that *Hippomedon kergueleni, Orchomene rotundifrons* and *Cheirimedon femoratus* prefer smaller depths, while *Orchomene plebs* and *Waldeckia obesa* slightly greater ones.

Interesting changes in the specific composition and abundance of assemblages occurring in the same stations in various seasons were observed besides the phenomenon of spatial replacing of species. As it follows from the synthetic diagram (Fig. 13) the smallest similarities between summer and winter assemblages occured in stations IA, IB and IIB, whereas the winter assemblage in station IB is still most similar to the assemblage occurring in this station in summer. In the case of stations ID, IE, IID and IIE winter and summer assemblages are quite similar. In station IC the winter assemblage becomes most similar to the summer assemblage of the station IIC, whereas the winter assemblage of station IIC to the summer assemblage of the neighbouring station IIB, which lies however at a shallower depth. It is worth stressing that winter assemblages, especially in the stations of section II, are probably less stable, which is evidenced by the low values of their diversity indices (Fig. 9). The distribution of similarities between the remaining stations is very close to the distribution obtained on the basis of comparing the dominance structures of summer assemblages (Fig. 10).

From figures 11 and 13 it follows that *Cheirimedon femoratus*, abundant in winter at depths of 5 and 15 m of section I, is replaced in summer by *Hippomedon kergueleni*. At these depths in summer the abundance of *Orchomene rotundifrons* increased but the abundance of *Orchomene plebs* decreased. At a depth of 30 m *Hippomedon kergueleni* replaced in summer *Orchomene plebs*, which was abundant in winter. As in the above mentioned stations, the abundance of *Cheirimedon femoratus* and *Waldeckia obesa* decreased in summer, and that of *Orchomene rotundifrons* increased. In station ID (depth 60 m) *Orchomene plebs* was the most common species both in summer and in winter, but in winter its abundance was higher than in summer. The proportions of the remaining species of *Amphipoda* in the compared seasons were similar to the proportions for shallower stations. Among necrophagous invertebrates other than *Amphipoda*, the abundances of *Parborlasia corrugatus, Harpovoluta charcoti, Neobuccinum eatoni, Cuenotaster involutus, Diplasterias brucei* and *Odontaster validus* in summer were much higher than in winter. Much higher abundances in winter than in summer were observed for *Glyptonotus antarcticus, Lysasterias hemiora, Lysasterias perrieri* and *Neosmilaster georgianus*. This evidences for the seasonal replacing of the above mentioned groups of species.

When comparing the abundances of species collected in the stations of section II (Figs. 12 and 13) one can see that the abundance values for *Cheirimedon femoratus* and *Waldeckia obesa* as well as for *Labidiaster annulatus* and *Ophionotus victoriae* were much higher in winter. In the case of the remaining species abundance usually increased in summer; of particular interest were the dramatic summer increase in the abundance of *Hippomedon* *kergueleni* and *Orchomene rotundifrons* as well as the appearence of eight species in summer assemblages, species that were absent in winter.

The seasonal replacing of species within assemblages among others may be due to the periodical changes in their feeding preferences. Basing on distinct differences between summer and winter abundances (WL) of necrophagous invertebrates three groups of species were distinguished: 1) group of species displaying stronger inclinations to winter necrophagy, 2) group of species displaying stronger inclinations to summer necrophagy, 3) group of ambivalent species. To the first group the following species are included: *Cheirimedon femoratus, Waldeckia obesa, Lysasterias perrieri* and *Neosmilaster georgianus* as well as *Glyptonotus antarcticus, Labidiaster annulatus* and *Ophionotus victoriae*. The second group is represented by *Parborlasia corrugatus, Harpovoluta charcoti, Neobuccinum eatoni, Hippomedon kergueleni, Orchomene rotundifrons, Diplasterias brucei* and *Psilaster charcoti* as well as *Cirolana* cf. *oculata, Cuenotaster involutus* and *Odontaster validus*. The third group is composed of the remaining 6 species: *Chlanidota elongata, Orchomene plebs, Lysasterias digitata, Lysasterias hemiora, Perknaster antarcticus* and *Porania antarctica glabra*.

4.2.3. Forms of the competitive community of necrophagous invertebrates

Taking into account the above discussed relations an attempt was made at distinguishing the forms of the competitive community of necrophagous invertebrates occurring in the investigated parts of the Admiralty Bay. The concept of the competitive community was accepted after Trojan (1975) assuming that all criteria determining the existence of a system to which this concept is applied are fulfilled. All species in question belong to the same food niche. Feeding competition undoubtedly occurs among species cooccurring in the characteristic structure.

The concept of the "form of the community" was applied to the unit constituting a part of a competitive community of necrophagous animals. It has the characteristic composition and species dominance structure and displays more significant differences than similarities in relation to other parts of the community. It has also defined range limits. These limits are not sharp and forms of the community replace each other more or less gradually depending on the environmental gradient. Such an understanding of the separated unit is in agreement with one of Whittaker's hypothesis (Whittaker 1970, after Collier et al. 1978), which refer to the changes of biocenoses in space.

Basing mainly on the synthetic diagram (Fig. 13) three spatially and seasonally changeable forms of the competitive community of necrophagous invertebrates were distinguished.

The first of these forms was created on the basis of assemblages occurring in stations IA and IB in summer as well as in stations IA, IB and IIB in winter. Its range is from 5 to 15 m of depth where rocky, stony or stony-gravel substrate occurs. The total of 12 species of necrophagous invertebrates occurred there in the course of a year. In summer *Hippomedon kergueleni* and *Orchomene rotundifrons* were species dominating with regard to abundance. As regards biomass, *Hippomedon kergueleni* was dominant, whereas *Hippomedon kergueleni, Orchomene rotundifrons, Cheirimedon femoratus, Chlanidota elongata* and *Orchomene plebs* were dominant as regards to the role of species in an assemblage. In winter assemblages *Cheirimedon femoratus, Orchomene plebs* and *Hippomedon kergueleni* dominated in respect to the abundance. The starfishes *Neosmilaster georgianus* and *Lysasterias perrieri* appeared frequently but not in great abundance.

The second form of the community was distinguished by joining the most similar assemblages from stations IC, IIC and IIB for summer and IC and IIC for winter. This second form of the community covers the depth ranging from 15 to 30 m in places of the bottom of mud and gravel with an admixture of stones. In total 17 species of necrophagous invertebrates occurred there in summer and in winter. In summer *Hippomedon kergueleni* and *Orchomene plebs* were dominant in abundance, while *Hippomedon kergueleni, Lysasterias hemiora, Odontaster validus* and *Orchomene plebs* were dominant in weight. As regards to the role in summer assemblages *Hippomedon kergueleni* and *Orchomene plebs* dominated, but *Orchomene rotundifrons, Cheirimedon femoratus, Waldeckia obesa, Glyptonotus antarcticus, Chlanidota elongata, Lysasterias hemiora, Odontaster validus* and *Ophionotus victoriae* had also high “role” indices. *Cheirimedon femoratus, Orchomene plebs* and *Waldeckia obesa* dominated in abundance in winter, and *Glyptonotus antarcticus* was also fairly abundant there.

The third form of the community of necrophagous invertebrates was founded on the basis of seven very similar assemblages occurring in summer in stations ID, IE, IID, IIE, and in winter in stations ID, IID and IIE. The range of this third form covers the depth from 60 to 90 m, where the bottom is covered with mud with small admixture of gravel and stones. In total 21 species occurred there in summer and winter assemblages. In summer assemblages *Orchomene plebs* dominated in abundance, and *Waldeckia obesa* was the second on the list. *Parborlasia corrugatus* or *Ophionotus victoriae* were dominants in respect to the biomass. The greatest role in assemblages had *Orchomene plebs, Waldeckia obesa, Harpovoluta charcoti, Neobuccinum eatoni* as well as *Parborlasia corrugatus* and *Ophionotus victoriae. Waldeckia obesa, Orchomene plebs, Cheirimedon femoratus* and *Ophionotus victoriae* were most abundant in winter assemblages.

One should remember that there are few species which belong exclusively to only one of the distinguished forms of the community. To these species belong: *Lysasterias perrieri* which occurred exclusively in the assemblages of the first form and *Harpovoluta charcoti, Neobuccinum eatoni, Cuenotaster involutus, Diplasterias brucei* and *Psilaster charcoti* which occurred only in the third form. There are no such characteristic species for the second form. *Neosmilaster georgianus* is the only species common to the first and second form, and *Parborlasia corrugatus, Glyptonotus antarcticus, Labidiaster annulatus, Lysasterias hemiora* and *Porania antarctica glabra* are the only species common to the second and third form. There are no species common exclusively to the first and third form. The remaining ten species of necrophagous invertebrates occurred either in winter or in summer assemblages of all these three forms.

The three distinguished forms of the community of necrophagous invertebrates have zonal distribution that is correlated with the type of bottom. One can possibly regard the distribution of the second form of the community as corresponding to the ecotone distribution. It should be born in mind however that the effect of contact, which is characteristic for ecotone, is not univocal in the case of necrophagous invertebrates. At the best, it manifests itself in an increase in the diversity, in overlapping of the range of species common to neighbouring forms of community, but it is not evidenced by an increase in the total abundance of necrophagous invertebrates.

5. Discussion

Specific conditions prevailing in cold Antarctic waters have forced animals living there to a number of adaptations. One of such adaptations is necrophagy (Arnaud 1977). Necrophagy is found frequently among Antarctic benthic invertebrates. Arnaud (1964) pointed out to the common occurrence of necrophagy among *Echinodermata* living in the Dumont d'Urville Sea, at the coast of Adelie Land. In his subsequent works (Arnaud 1970, 1974, 1977; Arnaud and Hureau 1966) this author paid much attention to the problems concerning the necrophagy of Antarctic animals, contributing to the explanation of various aspects of this phenomenon. The frequent occurrence of necrophagy is explained by Arnaud by finding and using of such feeding method which is least energy consuming for the organisms in question. It is well known that carcasses of animals occur on the sea bottom in all seasons. They include both dead benthic and planktonic invertebrates, dead fishes, as well as dead seals and penguins wounded by leopard seals and killer-whales or dying because of many other causes. Consequently, this kind of food is easily and frequently accessible. Of course, the energy loss of the carrion consuming animals is much lower than that of the predators which hunt for animals before consuming them. Also, it is worth mentioning that necrophagy does not usually occur as the only, or even main form of feeding, but can be only a complement to the diet of other origin. It has been proved that necrophagous animals are most frequently predators or phytophagous animals of an opportunistic diet, which compete with each other for food resources (e.g. Dearborn 1967, Temnikow, Brand and Moe 1976, Arnaud 1977, Dearborn 1977, Dearborn, Edwards and Fratt 1981, Fratt and Dearborn 1984).

Wide range of the occurrence of many Antarctic necrophagous animals may be an evidence that the opportunistic diet and such trophic adaptation as necrophagy is an advantage for these organisms. Out of 23 species of necrophagous invertebrates found in the Admiralty Bay, as much as 74% have circumantarctic distribution, 13% occur in Western Antarctica and Subantarctica, and only three (i.e. also 13%) have their range of occurrence limited to Western Antarctica (Arnaud et al. 1986).

The common occurrence and great abundance of necrophagous benthic invertebrates in the whole Antarctica caused that in the course of many scientific investigations they were frequently sampled. Together with other invertebrates they were caught during diving and using dredges and samplers (e.g. Bellisio, Lopez and Tomo 1972, Dayton et al. 1974). They were also selectively collected using baited traps (e.g. Littlepage and Pearse 1962, Tressler 1964, Jażdżewski 1983). This material, however, was then used in rather general ecological considerations. Some necrophagous species have been treated in monographic studies, which widely discussed their ways of feeding, breeding biology or population dynamics. These species are: *Glyptonotus antarcticus* (Dearborn 1967), *Odontaster validus* (Pearse 1969), *Cheirimedon femoratus* and *Hippomedon kergueleni* (Bregazzi 1972a, 1972b, 1973a, 1973b), *Orchomene plebs* (Rakusa-Suszczewski 1982), and also *Ophionotus victoriae* (Fratt and Dearborn 1984).

However synecological studies on all necrophagous species inhabiting particular habitats so far are very scarce. The only works treating necrophagous animals in a more complex way are above-mentioned papers by Arnaud (1964, 1970, 1974) and Hoshiai (1968). However also there autecological approach to the problem prevailed. No attention has ever been paid to mutual biological relations occurring between necrophagous invertebrates, which according to the present author, form a competitive community. Therefore it is difficult to evaluate if the dominance structure of the described community, and the abundance or biomass of invertebrates forming this community are typical of all the regions of Antarctica. However, all possible comparisons with the results of investigations of the above-mentioned authors suggest that the described system is typical of, at least, the region of Western Antarctica.

One of the problems worth particular discussing and comparing is seasonal necrophagy. This phenomenon consists in the inclination of a given species to feed on carrion in a particular season of the year. Arnaud (1964) has paid attention to such a seasonality in his work on necrophagous *Echinodermata* of Adelie Land, and then frequently and widely referred to this phenomenon in his latter works (Arnaud 1970, 1974, 1977). The causes of seasonality in necrophagous behaviour are found about by this author in changes in availability and abundance of certain food types (mainly *Diatomeae*), that are, on the other hand, caused by winter oligotrophy of Antarctic waters. This view, accepted also by the present author, was supported by observations done by other investigators of Antarctic benthos (e.g. Pearse 1969, Kauffman 1974). Arnaud (1974) stresses, that some species of benthic animals (e.g. *Odontaster validus*) which are necrophagous in winter, are basically phytophagous in summer. This author states also that his investigations did not reveal the existence of any species which might exhibit a seasonal summer necrophagy. The present investigations proved that there occurred a group of animals which displayed stronger inclination to feed on carrion in winter. However, it was also possible to distinguish a group of invertebrates whose inclination to necrophagy was stronger in summer. Of course, this does not mean that such species were caught in baited traps only in summer. Still, their abundance and frequency in the catches were higher than in winter. The discovery of the existence of the "summer necrophagy" does not disprove Arnaud's (1974) concept about changes in necrophagous behaviour caused by the availability of food during winter oligotrophy. On the contrary, it is a proof in its support and complements this concept. As it has already been mentioned, according to this concept "winter" necrophagous animals in summer prefer food of plant (*Diatomeae*). When this food type is scarce they have to feed on carrion. However when a sufficient amount of the preferred food type appears again they easily give up feeding on dead animals. As a result their place in the ecological niche empties. One may assume that the abundance of carcasses in summer is at least as high as that in winter. Probably, it is even higher, considering the appearence of pieces of carrion which remain after leopard seals' and killer-whales' feeding and carcasses of animals dying because of the furrowing and rubbing influence of ice-pack and icebergs. In this way there appears a certain surplus of this food type, which is eagerly used by "summer" necrophagous animals. To learn what basic food types are the components of the diet of the "summer" necrophagous animals in winter, further, deep studies have to be carried out. There is a good reason to believe, however, that the feeding behaviour of animals is influenced by local environmental conditions. As an example *Odontaster validus* may be mentioned; this species was commonly known as exhibiting a seasonal "winter" necrophagy (Arnaud 1974), whereas in the Admiralty Bay it showed stronger inclination to consume carrion in summer.

Zonal distribution of species correlated with change in depth and the kind of sediment stated in the present work is concordant with observations of other authors concerning the distribution of benthic forms on the bottom of Antarctic shelf (Bullivant and Dearborn 1967, Gallardo and Castillo 1969, Dayton, Robilliard and Paine 1970, Gruzov and Pushkin 1970, Dayton and Robilliard 1971, Hedgpeth 1971, Bellisio, Lopez and Tomo 1972, Arnaud 1974, Dayton et al. 1974, DeLaca and Lipps 1976, Richardson and Hedgpeth 1977, Everitt, Poore and Pickard 1980). Data included in the works of these authors prove that the distribution of benthic fauna has always a mosaic, but at the same time, zonal character and that there exists a very strong correlation in this respect with the character of the inhabited substrate.

The conceptual model of main trophic relations conditioning the circulation of matter and energy flow in the coastal part of the Antarctic ecosystem, which was put forward by Rakusa-Suszczewski (1980b), indicates to a significant role played in the ecosystem by benthic animals. They constitute a link widely connected to all trophic levels of the ecosystem. This is, among other reasons, due to the fact that animal benthos is extremely heterogenous and displays a wide range of adaptations to various food types. Among other equally important benthic communities, the competitive community of necrophagous animals deserves attention.

It is well known that the decomposition of organic matter of animal origin is extremely slow in cold Antarctic waters. Dayton (1970) states that seal flesh protected against *Amphipoda* may remain in the sea in an almost unchanged condition for 6 weeks. This has been proved by experiments which Rakusa-Suszczewski and Zdanowski (1980) have carried out in the water of the Admiralty Bay. Observing the process of autolytic and bacterial decomposition of krill, they recorded that its rate was extremely slow and might be significantly accelerated by raising the temperature and by mechanical washing out. Taking into account the above information one might expect a wealth of remnants of dead animals on the sea bottom. However, sea sediments in Antarctica contain extremely small amounts of organic compounds and usually the smell of hydrogen sulfide, which is typical of decomposition processes is not noticed (Tressler 1964, Richardson and Hedgpeth 1977). This is due to the community of necrophagous animals which concentrate at carrion lying on the bottom in hundreds, or even thousands of individuals and quickly and efficiently consume all dead organic remnants.

In spite of the fact that some necrophagous animals may live for many dozens of years (Pearse 1969, estimates that some specimens of *Odontaster validus* may live over 100 years) it is obvious that most of them do not constitute the highest trophic level of the ecosystem. Much of the matter which is accumulated in their bodies may quickly pass to further stages of circulation and feed subsequent, higher trophic levels. It is known, for instance, that the long-living starfish *Odontaster validus* is consumed by a much larger starfish *Macroptychaster acrescens* (Dayton et al. 1974, Dearborn 1977), as well as an actinian *Urticinopsis antarcticus* and a starfish *Labidiaster annulatus* (Dearborn 1977). The fragments of *L. annulatus*, whose inclination to cannibalism was also recorded (ibid.), were found in the stomachs of the ophiuroid *Ophionotus victoriae* (Fratt and Dearborn 1984). This ophiuroid also displays an inclination to cannibalism (Dearborn 1977, Fratt and Dearborn 1984) being on the other hand consumed by the starfish *Labidiaster annulatus* (Dearborn 1977). Large necrophagous snails *Neobuccinum eatoni* were consumed by fishes *Trematomus hansoni* and *T. bernacchii* (Arnaud and Hureau 1966) and by the starfish *Labidiaster annulatus* (Dearborn 1977). The starfishes *Odontaster validus* and *Labidiaster annulatus* may prey on the isopod *Glyptonotus antarcticus* (ibid.). This isopod is also consumed by fishes *Trematomus bernacchii* (Dearborn 1967) and *Notothenia coriiceps neglecta* (Richardson 1975, Linkowski, Presler and Żukowski 1983). Amphipods from the family *Lysianassidae* are consumed mainly by fishes, but there are cases recorded when they were also eaten by other animals. *Waldeckia obesa* is consumed by *Trematomus bernacchii* (Arnaud and Hureau 1966) and by *Notothenia coriiceps neglecta* and *N. rossi marmorata* (Linkowski, Presler and Żukowski 1983). Single specimens of these amphipods were also recorded in the stomachs of the penguins *Pygoscelis antarctica* (Chevreux 1905) and *P. papua* (Jażdżewski 1981). *Orchomene plebs* was found in the stomachs of fish species *Notothenia nudifrons* and *N. coriiceps neglecta* (Linkowski, Presler and Żukowski 1983), but was also recorded in the diet of the penguins *Pygoscelis adeliae* (Emison 1968). The list of predators feeding on the amphipods *Cheirimedon femoratus* and *Hippomedon kergueleni* is large. Besides such invertebrates as, for instance, *Glyptonotus antarcticus* (Bregazzi 1972a), they are consumed by the fish *Notothenia coriiceps neglecta* and *N. rossi marmorata* and, perhaps, by other representatives of the same family (Bregazzi 1972a, Thurston 1974, Richardson 1975, Linkowski, Presler and Żukowski 1983). The investigations of feeding preferences of fishes carried out in the Admiralty Bay proved, that both *Hippomedon kergueleni* and *Cheirimedon femoratus* are consumed willingly and in large quantities by *Notothenia coriiceps neglecta* and *N. rossi marmorata*. It was also noticed that *Ch. femoratus* prevailed in the diet of these fishes in winter, whereas *H. kergueleni* decisively dominated in summer (Linkowski, Presler and Żukowski 1983). Both amphipod species were recorded also in the stomachs of Antarctic birds. Bregazzi (1972a) mentioned them in the diet of *Daption capensis*, while Chevreux (1906) and Jażdżewski (1981) observed them in the stomachs of penguins *Pygoscelis antarctica* and *P. adeliae*.

All above data suggest that the competitive community of necrophagous invertebrates of the bottom of the Antarctic shelf significantly contributing to the decomposition of dead animal remnants, seriously accelerates the rate of matter and energy circulation in the Antarctic ecosystem.

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6. Резюме

В 1977 и 1980 годах в бухте Адмиральти (о. Кинг Джордж, Южные Шетландские о-ва) были проведены исследования некрофагических бентосных беспозвоночных. Используя ловушки с мясной приманкой, опускаемые со льда или устанавливаемые из моторной лодки на двух выбранных разрезах (фиг. 1 и 2) и поднимаемые через регулярные отрезки времени, было собрано 160 проб, содержащих почти 300 тысяч особей, принадлежащих к различным группам животных. Серия проб, собранных ловушками без приманки, а также несколько других критерий оценки разрешило выселекционировать среди 100 встреченных в ловушках таксонов 23 вида животных (немертины, моллюски, ракообразные, иглокожие) с несомненно некрофагическими склонностями и 10 видов, подозреваемых в некрофагии. Материал был разработан при помощи повсеместно используемых статистических методов и показателей, а также показателей нововведенных. Установлено, что некрофагические беспозвоночные образуют скопления, отличающиеся составом и структурой доминирования видов (фиг. 4—7). В зависимости от места выступания и времени года изменяется численность скоплений (фиг. 8). Обнаружено, что обычно существует положительная корреляция между увеличением глубины и биомассой летних скоплений некрофагов, в это же время индексы общего разнообразия Шаннона-Вивера указывают на высокое доминирование немногих видов на небольших (5 и 15 м) и больших (90 м) глубинах и более равное участие большего числа видов в структуре доминирования скоплений на промежуточных глубинах (30 и 60 м) (фиг. 9). Выделено несколько групп видов, которые обнаруживают подобные предпочтения мест обитания и заменяются в скоплениях (фиг. 11, 12 и 13). Сравнивая численность некрофагических беспозвоночных в скоплениях, находящихся в тех же самых станциях, но в различных временах года, определено сезонное замещение видов (фиг. 11—13). Выделено 3 группы некрофагических беспозвоночных: 1. некрофаги с более сильной склонностью к некрофагии зимой, 2. некрофаги с более сильной склонностью к некрофагии летом и 3. амбивалентные некрофаги.

Обнаружено, что некрофагические беспозвоночные, выступающие на дне бухты Адмиральти образуют конкурентное сообщество некрофагов. Выделено 3 взаимозаменяющиеся формы этого сообщества, которые размещаются зонально и связаны с характером отложений.

7. Streszczenie

W latach 1977 i 1980 przeprowadzono w Zatoce Admiralicji Wyspy Króla Jerzego badania nad nekrofagicznymi bezkręgowcami bentosowymi. Stosując pułapki z przynętą mięsną, opuszczane z lodu lub stawiane z łodzi motorowej na dwu wybranych przekrojach (rys. 1 i 2) i podnoszone w regularnych odstępach czasu, zebrano ok. 160 prób zawierających blisko 300 tysięcy osobników należących do różnych grup zwierzęcych. Seria prób zebranych pułapkami pozbawionymi przynęty oraz kilka innych kryteriów oceny pozwoliło na wyselekcjonowanie spośród blisko 100 spotykanych w pułapkach taksonów 23 gatunków zwierząt (wstężnice, mięczaki, skorupiaki i szkarłupnie) o niewątpliwie nekrofagicznych skłonnościach oraz 10 gatunków podejrzanych o nekrofagię. Materiał opracowano przy użyciu powszechnie stosowanych metod statystycznych i wskaźników, a także wskaźników nowo zaproponowanych. Ustalono, że bezkręgowce nekrofagiczne tworzą zgrupowania różniące się składem i strukturą dominacji gatunków (rys. 4—7). W zależności od miejsca występowania i pory roku zmienia się liczebność zgrupowań (rys. 8). Stwierdzono, że na ogół istnieje korelacja dodatnia pomiędzy wzrostem głębokości i biomasą letnich zgrupowań nekrofagów (rys. 8). Bogactwo gatunkowe zgrupowań na ogół zwiększa się ze wzrostem głębokości, zaś wskaźniki ogólnej różnorodności Shannona-Weavera wskazują na wysoką dominację niewielu gatunków na głębokościach małych (5 i 15 m) i dużych (90 m), i bardziej wyrównany udział większej liczby gatunków w strukturze dominacji zgrupowań na głębokościach pośrednich (30 i 60 m) (rys. 9). Wydzielono kilka grup gatunków, które wykazują podobne preferencje siedliskowe i wzajemnie zastępują się w zgrupowaniach (rys. 11, 12 i 13). Porównując liczebności bezkręgowców nekrofagicznych w zgrupowaniach obecnych na tych samych stanowiskach, lecz w różnych porach roku stwierdzono sezonowe zastępowania się gatunków (rys. 11—13). Wydzielono trzy grupy bezkręgowców nekrofagicznych: 1. nekrofagi o silniejszych skłonnościach do nekrofagii zimą, 2. nekrofagi o silniejszych skłonnościach do nekrofagii latem i 3. nekrofagii ambiwalentne. Stwierdzono, że bezkręgowce nekrofagiczne występujące na dnie Zatoki Admiralicji tworzą zespół konkurencyjny nekrofagów. Wyróżniono trzy zastępujące się formy tego zespołu, które są rozmieszczone strefowo i związane z rodzajem podłoża.

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