TWO BIVALVE COMMUNITIES IN A SHALLOW AND SANDY BOTTOM IN RAUNEFJORDEN, WESTERN NORWAY

BJÖRN TUNBERG

SARSIA

TUNBERG, BJÖRN 1981 12 31. Two bivalve communities in a shallow and sandy bottom in Raunefjorden, western Norway. – *Sarsia* 66: 257–266. Bergen. ISSN 0036–4827.

Ninety-nine quantitative substrate samples of 0.2 m² each, were taken at regular intervals between November 1975 and October 1976, from sandy bottoms at 0.3–13.3 m depth. The sediment was rich in $CaCO_3$. Thirty-two bivalve species (3685 individuals) were obtained. *Lucinoma borealis* was by far the most common species (59.6 % by number) followed by *Dosinia exoleta* (11.6 %) and *Astarte montagui* (5.8 %).

Most species showed a specific preference concerning sediment structure, and two distinct groups or 'communities' of bivalves could be distinguished, and their distributions were shown to be correlated with the grain-size distribution in the sediment.

It was not possible to explain the specific distribution patterns by means of feeding methods. Both types, i.e. deposit- and suspension-feeders, were spread throughout the sampling area. Species which are deposit-feeders made up only 1.9 % of the individuals sampled, and 81 % of the species were suspension-feeders, which indicates that the biotope was more suitable for suspension-feeding bivalves.

Björn Tunberg, Institute of Marine Biology, University of Bergen, N-5065 Blomsterdalen, Norway. – Present address: Kristineberg Marine Biological Station, S-450 34 Fiskebäckskil, Sweden.

INTRODUCTION

The species composition and distributional patterns of the macrofauna of level-bottom environments have been described from a great many areas, especially within sublittoral soft bottoms. Quantitative studies of the benthic macrofauna in shallow and sandy areas are scarce, probably because of technical sampling problems. Owing to the coarseness of the sediment, the substrate samples from this type of bottoms are also comparatively big, even if the finer fractions are discarded. Sorting is therefore very time-consuming.

Correlation between the grain-size distribution and diversity has been demonstrated in many studies (e.g. GAGE 1972), but other factors are probably also important for species diversity. WHITLATCH (1981) states that standard methods may be largely inadequate for understanding many aspects of organism-sediment relationships in marine benthic environments.

The aim of this work was to examine composition, diversity patterns, and distribution of bivalve species in a shallow and sandy bottom in Raunefjorden, western Norway, and to ascertain if it were possible to distinguish between different bivalve 'communities', and then mainly in relation to sediment structure.

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 in 1975 and 1976 within a delimited area at Eggholmane (Fig. 1), 60°15′36″ N, 5°13′ E (Institute of Marine Biology Ref. numbers E 191–75 and E 298-76). Its size was about 49 800 m², of which 11 200 m² (22 %) was land (islets and skerries) and 38 600 m² (78 %) water, and the maximum depth was c. 14 m.

Bottom conditions and depths were investigated by means of c. 600 soundings and visual inspection through SCUBA diving. Large parts of the bottom consisted of rocks, boulders, and pebbles, and these were excluded from the survey (Fig. 1, hatched areas). The remaining area was divided into nine sub-areas, A–I (Fig. 2), all with different characteristics. Each sub-area was divided into numbered squares of 25 m². Before each substrate sampling occasion, one square was randomly selected within each sub-area, and the samples were taken in the middle of these squares. In that way, substrate samples were taken from different depths and on different types of sediment on each sampling occasion (see Table 1 and below).

Quantitative fauna samples were collected 11 times with regular intervals during the period November 1975 to October 1976 (Fig. 3).

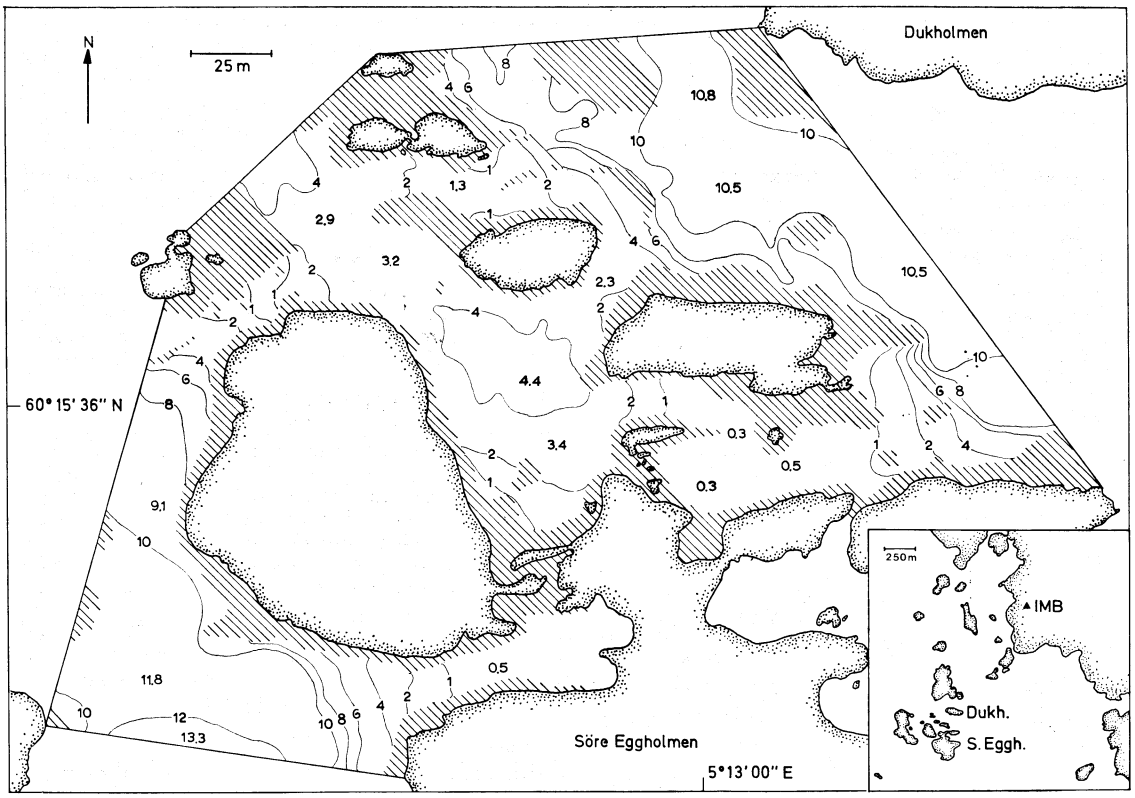

Fig. 1. Sampling area. Hatched parts indicate rock/pebble bottom. Some depths and isobates are shown for 1, 2, 4, 6, 10, and 12 m depth. All depths have been corrected to LWS. IMB = Institute of Marine Biology.

The 11×9 samples were collected with a diver-operated, air-driven, suction sampler, and collected in a sieve, the bottom of which was a perforated steel plate with circular 5-mm holes.

Sampling of sediment for grain-size and $CaCO_3$ analysis was carried out on 1 December 1976 and between 20 February and 3 June 1977, at 16 randomly selected points (Fig. 2, numbered dots). Fiberglass tubes (inner Ø 56 mm) were used by a SCUBA diver for sediment coring. Each core was divided into four 40 mm sections which were subsequently dried and weighed. A 5 g sub-sample was taken for $CaCO_3$ analysis and the remaining sediment was sieved under water through eight sieves (wire netting) with mesh sizes 8, 4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm. Sediment not retained on the finest sieve was determined by subtraction from the total weight. The other fractions were dried and weighed, and $CaCO_3$ analysis was made according to a direct titration method (BARNES 1959). Description of sediment structure follows the designations by WENTWORTH (1922).

Grain-size distribution may be illustrated. by means of a cumulative curve (PETTIJOHN 1957) The median particle diameter was obtained from this curve. The sorting or spread of the data was measured by using a coefficient of sorting (Inclusive Graphic Standard Deviation), described in GRAY (1981).

Temperature was measured in connection with quantitative sampling of substrate, except on 2 February 1976 (Sampling No 3). The measurements were made about one cm above the sediment surface, and with an accuracy of $\pm$ 1/10° C.

Computation of correlation coefficients was carried out by using the following expressions:

$$\text{Correlation coefficient} = \frac{Sxy}{SxSy}$$

where

$$S_{xy} = \frac{1}{n-1}\left(\Sigma x_i y_i - \frac{1}{n}\Sigma x_i \Sigma y_i\right)$$

$$S_x = \sqrt{\frac{\Sigma x_i^2 - n\bar{x}^2}{n-1}}$$

$$S_y = \sqrt{\frac{\Sigma y_i^2 - n\bar{y}^2}{n-1}}$$

The calculated values were not tested for significance.

The Shannon-Wiener index (H′) was used as a measure of species diversity, and evenness (J) was defined as H'/H'_{max} where H'_{max} is the diversity when the species are equally distributed.

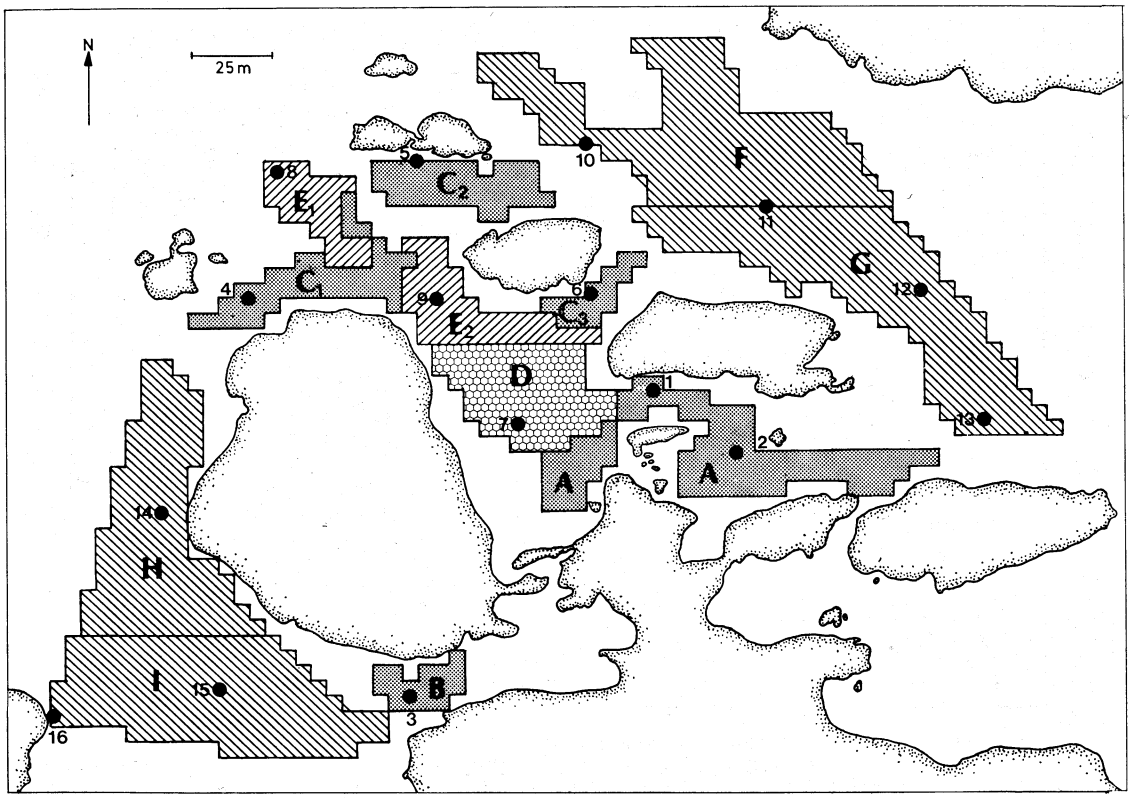

Fig. 2. The nine sub-areas, A–I, within the sampling area. The dots show the 16 sediment sampling points for grain-size and $CaCO_3$ analysis.

RESULTS AND DISCUSSION

Sediment

The results of the analysis of grain-size distribution is presented in Fig. 4. It shows that the 0–40 mm sections of points 1 and 3–6 had a similar sediment structure, and this also applies for points 10–15. The former points all had sediments with median phi-values between 0 and + 1 (coarse sand), and the latter between + 1 and + 2 (fine sand), except point 14 which had a value of + 0.94. The core taken at point 4 contained one living specimen of *Dosinia exoleta*, which took up the greater part of the core in 80–120 mm depth. (As a result of the area fusions described below, points 1 and 3–6 were taken in secondary area 1, and points 10–15 in secondary area 4).

Point 2, in sub-area A, had a phi-value in the 0–40 mm layer corresponding to fine sand, and this sediment was black and had a faint smell of H_2S.

Point 16, in sub-area I, was taken on a slope in rather shallow water (5.7 m), and the sediment structure, in the 0–40 mm layer, was different from the rest of this sub-area.

Point 7, in sub-area D (sec. area 2), had a rather fine sediment in the 0–80 mm layer, but a strong increase of coarse particles deeper down (mainly fragments of *Mya*).

The 0–40 mm layer at points 8 and 9, in sub-area E (sec. area 3), was dominated by very coarse sand, with median phi-values of – 0.32 and – 0.14.

The analysis of sorting shows that most parts of most cores fall within the groups poorly sorted or very poorly sorted sediments (Fig. 4). Point 10, in 0–40 mm, was moderately sorted. Point 5, in 0–40 mm and 120–160 mm, and point 9, in 80–120 mm were extremely poorly sorted.

The $CaCO_3$ content in the sediment was consistently high, except in the SW part of sub-area A (point 2). The measured values may be summarized as follows: over 85 %;

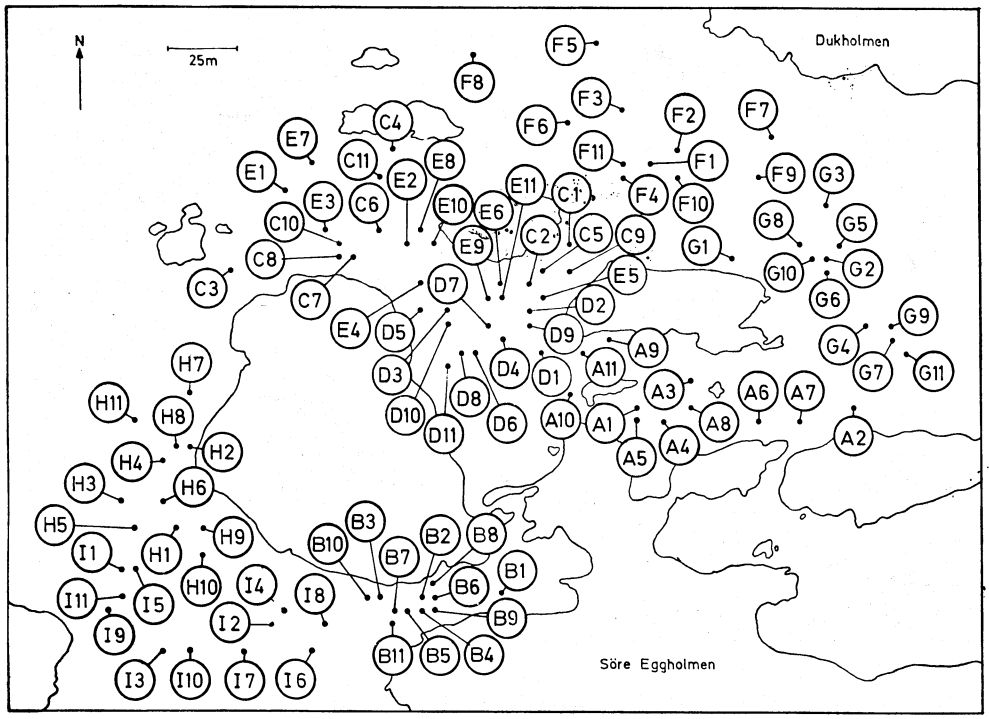

Fig. 3. Quantitative substrate sampling points. Letters denote sub-areas (cf. Fig. 2″, and figures denote collection numbers. Because of a slightly different division into sub-areas at collection No 1, point B1 is situated outside sub-area B.

A (p. 1), C_1, C_2, C_3, H, I (p. 6), about 80 %; B, about 70 %; E_2, F, F–G, about 65 %; G (p. 13), I (p. 15), about 60 %; D, G (p. 12), about 55 %; E_1, about 5 %; A (p. 2).

Temperature and salinity

The lowest temperature, 3.6° C (sub-area A), was measured on 25 March, and the highest, 17.7° C (sub-area A), on 6 July. During the winter, the temperature was relatively homogeneous all over the area, whereas during the summer the deepest sub-areas (F–I) were considerably colder than the more shallow ones. In July these deep areas had an average temperature of 13.6° C, the others 17.0° C.

The salinity in the area remained fairly constant (c. 33 ‰) throughout the year.

Sub-areas

Sediment analyses, and the result of the analysis of macrofaunal distribution within the area, gave valuable information concerning the nature of the sub-areas. This information, together with what had earlier come to hand about the area, showed that the resemblance between sub-areas A, B, C and F, G, H, I respectively was so far-reaching that they could be fused into two large areas. Sub-areas D and E both had features distinctive enough to make it necessary to treat them separately.

A small part of sub-area A, in very shallow water (at sediment sampling point 2, and to the SW of it), had fine sediment with little $CaCO_3$. Only a few bivalves were found here, probably due to the contamination of H_2S (mentioned earlier). Therefore this part of sub-area A, 150 m² (substrate sampling points A1, A4, A5, and A8), was excluded from the survey.

These fusions of areas made the results of the statistical work more reliable.

To avoid misunderstanding, the four groups of areas are from this point on called secondary areas, and have been given the numbers 1–4 (Table 2). A result of the new grouping was that the number of quantitative substrate samples was not the same within all secondary areas (see Table 2), which must be taken into consideration when drawing conclusions about the occurrences of the different species (see below).

Table 1. The nine sub areas at Eggholmane, divided according to depth and bottom conditions.

Sub. area	Area m²	% of total	Depth (m) Min	Max	Aver	Observations
A	2075	9.9	0.2	2.7	1.0	Varying bottom conditions. Somewhat muddy, and with blackish color in the SW. In the other parts, rather coarse and white shell sand.
B	400	1.9	0.5	3.6	2.0	Light shell sand with small pebbles. A few brown algae. Heavy slope in the W part.
C_1	1850	10.5	3.7	3.0	2.1	Light shell sand. Bottom smooth and homogenous.
C_2			0.8	3.4		
C_3	350		1.8	3.4		Some boulders, which had a rich growth of macroalgae.
D	1525	7.3	2.7	4.5	4.0	Greyish sand with many stones and pebbles.
E_1	1625	7.8	2.9	4.4	3.6	Light greyish sand. Bottom smooth, homogenous.
E_2			3.0	4.4		
F	3550	17.0	7.3	11.8	10.0	Dark grey sand, many big boulders.
G	3525	17.0	5.7	10.7	9.3	Dark grey sand, many big boulders.
H	2750	13.2	6.4	11.2	9.3	Dark grey sand, lots of pebbles.
I	3250	15.6	4.3	13.3	10.9	Dark grey sand, lots of pebbles.

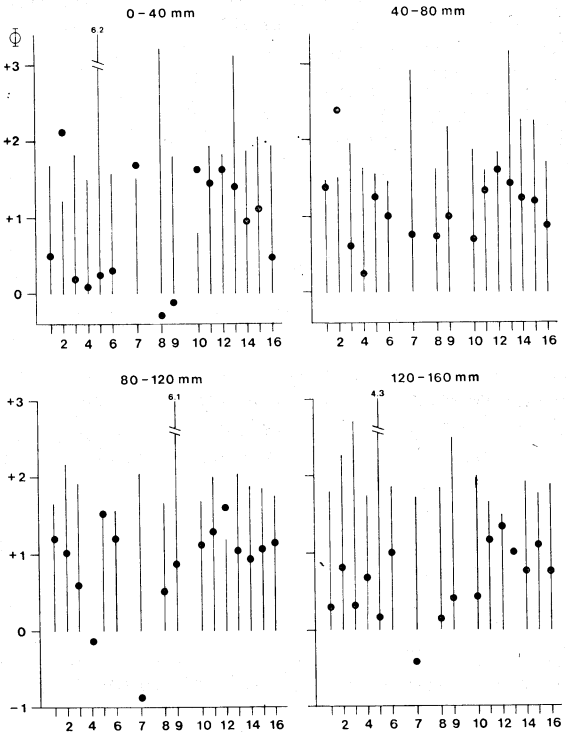

Fig. 4. Grain-size distribution in different depths of the sediment, at 16 points (Fig. 2) within the survey area, represented by median values (dots) and coefficients of sorting (bars). Points 1 and 3–6 were taken in secondary area 1, point 7 in sec. area 2, points 8 and 9 in sec. area 3, and points 10–15 in sec. area 4. (See the text for the reasons for excluding point 2 from sec. area 1, and point 16 from sec. area 4.)

Bivalves

The quantitative samples contained 32 bivalve species (3685 individuals, Table 3). Three more, *Modiolus modiolus* (L.), *Pecten maximus* (L.), and *Chlamys varia* (L.) were observed during SCUBA dives. The sandy shore behind sub-area B also had a large population of *Cerastoderma edule* (L.). Thus the total number of species amounted to 36.

The outcome of the correlation analysis for the separate sampling points (Table 4, part I), and sub-areas (Table 4, part II), where the occurrences of the twelve most common species were tested towards each other, made it possible to distinguish between two distinct groups, A and B. Most individuals of the bivalves in Group A were found in secondary area 1 (coarse clean sediment in shallow water), and the ones in Group B mostly in secondary area 4 (fine sediment on deeper water). Within each of these groups almost all species were positively correlated to each other, and negatively correlated to the bivalves in the opposite group. *Venus fasciata*, however, showed no correlation whatsoever to *Astarte montagui* and *Corbula gibba* in Group B. Its relation to the other species also made it necessary to place it in an inter-

Table 2. Secondary areas. N = number of samples (0.2 m²) collected within each secondary area. Average values of median grain diameter were calculated as follows: Sec. area 1 = sediment sampling points 1 and 3–6, sec. area 2 = point 7, sec. area 3 = points 8 and 9, sec. area 4 = points 10–15 (see the text and Fig. 4).

Sub-area	Sec. area	Size m²	% of total	N	Bivalve diversity	Bivalve evenness	Aver. values of median grain diam. (mm) in different sediment depths (mm) 0–40	40–80	80–120	120–160
ABC	1	4 325	21.1	29	2.88	0.61	0.8	0.6	0.6	0.7
D	2	1 525	7.4	11	2.54	0.61	0.3	0.6	1.8	1.3
E	3	1 625	7.9	11	2.29	0.56	1.2	0.6	0.6	0.8
F–I	4	13 075	63.6	44	1.64	0.38	0.4	0.4	0.5	0.5

mediate position. Noteworthy is also that *Parvicardium scabrum* and *Gari depressa* in Group A showed a strong positive correlation when subareas were compared, but a weak negative correlation when sampling points were compared. The same condition also applies for *Astarte montagui* and *Gari fervensis* in Group B.

According to TEBBLE (1966), *Astarte montagui* (Group B), in British waters, not only occurs in muddy sand, but also in clean sand and sandy gravel. In Raunefjorden 98 % of the individuals were found in the fine sediments of area 4. JEFFREYS' (1863) description of the habitat (sand often mixed with mud) corresponds much better to the result of this survey.

Lucinoma borealis (Group B) was very common all over the area, but 84 % of the individuals were found within area 4. Because of its high density, up to 500 individuals/m², it must be an important species here.

Thyasira flexuosa (Group B) was almost exclusively found in area 4 (97 %), and this preference of habitat corresponds very well with notes in the literature.

Montacuta ferruginosa was only found on four occasions. According to GAGE (1966), this species is typically found unattached in the burrows of spatangoids. In this survey, sea urchins occurred together with the bivalve only once, at point E5, one *Echinocardium cordatum* (PENNANT) and one *E. flavescens* (MÜLLER).

Parvicardium scabrum (Group A) preferred the coarse, clean sediment of area 1, 83 % of all individuals being found here. It did not occur at all in area 4, which is rather notably, as TEBBLE (1966) states the minimum depth for this species to be about 9 m in British waters.

Dosinia exoleta (Group A) and *D. lupinus* (Group B) have different demands on sediment structure; 74 % of the individuals of *D. exoleta* were found in area 1, and 82 % of those of *D. lupinus* in area 4. In spite of the fact that the two species obviously prefer different types of sediment, they were obtained in the same samples on several occasions. *D. lupinus* seemed to be a little bit more specific in its choice of habitat. GLEMAREC (1973) characterized *D. lupinus* as a typical inhabitant of 'coastal' muddy sands, and *D. exoleta* of infralittoral gravel, in North Gascony.

Venerupis pullastra was not found deeper than 1.3 m. It usually prefers muddy sand and sandy gravel (è.g. QUAYLE 1952), but at Eggholmane it was found only in clean shell sand.

Gari fervensis (Group B) and *G. depressa* (Group A), were only once found together (point B4). *G. depressa* did not occur in area 4, 67 % of all individuals being collected within area 1. It is also noteworthy that this species was common also in the stratified sediments of areas 2 and 3. Even though *G. fervensis* occurred sporadically over all the sampling area, it perferred the sediments of area 4, where 83 % of all individuals were found.

According to JEFFREYS' (1863) *G. depressa* occurs intertidally in British waters, but the rest of the species within this genus are sublittoral, although *G. fervensis* is occasionally taken at LWS. YONGE (1949) found this species in fine substrata of sandy or muddy gravel at moderate depths in the Clyde Sea area.

Mya truncata was placed in Group A, but occurred over all the area. Its relatively high density in the stratified and coarse sediments of area 2 is noteworthy.

Of the 32 specimens collected of *Corbula gibba* (Group B), 26 (84 %) were found in area 4. Only one individual was found in area 1. YONGE (1946) states that *C. gibba* is a typical inhabitant of thick, muddy sands with admixed gravel and small stones.

Thracia villosiuscula (Group A) and *T. phaseolina* presumably prefer the same type of habitat, but too few of the latter species were found to draw any certain conclusions concerning distributional pattern. Eighty-four per-

Table 3. Distribution and feeding methods of the bivalve species found at Eggholmane. N = total number of individuals found in the 99 samples of 0.2 m². Feeding method: D = deposit feeder, S = suspension feeder. The numerals within brackets are standard deviation values.

Rank	N	Species	Feeding method	Depth distr. (m) min	max	Average number of individuals per 0.2 m² Totally	Secondary area 1	2	3	4	% of total	Cumulative %
1	2194	Lucinoma borealis (L.)	S	0.3	13.3	22.2 (24.1)	5.6 (7.3)	8.7 (5.4)	8.0 (5.4)	41.5 (23.9)	59.6	59.6
2	428	Dosinia exoleta (L.)	S	0.5	11.9	4.3 (9.7)	9.6 (15.0)	1.3 (3.0)	5.0 (6.5)	1.0 (2.1)	11.6	71.2
3	213	Astarte montagui (DILLWYN)	S	1.7	13.3	2.1 (4.6)	0.1 (0.3)	-	-	4.7 (6.0)	5.8	77.0
4	142	Dosinia lupinus (L.)	S	1.8	12.6	1.4 (2.4)	0.4 (1.0)	0.3 (0.9)	0.7 (1.1)	2.7 (3.1)	3.9	80.9
5	141	Thracia villosiuscula (MACGILLIVRAY)	S	0.3	10.5	1.4 (3.1)	4.3 (4.6)	0.6 (1.0)	0.6 (1.0)	0.2 (0.5)	3.8	84.7
6	119	Ensis sp.	S	0.3	11.9	1.2 (2.2)	0.8 (1.7)	1.8 (1.8)	0.5 (0.9)	1.5 (2.8)	3.2	87.9
7	75	Thyasira flexuosa (MONTAGU)	S	3.2	11.9	0.8 (1.7)	-	-	0.1 (0.3)	1.7 (2.3)	2.0	89.9
8	64	Mya truncata L.	S	0.3	13.3	0.7 (1.3)	1.0 (1.9)	1.2 (1.2)	0.1 (0.3)	0.4 (0.8)	1.7	91.6
9	52	Venerupis pullastra (MONTAGU)	S	0.3	1.3	0.5 (2.1)	1.6 (3.4)	-	-	-	1.4	93.0
10	46	Gari fervensis (GMELIN)	D	0.9	10.7	0.5 (1.3)	0.1 (0.4)	0.1 (0.3)	0.3 (0.5)	0.9 (1.9)	1.3	94.3
11	43	Venus fasciata (DA COSTA)	S	0.3	11.4	0.4 (0.9)	0.8 (1.1)	0.4 (0.9)	-	0.3 (0.7)	1.2	95.5
12	31	Corbula gibba (OLIVI)	S	1.8	11.9	0.3 (0.8)	-	0.2 (0.4)	0.2 (0.4)	0.6 (1.0)	0.8	96.3
13	24	Parvicardium scabrum (PHILIPPI)	S	0.5	4.2	0.2 (0.8)	0.6 (1.2)	0.3 (0.7)	0.1 (0.3)	-	0.7	97.0
14	20	Gari depressa (PENNANT)	D	0.3	3.8	0.2 (0.5)	0.4 (0.7)	0.1 (0.3)	0.5 (0.7)	-	0.5	97.5
15	13	Cochlodesma praetenue (PULTENEY)	S	0.3	10.7	0.1 (0.4)	0.1 (0.4)	0.5 (0.7)	0.1 (0.3)	0.1 (0.3)	0.4	97.9
16	13	Venus ovata (PENNANT)	S	0.9	10.5	0.1 (0.4)	0.1 (0.3)	0.4 (0.9)	-	0.1 (0.3)	0.4	98.3
17	13	Thracia phaseolina (LAMARCK)	S	0.5	10.8	0.1 (0.7)	0.3 (1.2)	0.1 (0.3)	0.1 (0.3)	0.1 (0.2)	0.4	98.7
18	8	Arctica islandica (L.)	S	2.2	12.6	0.1 (0.3)	0.1 (0.2)	-	-	0.1 (0.4)	0.2	98.9
19	7	Hiatella arctica (L.)	S	0.3	10.8	0.1 (0.3)	-	-	-	0.1 (0.4)	0.2	99.1
20	7	Mysia undata (PENNANT)	S	2.3	10.8	0.1 (0.3)	-	-	-	0.1 (0.4)	0.2	99.3
21	7	Montacuta ferruginosa (MONTAGU)	S	3.7	11.2	0.1 (0.4)	0.1 (0.4)	0.4 (0.9)	-	-	0.2	99.5
22	5	Spisula subtruncata (DA COSTA)	S	2.7	3.5							
23	4	Venus striatula (DA COSTA)	S	0.6	8.4							
24	3	Acanthocardia echinata (L.)	S	8.4	10.4							
25	3	Mya arenaria L.	S	0.9	1.3							
26	3	Lyonsia norvegica (GMELIN)	S	10.4	11.3							
27	2	Macoma baltica (L.)	D	0.5								
28	1	Parvicardium ovale (SOWERBY)	S	3.2								
29	1	Venerupis aurea (GMELIN)	S	0.6								
30	1	Tellina tenuis (DA COSTA)	D	0.9								
31	1	Tellina fabula GMELIN	D	4.3								
32	1	Macoma calcarea (CHEMNITZ)	D	3.2								

Table 4. Correlation coefficients for the twelve most common species. Part I: Comparison between sampling points (N = 99). Part II: Comparison between sub-areas (N = 9). All values have been multiplied by 100. The groups, A and B, were established on the basis of the correlation coefficients. Group A: species in coarse clean sediment in shallow water, Group B: species in fine sediment in deeper water. *Venus fasciata* has been placed in an intermediate position (see the text).

		Thracia villosiuscula	Dosinia exoleta	Gari depressa	Mya truncata	Parvicardium scabrum	Venus fasciata	Lucinoma borealis	Dosinia lupinus	Thyasira flexuosa	Gari fervensis	Astarte montagui	Corbula gibba
	Thracia villosiuscula		+71	+78	+71	+77	+64	-70	-45	-54	-38	-54	-52
	Dosinia exoleta	+71		+51	+27	+43	+69	-60	-35	-50	-29	-52	-51
A	Gari depressa	+30	+24		+49	+62	+20	-77	-51	-64	-42	-61	-53
	Mya truncata	+20	+07	+35		+39	+34	-54	-36	-35	-22	-40	-31
	Parvicardium scabrum	+17	+07	-09	+16		+56	-65	-50	-58	-54	-57	-52
	(Venus fasciata)	+26	+06	+04	+06	+11		-21	-14	-38	-16	-14	-36
	Lucinoma borealis	-34	-30	-29	-16	-21	-13		+80	+79	+72	+89	+74
	Dosinia lupinus	-07	-01	-19	-08	-10	-08	+50		+87	+97	+79	+94
B	Thyasira flexuosa	-18	-16	-16	-04	-15	-06	+43	+51		+88	+68	+95
	Gari fervensis	-14	-11	-10	-06	-09	-11	+33	+45	+35		+68	+95
	Astarte montagui	-17	-10	-17	-06	-16	00	+46	+35	+16	-01		+65
	Corbula gibba	-16	-11	-13	-16	-11	00	+31	+15	+27	+02	+16	

I II

cent of all *T. villosiuscula* individuals were found in area 1, and only 6 % in area 4. According to ALLEN (1961), in his study of the British species of *Thracia*, *T. phaseolina* mainly occurs in sands and muddy sands, and *T. villosiuscula* in sandy gravels.

It is not possible to draw any certain conclusions concerning habitat preference for the other species, because they were found too sporadically (see Table 5 for a complete list).

An analysis of dominance (cf. SANDERS 1960) was made, which shows that *Lucinoma borealis* alone dominated sub-areas D, F, G, H, and I. *Dosinia exoleta*, *Thracia villosiuscula*, and *Lucinoma borealis* were dominant species in sub-area A, and *Dosinia exoleta* in sub-area C.

Twenty-six (81 %) of the 32 species collected, are known to be suspension-feeders. It was not possible, however, to relate the distributional patterns to the feeding methods, since both types were spread over all the area. On the other hand, only 71 individuals or c. 1.9 % were deposit-feeders. This fact shows that the sediment within this survey area was too coarse to be handled by most deposit-feeding species.

Areas 2 and 3 had a bivalve fauna that was rather low in density. The highly stratified and coarse sediments, especially in area 2, obviously had a negative effect on many species. On the other hand, the diversity indices of these areas were rather high, especially when compared with area 4, which had a very low index. The reason for this is not clear, but the following conditions may be of importance: Tidal currents were stronger in the shallower parts of the sampling area, which probably increased the variety of available food. JACKSON (1972), in his study of mollusc populations in Jamaica, says that there was no correlation between bivalve diversity and the total quantity of food available, but bivalve diversity increased with the variety of available food. He also found that biological factors, such as predation, were of great importance in determining faunistic differences between certain areas. Competition may also be an important factor. *Lucinoma bo-*

Table 5. The bivalves found in the quantitative samples (cf. Fig. 3). Letters denote sub-area (cf. Fig. 2), and numerals denote collection number (regular intervals from October 1975 to November 1976). Numerals within brackets= number of individuals in the samples of 0.2 m². Zero values have been omitted.

Venus striatula	A: 6(1). D: 9(1). E: 11(1). F: 6(1).
Venerupis aurea	A: 6(1).
Venerupis pullastra	A: 3(11), 6(4), 7(1), 8(2). B: 1(1), 2(3), 4(5), 6(14), 8(3), 9(8).
Mysia undata	C: 1(1). G: 6(1), 7(2), 10(1).
Spisula subtruncata	A: 10(2), 11(1). B: 10(1). D: 11(1).
Tellina tenuis	B: 9(1).
Tellina fabula	D: 7(1).
Macoma baltica	A: 5(2).
Macoma calcarea	E: 10(1).
Gari fervensis	B: 2(2), 4(1), 9(1). D: 8(1). E: 4(1), 6(1), 11(1). F: 1(1), 2(3), 3(2), 5(3), 8(1), 9(9), 10(1). G: 2(1), 3(8), 4(1), 8(1). H: 3(1), 5(1), 11(1). I: 5(2), 7(2).
Gari depressa	A: 2(1), 3(1), 6(1), 7(1), 8(1), 9(1). B: 4(2), 7(3). C: 9(1). D: 5(1). E: 3(2), 5(1), 8(1), 10(1).
Ensis sp.	A: 6(3), 8(1), 11(1). B: 4(1), 5(3), 6(1), 7(9), 11(1). C: 6(1), 7(2), 9(2). D: 2(1), 4(3), 5(5), 6(2), 7(4), 9(2), 11(3). E: 1(1), 4(1), 5(3), 11(1). F: 1(1), 5(1), 6(8), 7(14), 8(3), 9(4), 10(8). G: 2(4), 5(3), 6(1), 8(1), 10(3). H: 2(1), 4(4), 5(1), 6(1). I: 1(1), 2(1), 5(6), 9(1).
Mya truncata	A: 3(6), 6(3), 9(4). B: 2(1), 4(5), 5(1), 6(7), 7(3), 8(2). C: 2(1). D: 3(1), 4(1), 5(3), 6(3), 8(2), 10(2), 11(1). E: 2(1). F: 2(3), 5(1), 7(1). G: 6(2), 10(1). H: 4(1), 6(3), 10(2). I: 3(1), 6(1), 10(1).
Mya arenaria	B: 4(1), 9(1). D: 2(1).
Corbula gibba	A: 2(1). D: 7(1), 8(1). E: 1(1), 7(1). F: 1(2), 3(5), 4(2), 6(1), 7(1). G: 2(2), 4(2), 7(1), 11(1). H: 2(1), 9(2), 10(1). I: 2(1), 9(2).
Hiatella arctica	A: 3(1). F: 2(1), 7(1), 11(1). G: 5(2). H: 9(1).
Cochlodesma praetenue	A: 3(1), 11(2). B: 11(1). D: 3(2), 4(1), 6(1), 10(1). E: 4(1). F: 9(1). G: 3(1). I: 7(1).
Thracia phaseolina	B: 8(1), 9(7). C: 8(1). D: 7(1). E: 11(1). F: 9(1). H: 6(1).
Thracia villosiuscula	A: 2(1), 3(10), 6(5), 7(12), 8(2), 9(8), 10(7), 11(2). B: 1(1), 2(2), 3(3), 4(3), 5(6), 6(1), 7(7), 9(1), 10(22), 11(3). C: 1(5), 2(1), 4(6), 5(1), 7(3), 8(1), 9(2), 10(1), 11(2). D: 2(1), 3(1), 6(2), 10(3). E: 1(3), 3(1), 7(1), 10(2). F: 7(1), 8(3), 11(1). H: 2(1), 8(1). I: 4(1).
Lyonsia norvegica	F: 7(1). G: 8(1). H: 5(1).
Astarte montagui	B: 3(1), 5(1), 7(1), 10(1). F: 1(7), 2(6), 3(1), 7(21), 10(9), 11(15). G: 2(7), 3(4), 5(8), 6(4), 7(2), 8(7), 9(4), 10(26), 11(1). H: 3(1), 4(2), 5(1), 6(4), 9(1), 10(1). I: 1(13), 2(11), 3(8), 4(8), 6(3), 7(6), 9(11), 10(2), 11(3).
Lucinoma borealis	A: 2(11), 3(4), 5(3), 6(2), 7(2), 8(1), 9(1), 10(6), 11(1). B: 5(3), 7(2), 11(11). C: 1(23), 2(26), 3(2), 4(2), 5(22), 6(8), 7(11), 8(13), 9(6), 10(6), 11(17). D: 2(12), 3(7), 4(10), 5(5), 6(10), 7(14), 8(17), 9(9), 10(12). E: 1(21), 2(10), 3(4), 4(17), 5(12), 7(2), 8(8), 10(14). F: 1(54), 2(78), 3(49), 4(33), 5(22), 6(43), 7(15), 8(4), 9(45), 10(79), 11(61). G: 1(4), 2(64), 3(68), 4(47), 5(50), 6(64), 7(100), 8(44), 9(46), 10(66), 11(65). H: 1(19), 2(8), 3(70), 4(34), 5(74), 6(39), 7(3), 8(13), 9(25), 10(24). I: 1(26), 2(39), 3(34), 4(35), 5(68), 6(42), 7(55), 8(10), 9(40), 10(45), 11(23).
Thyasira flexuosa	C: 2(1). E: 10(1). F: 1(7), 2(8), 3(5), 6(7), 7(1), 8(3), 9(1). G: 3(7), 4(1), 5(1), 6(1), 8(1), 9(1), 10(1), 11(1). H: 1(5), 4(3), 5(3), 6(2), 7(2), 9(2). I: 4(5), 6(3), 9(2).
Montacuta ferruginosa	C: 2(2). E: 2(3), 5(1). I: 2(1).
Arctica islandica	C: 4(1), 11(1). F: 1(1), 6(1). H: 3(2). I: 3(2).
Acanthocardia echinata	F: 1(1), 6(1). G: 10(1).
Parvicardium ovale	E: 10(1).
Parvicardium scabrum	A: 6(2), 8(2), 9(3), 10(2), 11(2). B: 6(1), 11(2). C: 5(1), 11(5). D: 5(1), 8(2). E: 6(1).
Dosinia exoleta	A: 2(2), 6(13), 7(7), 9(22), 10(3). B: 2(8), 3(7), 4(14), 5(9), 6(1), 7(27), 9(1), 10(66). C: 1(7), 2(2), 4(55), 5(8), 6(1), 7(5), 8(5), 9(21), 10(27), 11(9). D: 6(10), 8(2), 10(2). E: 1(12), 3(2), 4(1), 5(3), 6(2), 7(21), 8(8), 10(6). F: 1(1), 2(2), 4(2), 5(4), 7(13), 8(4). G: 1(2), 3(1), 5(1), 6(2), 9(2), 10(2), 11(2). H: 2(1). I: 1(1), 8(1), 9(2).
Dosinia lupinus	A: 2(1), 6(1), 10(1). B: 10(5). C: 2(2), 5(1), 7(1), 10(1), 11(1). D: 8(3). E: 4(3), 6(2), 10(2), 11(1). F: 1(5), 2(9), 3(4), 4(2), 5(7), 6(8), 7(6), 8(4), 9(2), 10(12), 11(2). G: 1(1), 3(12), 4(2), 5(5), 6(2), 7(2), 9(2), 10(2), 11(3). H: 5(2), 6(1), 9(1), 10(2). I: 1(4), 3(6), 5(1), 7(2), 8(2), 9(2), 11(2).
Venus ovata	B: 4(1), 9(1), 10(1). C: 8(1). D: 6(3), 8(1). F: 7(1). G: 2(1), 6(1). H: 8(1). I: 6(1).
Venus fasciata	A: 6(1), 7(3). B: 3(2), 5(3), 6(1), 7(1), 11(2). C: 5(1), 6(2), 7(1), 8(1), 10(3), 11(2). D: 2(3), 11(1). F: 1(1), 3(1), 7(1). G: 4(3), 5(2), 8(2). I: 1(2), 4(1).

realis was extremely dominant in area 4, which may be a result of competition, but it is impossible to draw any certain conclusions from the information obtained in this survey.

I have chosen to use the word 'communities' for the two groups of bivalves found in this investigation, even if the community concept is a controversial issue. Group A, which was found in shallow water and in coarse clean sediment (secondary area 1), and Group B, which was found in deeper water and in fine sediment (secondary area 4), were quite distinct.

Although sediment structure seemed to be the overall important factor for the establishment of these bivalve 'communities', there are definitely also other factors that may influence distribution (some of which were mentioned above). GLEMAREC (1973) considers temperature, or more exactly variations in temperature, to be the factor involved in separating 'communities' on the North Gascony continental shelf. Temperature variations during 1975–76, at Eggholmane, were less in area 4 than in area 1; about 12.0° C in the former and 14.1° C in the latter. The difference in temperature between these areas during the summer (about 3.5° C in July) is noteworthy, but probably too small to have any significant effects.

Other factors may also be of importance, but it was not within the scope of this study to analyse these questions.

ACKNOWLEDGEMENTS

I wish to thank Cand. real. Torleiv Brattegard for guidance during the field work and critical reading of the manuscript, Prof. Hans Brattström for editorial help and critical reading, Cand. real. Stefan Mattson for fruitful discussions and valuable help during the field work, and Prof. William C. Summers for valuable comments of the manuscript and correction of the English.

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Received 31 August 1981.