A comparison of the macrofaunal community structure and diversity in two arctic glacial bays – a 'cold' one off Franz Josef Land and a 'warm' one off Spitsbergen

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Abstract

The species composing the bottom fauna of Skoddebukta, a tidal glacier bay off West Spitsbergen (77°N), and Tikhaia Bay off Franz Josef Land (Hooker Island 80°N) were studied. Skoddebukta contained transformed Atlantic waters at a temperature of $> +4°C$ in summer, while the Arctic waters of Tikhaia Bay were at their summer maximum temperature of $< -0.5°C$. The glaciers were of different types: 'warm' at Skoddebukta and 'cold' at Tikhaia Bay. Over 210 benthic taxa were identified at both sites, 30% of species being common to both. The zoogeographical status of the fauna was similar in both bays. Cluster analysis of the samples revealed the existence of 7 associations. The associations mostly influenced by glacier or river outflow were significantly dominated by deposit feeders and displayed low diversity. The Tikhaia Bay community was more diverse than that in Skoddebukta, which is due to its better trophic conditions and lower level of inorganic sedimentation-induced disturbance.

1. Introduction

Polar marine basins, where the presence of a nearby glacier affects the hydrology, type of bottom sediments, level of sedimentation, water turbidity and nutrient supply, and hence the primary production, provide a specific habitat for benthic fauna (Pearson, 1980). The influence of glacial or glaciofluvial inflows on the macrobenthos of fjords and bays has been described for a number of localities in the Canadian Arctic (Thomson, 1982; Syvitski *et al.*, 1989), Greenland (Schmid and Piepenburg, 1993) and Svalbard (Gulliksen *et al.*, 1984; Węsławski *et al.*, 1990a; Kendall, 1994).

While the sublittoral benthos of Spitsbergen is relatively well-known as regards the taxonomy of animal groups like the Amphipoda (Bruggen, 1907; Stephensen, 1935–1942), few recent ecological studies have been done. Moreover, the benthic fauna of neighbouring Franz Josef Land is unknown in the western literature since a number of Russian studies (except those by Golikov and Averintsev (1977), Averintsev (1992) and Matishov (1993)) have not been translated. The aim of the present study is to compare the benthic fauna of two glacial bays – Skoddebukta off Spitsbergen and Tikhaia Bay off Franz Josef Land, two localities that are similar with respect to their geographical position, sediment type, salinity, overall size, and the presence of a tidal glacier. The major differences are in the water temperature – high off Spitsbergen (> +4°C in summer) and low off Franz Josef Land (maximum −0.7°C) and in the type of glacier – 'warm' in Skoddebukta and 'cold' in Tikhaia Bay.

There are a number of definitions and concepts of ecological organisational units such as community, assemblage, association or biome. A comprehensive list of these definitions proposed by the twentieth-century ecological literature is provided in Schrader-Frechette and McCoy (1993). In our study we use the term community to describe the whole macrofauna inhabiting the bay (which has well-defined boundaries) in accordance with the Schrader-Frechette and McCoy (1993) concept of community as a group of species recognised by quantitatively definable boundaries and/or by the interactions of their component species. According to these authors, an association is a community type or category recognised primarily through the appearance of the largely non-interacting species composing it, defined in terms of the appearance of component species rather than by any quantitative criterion or interacting species. A similar concept was applied by Thomson (1982), who defined such associations as groups of species tending to occur together and found under similar environmental conditions in different parts of the study area.

One of the most common measures of community structure is its diversity, which reflects the complexity of the biological interactions within it, the stage of its development, and the diversity and stability of the habitat. The problem of the biodiversity of the Svalbard benthic fauna was recently raised in Kendall and Aschan (1993) with regard to latitudinal gradients in the diversity of the macrobenthic infauna of soft sediments. In our study we aimed to compare community diversity in two bays, as well as the diversity of the associations within each of them.

2. Materials and methods

Material was collected at 35 stations in Skoddebukta (Spitsbergen) in July 1980 and at 24 stations in Tikhaia Bay (Hooker Island, Franz Josef Land) in August 1992 (Figs. 1 and 2). The irregular location of stations at the latter site was due to the difficult ice conditions. A rectangular dredge (80 x 30 cm) with a net of 1 mm mesh was used in Skoddebukta; in Tikhaia Bay samples were taken with a triangular dredge (30 x 30 cm) and a net of the same type. 5 to 10 l quantitative samples were sieved on a 1 mm mesh, and preserved in 4% formaldehyde solution.

The animals were identified at the lowest possible taxonomic level. The representativeness of the material collected was verified by plotting the number of species against the number of samples analysed. The percentage of samples was determined in which all the species present in the study material were found.

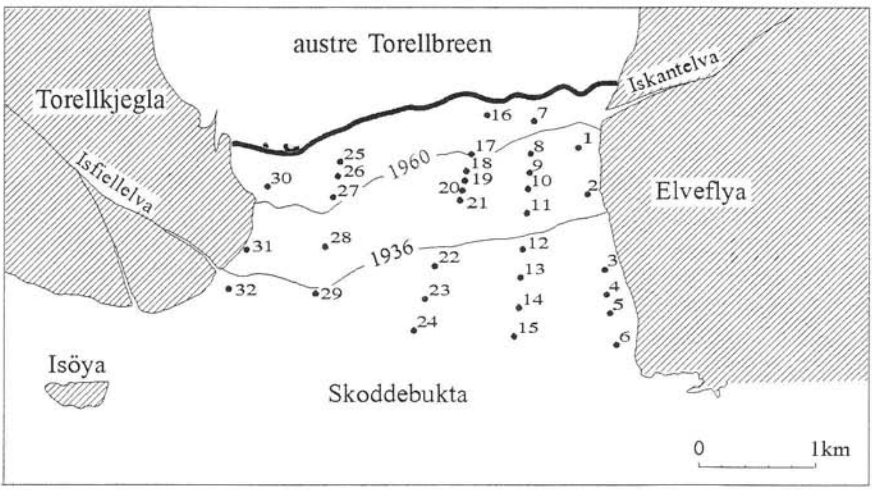

Fig. 1. The location of the sampling stations in Skoddebukta. The positions of the glacier front in 1936, 1960 and at the time of sample collection (1980) have been plotted

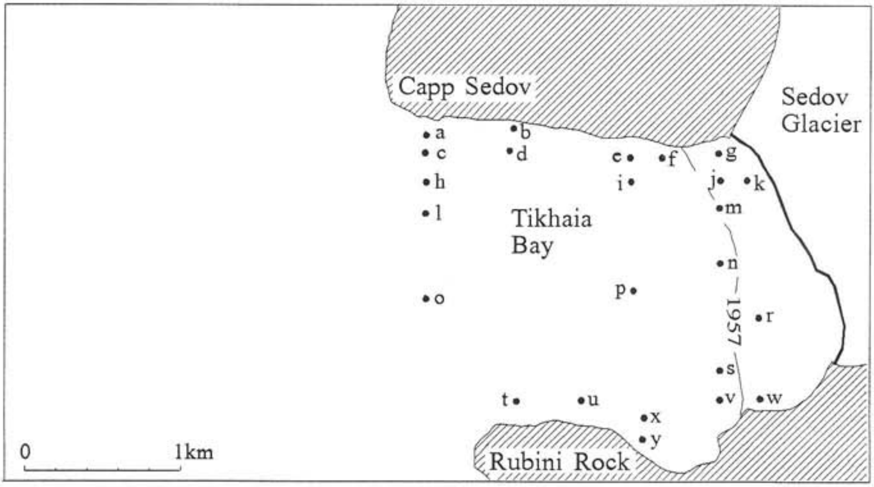

Fig. 2. The location of the sampling stations in Tikhaia Bay. The positions of the glacier front in 1957 and at the time of sample collection (1992) are plotted

The frequency (F%, the percentage of samples comprising specimens of a given species) and the dominance (D%, the proportion of the abundance of the species in question in the total abundance of macrofauna) were calculated for each species. These were classified according to their zoogeographical status, trophic ecology and maximum length. Zoogeographical distribution and maximum length were cited after Anisimova *et al.* (1992), Gromisz and Legeżyńska (1992), Różycki (1991), Węsławski (1991), Węsławski *et al.* (1990b), and Gajewska (1948). Three zoogeographical species groups were distinguished:

(1) arctic – occurring only in high arctic regions as defined by Dunbar (1968),

(2) arcto-boreal – occurring in both arctic and in boreal waters,

(3) boreal – occurring mainly in the North Atlantic; the northernmost boundary is in the European Arctic,

(4) cosmopolitan – organisms with an extensive distribution reaching south to the Mediterranean and tropical regions.

With regard to their feeding preferences, species were classified into trophic types: (1) suspension feeders, (2) deposit feeders, (3) carnivores (Gromisz and Legeżyńska, 1992; Kuznetsov, 1964; Fish and Fish, 1989; Aitken, 1990; Syvitski *et al.*, 1989; Schmid and Piepenburg, 1993).

Cluster analysis was applied to the species abundance data,[1] which were double-root transformed. Group average linking of Bray-Curtis similarities was performed and the similarity index calculated according to the Bray-Curtis (1957) formula:

$$S_{jk} = \frac{\sum_{i=1}^{s} \mid Y_{ij} - Y_{ik} \mid}{\sum_{i=1}^{s} (Y_{ij} + Y_{ik})}, \tag{1}$$

where

j, k – samples compared,

Y – abundance value for the i-th species,

s – number of species.

The faunal associations were distinguished from this cluster analysis. The typical species for each association were determined by the use of similarity breakdown analysis (Clarke, 1993) on the basis of their high contribution to the average similarity within the group (avS_i) and the high $\mathrm{avS}_i/\mathrm{SD}(\mathrm{S}_i)$ ratio.

Several species diversity measures were used: the number of species, the Shannon-Weaver Index and k-dominance curves. The Shannon-Weaver Index was calculated from

$$H = \sum_{i=1}^{s} \frac{n_i}{n} \log \frac{n_i}{n}, \tag{2}$$

where

s – number of species,

n_i – abundance of i-th species,

n – total macrofaunal abundance.

The k-dominance curves were obtained by plotting percentage cumulative abundance against species rank (Lambshead *et al.*, 1983).

3. Study area

Skoddebukta is an open, tidal-glacier bay off the west coast of Spitsbergen. The Torellbreen glacier, forming a 40–80 m high cliff over 3 km in length, flows into the bay. The bay is 2.5 x 3 km in size, and is relatively deep, most of it being between 20 and 50 m deep. Two conspicious underwater moraines mark the former glacier front line. Torellbreen is retreating relatively slowly: about 1 km of the sea bottom was newly exposed between 1960 and 1980. The bottom is covered with gray silty clay with

[1]The cluster and 'similarity breakdown' analyses, and the k-dominance plots were performed with use of programs from the PRIMER package kindly provided by the Plymouh Marine Laboratory.

numerous dropstones (Filipowicz and Giżejewski, 1992). The water temperature in summer ranges from +4 to +6°C, and the salinity from 30 PSU at the surface to 34.2 PSU at the bottom. A well-defined pycnocline occurs at a depth of 20–25 m in summer. The glacier discharges large amounts of turbid, sediment-laden freshwater into the bay; water transparency is less than 1 m in the main plume, and used to be 3 to 6 m in the outer part of the bay. Sedimentation is probably comparable to that at Recherfjorden, Bellsund, and reaches 20 g d.w. m^{-2} day^{-1}.

Tikhaia Bay is similar in size to Skoddebukta, with a shorter glacier front (about 2 km in length and 20–30 m high). The Jurij Lednik (glacier) is not very active, and its retreat from 1957 to 1992 has been estimated at less than 1 km. The bay is a deep basin, most of it being between 50 and 100 m deep. The bottom is covered with brownish-grey silt, with numerous dropstones. In summer the water temperature ranges from −0.7 to −1°C, the salinity from 33.4 to 34.01 PSU. There is a very weak vertical gradient in the T/S profile (Swerpel, 1992), the surface water is slightly colder and less saline because of the presence of permanent ice floes. Glacial discharge is limited to a few weeks in August; water transparency is from 7 to 11 m all over the bay, decreasing to 2 m at the glacier cliff (Wiktor and Zajączkowski, 1992). Sedimentation rates range from 1 to 2 g d.w. m^{-2} day^{-1}.

4. Results

4.1. Species composition

The increase in species number *vs.* the sample number collected was plotted for both data sets (Fig. 3). The number of species stops increasing after the 16th sample in the material from both Skoddebukta and Tikhaia Bay. Thus, in both cases, the total number of species present were found in less than 70% of samples.

The species list consists of 211 taxa (Tab. 1), the majority of which belong to 3 groups: Annelida, Crustacea and Mollusca. In the two bays about 30% of species were Crustaceans, Amphipoda being the most abundant class. The proportions of Annelida varied from 24% in Skoddebukta to 34% in Tikhaia Bay; the corresponding figures for Mollusca were 39% and 26%. 67 taxa (31%) were found at both sites, 42 (21%) were present in Skoddebukta only, and 102 in the Tikhaia Bay material only, which means that almost half of the taxa identified were found only at the latter site. 10 of the 16 most common species (frequency > 50%) were found in both localities. Thirteen species occurred with a frequency exceeding 25% at both sites – *Yoldia hyperborea, Macoma moesta, Anaitides greonlandica, Paroedicerus lynceus, Harmathoe imbricata, Pontoporeia femorata, Serripes greonlandicus,*

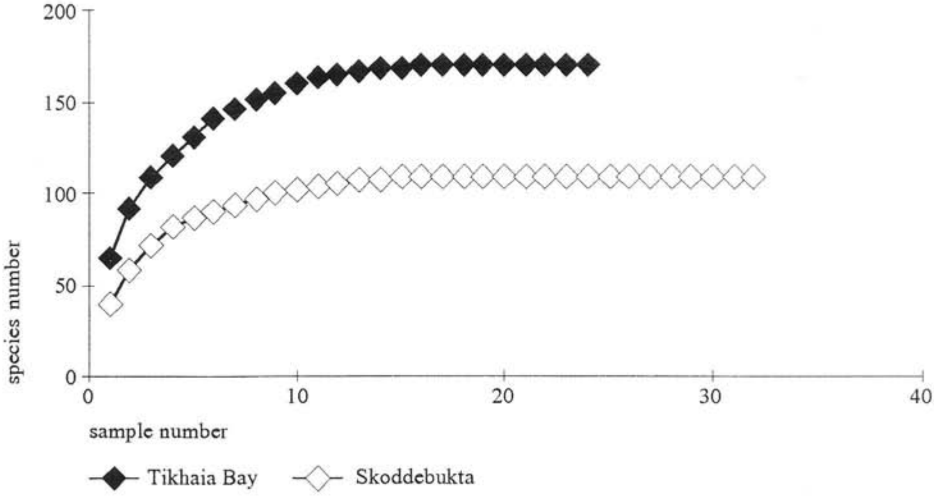

Fig. 3. The increase in the number of species *vs.* the sample number for both data sets

Table 1. Checklist of the macrofaunal taxa found in the material examined. The maximum length of the taxa specimens is given. The taxa are classified according to their zoogeographical status (A – arctic, AB – arcto-boreal, B – boreal, C – cosmopolitan) and trophic type (S – suspension feeders, D – deposit feeders, C – carnivores)

	Taxa	Skoddebukta D%	F%	Tikhaia Bay D%	F%	Max. length	Zoo-geogr. status	Trophic type
	Annelida							
1	*Aglaophamus malmgreni*			0.0	4	120	C	D
2	*Ammotryphane aulogaster*	0.07	6			60	AB	D
3	*Ampharete* sp.	24.16	31	0.1	8	30	N	D
4	*Amphitrite birulai*	0.02	6			20	A	D
5	*Amphitrite cirrata*	0.02	9			20	C	D
6	*Anaitides groenlandica*	0.44	53	0.6	46	450	AB	C
7	*Anaitides* sp.			0.0	4	150	C	C
8	*Antinoella sarsi*	0.50	53	0.6	58	68	AB	C
9	*Apistobranchus tullbergi*			0.1	13			D
10	*Artacama proboscidea*			0.1	8	80	AB	D
11	*Autolytus prolifer*			0.0	4	100	C	C
12	*Axionice flexuosa*			0.2	17	60	A	D
13	*Brada inhabilis*			0.3	13	40	A	D
14	*Brada villosa*	2.23	19	2.2	29	44	AB	D

Table 1. (continued)

Taxa	Skoddebukta D%	F%	Tikhaia Bay D%	F%	Max. length	Zoo-geogr. status	Trophic type
15 *Capitella capitata*	0.73	31	0.3	13	120	C	D
16 *Chaetosone setosa*	0.64	34	0.1	17	25	C	D
17 *Chone dunesi*			0.1	4	35	C	S
18 *Chone infundibuliformis*			0.0	8	120	AB	S
19 *Chone* spp.			0.0	4	35	N	S
20 *Diplocirrus hireutus*			0.1	8	30	A	D
21 *Diplocirrus* sp.			0.0	4	30	N	D
22 *Eteone flava*	0.02	6	0.2	21	120	AB	C
23 *Eteone longa*			0.1	21	160	C	C
24 *Eteone* sp.	0.25	22			100	N	C
25 *Eteone spitsbergensis*	0.04	6	0.1	17	100	AB	C
26 *Euchone nodosa*			0.1	13	30	AB	S
27 *Euchone papillosa*	0.01	3	0.2	13	30	AB	S
28 *Flabelligera affinis*			0.1	8	60	C	D
29 *Gattyana cirrosa*	0.12	16	0.0	4	50	AB	C
30 *Harmathoe imbricata*	0.17	34	1.0	38	65	C	C
31 *Harmathoe impar*			0.2	21	25	AB	C
32 *Harmathoe longisetis*			0.1	8	60	C	C
33 *Harmathoe* sp.			0.0	4	60	N	C
34 *Harmothoe nodosa*	0.01	3			90	AB	C
35 *Laonome kroyeri*			0.0	4	30	AB	S
36 *Leitoscoloplos armiger* s.l.	6.43	75	3.9	63	120	C	D
37 *Lumbrinereis fragilis* s.l.	0.24	19	0.6	54	380	AB	C
38 *Lyssipe labiata*	0.05	9			22	C	D
39 *Maldane sarsi*			0.6	17	110	C	D
40 *Neoamphitrite affinis*			0.1	13	110	AB	D
41 *Neoamphitrite groenlandica*			0.1	4	100	AB	D
42 *Nephtys ciliata*	0.01	6	0.1	13	300	C	C
43 *Nereimyra punctata*	0.04	6	4.2	13	25	B	D
44 *Nereis pelagica*			0.0	4	120	B	D
45 *Nicomache* sp.			0.0	4		N	D
46 Oligochaeta n.det			0.0	4	5	N	D
47 *Onuphis conchylega*			0.0	4	150	C	C
48 *Ophelina acuminata*			0.0	4	60	AB	D
49 *Ophelina cylindicaudata*			0.5	13	150	A	D
50 *Owenia fusiformis*	0.08	6			100	C	D
51 *Pholoe minuta*	0.01	3	0.1	8	25	C	C
52 *Pinosyllis compacta*			0.0	4			D
53 *Polydora quadrilobata*	5.67	13	1.1	29	25	AB	D
54 *Proclea malmgreni*			0.1	21	30	AB	D

Table 1. (continued)

Taxa	Skoddebukta D%	F%	Tikhaia Bay D%	F%	Max. length	Zoo-geogr. status	Trophic type
55 *Sphaerodorum gracilis*			0.2	21	60	AB	D
56 *Sphaerodropsis minuta*			0.0	4			D
57 *Spio filicornis*	0.50	31	0.4	25	30	C	D
58 Spionidae n.det			0.0	4	30	N	D
59 *Spirorbis spiryllum*			0.2	8	10	AB	S
60 *Terebellides stroemi*	0.03	6	5.4	63	75	C	D
61 *Terebellidomorpha* n.det			0.0	4	75	N	D
62 *Thelepus cincinatus*			0.1	4	200	AB	D
63 *Trichobranchus glacialis*			0.1	13	30	AB	D
64 *Typosyllis cerstedi*			0.0	8	30	AB	C
65 *Typosyllis cornuta*	0.01	3	0.0	4	50	A	C
66 *Typosyllis faeciata*			0.3	21	5	AB	C
Crustacea							
67 *Acanthostepheia behrigiensis*			0.6	38	37	A	D
68 *Acanthostepheia malmgreni*			0.1	4	45	A	D
69 *Ampelisca eschrichti*	0.01	6			35	AB	S
70 *Ampelisca* sp.			0.0	4	30	N	S
71 *Anonyx nugax*	0.03	13	0.4	33	41	AB	D
72 *Anonyx sarsi*			0.1	8	30	AB	D
73 *Apherusa glacialis*			0.2	13	20	A	D
74 *Arrhis phyllonyx*			0.6	29	20	A	D
75 *Atylus carinatus*	0.01	3	0.1	8	21	A	D
76 *Balanus balanus*	0.08	6	0.0	4	50	AB	S
77 *Byblis gaimardi*	0.03	16			23	AB	S
78 *Calathura brachiata*			0.1	13	45	AB	C
79 *Caprella septentrionalis*	0.01	3	0.1	4	26	AB	D
80 *Dajus mysidis*			0.0	4	4	AB	D
81 *Diastylis glaber*	0.01	6			28	AB	D
82 *Diastylis oxyrhyncha*	2.29	53			14	A	D
83 *Diastylis scorpionides*			0.5	38	11	A	D
84 *Erytrops erythropthalma*			0.0	4	10	AB	D
85 *Eualus gaimardi*	1.46	50	0.1	4	60	AB	D
86 *Eudorella emarginata*			0.0	4	12	AB	D
87 *Eusirus cuspidatus*			0.0	4	39	A	D
88 *Gammarellus homari*	0.18	16	1.8	13	35	AB	D
89 *Gammarus oceanicus*	0.01	3			38		D
90 *Gammarus setosus*	0.02	3	0.0	4	34	AB	D
91 *Halirages fulvocintus*			1.2	38	20	AB	D
92 *Haploops tubicola*			0.1	13	13	AB	D
93 *Hyas araneus*	0.24	34			100	AB	C

Table 1. (continued)

	Taxa	Skoddebukta D%	F%	Tikhaia Bay D%	F%	Max. length	Zoo-geogr. status	Trophic type
94	*Ischyrocerus anguipes*	0.16	16	0.5	8	17	AB	D
95	*Ischyrocerus* sp.			0.1	17	17	N	D
96	*Labbeus polaris*			0.5	21	70	AB	D
97	*Melita formosa*	0.27	38	0.2	4	18	A	D
98	*Menigrates obtusifrons*			0.0	4	13	B	D
99	*Menigrates* spp			0.2	13	13	N	D
100	*Metacaprella horrida*			0.1	13	20	A	D
101	*Monoculodes borealis*	0.01	3	0.3	21	15	AB	D
102	*Monoculodes longirostris*	0.14	19	0.0	8	18	A	D
103	*Monoculodes packardi*			0.0	4	7	AB	D
104	*Munna spitsbergensis*			0.1	25	5	A	D
105	*Munnopsis typica*			0.0	4	18	A	D
106	*Mysis arcticoglacialis*			0.0	4	25	A	D
107	*Mysis oculata*	3.01	69	7.0	75	39	AB	D
108	*Onisimus caricus*			1.3	21	29	A	D
109	*Onisimus edwardsi*			0.6	21	15	A	D
110	*Onisimus littoralis*	0.28	13	0.1	21	25	A	D
111	*Orchomene minuta*	0.07	6	0.6	17	11	A?AB	D
112	Ostracoda n.det			0.8	25	3	N	D
113	*Pagurus pubescens*	0.22	31			100	B	D
114	Pantopoda n.det			0.2	17	10	N	D
115	*Parapleustes bicuspis*	0.02	3			12	AB	D
116	*Paroediceros lynceus*	0.91	44	0.4	25	25	A	D
117	*Pleustes medius*	0.01	6			20	A	D
118	*Pleustes panoplus*	0.01	3	0.2	25	21	A	D
119	*Pontoporeia femorata*	0.55	25	0.5	33	16	AB	D
120	*Rozinante fragilis*			0.1	13	20	A	D
121	*Sabinea septemcarinata*	0.71	41	0.1	17	80	A	D
122	*Sclerocrangon boreas*	0.01	3	0.0	4	90	B	D
123	*Sclerocrangon ferox*			0.1	8	130	A	D
124	*Spirontocaris spinus*	0.01	3	0.0	4	40	AB	D
125	*Spirontocaris turgida*	0.07	16	0.0	4	60	A	D
126	*Synidothea bicuspidata*	0.01	3	0.0	8	30	AB	D
127	*Synidothea nodulosa*	0.08	3			30	AB	D
128	*Syrrhoe crenulata*			0.2	8	12	AB	D
129	Tanaidacea n.det			0.0	8	5	N	D
130	*Weyprechtia pinguis*	0.25	19	0.7	25	25	A	D
	Mollusca							
131	*Arcidea jeffreysii*			0.0	4	11	A	D
132	*Astarte borealis*			2.0	50	55	AB	S

Table 1. (continued)

	Taxa	Skoddebukta D%	Skoddebukta F%	Tikhaia Bay D%	Tikhaia Bay F%	Max. length	Zoo-geogr. status	Trophic type
133	*Astarte crenata*			0.8	38	45	A	S
134	*Astarte eliptica*			0.3	21	35	AB	S
135	*Astyris rosacea*	0.01	6	0.0	4	10	AB	D
136	*Buccinum angulosum*	0.03	6			55	A	C
137	*Buccinum fragile*	0.09	19			60	AB	C
138	*Buccinum glaciale*	0.01	3	0.2	21	80	A	C
139	*Buccinum undatum*	0.03	13			161	AB	C
140	*Bucinum cyaneum*			0.0	4	56	A	C
141	*Cardium ciliatum*	0.07	22			60	A	S
142	*Cylichna alba*	0.15	16	5.7	29	11	AB	C
143	*Cylichna arctica*	0.01	6			9	A	C
144	*Cylichna occulta*			0.0	4	9	A	C
145	*Cylichna scalpta*	0.06	16			9	A	C
146	*Dacrydium vitreum*			0.1	13	6	A	D
147	*Diplodonta torelli*	0.01	3			25	A	D
148	*Hiatella arctica*	0.10	22	1.0	13	70	K	S
149	*Liocyma fluctuosa*	1.72	22	0.1	4	30	A	S
150	*Lyonsia arenosa*	0.05	6			40	A	D
151	*Macoma calcarea*			0.5	17	54	AB	D
152	*Macoma moesta*	3.32	63	0.7	29	35	A	D
153	*Macoma torelli*	0.05	13			20	A	D
154	*Margarites coastalis*			1.4	25	25	A	C
155	*Margarites groenlandicus*	0.01	3	5.2	33	12	AB	C
156	*Musculus laevigatus*			0.3	17	70	A	S
157	*Musculus niger*			0.2	29	45	AB	S
158	*Musculus* sp.	0.43	41			40	N	S
159	*Mya pseudoarenaria ?*			0.0	4	40	AB	S
160	*Mya trunctata*	0.03	3	0.3	25	80	AB	S
161	*Natica clausa*	0.08	22	0.0	4	40	AB	C
162	*Neptunea borealis*	0.01	3			13	A	D
163	*Nucella lapilus*	0.01	6			30	B	C
164	*Nucula delphinodonta*	0.13	22			5	B	D
165	*Nuculana minuta*	0.09	13			20	AB	D
166	*Nuculana pernula*	0.95	31	0.7	42	38	AB	D
167	*Nuculoma tenuis*	0.64	34	0.0	4	18	AB	D
168	Nudibranchia n.det	0.01	3	0.1	4	20	N	D
169	*Oenopta harpularia*	0.10	6			15	AB	C
170	*Oenopta nobilis*			0.1	8	22	AB	C
171	*Oenopta piramidalis*	0.01	3	0.0	4	16	A	C
172	*Oenopta scalaris*	0.26	16			26	AB	C

Table 1. (continued)

Taxa	Skoddebukta D%	F%	Tikhaia Bay D%	F%	Max. length	Zoo-geogr. status	Trophic type
173 *Oenopta violacea*	0.02	3	0.1	8	7	AB	C
174 *Onoba mighelsi*			0.0	8	4	AB	D
175 *Pandora glacialis*			0.1	4	30	A	D
176 *Philline finmarchica*			0.6	13	7	AB	D
177 *Polynices nanus*	0.01	6			6	B	D
178 *Polynices pallidium*	0.03	13			25	AB	D
179 *Portlandia arctica*	3.96	34	0.2	13	39	A	D
180 *Retusa obtusa*			0.1	13	3	AB	C
181 *Retusa partenuis*	0.01	3			3	A	C
182 *Serripes groenlandicus*	0.14	28	1.8	29	85	A	S
183 *Thracia myops*			0.0	4	35	AB	S
184 *Thyasira flexuosa*			3.1	33	8	AB	S
185 Thyasiridae n.det	10.86	72			8	N	S
186 *Velutina velutina*	0.01	3			25	AB	D
187 *Volutopsius defromis*	0.01	3			100	A	D
188 *Yoldia hyperborea*	9.04	66	0.4	29	46	A	D
189 *Yoldiella frigida*			0.0	4	7	A	D
190 *Yoldiella lenticula*			0.0	4	10	A	D
Chordata							
191 *Eumicrotremus* sp.			0.2	13	100	N	C
192 *Liparis fabricii*	0.03	16	0.0	8	180	A	C
193 *Lumpenus lampraeteformis*	0.12	22			200	AB	C
194 *Myoxocephalus scorpius*	0.30	22	0.1	13	600	AB	C
Coelenterata							
195 Anthozoa n.det	0.03	6	0.1	4	50	N	S
Echinodermata							
196 *Elpidia glacialis*			0.0	4	20	A	D
197 *Henricia* sp.			0.0	4	120	N	D
198 *Myriotrochus rinkii*	72.93	31	0.4	13	60	AB	D
199 *Ophiacanta bidentata*			0.9	29	12	AB	D
200 *Ophiocten sericeum*	0.08	19	8.3	67	18	AB	D
201 *Ophiura robusta*			10.4	38	10	AB	D
202 *Ophiura sarsi*			0.0	4	40	AB	D
203 *Stegophiura nodosa*	9.89	63			20	AB	D
204 *Strongylocentrotus droebachiensis*			0.1	8	90	AB	D
Bryozoa							
205 *Alcyonidium disciformae*	0.02	3	4.8	33	100	A	S
206 *Alcyonidium gelatinosum*			0.1	8	150	AB	S

Table 1. (continued)

	Taxa	Skoddebukta D%	F%	Tikhaia Bay D%	F%	Max. length	Zoo-geogr. status	Trophic type
	Protozoa							
207	*Cornuspira foliacea*			0.3	8	13	K	D
208	Foraminifera n.det			0.5	13	5	N	D
209	*Miliolina* spp.			0.0	4	2	N	D
	Priapulida							
210	*Priapulus caudatus*	0.24	25	0.4	8	80	AB	D
	Sipulunculida							
211	*Phascolosoma* sp.	0.16	44			20	N	D

Nuculana pernula, Spio filicornis, Antinoella sarsi, Leitoscoloplos armiger s.l. and *Mysis oculta*. The last three are common species in both areas (frequency > 50%). *Astarte borealis*, a common species in Tikhaia Bay, was absent in Skoddebukta; the reverse applied to the Thyasiridae, *Stegophiura nodosa* and *Diastylis oxyryncha*.

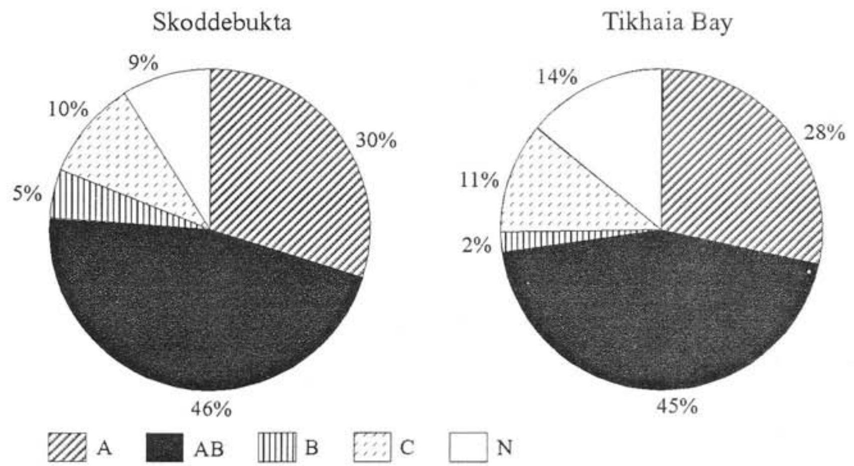

Fig. 4. The ratios of organisms of different zoogeographical status to the total number of species. The species were classified as: A – arctic, AB – arcto-boreal, B – boreal, C – cosmopolitan. The zoogeographical status of the higher taxa was not determined (N – non-classified)

The fauna of both areas enjoy a similar zoogeographical status (Fig. 4): about 30% of species have been classified as typical of the arctic zone, 45% are arcto-boreal and 10% cosmopolitan. The proportion of boreal species in the total number of species varied slightly, from 2% in Tikhaia Bay to 5% in Skoddebukta.

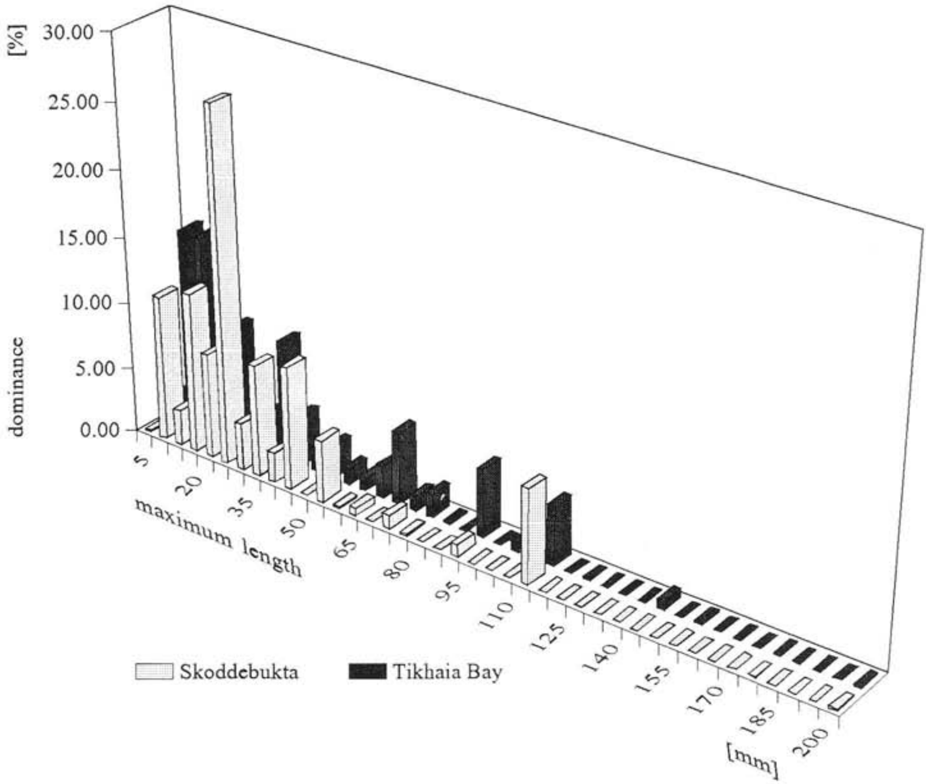

Fig. 5. The distribution of ratios of species characterised by different L_{max} (for $L_{max} \leq 200$ mm) to the total macrofauna abundance in Skoddebukta and Tikhaia Bay

The frequency of species' maximum length was similar in the two bays, the most common length classes being 10–20 mm (Fig. 5). Animals of maximum length from 60 to 100 mm were more common in Tikhaia Bay.

4.2. Faunal associations

Cluster analysis of samples revealed the existence of 4 benthic associations in Skoddebukta (S1, S2, S3, S4; Figs. 6 and 7) and 3 in Tikhaia Bay (T1, T2, T3; Figs. 8 and 9). There were samples in both sets that could not be

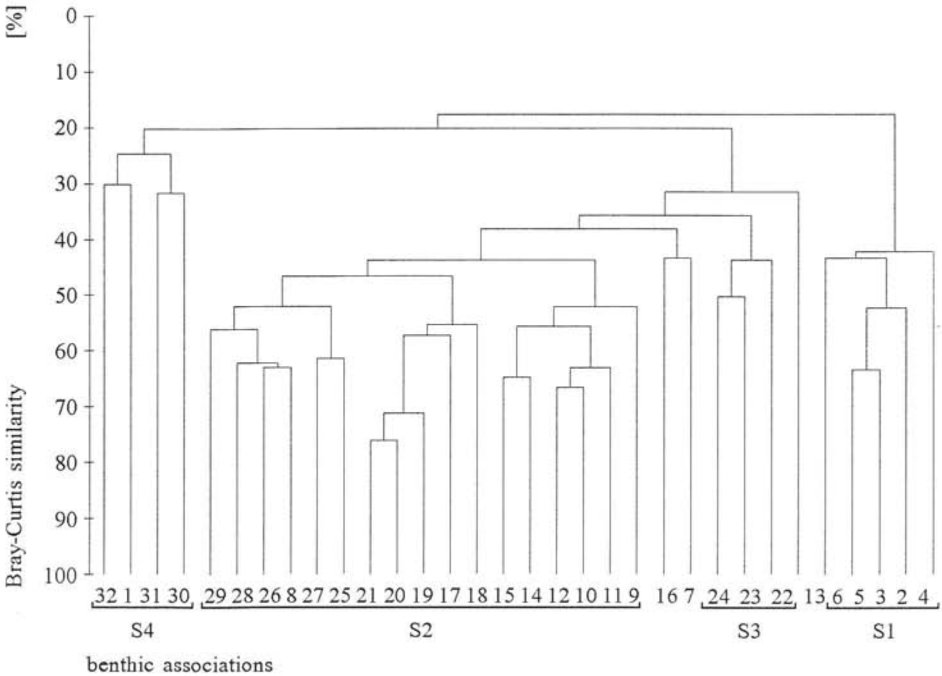

Fig. 6. The result of the cluster analysis of samples from Skoddebukta performed using the Bray-Curtis similarity index and double-root data transformation

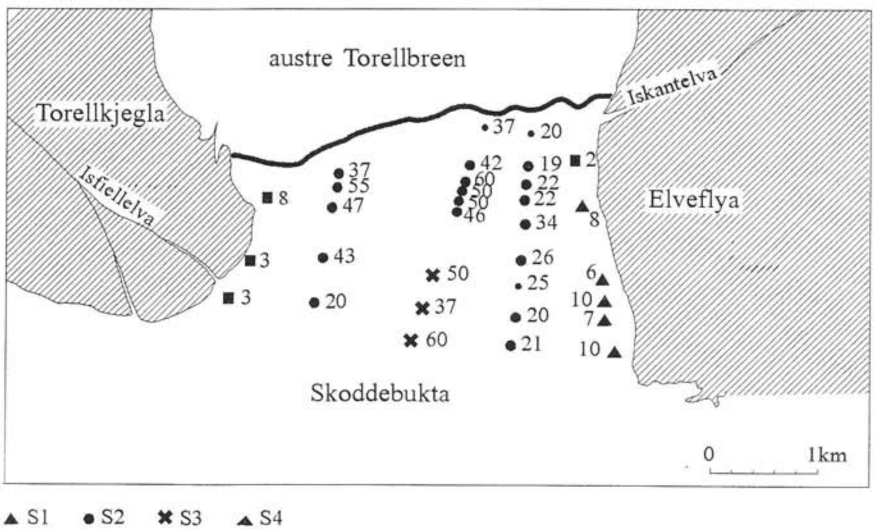

Fig. 7. The distribution of the associations distinguished in Skoddebukta. The small dots represent stations not included in any association. The depths of the sampling sites at each station are given

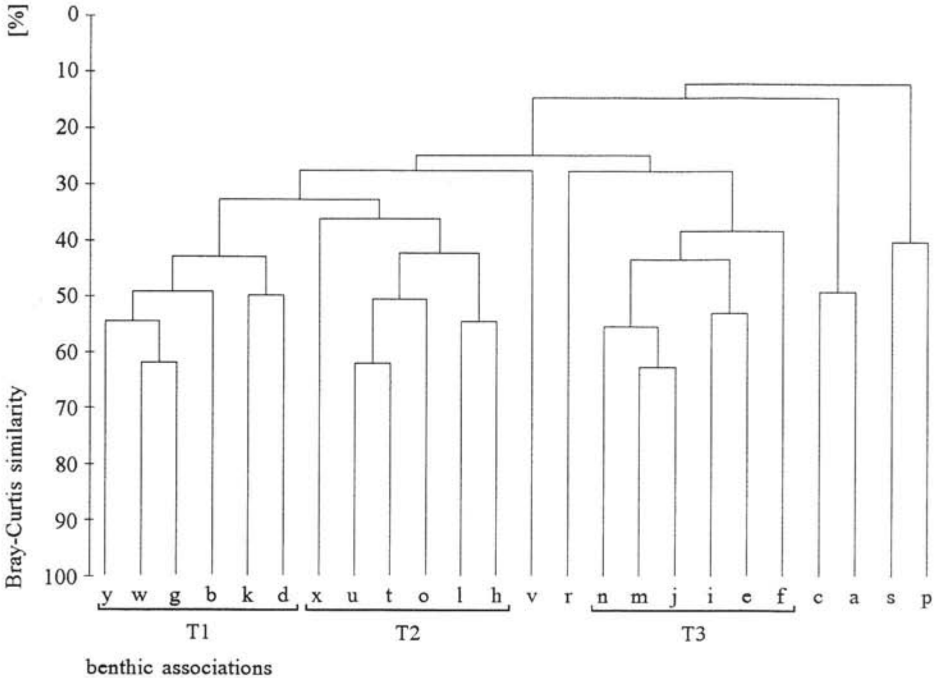

Fig. 8. The result of the cluster analysis of samples from Tikhaia Bay performed using the Bray-Curtis similarity index and double-root data transformation

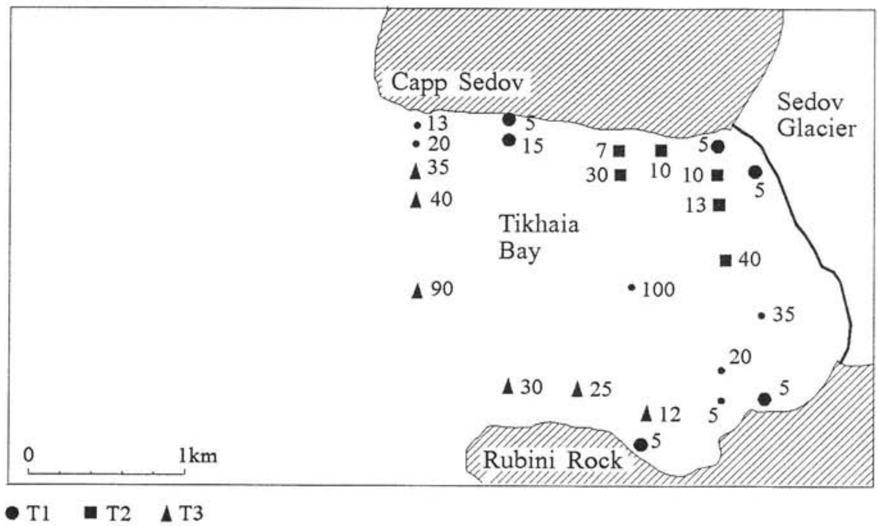

Fig. 9. The distribution of the associations distinguished in Tikhaia Bay. The small dots represent stations not included in any association. The depth of the sampling sites at each station are given

included in these associations. As they did not form any other distinct groups either, they are not covered by the following analysis.

Association S1 is found on the shallow (mean depth 8.5 m), stony bottom, covered by macrophytes, situated along the south coast of Skoddebukta. The most prominent organisms (Tab. 2) here are crustaceans (*M. oculta, Weyprechta pinguis, Eualus gaimardi, Gammarellus homari*), the fish feeding on them *Myoxocephalus scorpius* and the bivalve *Liocyma fluctuosa.*

Table 2. The species characteristic of the associations distinguished in the two bays. The frequency (F%), dominance (D%), contribution to the average similarity within the group (avS_i) and the $avS_i/SD(S_i)$ ratio are given for each species. The average similarity within the group (av. sim.) and its standard deviation are given for each association

Tikhaia Bay				
Species	F%	D%	avS_i	$avS_i/SD(S_i)$
Ass. T1 av. sim. = 38.98	SD = 7.153			
Alcyonidium disciforme	100	9.39	3.8	5.49
Mysis oculta	100	9.97	3.6	7.18
Ophiocten sericeum	100	7.87	3.1	6.91
Serripes groenlandicus	100	3.58	2.6	2.83
Lumbrinereis fragilis s.l.	100	0.76	1.9	4.12
Antinoella sarsi	100	0.59	1.8	4.89
Leitoscoloplos armiger s.l.	83	3.54	1.6	1.33
Brada villosa	83	4.21	1.4	1.28
Cylichna alba	67	11.15	1.3	0.75
Yoldia hyperborea	83	0.63	1.2	1.27
Diastylis scorpionides	83	0.80	1.2	1.23
Ass. T2 av. sim. = 33.44	SD = 7.809			
Astarte borealis	83	2.45	3.3	3.4
Astarte crenata	83	1.54	3	2.93
Ophiocten sericeum	83	12.41	2.8	1.31
Terebellides stroemi	83	1.68	2.8	2.63
Ophiura robusta	50	22.79	2.5	0.74
Harmathoe imbricata	83	1.47	1.7	1.25
Nuculana pernula	67	0.70	1.6	1.22
Ostracoda n.det	50	1.26	1.6	0.7
Anaitides groenlandica	83	1.33	1.6	1.26

Table 2. (continued)

Tikhaia Bay				
Species	F%	D%	avS_i	$avS_i/SD(S_i)$
Ass. T5 av. sim. = 41.90 SD = 9.557				
Leitoscoloplos armiger s.l.	100	15.58	8.1	5.03
Terebellides stroemi	100	14.77	6.6	2.4
Mysis oculta	83	6.33	4.4	1.12
Acanthostepheia behrigiensis	83	2.11	4.1	1.24
Antinoella sarsi	83	1.30	3.1	1.27
Skoddebukta				
Ass. S1 av. sim. = 43.01 SD = 10.965				
Mysis oculta	100	30.11	9.6	2.91
Weyprechta pinguis	100	3.06	6.1	4
Myoxocephalus scorpius	100	3.64	5.8	5.93
Liocyma fluctuosa	80	21.09	4.6	1.12
Eualus gaimardi	80	13.48	3.9	1.1
Gamarellus homari	80	2.23	3.8	1.11
Ass. S2 av. sim. = 42.98 SD = 9.195				
Yoldia hyperborea	100	9.56	6.4	2.5
Thyasiridae n.det	94	11.93	4.8	1.55
Stegophiura nodosa	94	10.45	3.4	1.35
Macoma moesta	94	3.60	3.3	2.13
Leitoscoloplos armiger s.l.	94	6.98	3.1	1.41
Diastylis oxyryncha	94	2.58	2.7	1.58
Ass. S3 av. sim. = 40.76 SD = 2.883				
Mysis oculata	100	9.76	6.4	4.09
Thyasiridae n.det	100	9.45	5.7	7.11
Pagurus pubescens	100	2.74	5.2	7.53
Eualus gaimardi	100	3.35	4.6	5.64
Melita formosa	100	3.96	4.6	5.64
Ass. S4 av. sim. = 26.3 SD = 7.644				
Phascolosoma sp.	100	3.93	8.8	6.01
Spio filicornis	75	3.06	3.9	0.91

S2 is found on the muddy and sandy-muddy bottom of the deeper, central part of the bay (depth from 19 to 60 m, average 29.4 m). The characteristic species here are the bivalves *Y. hyperborea*, *M. moesta* and Thyasiridae – the ophiuroid *S. nodosa* and the cumacean *D. oxyryncha.*

On the muds and gravels of the deepest bottom (mean depth 52 m) organisms typical of association S3 were found: these were the crustaceans *M. oculta, Pagurus pubescens, E. gaimardi, Melita formosa*, and Thyasiridae.

Association S4 consists of samples taken close to the river mouths and on the shallow muddy-sandy bottom influenced by the river inflow. The organisms characteristic of this association are the sipunculid *Phascolosoma* sp. and the polychaete *S. filicornis.*

The first association distinguished in Tikhaia Bay, T1, consists of samples taken in shallow, coastal waters (average depth 6.7 m), on bottoms of different types, varying from muds to stones. As a result of the similarity breakdown analysis we selected a number of species characterised by high avS_i and a high $avS_i/SD(S_i)$ ratio (Tab. 2). The most typical ones are the bryozoids *Alcyonidium disciforme, M. oculta* and *Ophiocten sericeum.* The other characteristic species here are the molluscs *S. greonlandicus, Y. hyperborea*, the polychaetes *Lumbrinereis fragilis* s.l., *A. sarsi, Brada villosa, L. armiger* s.l. and the crustacean *Diastylis scorpionides.*

The central, deeper part of the bay (depth from 20 to 50 m), with a muddy bottom is occupied by organisms forming association T2. The characteristic organisms here are the bivalves *A. borealis, Astarte crenata, N. pernula*, the polychaetes *Terebellides stroemi, H. imbricata, A. groenlandica* and the ophiuroids *O. sericeum, Ophiura robusta.*

Association T3 is situated in the region strongly influenced by the glacier. The samples were taken at different depths (5–20 m) on the muddy bottom. The typical species are the euryhaline polychaetes *L. armiger* s.l., *T. stroemi, A. sarsi* and the crustaceans *M. oculta, Acanthostepheia behrigiensis.*

As regards the trophic ecology of the organisms, deposit feeders were significantly dominant in all the associations (Fig. 10). The highest ratios of this group to the total abundance – 83% and 77% – were recorded in S2 and S3, the deep water associations in Skoddebukta. The most abundant deposit feeders there included *Ampharete* sp., *S. nodosa, Y. hyperborea, L. armiger* s.l., *Polydora quadrilobata* and *Portlandia arctica* in S2, and *Y. hyperborea, P. femorata, M. oculata, Chaetosone setosa* and *L. armiger* s.l. in S3. Thyasiridae made up most of the 10% of suspension feeders in these two associations. At similar depths in Tikhaia Bay (T2) the proportion of deposit feeders was lower (66%), the most important of them

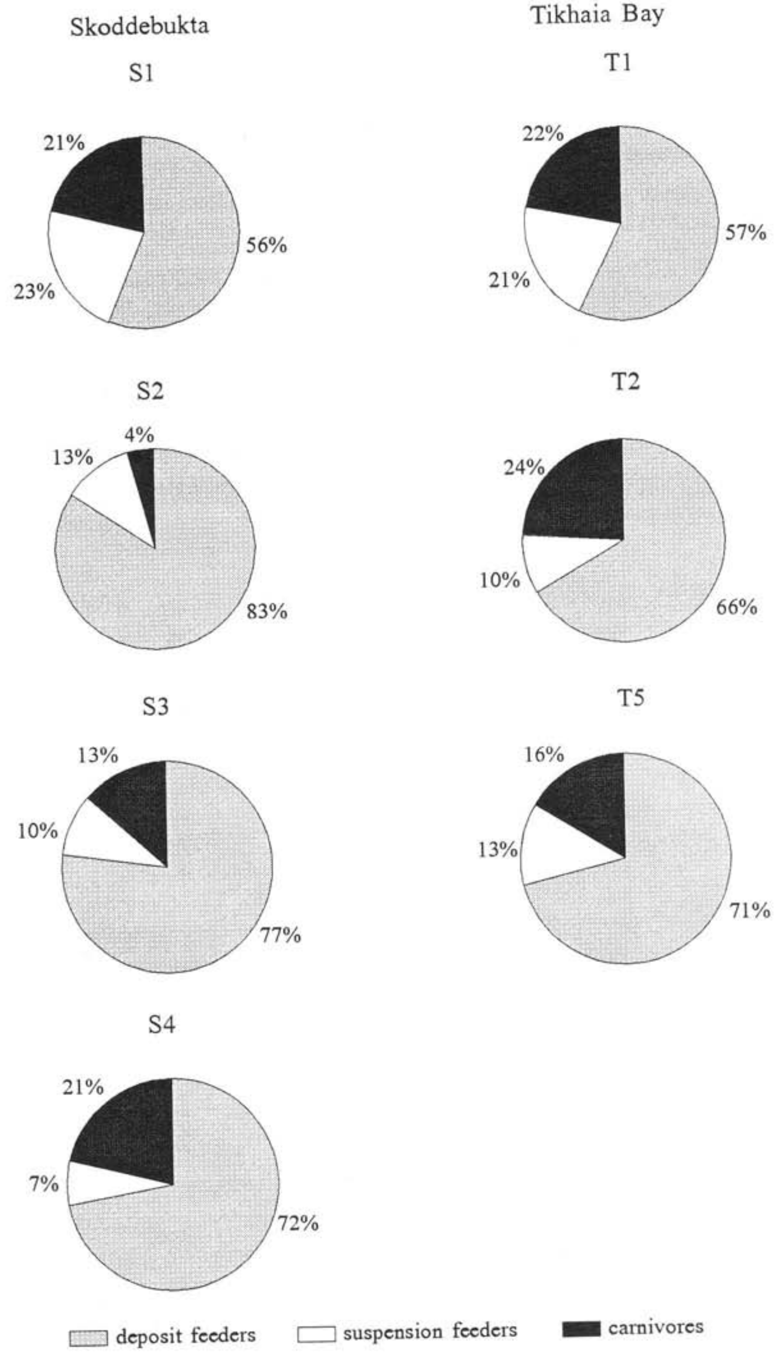

Fig. 10. The distribution of ratios of organisms of different trophic types to the total faunal abundance in the associations

being *O. robusta, O. sericeum, G. homari* and *Haligrades fulvocintus*. The suspension-feeding bivalves *Hiatella arctica, A. borealis, A. crenata, Musculus laevigatus* constituted much of the 10% of suspension feeders. The very high percentage of carnivores (24%) is due to the abundant occurrence of the carnivorous gastropod *Margarites groenlandica*.

A very similar distribution of feeding types was observed in the two shallow water associations – S1 in Skoddebukta and T1 in Tikhaia Bay. The proportions of deposit feeders were relatively low – *ca* 56%. In both bays the most important deposit feeders were the crustaceans *M. oculata, B. villosa* and the ophiuroids – *S. nodosa* in S1 and *O. sericeum* in T1. In the latter area deposit-feeding annelids – *Nereimyra punctata, T. stroemi, L. armiger* s.l. – were also abundant. Suspension feeders and carnivores made up about 20% of the fauna in these associations. In S1 the most important suspension feeder was the bivalve *Liocyma fluctuosa*, while in T1 they were the bryozoid *A. disciforme*, the bivalve *S. groenlandicus*. The carnivores are represented by an amphipod *E. gaimardi* and a fish *M. scorpius* in S1, gastropods *Cylichna alba* and *Margarites coastalis* in T1.

Deposit feeders made up *ca* 70% of the fauna, both in the glacier-influenced association in Tikhaia Bay (T3) and in the river-influenced association in Skoddebukta (S4). Among the most abundant deposit feeders in these associations were the polychaetes *L. armiger* s.l., *T. stroemi* and *P. quadrilobata* in T3, *Capitella capitata, L. armiger* s.l. in S4 and the isopod *M. oculata* in both areas. Besides these, *P. lynceus, M. moesta, Phascolosoma* sp. and *S. nodosa* occurred abundantly in S4, and *Ophelina cylincaudata, O. sericeum* and *M. moesta* in T3. The most significant suspension feeders in both bays were Thyasiridae; the whole group made up 7% of the fauna in S4 and 13% in T3. The carnivores here were mostly amphipods – *Onisimus caricus* in T3, *Onisimus littoralis* and *A. groenlandica* in S4, and polychaetes – *A. sarsi* and *L. fragilis* s.l. in T3 and *A. sarsi* and *Eteone* sp. in S4.

4.3. Diversity

Both the Shannon-Weaver Index and the k-dominance curves show the Tikhaia Bay fauna to be much more diverse than that of Skoddebukta. The Shannon-Weaver Index in Skoddebukta varied from 0.383 at station 13 to 2.489 at station 10, with a mean value of 1.814. The average for Tikhaia Bay was 2.044, the maximum at station d was 3.005, and the minimum at station l was 1.105. The frequency distribution of the diversity index for both bays is shown in Fig. 11 and the k-dominance curves for both bays are plotted in Fig. 12. As the curves do not intersect at any point, the data sets

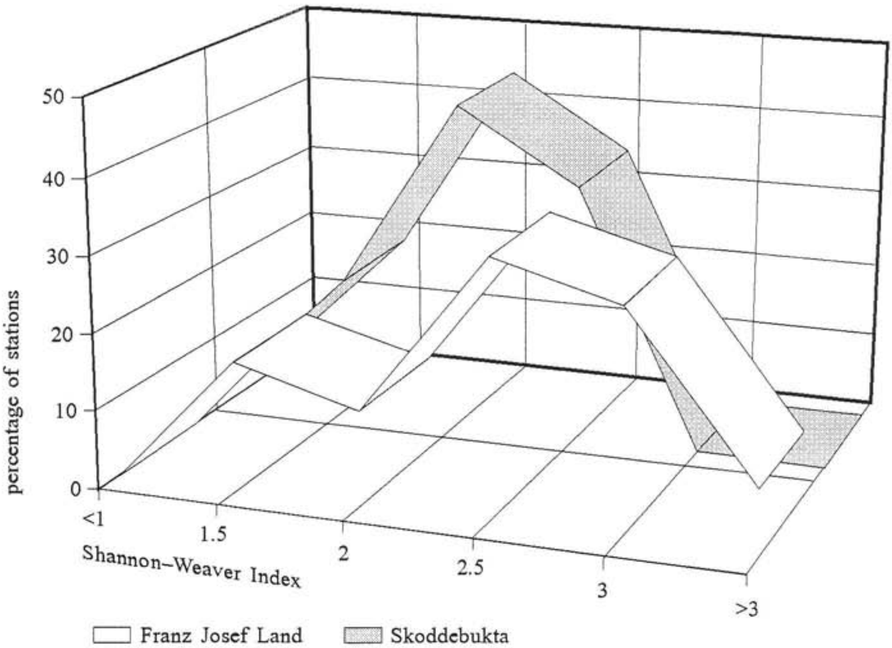

Fig. 11. Percentage of stations with a given Shannon-Weaver Index in Skoddebukta and Tikhaia Bay

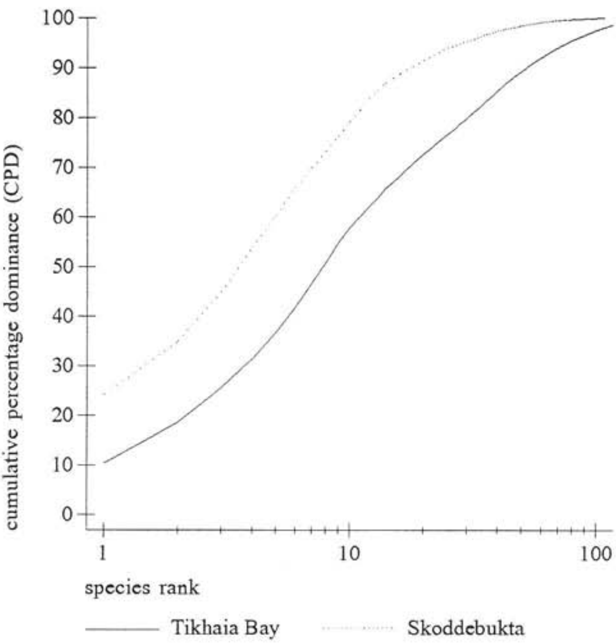

Fig. 12. K-dominance curves plotted for both data sets

are comparable in terms of intrinsic diversity (Lambshead *et al.*, 1983). The Skoddebukta curve always lies above the Tikhaia Bay curve.

The diversity in the associations was compared. In Tikhaia Bay the lowest Shannon-Weaver Index and the lowest number of species were recorded in T3, the highest values of both parameters in T1 (Tab. 3). Since the k-dominance curves for T3 and T2 intersect, these associations are not comparable in terms of intrinsic diversity (Lambshead *et al.*, 1983). Fig. 13 shows that association T1 is more diverse than either T2 or T3.

Table 3. The average number of species per sample (n) and the Shannon-Weaver Index (H) for the associations distinguished in the two bays

	Skoddebukta				Tikhaia Bay		
Associations	S1	S2	S3	S4	T1	T2	T3
n	14.2	25.4	16	8.8	43.8	33	16.2
H	1.693	1.852	2.015	1.757	2.830	2.409	2.098

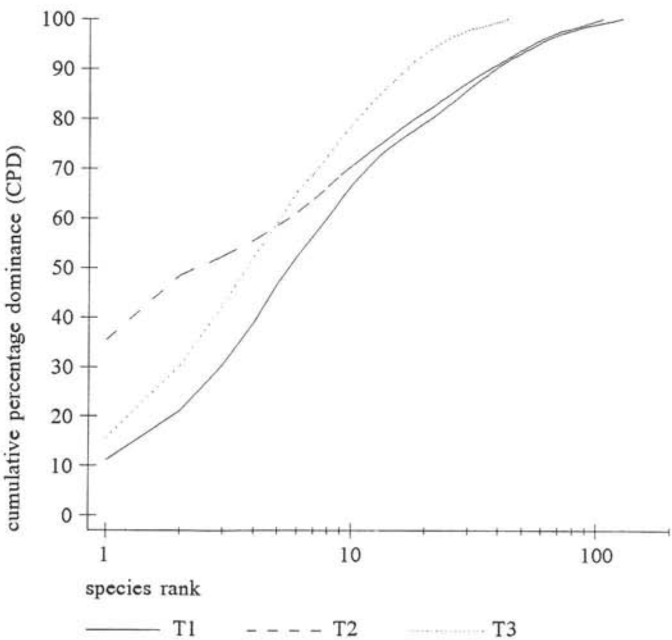

Fig. 13. K-dominance curves plotted for the associations in Tikhaia Bay

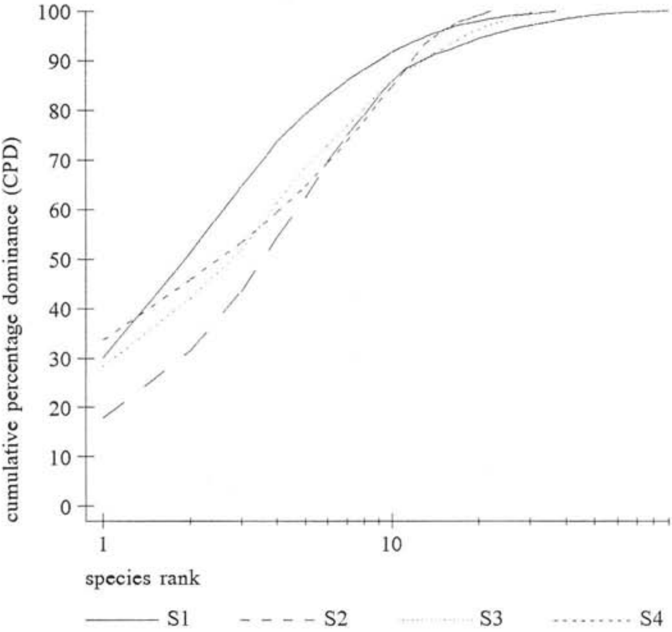

Fig. 14. K-dominance curves plotted for the associations in Skoddebukta

In Skoddebukta the highest Shannon-Weaver Indices were recorded in the deepest, outermost association S3, the lowest in the macrophytic association S1. S2 was characterised by the highest number of species and high Shannon-Weaver Indices. The samples from S4 contained the smallest number of species and calculated values of the Shannon-Weaver Index were not high. It is difficult to interpret the k-dominance curves plotted for the Skoddebukta associations (Fig. 14) since most of the curves intersect each other. It can only be stated that S3 was more diverse than S1.

5. Discussion

The species/sample plots showed that the material collected was representative of the two bays. In both, the total number of species present were found in less than 70% of samples. All of these were taken with a dredge, which may have affected the species composition. The disadvantage of this gear is that is does not dig deeply enough to sample the majority of the burrowing animals inhabiting the top 10 cm of sediment (Holme, 1964). Hence some infaunal species (mostly polychaetes and bivalves) could have been underrepresented in this analysis. The other group which might have been underrepresented in the material due to the sampling method are hard-bottom organisms. On the other hand the rectangular dredge is a suitable piece of equipment for sampling epifauna (Holme, 1964), and the number of mobile and scarce hyperbenthic species collected can be much higher as compared to the grab samples.

The species list consists of 211 taxa, all of which are known from the published checklists of the coastal fauna of Svalbard (Gulliksen and Holthe, 1992) and Franz Josef Land (Matishov, 1993).

In both areas the fauna was dominated by arctic-boreal elements (*ca* 45% of species). The scarcity of typically arctic species is characteristic of the arctic marine benthos and is explained by the brief period of its evolution, which has not allowed much speciation to occur so far (Curtis, 1975). In the material collected, arctic species comprised *ca* 30% of the macrofauna. The very similar zoogeographical status of the fauna in the two bays is surprising, since Franz Josef Land is commonly regarded as a typically high-arctic locality, while west Spitsbergen falls within the subarctic category (Dunbar, 1968; Atlas Arktiki, 1980). One explanation for this is the dominance of polychaetes and bivalves – animals with very wide distributions, and hence poor as a tool in zoogeographical analysis. If one considers the Amphipoda only, one can see more clearly the predominance of high-arctic species (*O. carinus, Acanthostepheia malmgreni, Acanthostepheia behrigiensis, Syrrhoe crenulata*) in Tikhaia Bay (Tab. 1). The much stronger influence of Atlantic waters in the ocean-exposed, 'warm' Skoddebukta is reflected in the slightly higher proportion of boreal species in this area.

The length-frequency distribution of the benthos in both bays was similar; medium-sized hyperbenthos 60–100 mm in length is more common in Tikhaia Bay. That would fit well the general theory that the arctic benthos tends to be larger than the boreal-subarctic (Thorson, 1936).

The glacial impact on the macrofauna is connected mostly with the fresh meltwater discharge and high sedimentation rates (Görlich *et al.*, 1987). The glaciomarine sedimentation depends on the type of glacier (grounded or floating), amount of meltwater, sea-bottom relief and pattern of oceanic currents and wind regime (Edwards, 1985). The main difference between the glaciers in the two bays – the Torellbreen and the Sedov glaciers – is in the amount of meltwater discharge and hence in the transported sediments that result from the nature of the glaciers. The Torellbreen is a 'warm', active subarctic glacier typical of western Svalbard (Baranowski, 1977). The glaciers on Franz Josef Land are 'cold' polar glaciers calving during less than one month in a year (Węsławski, 1993a). The differences in the sedimentation rates are reflected in the different reductions in water transparency – from 2 to 13 m on Franz Josef Land and from 0.5 to 2 m in Svalbard glacier bays (Węsławski and Stempniewicz, 1995).

With respect to water depth we have distinguished four shallow water associations (S1, S4, T1, T3). The S1 association matches very well Péres' (1982) description of typically arctic, infralittoral hard-bottom faunal communities connected with algal assemblages, consisting mostly of Crustaceans – gammarids, decapods, shrimps, amphipods – and the fishes feeding on them. The shallow bottom inhabited by organisms of association T1 is much more diversified, varying in sediment type from muds to stones, as well as in macrophyte coverage, and this has given rise to numerous characteristic species. The most typical organism, with high dominance and frequency, was *A. disciforme*, a flat, immobile, filter-feeding animal regarded as an indicator of low sedimentation areas. Hence we assume that besides the depth limit, the discriminating factor for this association must have been the relatively low sedimentation, as compared to the glacier-impacted association T3. The occurrence of an *A. disciforme* community on the muddy-sandy shallow (12–16 m) bottom of the Laptev Sea has been reported by Golikov and Averintsev (1977). T3 consists of samples taken at different depths on a bottom significantly influenced by the glacier. The meltwater flows over this region in accordance with the circulation pattern of water masses in Tikhaia Bay. Averintsev (1992) observed a strong permanent flow streaming counterclockwise from south to north, from Rubini Rock along the Sedov Glacier towards Cape Sedov. The waters in Tikhaia Bay are not stratified (Swerpel, 1992), so the meltwaters with suspended inorganic matter do not flow over the deeper layers bounded by the pycnocline, but mix more readily with the whole water column and reach the bottom. The organisms living in these conditions are euryhaline, active polychaetes and crustaceans. A unique environment is produced by the two rivermouths in Skoddebukta, which is inhabited by polychaetes and a *Phascolosoma* sp. sipunculid. The central, deep, soft-bottom of both bays are inhabited by associations consisting largely of bivalves, ophiuroids and polychaetes: *Y. hyperborea* is the most typical species in Skoddebukta and *A. borelis* and *A. crenata* in Tikhaia Bay. The *Y. hyperborea* communities are typical of the subarctic, circalittoral shelf bottom covered by terrigenous muds (Péres, 1982). There are also several records of arctic communities with different *Astarte* spp. being the predominant organisms, *e.g.* the *Eudendrium ramosum* community with *Astarte montagui* and *Ophiacanta bidentata* as typical forms found on the muddy-sandy deep bottom (32–38 m) at Heis Island (Franz Josef Land) reported by Golikov and Averintsev (1977). In the central part of Skoddebukta we classified one more association – S3, which is probably representative of the fauna of the deep regions outside the bay. The action of oceanic currents is reflected here in the presence of well-washed gravel and shells, and typical species are crustaceans, including *P. pubescens* – a decapod living in empty gastropod shells.

The trophic structure of the fauna in the bays was influenced mostly by the bottom sediment type and the rate of inorganic sedimentation. Long and Lewis (1987) found a correlation between the proportion of deposit and suspension feeders to sediment grain size. They observed an increase in deposit feeders and a decrease in suspension feeders as the sand-to-pelite ratio increased. High levels of inorganic sedimentation may also bring about a decrease in the number of suspension-feeding animals. The impact of inorganic suspension on these organisms is connected with two processes: the dilution by inorganic particles of the nutritious suspensions which may be ingested by these animals (mostly non-selective), and the risk of gill clogging, dangerous to invertebrates (*e.g.* bivalves) employing a mesh-like gill as a filtering organ (Moore, 1977). So the muddy bottom and inorganic suspension carried by glaciers and rivers in the regions studied have produced a predominance of deposit feeders in the macrofauna. In both bays, suspension feeders were the most abundant and deposit feeders least important in shallow waters not exposed to the impact of river or glacier and on a stony or mixed bottom – conditions unique to the S1 and T1 associations. In S2, S3, S4 and T3 the proportion of suspension feeders was about 10%, the most abundant of them being Thyasiridae. Schmid and Piepenburg (1993) have classified *Thyasira gouldi* as a facultative filter-feeder, so we may expect that other species of this family are also able to change their mode of feeding depending on environmental conditions. In Kuznetsov's (1964) classification, *Thyasira* spp. were included among the mobile suspension feeders. These are characterised by the 'poorer' development of their filtering organs, and inhabit regions with higher concentrations of inorganic suspensions than do sessile suspension feeders. Other bivalves – *H. artcica, A. borealis, A. crenata, M. laevigatus* – were responsible for a similar 10% proportion of suspension feeders in T2 in extensive central part of Tikhaia Bay. Two of them – *A. borealis* and *A. crenata* – were also classified as species characteristic of this association, as they had the highest avS_i and $\mathrm{avS}_i/\mathrm{SD}(\mathrm{S}_i)$ ratio in the similarity-breakdown analysis. In S2, the parallel association in Skoddebukta, the most typical organism was *Y. hyperborea*, a deposit-feeding bivalve. The following seems to be typical of arctic glacier bays and fjords: suspension-feeding bivalve associations in conditions of low sedimentation provided by an inactive, 'cold' or retreating glacier, and associations characterised by deposit-feeding bivalves in regions of high sedimentation, influenced by active, 'warm' glaciers. Syvitski *et al.* (1989) reported *Portlandia arctica* (a deposit-feeding bivalve) associations in fjords experiencing exceptionally high to moderate rates of sedimentation caused by active glaciers, and the Onuphid association, consisting of echinoids and filter-feeding bivalves (*Chlamys* sp., *Astarte* spp., *Miodolaria* sp.), in a fjord with a retreating glacier, minimal glacial impact and low levels of sedimentation.

In his study of arctic and subarctic marine benthos Curtis (1975) found that the numbers of species were much higher in areas of mixing between cold polar and warm non-polar waters (*e.g.* Barents Sea, Bering Sea) than in cold arctic waters. The potential pool of species available in the Atlantic waters off West Spitsbergen is at least three or four times as large (over 2000 species according to Gulliksen and Holthe, 1992) as the *ca* 500 species expected at Franz Josef Land (Matishov, 1993; Węsławski and Stempniewicz, 1995). This does not agree with our results, as we found almost three times as many species in the 'cold' Tikhaia Bay as in the 'warm' Skoddebukta, which experiences the mixing of Atlantic and Arctic water masses. Similarly, the Tikhaia Bay fauna proved to be more diverse than that in Skoddebukta when we applied such measures of diversity as the species number per sample, the Shannon-Weaver Index and k-dominance plots. In his comparison of the ecosystems of Tikhaia Bay and Isbjornhamna (Svalbard, Hornsund) Węsławski (1993a) found similar differences, and explained them by the higher primary production resulting from the prolonged phytoplankton bloom and faster sedimentation of organic particles due to the weak stratification of the water column in Tikhaia Bay. The theory attributing higher diversity to increased productivity was propounded by Connell and Orias (1964). The physical stability of the environment and the level of disturbance are very important factors influencing faunal diversity (Connell, 1978). Kendall and Aschan (1993) indicated that the sedimentation of silt from melt water carried by the river Gipsvika caused natural disturbances in Sassenfjord affecting the diversity of the benthic assemblage. Thus the higher diversity of the Tikhaia Bay benthos is due to both the higher productivity and the lower levels of sedimentation-induced natural disturbances in this region, as compared with Svalbard's 'warm' glacier bays. This agrees well with Huston's (1979) theory, which links high diversity with the high population growth rates such as are normally associated with high productivity and a low incidence of disturbance. Glacier- or river-induced sedimentation also seems to be the decisive factor responsible for the diversity differences between the associations in the two bays. Ignoring the very low diversity measures recorded in association S1, which we think are artefacts resulting from the inefficiency of the dredge used to sample the stony bottom fauna, we observed the lowest diversity in the glacier-impacted association T3 in Tikhaia Bay and in the river-influenced association S4 in Skoddebukta. A similar situation was reported by Schmid and Piepenburg

(1993) in Disko Fjord (West Greenland), where the benthic assemblage inhabiting the part of the fjord isolated by a sill and influenced by aestival river outflow showed the lowest number of species per sample and the lowest Shannon-Weaver Indices among the assemblages distinguished.

In his dissertation on the sensitivity of Svalbard's marine ecosystem to climatic changes, Węsławski (1993b) outlined a possible scenario of the consequences of climatic warming to this ecosystem. Regarding the sublittoral benthos, he predicted a decline in benthos biomass in areas of increased glacial sedimentation. Our results lead to the conclusion that the warming of the Arctic may cause a drop in benthic biodiversity owing to the increase in mineral sedimentation from meltwaters.

6. Conclusions

- 31% of all species were common to both bays, while 71% of the most frequent species were found in both localities.
- The zoogeographical status of the fauna was similar, regardless of the different geographical status of the bays (the high-arctic Tikhaia Bay and the subarctic Skoddebukta).
- The principal factors responsible for the distribution of macrofaunal species were depth, bottom type, and glacier or river impact resulting in increased inorganic sedimentation.
- Deposit feeders dominated the fauna in both localities. Their proportions were highest in associations inhabiting muds and experiencing high levels of inorganic sedimentation.
- The largest, central parts of the two bays were inhabited by the *Yoldia hyperborea* (a deposit-feeding bivalve) association in Skoddebukta and by the *Astarte* spp. (suspension-feeding bivalves) association in Tikhaia Bay.
- The 'warm' subarctic bay at Spitsbergen, with a potential species pool of 2000 was less diverse than the 'cold' high-arctic locality with a potential species pool of 500.
- The higher mineral sedimentation rates (disturbance) at Spitsbergen together with the higher production and pelago-benthic coupling (trophic conditions) in Franz Josef Land are said to be responsible for the richer and more diverse communities in the 'cold' locality.

- The level of inorganic sedimentation was responsible for the diversity differences between the associations in the two bays.
- The possible warming of the Arctic will cause the benthic biodiversity to decline, owing to the increase in mineral sedimentation from meltwaters.

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