QUANTITATIVE DISTRIBUTION OF THE MACROFAUNA IN A SHALLOW, SANDY BOTTOM IN RAUNEFJORDEN, WESTERN NORWAY

BJÖRN TUNBERG

SARSIA

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Fifty-four quantitative (0.2 m²) substrate samples were taken between Nov. 1975 and May 1976, in the archipelago of Eggholmane near Bergen. The sediment was rich in $CaCO_3$, and grain-size distribution varied from fine to very coarse sand. In all, 75 species (3087 individuals) were collected, the most abundant of which were *Lucinoma borealis* (41.4 ‰, by number), *Ophiura albida* (8.2 %), and *Dosinia exoleta* (5.5 %). Species diversity increased in the shallower parts of the study area, and a correlation and cluster analysis showed that it was possible to distinguish distinct groups or 'communities' of species. Their distribution was correlated with depth and the grain-size distribution of the sediment. The most characteristic species of these two 'communities' were *Thracia villosiuscula* and *Dosinia exoleta* in coarse, clean sediment in shallow water, and *Lucinoma borealis* and *Ophiura albida* in fine sediment in deeper water.

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INTRODUCTION

In a previous paper (TUNBERG 1981) two bivalve species groups or 'communities' in a shallow, sandy bottom in Raunefjorden were described. These groups were distinct and could be related to the grain-size distribution of the sediment. The remaining macrofaunal element was, however, not dealt with, although this component was examined at the first 54 (9 × 6) of the total 99 (9 × 11) samples that were collected.

The present study deals with the composition, diversity patterns, and distribution of all macrofaunal species within the area. Comparative analyses were carried out to ascertain whether or not the additional information obtained further confirmed the presence of two macrofaunal species groups or 'communities'.

This survey is part of a study on population dynamics of the bivalve *Dosinia exoleta* (L.) (TUNBERG 1979).

MATERIAL AND METHODS

The survey was carried out within a delimited area at Eggholmane, 60°15′36″N, 5°13′E (Institute of Marine Biology Ref. Numbers E 191-75 and E 298-76.)

The survey area was divided into nine sub-areas, A–I (Fig. 1), which together with the sampling technique, sediment analyses, and correlation analysis are described in detail in TUNBERG (1981). The coefficient of Czekanowski (BRAY & CURTIS 1957) was used for a quantitative analysis of the similarity between the samples (species composition). Sorting was done by using the computer program *BMDP1M-Cluster analysis of variables*, and the single linkage method (nearest neighbour) was used as clustering strategy. The analysis was made using the actual number of specimens of each species. The Shannon-Wiener index (H′) was used as a measure of species diversity, and 'evenness' was defined as H'/H'_{max}, where H'_{max} is the diversity when the species are equally distributed.

Quantitative fauna samples were collected six times at regular intervals during the period November 1975 to May 1976. On each occasion one sample was taken in each sub-area (i.e. a total of 54 samples of 0.2 m², 16 cm deep, were collected). The substrate sampling points (A–I, 1–6) are shown in fig. 3 in TUNBERG (1981).

RESULTS

The outcome of the sediment analysis was presented in TUNBERG (1981).

Water temperature during the survey period varied between 3.6° C (25 March, sub-area A) and 12.1° C (6 Nov., sub-area H). Temperature variations between the different sub-areas were relatively small. The salinity remained fairly constant (c. 33 ‰) throughout the period.

The 54 quantitative samples contained 75 species (Table 1A and 1B) of which 33 (44 %) were molluscs (26 bivalve species), 18 (24 %)

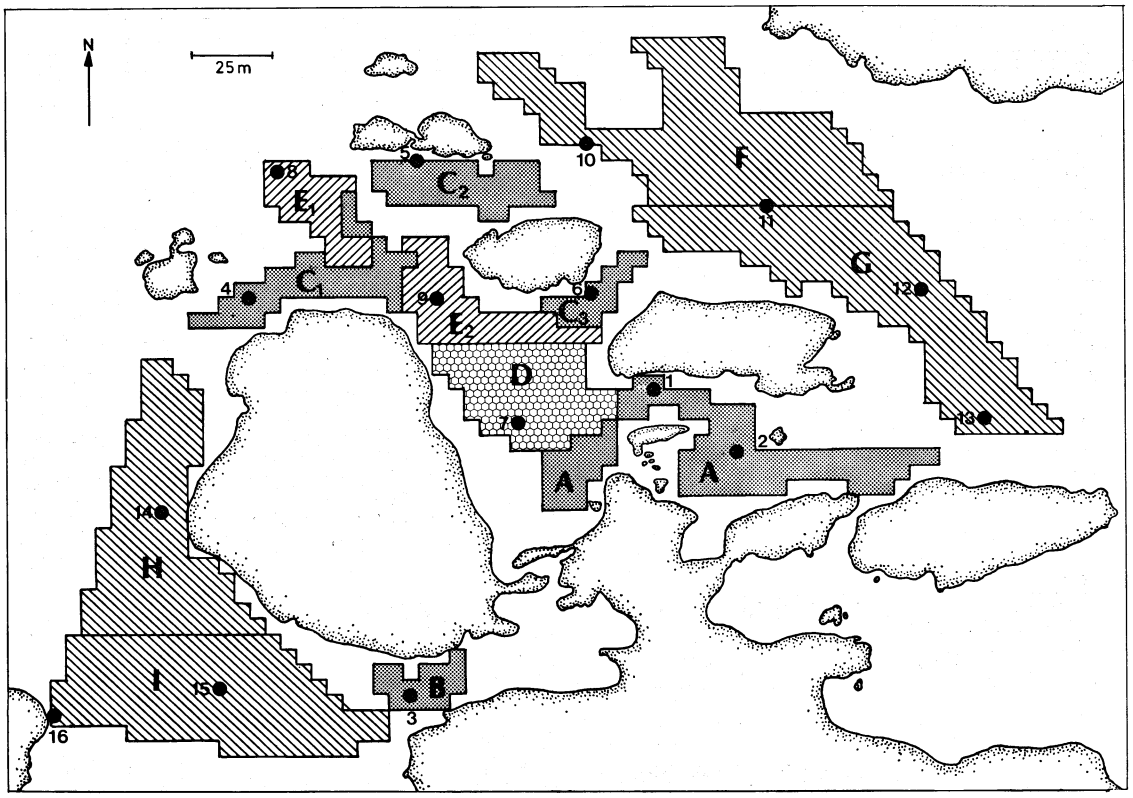

Fig. 1. The nine sub-areas, A–I, within the sampling area. The dots show the 16 sediment sampling points for grain-size and $CaCO_3$ analysis.

polychaetes, 11 (15 %) crustaceans, and 9 (12 %) echinoderms. Of the 3087 individuals collected, 2051 (66.5 %) were molluscs (1947 bivalves), 307 (10 %) polychaetes, 171 (5.5 %) crustaceans, and 367 (12 %) echinoderms.

Species groups

The outcome of the correlation analyses (see TUNBERG 1981) are shown in Table 2 (part I for sampling points and part II for sub-areas) and Fig. 2. The 26 most abundant species were tested against each other (quantitative distribution), with the exception, however, of *Littorina littorea* and *Ophiocomina nigra* (see below). It was possible to distinguish between two groups, I and II, with 5 and 12 species respectively. Group II was more distinct than Group I. The habitat preferences of the remaining 9 species were more uncertain and will be discussed below. It should be stressed, however, that several of the species in this analysis are more or less motile, which possibly may lower the value of the results of distributional patterns of these species.

Group I includes species 13–17, and Group II includes species 1–12 (Table 2). Most individuals of the species in Group I were found in sub-areas A–E (coarse, clean sediment in shallow water), and the ones in Group II were mostly in sub-areas F–I (fine sediment in deeper water). Within each of the two groups all species were positively correlated with each other, and negatively correlated with the species in the other group although a few exceptions were noted in the comparison based on sampling points. For example, *Pectinaria auricoma* and *Astarte montagui*, both in Group II, showed a weak negative correlation. This also applied to the pairs *Pectinaria auricoma* and *Gari fervensis*, and *Lepidopleurus asellus* and *Corbula gibba*, all in Group II. Even though *Lepidopleurus asellus* was connected with Group II, it is only found attached to hard substrata such as pebbles and shell fragments. *Cirriformia tentaculata*, in Group I, showed a low positive correlation with *Edwardsia tuberculata* and *Notomastus latericeus*, both in Group II, and it showed no correlation whatso-

Table 1A. Distribution of the species represented in the samples by a total of more than five individuals. N = total number of individuals found in the 54 quantitative samples of 0.2 m². Numerals in brackets are standard deviation values. Depth distribution values of the bivalves were obtained from 99 quantitative samples (see TUNBERG 1981).

Rank	N	Species	Depth distr.(m) min	max	Average number of individuals per 0.2 m²										% of total
					Totally	Secondary area A	B	C	D	E	F	G	H	I	
1	1278	Lucinoma borealis (L.)	0.3	13.3	23.7(23.8)	3.3(4.1)	0.5(1.2)	13.8(11.1)	7.3(4.4)	10.7(7.8)	46.5(19.2)	49.5(23.8)	40.7(26.7)	40.7(14.5)	41.4
2	252	Ophiura albida FORBES	0.3	12.0	4.7(6.7)	0.7(1.2)	1.0(1.1)	2.3(2.1)	0.5(0.8)	4.5(6.0)	12.2(8.6)	5.7(4.1)	8.2(9.2)	8.4(10.9)	8.2
3	170	Dosinia exoleta (L.)	0.5	11.9	3.2(7.6)	2.5(5.2)	6.5(5.2)	11.5(19.6)	1.7(4.1)	3.3(4.4)	1.5(1.5)	1.0(0.9)	0.2(0.4)	0.2(0.4)	5.5
4	111	Edwardsia tuberculata DÜBEN & KOREN	1.3	12.6	2.1(5.4)	- -	- -	0.2(0.4)	0.3(0.5)	1.2(1.2)	10.8(13.1)	3.3(3.9)	1.2(1.8)	1.5(1.8)	3.6
5	90	Cirriformia tentaculata (MONTAGU)	0.3	10.5	1.7(3.2)	2.7(3.5)	1.5(2.7)	3.3(5.3)	2.7(2.8)	3.5(4.9)	1.2(2.4)	- -	0.2(0.4)	- -	2.9
6	90	Astarte montagui (DILLWYN)	1.7	13.3	1.7(3.2)	- -	0.3(0.5)	- -	- -	- -	2.3(3.3)	3.8(3.4)	1.3(1.5)	7.2(4.9)	2.9
7	81	Dosinia lupinus (L.)	1.8	12.6	1.5(2.7)	0.3(0.5)	- -	0.5(0.8)	- -	0.8(1.3)	5.8(2.6)	3.7(4.4)	0.5(0.8)	1.8(2.6)	2.6
8	78	Pectinaria auricoma (O.F.MÜLLER)	2.3	10.8	1.4(3.5)	- -	- -	0.5(0.8)	0.3(0.5)	0.2(0.4)	4.5(7.3)	4.2(6.1)	3.0(2.2)	0.3(0.5)	2.5
9	75	Phoronis muelleri SELYS-LONGCHAMPS	1.8	10.5	1.4(5.7)	0.5(1.2)	- -	8.2(13.1)	- -	- -	3.8(9.4)	- -	- -	- -	2.4
10	60	Pagurus bernhardus (L.)	0.3	11.1	1.1(1.6)	0.7(1.2)	2.2(2.6)	1.7(1.9)	1.2(1.6)	1.7(1.0)	1.0(1.6)	0.2(0.4)	0.7(1.6)	0.8(1.6)	1.9
11	59	Thyasira flexuosa (MONTAGU)	3.2	11.9	1.1(2.2)	- -	- -	0.2(0.4)	- -	- -	4.5(3.6)	1.7(2.7)	2.2(1.9)	1.3(2.2)	1.9
12	57	Travisia forbesi JOHNSTON	0.5	12.0	1.1(1.9)	0.7(1.2)	1.8(1.5)	2.3(2.6)	0.3(0.5)	2.5(1.6)	1.5(3.7)	- -	0.2(0.4)	0.2(0.4)	1.9
13	55	Thracia villosiuscula (MACGILLIVRAY)	0.3	10.5	1.1(2.2)	2.7(4.1)	2.7(1.9)	2.2(2.6)	0.7(0.8)	0.7(1.2)	- -	- -	0.2(0.4)	0.2(0.4)	1.8
14	55	Leptosynapta inhaerens MÜLLER	0.5	12.6	1.0(1.1)	0.5(1.2)	1.8(1.6)	1.5(0.6)	0.5(0.6)	1.3(1.2)	1.0(1.3)	0.8(1.2)	1.0(1.1)	0.7(0.5)	1.8
15	51	Lunatia intermedia (PHILIPPI)	1.4	11.4	0.9(1.3)	0.2(0.4)	0.8(1.3)	1.0(1.6)	0.3(0.5)	1.0(1.3)	1.0(1.1)	2.3(1.5)	1.7(1.4)	0.2(0.4)	1.7
16	49	Pagurus cuanensis BELL	0.5	12.0	0.9(2.9)	0.2(0.4)	0.3(0.5)	2.2(2.8)	1.3(1.5)	3.5(8.1)	- -	- -	0.2(0.4)	0.5(0.8)	1.6
17	45	Mya truncata L.	0.3	13.3	0.8(1.6)	1.5(2.5)	2.3(2.9)	0.2(0.4)	1.3(1.4)	0.2(0.4)	0.7(1.2)	0.3(0.8)	0.7(1.2)	0.3(0.5)	1.5
18	44	Notomastus latericeus M.SARS	0.3	12.6	0.8(1.1)	0.2(0.4)	- -	0.5(0.6)	0.8(1.2)	0.5(0.8)	1.8(1.8)	1.8(1.6)	0.5(0.8)	1.2(0.8)	1.4
19	38	Venerupis pullastra (MONTAGU)	0.3	1.3	0.7(2.5)	2.5(4.5)	3.8(5.3)	- -	- -	- -	- -	- -	- -	- -	1.2
20	28	Gari fervensis (GMELIN)	0.9	10.7	0.5(1.3)	- -	0.5(0.8)	- -	- -	0.3(0.5)	1.5(1.4)	1.7(3.1)	0.3(0.5)	0.3(0.8)	0.9
21	27	Macropipus pusillus (LEACH)	1.3	11.3	0.5(0.8)	- -	0.2(0.4)	1.3(1.2)	0.3(0.8)	0.3(0.5)	0.7(0.8)	0.7(0.8)	0.8(0.7)	0.2(0.4)	0.9
22	27	Littorina littorea (L.)	0.4	8.4	0.5(1.9)	0.5(1.2)	2.7(4.8)	0.2(0.4)	0.7(1.6)	- -	0.5(1.2)	- -	- -	- -	0.9
23	26	Venus fasciata (DA COSTA)	0.3	11.4	0.5(0.9)	0.7(1.2)	1.0(1.3)	0.5(0.8)	0.5(1.2)	- -	0.3(0.5)	0.8(1.3)	- -	0.5(0.8)	0.8
24	22	Ophiocomina nigra (ABILDG)	3.2	10.6	0.4(2.6)	- -	- -	0.2(0.4)	- -	- -	0.2(0.4)	- -	3.3(7.7)	- -	0.7
25	18	Corbula gibba (OLIVI)	1.8	11.9	0.3(0.9)	0.2(0.4)	- -	- -	- -	0.2(0.4)	1.7(1.9)	0.7(1.0)	0.2(0.4)	0.2(0.4)	0.6
26	17	Lepidopleurus asellus (SPENGLER)	9.0	12.6	0.3(1.0)	- -	- -	- -	- -	- -	1.0(1.7)	- -	0.5(0.6)	1.3(2.0)	0.6
27	13	Macropipus arcuatus (LEACH)	0.3	11.1	0.2(0.2)	0.2(0.4)	- -	0.8(1.3)	0.2(0.4)	0.8(1.3)	- -	0.2(0.4)	- -	- -	0.4
28	13	Astropecten irregularis (PENNANT)	8.4	10.7	0.2(0.7)	- -	- -	- -	- -	- -	1.3(0.8)	0.8(1.3)	- -	- -	0.4
29	10	Terebellides stroemi M.SARS	1.3	10.8	0.2(0.5)	- -	- -	- -	0.2(0.4)	0.3(0.5)	0.3(0.8)	0.5(0.8)	0.2(0.4)	0.2(0.4)	0.3
30	9	Echinocardium flavescens (O.F.MÜLLER)	0.3	10.8	0.2(0.4)	0.3(0.5)	- -	0.3(0.5)	0.2(0.4)	0.3(0.5)	0.2(0.4)	- -	- -	0.2(0.4)	0.3
31	9	Echinocyamus pusillus (O.F.MÜLLER)	0.3	12.6	0.2(0.6)	1.6(0.2)	0.2(0.4)	0.3(0.5)	- -	- -	- -	- -	0.2(0.4)	0.2(0.4)	0.3
32	9	Gari depressa (PENNANT)	0.3	3.8	0.2(0.5)	0.5(0.6)	0.3(0.8)	- -	0.2(0.4)	0.5(0.8)	- -	- -	- -	- -	0.3
33	8	Upogebia stellata (MONTAGU)	1.4	10.8	0.2(0.5)	- -	- -	0.2(0.4)	0.2(0.4)	- -	0.5(1.2)	- -	0.2(0.4)	0.3(0.8)	0.3
34	7	Arctica islandica (L.)	2.2	12.6	0.1(0.4)	- -	- -	0.2(0.4)	- -	- -	0.3(0.5)	- -	0.3(0.8)	0.3(0.8)	0.2
35	7	Cochlodesma praetenue (PULTENEY)	0.3	10.7	0.1(0.4)	- -	- -	- -	0.7(0.8)	0.2(0.4)	- -	0.2(0.4)	- -	- -	0.2
36	7	Montacuta ferruginosa (MONTAGU)	3.7	11.2	0.1(0.5)	- -	- -	0.3(0.8)	- -	0.7(1.2)	- -	- -	- -	0.2(0.4)	0.2
37	6	Parvicardium scabrum (PHILIPPI)	0.5	4.2	0.1(0.4)	0.3(0.8)	0.2(0.4)	0.2(0.4)	0.2(0.4)	0.2(0.4)	- -	- -	- -	- -	0.2
38	6	Venus ovata (PENNANT)	0.9	10.5	0.1(0.5)	- -	0.2(0.4)	0.2(0.4)	0.5(1.2)	- -	- -	0.3(0.5)	- -	0.2(0.4)	0.2

Table 1B. Species represented in the samples by a total of less than six individuals. Sample location: Letters denote sub-areas and numerals denote collection numbers. Numerals in brackets = number of individuals in the samples of 0.2 m². Depth distribution values of the bivalves were obtained from 99 quantitative samples (see TUNBERG 1981).

Rank	N	Species	Depth distr.(m) min	max	Sample location
39	5	Chone infundibuliformis KRÖYER	1.8	10.2	A2(1), D4(1), G2(2), H4(1)
40	5	Galathea intermedia LILJEBORG	0.3	3.3	A3(1), B6(1), D2(1), E2(2)
41	5	Gibbula cineraria (L.)	0.4		B1(5)
42	4	Scoloplos armiger (O.F.MÜLLER)	8.4	10.8	F4(1), F5(1), H2(1), I4(1)
43	4	Owenia fusiformis DELLE CHIAJE	10.2	12.6	G6(1), I3(1), I4(1), I5(1)
44	4	Anapagurus chiroacanthus (LILJEBORG)	10.2	10.5	G6(3), H6(1)
45	4	Echinocardium cordatum (PENNANT)	0.6	3.7	A6(1), C4(1), E4(1), E5(1)
46	4	Hiatella arctica (L.)	0.3	10.8	A3(1), F2(1), G5(2)
47	3	Golfingia vulgaris (DE BLAINVILLE)	3.1	9.2	C5(1), E5(1), H4(1)
48	3	Ophelia limacina (RATHKE)	1.3	1.7	B2(2), B5(1)
49	3	Chone duneri MALMGREN	9.0	10.5	H1(1), H6(2)
50	3	Lepidochiton cinereus (L.)	1.8	10.4	A3(2), G3(1)
51	3	Mysia undata (PENNANT)	2.3	10.4	C1(1), F1(1)
52	2	Goniada maculata OERSTED	8.4	10.1	F4(1), F6(1)
53	2	Philocheras bispinosus (HAILSTONE)	10.0	12.0	F5(1), I5(1)
54	2	Ophiura texturata LAMARCK	10.2	10.8	F1(1), G6(1)
55	2	Acanthocardia echinata (L.)	8.4	10.4	F1(1), F6(1)
56	2	Venus striatula (DA COSTA)	0.6	8.4	A6(1), F6(1)
57	2	Macoma baltica (L.)	0.5		A5(2)
58	2	Mya arenaria L.	0.9	1.3	B4(1), D2(1)
59	1	Priapulus caudatus LAMARCK	10.8		F2
60	1	Arenicola marina (L.)	9.2		H4
61	1	Scalibregma inflatum RATHKE	10.0		F5
62	1	Harmothoe lunulata (DELLE CHIAJE)	9.2		H4
63	1	Glycera alba (O.F. MÜLLER)	10.6		H3
64	1	Nephtys caeca (FABRICIUS)	4.4		D3
65	1	N. ciliata (O.F.MÜLLER)	1.8		A2
66	1	Pista cristata (O.F.MÜLLER)	10.2		G6
67	1	Acmaea testudinalis (MÜLLER)	3.3		E2
68	1	Nassarius reticulatus (L.)	4.3		C2
69	1	Pirimela denticulata (MONTAGU)	1.4		C3
70	1	Macropipus holsatus (J.C.FABRICIUS)	1.3		D2
71	1	Macropodia rostrata (L.)	10.8		F2
72	1	Spatangus purpureus (O.F.MÜLLER)	0.6		A6
73	1	Venerupis aurea (GMELIN)	0.6		A6
74	1	Thracia phaseolina (LAMARCK)	0.5	10.8	H6
75	1	Lyonsia norvegica (GMELIN)	10.4	11.3	H5

ever with *Pectinaria auricoma* (Group II). *Pagurus bernhardus* (Group I) showed a weak positive correlation with *Corbula gibba*, *Mya truncata* (Group I) likewise with *Lepidopleurus asellus* and *Astropecten irregularis*, both in Group II.

Despite these divergenses from the main pattern, and although some of the values are rather low, the matrix shows that it is possible to distinguish between two distinct species groups.

As mentioned above, distributional relationships among the remaining 9 species and the two groups were more uncertain. *Lunatia intermedia* was found in the entire study site, but was most abundant in the deeper areas characterized by finer sediment (areas G and H). *Travisia forbesi*, and possibly *Pagurus cuanensis*, are probably also connected to Group I. *Travisia forbesi* was most abundant in the coarse, clean sediments of areas A, B, and C, but was to a great extent also found in area E (15 individuals). Its distribution was somewhat complicated because 9 individuals were also found in sub-area F, all in one single sample of 0.2 m² (F5). Many individuals of *Pagurus cuanensis* were also found in the intermediate areas D and E (see TUNBERG 1981 and below). Of the 21 individuals collected in sub-area E, 20 were found in one sample (E6), at a depth of 3.6 m. This sample was taken close to area C_3. 13 individuals of *Macropipus arcuatus* were found, 10 of which were collected in areas D and E (77 %).

Three species, *Macropipus pusillus*, *Venus fasciata*, and *Leptosynapta inhaerens* were evenly distributed throughout the area, and showed no preference for depth or sediment structure. *Phoronis muelleri*, which was only found in areas A, C, and F, was not possible to group (see TUNBERG & MATTSON 1979).

Littorina littorea and *Ophiocomina nigra* were not tested because of their distributional patterns. 12 specimens (of a total of 27) of *Littorina littorea* were found in sample B1, and the ones found in deeper areas were probably individuals that had fallen down from shallower parts with steep slopes. Of the 21 collected specicimens of *Ophiocomina nigra*, 19 were found in one sample (H6).

Terebellides stroemi (not tested) is probably also connected to Group II; 70 % of the individuals were found in areas F–I.

It was not possible to draw any certain conclusions concerning the other species because they were all found too sporadically.

Figs 3A and 3B show (cf. also the correlation analysis) a high degree of correspondence among the distributional patterns of the twelve species in Group II (characterized by *Lucinoma borealis* and *Ophiura albida*). Most species had a very low abundance rate in areas A–E. This rate increased greatly in area F, but showed a downward trend in areas G–I. The exception was *Ophiura albida*, the abundance rate of which increased further in areas G–I. *Astarte montagui* was also very abundant in area I.

Fig. 4 (Group I, characterized by *Thracia villosiuscula* and *Dosinia exoleta*) does not show the same distinct pattern. The abundance maxima for the five species in this group varied among areas A–E. A low abundance rate in areas F–I, however, was common to all.

Cluster analysis

The level of similarity among the 50 quantitative samples (not A1, A4, A5, and D1, which con-

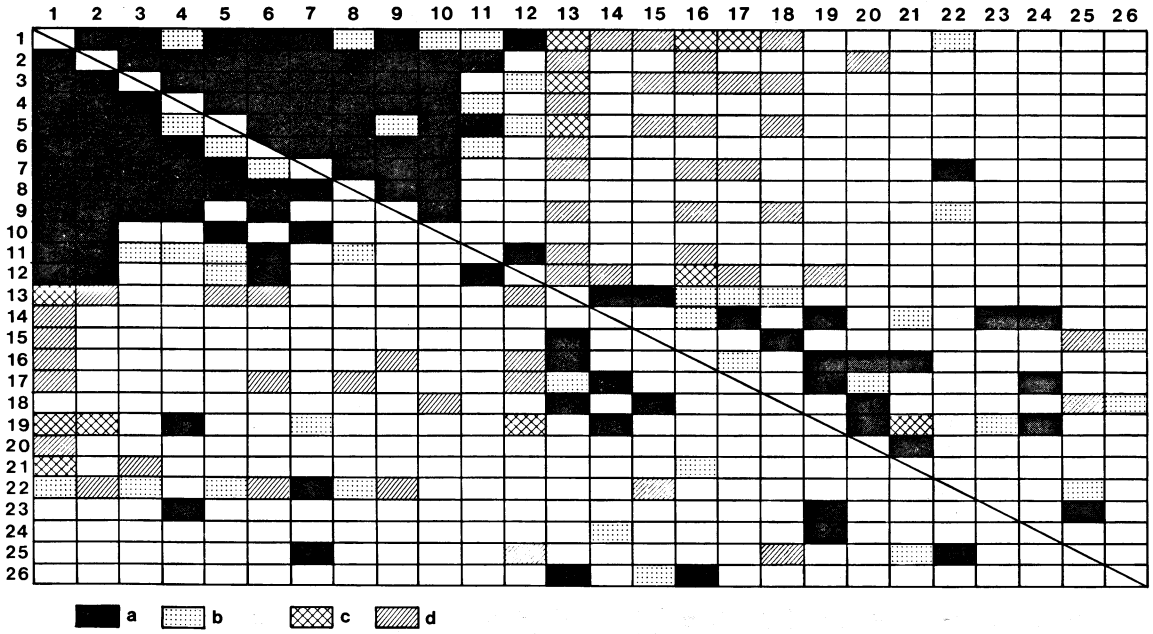

Fig. 2. Correlation coefficients (see Table 2). a) significant positive values (5 % level), b) values not significant but $\geq +0.50$ (sub-areas) and $\geq +0.20$ (sampling points), c) significant negative values, d) values not significant but ≤ -0.50 (sub-areas) and ≤ -0.20 (sampling points).

tained only one or no species at all) is presented in Fig. 5. The analysis is based on species composition in the samples, i.e. the same 26 species as in the correlation analysis.

Two groups, or clusters (Q_1 and Q_2), may be distinguished. Samples F1 through H6 (cluster Q_2), all have a high percentage of similarity. This cluster may possibly be extended to include samples C1 through F5. All samples in this extended cluster Q_2 (except C1, C5, and C2) were collected in the deeper parts of the area (with fine sediment), where species Group II was found. Cluster Q_1 includes samples A2 through D4, all collected in shallow parts of the area (with coarse, clean sediment), where species Group I was found.

It is noteworthy that samples C1, C5, and C2 have a stronger connection to cluster Q_2 than to Q_1. All three samples were taken close to each other in sub-area C_3 (Fig. 1). In this sub-area many specimens of *Lucinoma borealis* (Group II) were found, unlike other samples from shallow parts of the area. *Thracia villosiuscula* (Group I) was, however, also found here, which possibly indicates that this part of the area represented a transition zone.

The right side of Fig. 5 (samples E4 through B1) includes samples taken in shallower areas only, with the exception of G5. A3 and B6, forming a small cluster, were both taken in very shallow water (0.3 m and 0.5 m). *Venerupis pullastra* was found in abundance in both samples. Sample C3 was also taken in a rather shallow part of the area (1.4 m), and at a long distance from the other sampling points in sub-area C. Very few species (and individuals) were found in sample G5. The sediment was black and probably contaminated with H_2S. Few species were also found in D5; out of a total of 8 individuals found, 5 were specimens of *Lucinoma borealis*. C4 was dominated by only one species, *Dosinia exoleta* (51 out of a total of 69 individuals). E6, unlike the other samples from this sub-area, contained no specimens of *Lucinoma borealis*, but instead 20 individuals of *Pagurus cuanensis*. B1 was taken in shallow water (0.4 m) and somewhat outside sub-area B (see TUNBERG 1981). Of a total of 9 individuals, 7 were specimens of *Pagurus bernhardus*.

Diversity and dominance

Diversity and dominance indices of the nine sub-areas are presented in Table 3, which shows a marked decline of index values towards the deeper parts of the area (with finer sediment). Diversity indices for areas A–E lie between 3.6

Table 2. Correlation coefficients for the 26 most abundant species (not *Littorina littorea* and *Ophiocomina nigra*). Part I (lower left): Comparison of sampling points (N = 54). Part II (upper right): Comparison of sub-areas (N = 9). All values have been multiplied by 1000. Group I includes species 13–17 (found in coarse, clean sediment in shallow water), and Group II includes species 1–12 (found in fine sediment in deeper water) (see the text).

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	Lucinoma borealis		+824	+826	+640	+864	+753	+839	+653	+714	+636	+648	+729	-818	-537	-603	-790	-679	-580	-481	-453	-375	+550	-006	-272	+338	-223
2	Thyasira flexuosa	+528		+734	+912	+935	+867	+868	+830	+723	+894	+673	+429	-645	-443	-393	-586	-434	-300	-218	-508	-462	+355	+143	-146	+238	-264
3	Notomastus latericeus	+523	+387		+766	+687	+918	+774	+835	+806	+769	+481	+616	-778	-456	-617	-514	-585	-512	-359	-311	-249	+399	+067	-371	+224	-017
4	Edwardsia tuberculata	+281	+362	+576		+818	+930	+775	+935	+773	+988	+531	+287	-537	-312	-328	-317	-263	-251	+021	-327	-287	+243	+219	-086	+186	-163
5	Ophiura albida	+278	+342	+295	+200		+745	+776	+688	+644	+780	+750	+529	-749	-467	-525	-579	-387	-511	-139	-293	-298	+372	+085	-078	+286	-472
6	Dosinia lupinus	+541	+638	+482	+625	+216		+821	+962	+856	+940	+518	+483	-591	-369	-378	-476	-469	-296	-217	-465	-368	+318	+174	-246	+188	+057
7	Pectinaria auricoma	+294	+285	+479	+492	+450	+227		+853	+854	+803	+302	+302	-653	-407	-423	-596	-583	-339	-316	-495	-351	+726	+077	-131	+425	-138
8	Astropecten irregularis	+416	+355	+572	+574	+274	+482	+554		+908	+964	+319	+277	-487	-274	-264	-365	-380	-218	-073	-411	-281	+438	+188	-099	+219	+072
9	Gari fervensis	+458	+470	+360	+379	+012	+697	-027	+181		+814	+246	+411	-533	-338	-188	-564	-403	-564	-162	-438	-326	+651	-051	+023	+145	+181
10	Corbula gibba	+308	+280	+176	+080	+405	+164	+353	+183	+113		+460	+269	-493	-330	-273	-325	-340	-226	-019	-382	-298	+289	+188	-126	+154	-095
11	Lepidopleurus asellus	+306	+320	+262	+262	+201	+483	+116	+232	+065	-061		+771	-544	-467	-336	-590	-273	-299	-289	-364	-479	-211	-009	-261	-065	-261
12	Astarte montagui	+491	+297	+102	+013	+200	+359	-076	+083	+099	+096	+456		-575	-500	-328	-769	-498	-305	-527	-407	-438	+058	-213	-355	-125	+100
13	Thracia villosiuscula	-358	-233	-179	-159	-210	-262	-184	-187	-158	-145	-153	-223		+693	+792	+551	+545	+605	+438	+094	+224	-402	+242	+388	-167	-494
14	Dosinia exoleta	-250	-171	-185	-053	-119	-130	-144	-074	-055	-102	-112	-169	+006		+265	+605	+699	+069	+741	+442	+630	-067	+736	+697	+468	+253
15	Venerupis pullastra	-265	-140	-129	-108	-156	-148	-116	-101	-069	-108	-094	-149	+474	+040		+114	+410	+872	+176	-291	-280	-290	-232	+346	-528	+631
16	Cirriformia tentaculata	-266	-151	+160	+008	-106	-158	000	-077	-204	-103	-097	-268	+319	+006	+089		+583	+069	+697	+753	+757	-408	+378	+217	+035	-144
17	Pagurus bernhardus	-263	-068	-102	-115	-027	-206	-087	-203	-158	+068	-199	-210	+220	+298	-020	+159		+346	+819	+544	+409	-328	+275	+779	000	+060
18	Mya truncata	-163	-055	-069	-063	-198	-070	-106	+057	-040	-207	+048	-087	+403	+059	+814	+095	+030		-038	+884	-490	-356	-342	+133	-551	+569
19	Travisia forbesi	-285	-278	-101	+297	-162	+006	+206	+065	+114	-152	-192	-282	+163	+467	+028	+087	+011	+010		+672	-697	-103	+530	+766	+235	-141
20	Pagurus cuanensis	-213	-142	+040	-107	-169	-072	-077	-113	+003	+106	-091	-150	-097	-014	-044	+148	+097	-093	+161		+900	-136	+234	+328	+172	-454
21	Macropipus arcuatus	-277	-174	-202	-114	-075	-188	-137	-126	-142	-135	-117	-185	-152	-117	-097	+217	+163	-134	-025	+159		+047	+496	+363	+411	-315
22	Lunatia intermedia	+201	-242	+203	+154	+256	-253	+487	+264	-265	+087	+031	-005	000	-077	-213	-029	-178	-158	-112	+127	-157		+017	+258	+550	-063
23	Phoronis muelleri	-020	-124	+011	+289	-073	+102	-085	+139	+078	-084	-083	-132	+086	+103	-069	+007	-175	-084	+569	-040	-086	+102		+345	+761	-042
24	Leptosynapta inhaerens	-169	-142	-057	+086	+009	-134	-091	-032	-047	+033	+013	-140	+165	+217	-005	+167	+086	+046	+382	-082	+192	+098	+155		+326	+092
25	Macropipus pusillus	-043	-095	+128	-007	+150	-161	+279	-018	-152	+197	-065	-201	+080	+187	-183	+101	+170	-256	-112	+180	+228	+362	+084	+191		-271
26	Venus fasciata	-075	-059	+068	-130	-013	-031	+066	+022	-119	+102	-068	+126	+393	-032	+263	+282	+066	+121	-102	+017	-066	+056	-022	+066	+026	

II

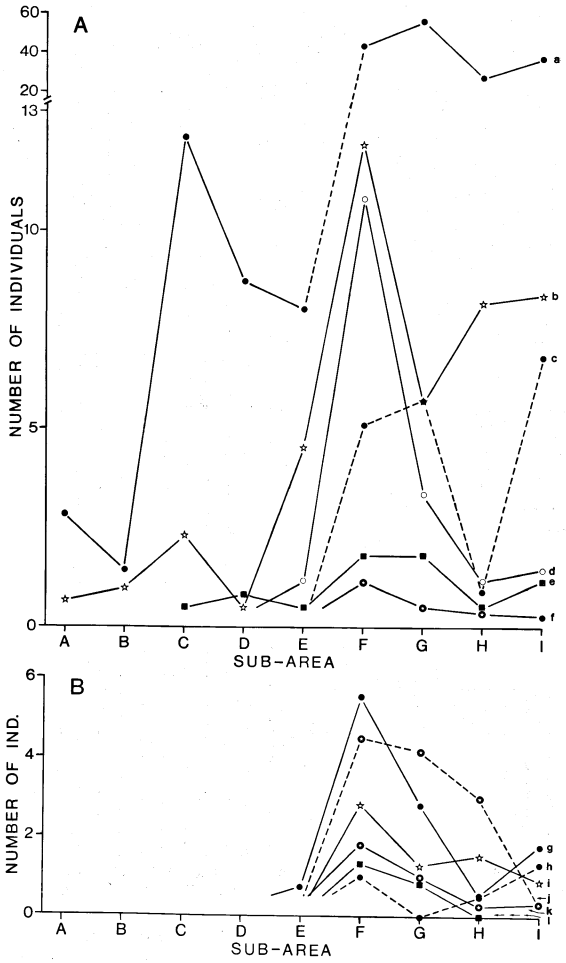

Fig. 3. Group II (The *Lucinoma borealis* and *Ophiura albida* group). Average number of individuals per 0.2 m² in the nine sub-areas. a) *Lucinoma borealis*, b) *Ophiura albida*, c) *Astarte montagui*, d) *Edwardsia tuberculata*, e) *Notomastus latericeus*, f) *Corbula gibba*, g) *Dosinia lupinus*, h) *Lepidopleurus asellus*, i) *Thyasira flexuosa*, j) *Pectinaria auricoma*, k) *Gari fervensis*, l) *Astropecten irregularis*. Values below 0.5 in sub-areas A–E are not included. NB! Average values of the bivalves were calculated from 99 samples (see TUNBERG 1981).

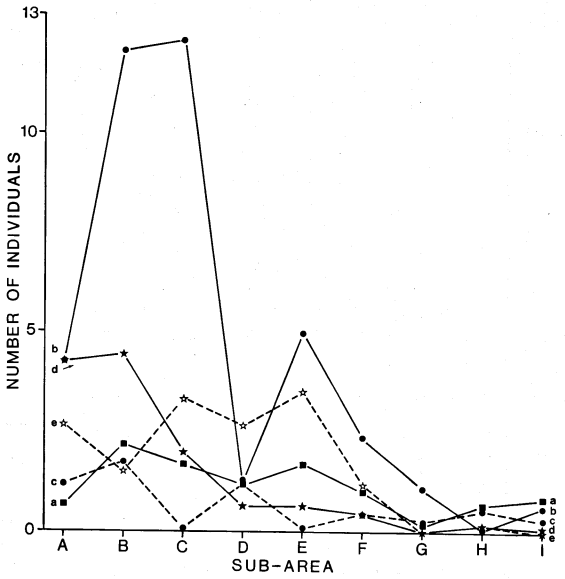

Fig. 4. Group I (The *Thracia villosiuscula* and *Dosinia exoleta* group). Average number of individuals per 0.2 m² in the nine sub-areas. a) *Pagurus bernhardus*, b) *Dosinia exoleta*, c) *Mya truncata*, d) *Thracia villosiuscula*, e) *Cirriformia tentaculata*. NB! Average values of the bivalves were calculated from 99 samples (see TUNBERG 1981).

and 4.2, for areas G–I between 2.5 and 2.7. Sub-area F holds an intermediate position with an index of 3.3. The highest value, 4.2, was noted for sub-area A, which was also the shallowest.

The cumulative curves (Figs 6A and 6B) show the rate at which new species are found with an increase in sample size (i.e. increased number of samples). The greatest number of species (36) was found in sub-area F, and lowest (25) in sub-area B. From the slope of the curves it seems reasonable to assume that if more than the existing six samples were taken, the number of species in each sub-area would increase, particularly for areas A, F, and H.

An analysis of species dominance (cf. SANDERS 1960) is presented in Table 4.

DISCUSSION

The two groups or 'communities' of species described, do not correspond to any of the communities described by PETERSEN (1913, 1918). Several of the species in the two groups are represented in different communities. Ap-

Table 3. Diversity indices (H'), Evenness (J), and Dominance (1-J) values of the nine sub-areas and of the whole sampling area. N = number of individuals, S = number of species.

Sub-area	A	B	C	D	E	F	G	H	I	TOT.
H'	4.21	3.92	3.62	3.96	3.74	3.34	2.67	2.65	2.46	3.83
J	0.83	0.84	0.72	0.80	0.78	0.64	0.55	0.51	0.50	0.62
1-J	0.17	0.16	0.28	0.20	0.22	0.36	0.45	0.49	0.50	0.38
N	147	195	344	148	237	665	516	422	413	3087
S	34	25	33	31	28	38	30	36	31	75

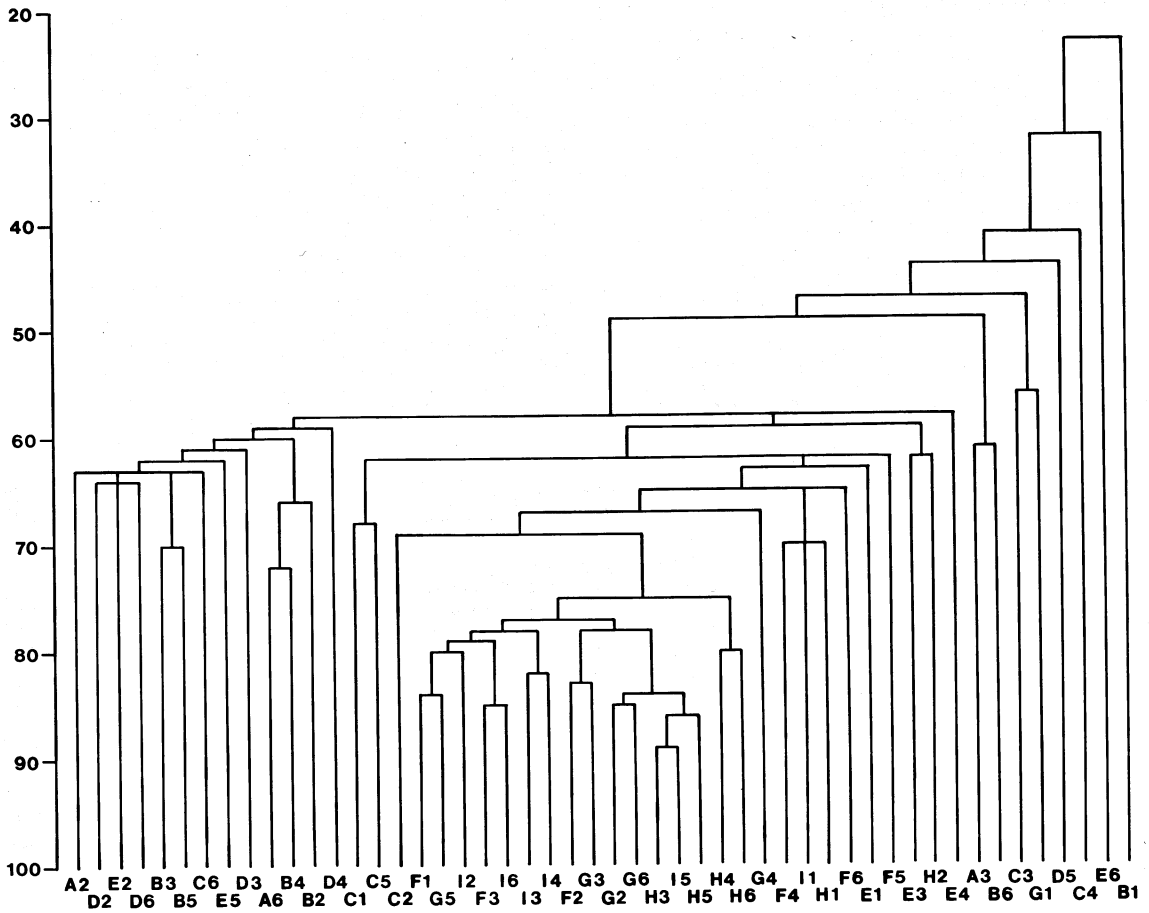

Fig. 5. Percent similarity (species composition) among 50 quantitative samples, based on the coefficient of Czekanowski (see the text).

parently the composition of the groups does not correspond to any of the so-called parallel communities (THORSON 1958).

The clean, coarse shell-sand bottom in the area occurs rather frequently in shallow areas along the Norwegian west coast, and this type of bottom was not found in the communities described by Petersen. This is also evident from the composition of his communities.

Because of the warm North Atlantic Current, the water temperature along the Norwegian west coast remains relatively high during the winter.

The strong tidal currents in the survey area

Table 4. Dominant species (cf. SANDERS 1960) in the nine sub-areas.

A	B	C	D	E
Lucinoma borealis	Dosinia exoleta	Lucinoma borealis	Lucinoma borealis	Lucinoma borealis
Cirriformia tentaculata	Venerupis pullastra	Dosinia exoleta	Cirriformia tentaculata	Ophiura albida
Thracia villosiuscula	Littorina littorea	Phoronis muelleri	Dosinia exoleta	Cirriformia tentaculata
Dosinia exoleta	Thracia villosiuscula		Pagurus cuanensis	Pagurus cuanensis
Venerupis pullastra	Mya truncata			

F	G	H	I
Lucinoma borealis	Lucinoma borealis	Lucinoma borealis	Lucinoma borealis
Ophiura albida			

prevent sedimentation of fine particles, and also keep the salinity at a very stable and high level (c. 33 ‰).

At present I am studying the macrofauna in a shell-sand bottom at a depth of 12 m outside Gullmarfjorden on the Swedish west coast. That area is under the strong influence of the low-salinity Baltic Current, and the salinity there has fluctuated both widely (20.4–31.8 ‰) and frequently during the 1.5 years that the survey has been in progress. The bottom-water temperature was also very low (0.8°C) during the winter. The species composition here, of more or less euryhaline species, corresponds relatively well to Petersen's shallow communities. Many polystenohaline species, such as the echinoderms *Echinus esculentus* L. and *E. acutus* LAMARCK, both of which were abundant over the whole survey area at Eggholmane, are not found in these communities. During certain periods the latter of these two species was so abundant within areas F–I that it almost completely covered the bottom.

THORSON (1957) defined Petersen's communities more precisely, but the species groups at Eggholmane differ also from these.

Figs 3A and 3B show that the species in Group II have similar distributional patterns in the nine sub-areas, and all show a clear preference for sub-area F, with medium sand and c. 70 % $CaCO_3$ (TUNBERG 1981). The quantitative distribution of the species in Group I, however, did not show the same uniform pattern (Fig. 2).

It is difficult to state whether the two groups in the Eggholmane area can be characterized as a continuum (SANDERS 1960; HUGHES & THOMAS 1971; LIE 1974) or as discrete communities. According to MILLS (1969) it is just as legitimate to regard the community as an abstraction from a series of continua as to characterize it in terms of a few abundant species. It should also be stressed here that within the survey area there was a sharp transition in the sediment structure and depth between the shallow sub-areas A–E and the deeper ones F–I (fig. 1 in TUNBERG 1981). The intermediate sub-areas D and E also, in certain areas, had very stratified sediments. D, in particular, often had a thin surface layer of very fine sediment, while the sediment deeper down was very coarse (fig. 4 in TUNBERG 1981).

Even though the area was rather protected from wave action, it was, as pointed out above, exposed to strong tidal movements, which complicated the situation. According to THORSON (1957) sandy bottoms similar to these are almost exclusively found in heavily exposed areas.

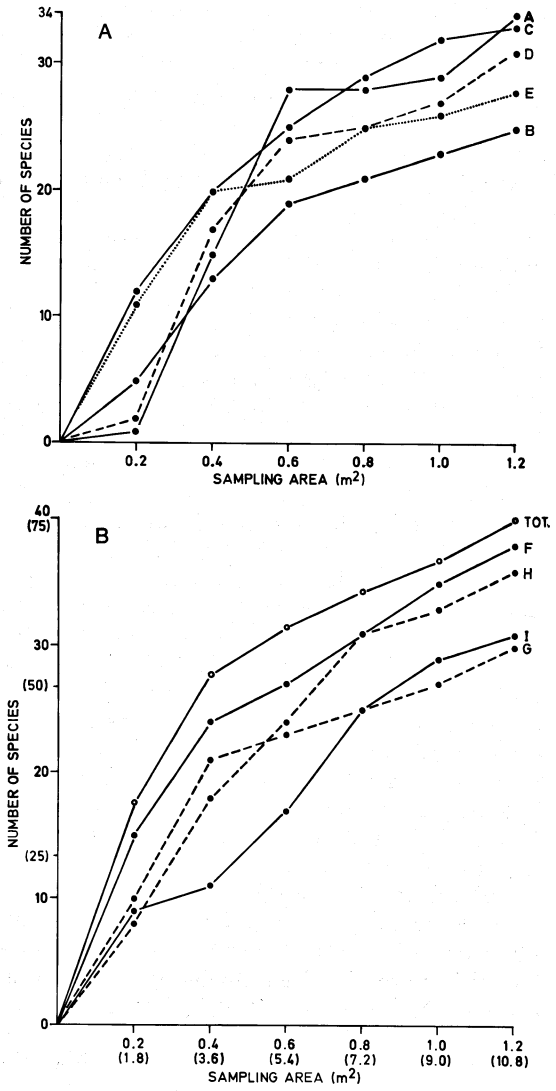

Fig. 6. Cumulative number of species with increased sample size (increased number of samples) in the nine sub-areas, A–I, and in the whole sampling area (TOT.). Numbers in parantheses are values of the whole sampling area.

There are also reasons to assume that the water exchange in the area increased the amount of available food, not only quantitatively, but also qualitatively. JACKSON (1972) states that shallow-water infaunal diversity is influenced by the variety of available food (see TUNBERG 1981). The high diversity indices in the shallow sub-

areas with stronger water movements seem to confirm this assumption. Most species (and also most individuals) were, however, found in sub-area F (Table 3). It must be taken into consideration that the high density of the bivalve *Lucinoma borealis* reduced the diversity indices in the deeper sub-areas. The high density of this species, especially in sub-areas F–I, is noteworthy. As far as I know, *Lucinoma borealis*, which can be said to be a character species of the whole survey area, has not been found in such high densities before. LIE (1978) found *L. borealis* to be the fourth most abundant species in the 'shore zone' in the nearby Fanafjorden, with an average density of 18.7 ind./0.6 m². BUCHANAN (1963), in his study of the benthic communities off the coast of Northumberland, found *L. borealis* in an average density of 8 ind./m² in the '*Cucumaria-Diastylis* variation' of PETERSEN'S (1913) *Amphiura filiformis–Amphiura chiajei* community. In the whole sampling area at Egghol-mane, the average density of this species was 22.2 ind./0.2 m², with a maximum value of 100 ind./0.2 m² (TUNBERG 1981). It is difficult to explain the reasons for the great differences between these areas. One reason could be that while conventional methods for taking quantitative samples may be inadequate for getting all individuals of this species, a deep burrower (personal observation), the suction sampler used in this survey was very efficient in taking samples deep into the substrate.

In conclusion, this survey confirms the assumption of the presence of two benthic macrofaunal 'communities' within the survey area, as proposed by TUNBERG (1981), despite the fact that all species did not follow the pattern that was proposed. It was possible to relate the quantitative distribution of the species to the structure of the sediment in this area. Other possible factors influencing distribution were, however, also discussed in TUNBERG (1981).

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