Distribution pattern analysis in a marine benthic community

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KURZFASSUNG: **Verteilungsmuster-Analyse in einer marinen benthonischen Lebensgemeinschaft.** Über die Mikroverteilungsmuster innerhalb der Tiergesellschaften des ozeanischen Benthals ist wenig bekannt. Derartige Informationen sind aber wesentlich für eine Beurteilung der Vorgänge bei der Probenentnahme und die Analyse der Mikrofundorte der vorhandenen Arten. In Fanafjorden, Norwegen, wurden entlang einer geraden Schnittlinie in einer Tiefe von 35 m 256 benachbarte Kernproben (ϕ 7,62 cm) entnommen. Alle von einem 0,5-mm-Sieb zurückgehaltenen Tiere wurden extrahiert und die Verteilungsbilder von elf Arten mittels der Bildanalysentechnik von GREIG SMITH (1957, 1961) analysiert. Diese Methode beruht darauf, daß die Befunde in Blöcken von stufenweise steigender Größe – mit Inhalten von (2^n) Proben – dargestellt werden. Drei Arten, *Myriochele heeri, Astrorhiza limicola* und *Labidoplax buski,* waren in fast allen Blockgrößen aggregiert. Fünf Arten, *Goniada maculata, Nephtys* sp., *Leptosynapta decaria, Lucinoma borealis* und *Dentalium entalis,* waren in fast allen Blockgrößen regellos verteilt. Drei weitere Arten, *Thyasira flexuosa, Owenia fusiformis* und *Euphisa aurata,* zeigten je nach Größe der Probe wechselnde Verteilungsbilder. Die Neigung einer Art zur Aggregation nimmt mit steigender Siedlungsdichte zu. Keine der untersuchten Arten wies bei irgendeiner Blockgröße eine regelmäßige Verteilung auf. Die Bedeutung dieser Ergebnisse für die multiple Stichprobenentnahme wird besprochen; es wird der Schluß gezogen, daß eine solche Stichprobenentnahme für eine Beurteilung der Mikroverteilung unzureichend ist.

INTRODUCTION

The concept of marine infauna communities has grown out of the initial quantitative studies by PETERSEN & JENSEN (1911) and PETERSEN (1913, 1915, 1918). The most numerous and conspicuous species were used to designate the community. More recently THORSON (1957) has shown that communities from similar environments over wide geographical ranges have similarities at generic or even specific level. In the past, communities have been diagrammatically represented with the species evenly distributed over the community diagrams, taking no account of possible inter- or intraspecific interaction, simply because nothing was known about these interactions. HOLME (1964) in his recent review on methods of sampling benthos emphasised the need for more detailed knowledge of micro-distribution. Attempts have been made to elucidate distribution patterns experimentally (HOLME 1950), by random multiple sampling (CLARK & MILNE 1955, URSIN 1960, M. L. JONES 1961) or by using a twin

scoop (HOLME 1953). However, GREIG SMITH (1952), studying plant communities showed that observed distribution patterns vary according to the sample size. GREIG SMITH (1957, 1961) and KERSHAW (1957) showed that if contiguous samples were taken along a straight line transect, individual samples could be blocked together statistically into consecutive pairs, fours, eights, etc. The variances of the blocked data could then be used as an indication of the distribution pattern, aggregated, random or even; the block size giving the linear dimension of the size of the pattern.

METHOD

Marine infauna communities were considered suitable for investigation using GREIG SMITH's (1957, 1961) method of pattern analysis. The lines of systematically spaced cores required for such an analysis could only be taken by diving.

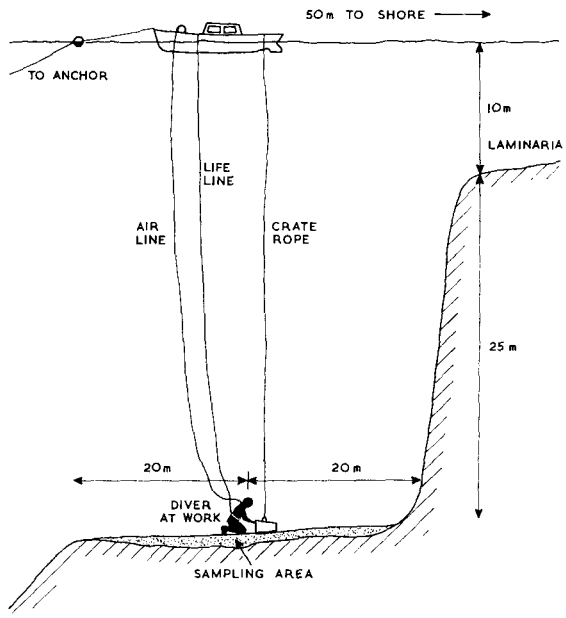

Fig. 1: Diagram showing the underwater features at the sampling area

In August 1962 a team of nine divers of the Bristol Norway Underwater Expedition visited Fanafjorden, Norway. An area at a depth of 35 m near Hollandervik on the north shore of the fjord was considered suitable (60° 15.1′ N; 5° 26.5′ E). An airline from a low-pressure compressor was used to supply the diver with air. This proved a valuable technique, since it relieved the diver's worries about having sufficient air for decompression after a 13 to 20 minute dive, and so allowed him to concentrate fully on the work. A transect line was laid out parallel to the shore along the

centre of a flat platform, 20 m from the base of an underwater cliff on one side and from the edge of the gentle slope into deeper water on the other (Fig. 1). The substrate was a fine sandy mud, and it appeared flat and uniform with a few stones and empty valves of *Cyprina islandica* scattered over the surface. Core samples were collected by hammering stainless steel tubes with a 7.62 cm internal diameter about 22.8 cm deep into the substrate. Each diver sampled one metre of the transect per dive, using a grid divided into eight sections (12.5×12.5 cm^2) to position each coring tube. Thus each sample was considered to be representative of a square $^1/_8 \times {}^1/_8$ m^2. The corers were sealed at the top with labelled rubber stoppers, and could then be drawn out without the loss of any sediment.

A total transect length of 32 m, i. e. 256 samples were collected within a ten day period, giving an actual total area sampled of 1.167 m^2. Each core was stored in a labelled polythene bag. After initial treatment for two hours with 7 % magnesium sulphate, the complete samples were preserved with 6 % sea-water formol with a small quantity of a dye, lissamine rhodamine B 200, added to facilitate the eventual extraction of the animals.

The samples were subsequently analysed in the Zoology Department at Bristol University. The bulk of each sample was sieved through a 0.5 mm sieve; the arbitrary limit put on the size of macrobenthos by McIntyre (1964). Subsamples were taken for substrate analysis (grade size, and organic matter and inorganic carbonate contents) and these were thoroughly handsorted prior to analysis. Two factors contributed towards the high efficiency of extraction, firstly less than 5 % of the substrate was retained by the 0.5 mm sieve, secondly the dye stained all the animals, making even the smallest stand out clearly. Five samples re-checked by an independent observer yielded no further animals.

In the analysis the numbers of an individual species occurring in each core were totalled into consecutive block sizes of 2^n cores ($n = 0$–8). The variances were then calculated at each block size. To give more direct comparisons with previous data of Holme (1950), Clark & Milne (1955), Ohba (1959), Ursin (1960), and M. L. Jones (1961), the results have been transformed into coefficients of dispersion.

$$\text{Coefficient of dispersion} = \frac{\text{Variance}}{\text{Mean}} = \frac{\Sigma (x - \bar{x})^2}{\bar{x}\,(n-1)}$$

The limits denoting significant aggregation or evenness are calculated using the formula

$$1 \pm 2 \sqrt{\frac{2n}{(n-1)^2}}$$

RESULTS

Table 1 shows the occurrence and abundance of some of the species, and gives a comparison with the community at station F1 off the Isle of Man, N. S. Jones (1956); the most similar in species composition of all described communities. The most notable differences are the absence of *Corbula gibba* and *Abra prismatica*, and the presence of *Thyasira flexuosa* and *Siboglinum fjordicum* in the Fanafjorden samples.

Table 1

Comparison of species occurring in Fanafjorden with those at Station F1, Isle of Man (JONES 1956)

Species	Fanafjorden Total No.	Fanafjorden Nos/m²	Station F1 Isle of Man Nos/m²
Myriochele heeri (MALMGREN)	209	179	70
Thyasira flexuosa (MONTAGU)	197	169	0*
Astrorhiza limicola (SANDAHL)	140	120	113
Owenia fusiformis (DELLA CHIAJE)	153	131	155
Nephtys incisa	78	67 *(incisa?)*	9
Labidoplax buski (MCINTOSH)	74	63	13
Lucinoma borealis (L.)	49	42	0
Goniada maculata (OERSTED)	33	28	4
Dentalium entalis (L.)	27	23	8
Leptosynapta decaria (ÖSTERGREN)	23	20	2 *(inhaerens)*
Euphysa aurata (FORBES)	24	21	0
Cylichna cylindracea (PENNANT)	17	14.5	0*
Nucula sp.	13	11	6 *(sulcata)*
Myrtea spinifera (MONTAGU)	8	7	0*
Cyprina islandica (L.)	8	7	0
Dosinia lupinus (MONTAGU)	7	6	9
Hiatella arctica (L.)	7	6	0*
Amphiura chiajei (FORBES)	4	3.5	4
Ophiura affinis (LÜTKEN)	5	4	0*
Asterias rubens (L.)	2	2	0*
Echinocardium cordatum (PENNANT)	2	2	0*
Siboglinum fjordicum (WEBB)	~ 200	–	0
Corbula gibba (OLIVI)	0	–	500
Abra prismatica (MONTAGU)	0	–	73

* Occurring at other nearby stations.

Eleven species were chosen for detailed analysis and the results are shown in Table 2. It should be noted that the results obtained from testing the significances of the variances and the coefficients of dispersion are identical.

Table 2

Coefficient of dispersion data. Values showing significant aggregation are given in italics

Block size	1	2	4	8	16	32	64	128
95 % Limit (Aggregation)	1.18	1.25	1.36	1.51	1.75	2.14	2.89	5.0
5 % Limit Evenness	0.82	0.75	0.64	0.49	0.25	—	—	—
Myriochele heeri (209)	*1.19*	*1.45*	*2.08*	*2.44*	*2.01*	*3.32*	*13.35*	*11.49*
Astrorhiza limicola (140)	*1.56*	*1.73*	*2.04*	*3.18*	*3.95*	*6.02*	*6.65*	0.029
Labidoplax buski (74)	*1.34*	*1.51*	*1.52*	*1.99*	*3.17*	*3.76*	*3.33*	4.38
Owenia fusiformis (153)	1.09	*1.31*	*1.48*	1.35	*2.11*	*2.22*	*3.74*	0.16
Thyasira flexuosa (197)	1.16	1.20	*1.41*	*1.98*	*1.96*	*2.64*	1.53	3.70
Euphysa aurata (24)	1.08	1.24	*1.40*	*1.89*	1.69	*2.48*	1.44	*6.00*
Nephtys sp. (78)	0.98	0.96	0.98	1.19	1.23	1.90	0.29	0.00
Lucinoma borealis (49)	0.93	0.91	0.90	0.93	0.98	0.72	*9.73*	*10.18*
Goniada maculata (33)	1.00	1.05	0.98	1.22	1.26	1.48	1.73	2.45
Dentalium entalis (27)	*1.20*	1.09	0.96	1.16	1.48	1.35	1.86	3.00
Leptosynapta decaria (23)	1.00	1.18	1.00	1.28	1.30	1.34	2.13	1.09

Three species, *Myriochele heeri*, *Astrorhiza limicola*, and *Labidoplax buski*, showed aggregation at nearly all block sizes (Fig. 2). The effective number of samples at the two highest block sizes is too small for much importance to be attached to the change in the pattern shown by two of these species at block size 128. KERSHAW (1957)

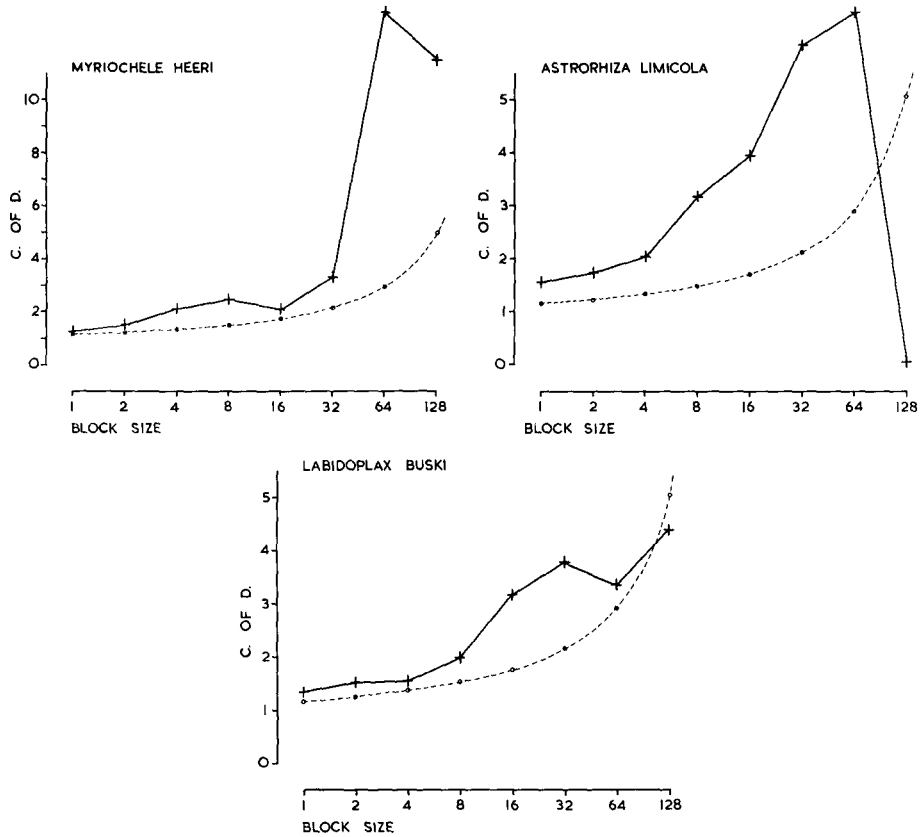

Fig. 2: Coefficient of dispersion/block size graphs for the three species showing aggregation at most block sizes. The limits of aggregation are shown by the dashed lines

recommended that the basic unit should not be more than half dimension of the smallest scale of pattern. The aggregation shown by all three species at block size 1 indicates that the core size was too large to detect the minimum size of pattern. Multiple random sampling of this community would have shown these species to have been aggregated over the whole range of sample sizes from $1/8 \times 1/8$ m^2 to 8×8 m^2, assuming that the dimensions of the patterns are the same in all directions.

Three species, *Owenia fusiformis*, *Thyasira flexuosa*, and *Euphysa aurata*, showed fluctuating distribution patterns (Fig. 3). *Owenia fusiformis* was randomly distributed at block sizes 1, 8, 128 and aggregated at block sizes 2, 4, 16, 32 and 64. Thus the individuals of this species were randomly distributed within aggregations of dimensions $1/4$ and

1/2 m, which were in turn randomly distributed within aggregations with dimensions of 2, 4, and 8 m. *Thyasira flexuosa* was randomly distributed at block sizes 1, 2, 64 and 128, and aggregated at block sizes 4, 8, 16 and 32. *Euphysa aurata* was random at block sizes 1, 2, 16 and 64, and aggregated at block sizes 4, 8, 32 and 128; a similar

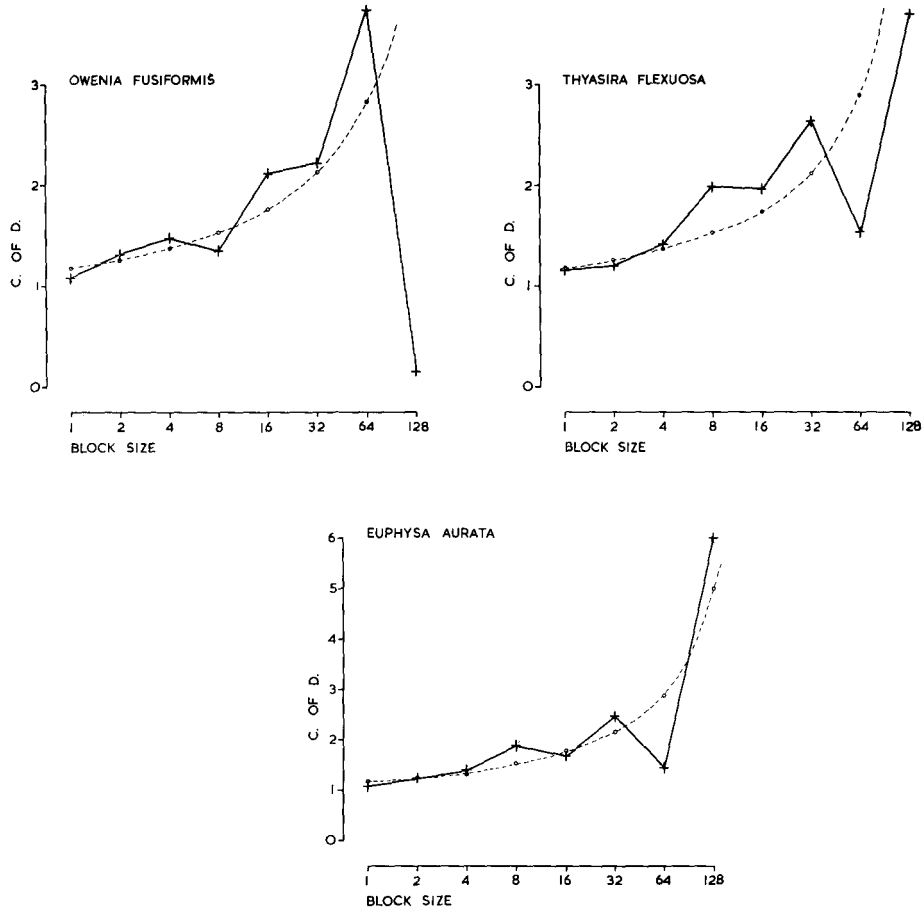

Fig. 3: Coefficient of dispersion/block size graphs for the three species showing fluctuating distribution patterns. The limits of aggregation are shown by the dashed lines

complex of aggregations within aggregations as found in *Owenia fusiformis*. *Euphysa aurata* was the only species showing a marked degree of aggregation that occurred at a density of below 60/m². Multiple random sampling would have given variable distribution patterns for these species depending of the size of sampler used.

The remaining five species, *Nephtys* sp. (? *incisa*), *Lucinoma borealis*, *Goniada maculata*, *Dentalium entalis*, and *Leptosynapta decaria*, were all randomly distributed at nearly all block sizes. Only *Dentalium entalis* (block size 1) and *Lucinoma borealis*

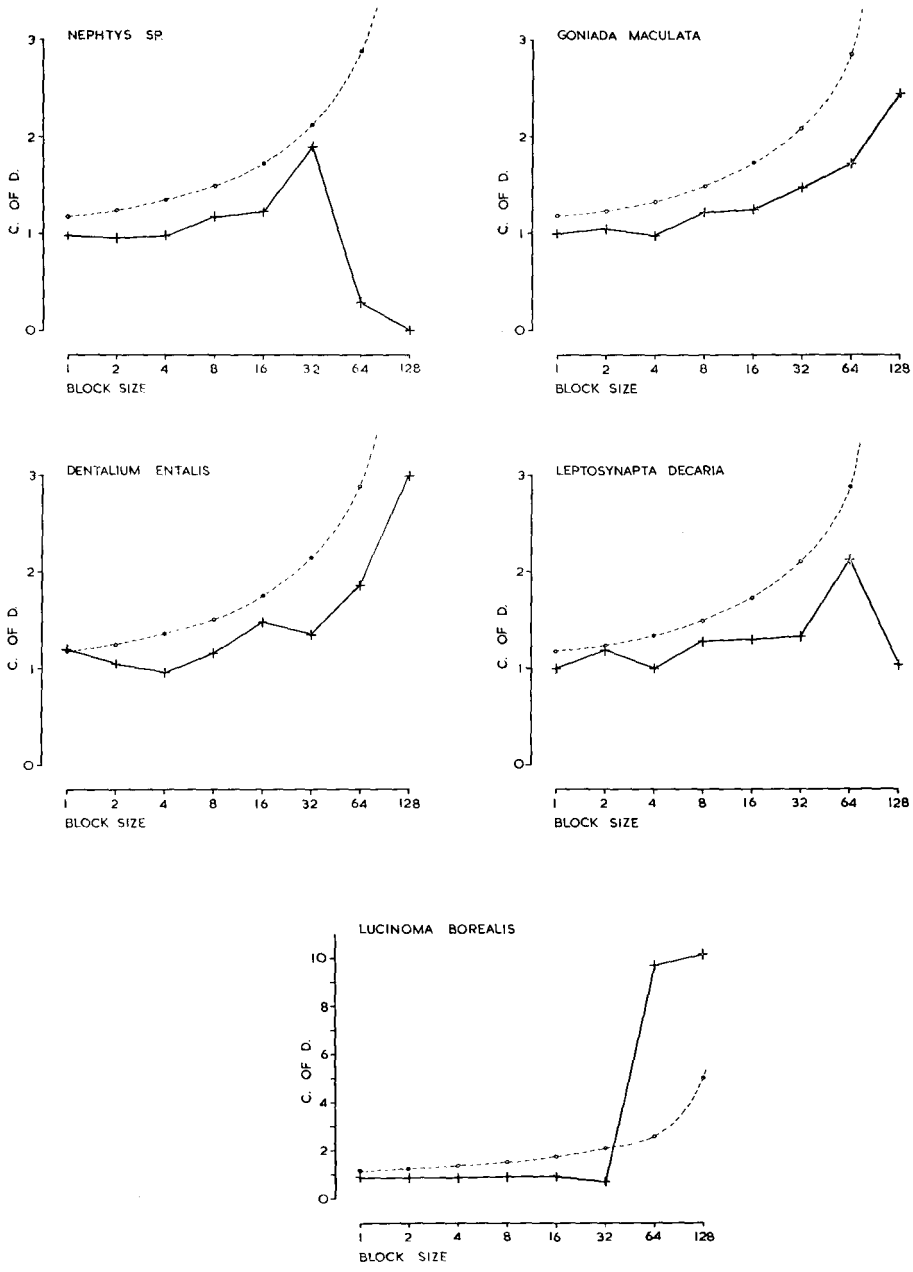

Fig. 4: Coefficient of dispersion/block size graphs for five species showing random distributions at nearly all block sizes. The limits of aggregation are shown by the dashed lines

(block sizes 64 and 128) showed any aggregation. Sudden aggregations at high block sizes only shown by *Lucinoma borealis* are typical of the result of crossing a community boundary (GREIG SMITH 1961), but the absence of similar phenomena in the distribution plots of the other species, suggests that no major community boundary was crossed during the survey.

DISCUSSION

In their studies of sublittoral communities CLARK & MILNE (1955) used ten repeated mud-bucket hauls. They concluded that the more numerous species were usually aggregated and further "that evidence of aggregation may disappear altogether if a smaller unit is used, simply because the mean per unit is reduced". The first conclusion is supported by the analysis of the Fanafjorden community since with the exception of *Nephtys* sp. all the species occurring at densities of over 60/m^2 were aggregated at four or more block sizes. The second conclusion is suspect since GREIG SMITH (1957) has shown that larger numbers of samples have to be taken to show aggregation in sparsely occurring species. This also refutes the suggestion by M. L. JONES (1961) that the test of significant aggregation or evenness for the coefficient of dispersion is only valid if the expected number of animals per sample is five or more. For example, *Euphysa aurata* would not have appeared aggregated in Fanafjorden using CLARK & MILNE's method.

None of the densities encountered in Fanafjorden approached those found by HOLME (1950) to result experimentally in an even distribution in *Tellina tenuis* caused by intraspecific interaction. All the species were probably too sparse for intraspecific competition to effect the distribution patterns since no example of an even distribution was found. The patterns that have been shown to exist were probably caused through interspecific interactions and the micro-habitat effects on the settlement behaviour of the larval stages. Large scale pattern may well be found to have different basic causes to smaller scale patterns. Covariance analysis (KERSHAW 1961) of interspecific relationships and the importance of minor substrate changes will give some indication of the underlying causes of these distribution patterns, and reports on these results will be published later.

It is clear from the variations in the distribution patterns shown by three species at the different block sizes, that multiple random sampling is not a suitable method for studying distribution patterns. Multiple random samples taken with a large size range of samplers would prove impractical due to the limitations of time and the difficulties of handling the gear. Without a systematic sampling technique, the results cannot be blocked statistically to show large scale patterns within the community. Since it is impossible to analyse the micro-habitats of infaunal species without knowledge of the distribution patterns, the technique described in this paper seems the most suitable for the study of shallow water benthos.

SUMMARY

1. 256 contiguous core samples (7.62 cm diameter) were collected along a 32 m straight line transect from a sandy mud substrate in Fanafjorden, Norway, at a depth of 35 m.
2. Eleven species found in the community were analysed using GREIG SMITH's method of pattern analysis.
3. Three species were aggregated at nearly all block sizes (i. e. the effective sample sizes) and five randomly distributed.
4. Three species showed fluctuating distribution patterns according to the block size. The distributions of these species could not be adequately studied from multiple random samples.
5. No species showed an even distribution at any block size.
6. It is concluded that the micro-distributions, and hence the micro-habitats, of infaunal species cannot be investigated using the more conventional sampling techniques for sampling the benthos, by grab, scoop or ship-operated corers.

ACKNOWLEDGMENTS

The authors wish to acknowledge the invaluable assistance of the leader of the expedition J. PARTRIDGE and all the other members, the help given to the expedition by H.R.H. the Duke of Edingburgh, Sir FOSTER ROBINSON, by many industrial concerns, and by many Norwegian friends especially Mr. P. SVENDSEN. One of the authors (M.V.A.) received a grant from the Browne Research Fund. The other author (H.H.A.) is grateful for financial aid received from a research grant awarded to Professor R. B. CLARK by the Science Research Council in support of this investigation. Professor R. B. CLARK gave great encouragement throughout and supervised the working up of the samples.

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Discussion following the paper by ANGEL & ANGEL

BARNES: Is it not true that the use of $1 + 2\sqrt{\frac{2n}{(n-1)^2}}$ as a test of dispersion is dependent on the *actual* form of the distribution – and does this not perhaps make it possible to invalidate "partially" some criticism of the earlier workers?

ANGEL: Possibly the statistical background to this paper is not entirely satisfactory, but the weaknesses it uncovers in the previous studies are genuine.

MASSÉ: Ne pensez-vous pas que vos cylindres sont trop petits pour capturer les gros individus? N'avez-vous pas par exemple coupé beaucoup de Polychètes ce qui rend la détermination souvent impossible?

ANGEL: We were interested in testing the methodology of grab sampling. We have chosen to analyse only a few of the species, all of which were extracted efficiently by our techniques.

FORSTER: How much should the pattern of distribution be considered static? Are dynamic changes possible? If the substrate is disturbed by storms in winter, would the pattern of distribution be changing slowly?

ANGEL: The pattern is initially caused by the settlement behaviour of the larvae. It is then modified by a variety of factors including migration of the adults and predation. Winter storms in a sheltered fjord are unlikely to disturb the substrate at such a depth, and this is supported by the muddy nature of the substrate.