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THE INFAUNA AND EPIFAUNA OF THE NORTHERN NORTH SEA

D. BASFORD, A. ELEFTHERIOU[1] AND D. RAFFAELLI[2]

Marine Laboratory, P.O. Box 101, Victoria Road, Torry, Aberdeen AB9 8DB, U.K.
[1] Department of Biology, University of Crete, P.O. Box 1470, Heraklion 71110, Crete, Greece
[2] Culterty Field Station, University of Aberdeen, Newburgh, Aberdeen AB4 OAA, U.K.

ABSTRACT

This paper compares the infaunal and epifaunal assemblages from surveys encompassing 121 grab stations and 152 Agassiz trawl samples respectively, collected between 1980 and 1985. The area surveyed is delimited by the Scottish, Norwegian and Danish coasts lying between 56°15'N and 60°45'N. Samples for infauna and environmental parameters were collected by Smith-McIntyre grab and Craib corer.

The epifaunal and infaunal assemblages were analysed separately by ordination techniques (DECORANA and TWINSPAN) to detect the major environmental gradients underlying the distribution and abundance of the fauna and to indicate which taxa were characteristic of different zones within the survey area.

The major determinant of infaunal community composition was sediment granulometry, with depth being of secondary importance. For the epibenthos, depth was the major factor and the sediment composition seemed less significant. Assemblages identified by TWINSPAN were characterised by particular species, but these 'community types' were seen to grade into one another along continuous environmental gradients. These findings are discussed in relation to previous North Sea benthic classification schemes.

1. INTRODUCTION

The offshore (>30 m depth) benthic infaunal community was originally described from very few samples collected in 1922 along transects across the northern North Sea (STEPHEN, 1923). Over the next four years (1922-1925) a more widespread area was sampled but the emphasis was on the inshore area with only a few samples being collected from deeper water (STEPHEN, 1933; 1934). These surveys were later augmented by several localised but much more intensively sampled areas (MCINTYRE, 1958; HARTLEY, 1977; LEVEL, 1980). General reviews of the communities using these data have been attempted by KINGSTON & RACHOR (1982) and HARTLEY (1984). However, neither the initial widely spaced transect surveys nor the dispersed sampling and localised surveys that followed provided sufficient data to allow the accurate mapping of community types (KINGSTON & RACHOR, 1982; HARTLEY, 1984). Similarly the environmental determinants of benthic assemblages could not be assessed realistically since little environmental data were available for most of the area. A larger scale survey was undertaken by DYER *et al.* (1982) and CRANMER *et al.* (1984), but they sampled only the epifauna. Here again no environmental parameters were measured. Furthermore, the question of whether the epifaunal communities can be used to predict infaunal distributions cannot be answered.

Attempts to define biological regions whithin the North Sea as a whole have been based largely on the temperature and thermal stability of the water column and the planktonic communities (GLÉMAREC, 1973; ADAMS, 1987). Benthic surveys have lent support to such divisions, in that different benthic assemblages seem to occur in different areas (MCINTYRE, 1958; KINGSTON & RACHOR, 1982; HARTLEY, 1984; DYER *et al.*, 1983). Just how homogeneous benthic assemblages are within these regions and whether faunal discontinuities exist between them remained undecided.

To resolve these questions we sampled a grid of 273 stations between 1980 and 1985 in the northern North Sea for infauna, epifauna and a range of physicochemical sediment parameters. Detailed accounts of the North Sea environment, its infauna and epifauna are given elsewhere (BASFORD & ELEFTHERIOU, 1988; ELEFTHERIOU & BASFORD, 1989; BASFORD *et al.*, 1989). Here we present an analysis of the epifaunal and infaunal surveys and we assess the major environmental gradients underlying the distributions of the infaunal and epifaunal assemblages. The benthic assemblages thus defined are compared with previous classification schemes put forward by other authors (GLÉMAREC, 1978; ADAMS, 1987).

Acknowledgements — Many people contributed directly or indirectly to this project. We are indebted to all of them. In particular we are grateful to our colleagues in the Benthos section of the Marine Laboratory, and others for their help with the faunal identification.

2. METHODS

Eight cruises were carried out in the spring or early summer between 1980 and 1985. Each station was visited once (Fig. 1) and at each, depth and bottom topography were determined by echosounder and four 0.1 m^2 samples were taken with a Smith-McIntyre grab. Three of these were sieved over 500 μm meshes and the organisms retained were preserved in 10% formalin for macrobenthic analysis. The fourth sample was subsampled for particle size analysis, total plant pigments and organic carbon content (BASFORD & ELEFTHERIOU, 1988). The fauna from one sample of each of the 119 selected stations reported here were identified and the organisms counted. Biomass was estimated as wet weight, later converted to dry weight by the application of the following conversion factors: polychaetes 15.5%; crustaceans 22.5%; echinoderms 8%; molluscs 8.5%; all other groups (miscellaneous) 15.5% (ELEFTHERIOU & BASFORD, 1989). Epifaunal samples were collected over the same period from 152 selected stations (Fig. 1) using a 2 m Agassiz trawl towed at 1.2 knots. The trawls covered an average distance of 920 m. Most of the fauna were identified on board. Specimens not immediately recognisable were identified later in the laboratory. The infaunal and epifaunal assemblages at the different stations were compared separately using

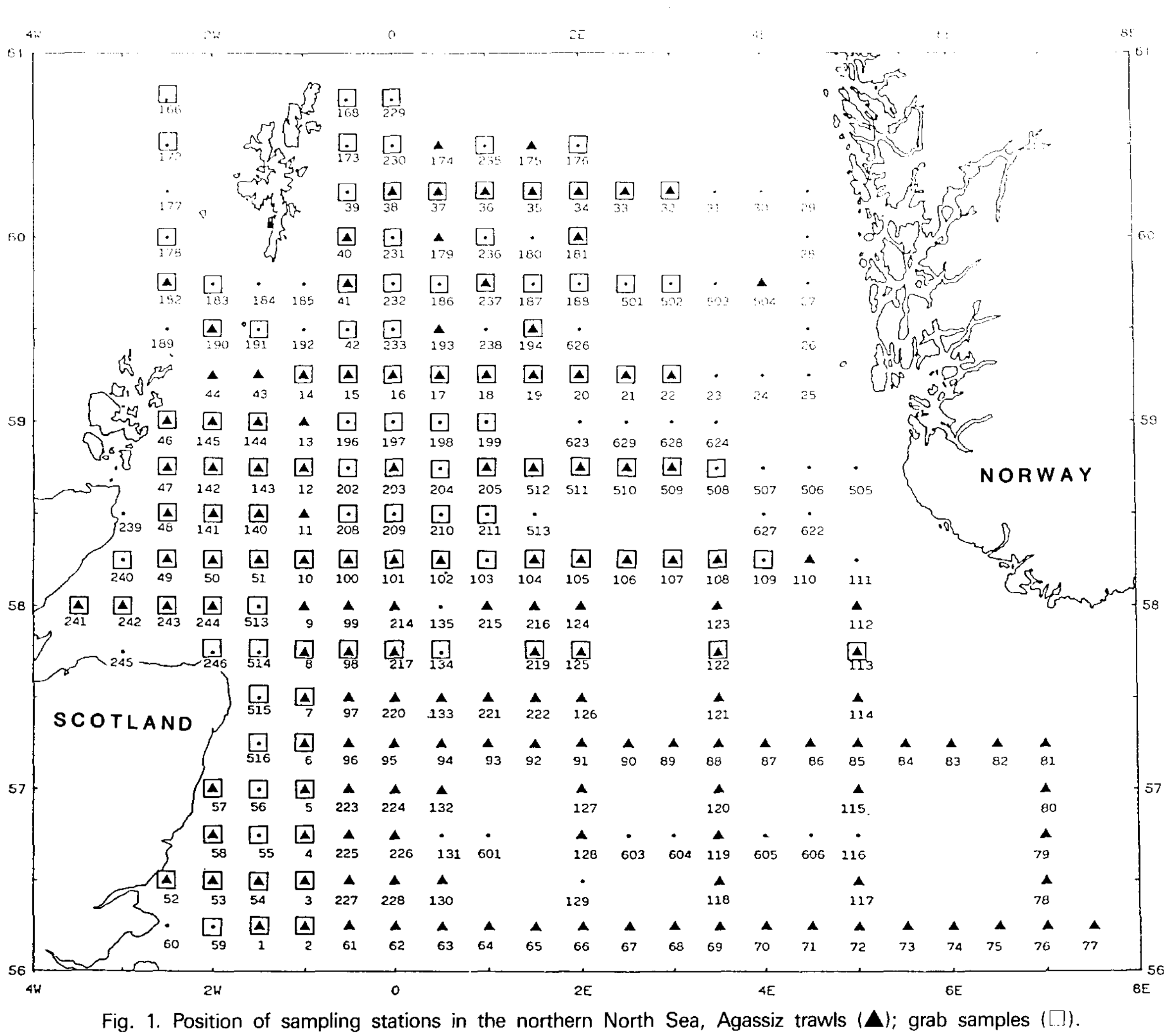

Fig. 1. Position of sampling stations in the northern North Sea, Agassiz trawls (▲); grab samples (□).

the ordination techniques of DECORANA (Detrended Correspondence Analysis) and TWINSPAN (Two-Way Indicator Species Analysis). A full account of both methods is provided by GAUCH (1982).

3. RESULTS

In order to interpret the distribution patterns of the fauna it is necessary to describe briefly the sedimentary environment of the survey area, (given in greater detail in BASFORD & ELEFTHERIOU (1988)). The sediments in the area vary from very coarse material (>6400 μm median diameter) between Orkney and Shetland, to finer (125 μm) and less well sorted towards the south and east, where the Atlantic inflow/Fair Isle current slows, following the 100 m depth contour (Fig. 2). The least well sorted and finest sediments containing large amounts of silt (>90%) occur in the Fladen Ground. In general the depth varies from 70-140 m with central depressions (*e.g.* Fladen Ground) penetrating to 200 m and shallower banks to the south east rising to 30 m. To the east the Norwegian Trench extends to >400m (Fig. 3). Chlorophyllous pigments are usually less than 4 $\mu g\ g^{-1}$ sediment with high values in the Moray Firth. The organic carbon was generally less than 3 $\mu g\ C\ g^{-1}$ sediment, except for the deeper Fladen Ground where values can be in excess of 10 $\mu g\ C\ g^{-1}$.

Five hundred infauna taxa were recorded from the grab samples and most were identified to species. Where the systematics of particular taxa or species complexes are poorly understood and remain unclear, individuals were identified only to generic level or above, e.g. *Thyasira* species and *Myriochele* sp. A full species list is available from the authors on request. The overall distribution patterns of the numbers of individuals and the total biomass at each station were derived by draw-

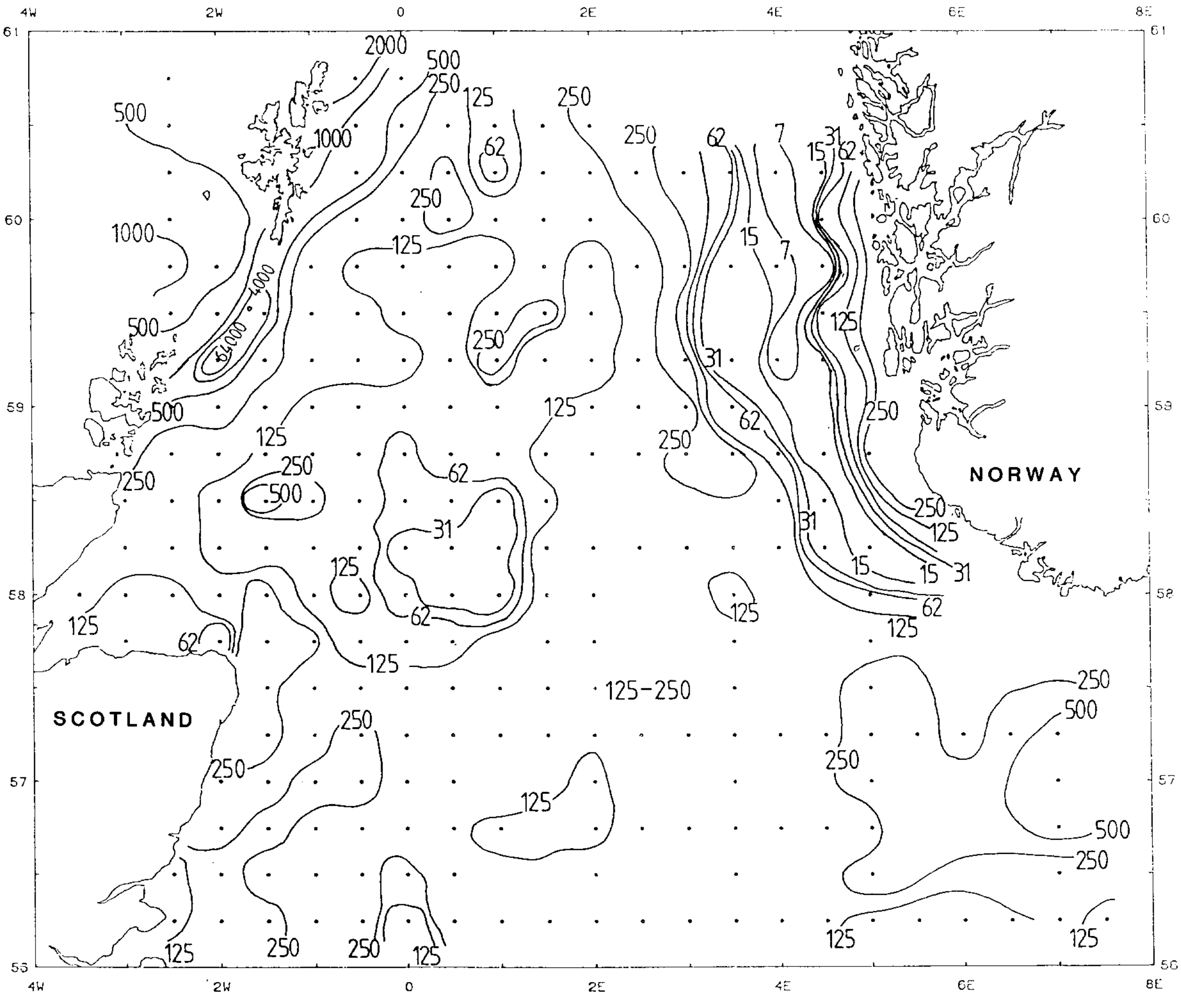

Fig. 2. Map showing sediment distribution in the northern North Sea (median diameter in μm). (BASFORD & ELEFTHERIOU, 1988).

ing contours around stations using the computer programme SURFACE as described by SAMPSON (1978). The greatest densities of infauna, (>6000 m^{-2}) were recorded south east of Shetland (Fig. 4). There were also high densities in the Moray Firth. The highest infaunal biomasses also occurred to the east of Shetland but these are not exactly coincident with the highest densities (Fig. 5). As far as the faunal abundance is concerned the high Shetland values were due mainly to the *Thyasira* bivalve complex, Foraminifera, and the polychaetes *Owenia fusiformis* (Chiaje) and *Heteromastus filiformis* (Claparède), whilst *Spatangus purpureus* (O.F. Müller) and Ascidians were responsible for the high biomasses. The number of species per station varied between about 30 and 60. There were no easily detectable patterns of species richness over the study area and therefore no map is provided. As far as feeding types are concerned, most of the Offshore Northern sector (ADAMS, 1987) was dominated by surface deposit feeders, whilst the siltier Fladen Ground was characterised by sub-surface deposit feeders (Fig. 6). The coastal stations with a wider range of sediment types supported a broader spectrum of feeding types with carnivores and filter feeders being dominant in the coarser sediments. However, there were no easily defined spatial patterns in the coastal sector.

One hundred and ninety-six taxa of epifauna were recorded from the Agassiz trawl samples. Epifaunal species richness was highest to the south of Shetland (Fig. 7). This area also had a high infaunal species richness mainly due to Polychaeta, but in the case of the epifauna many groups contributed to higher species richness including Echinodermata, Mollusca, Tunicata, Anthozoa, Porifera and colonial Bryozoans. Low species richness was recorded in localised areas widely distributed throughout the North Sea, often coinciding with silty sediments. This may in part reflect the lower efficiency of the trawl on these sediments. Abundances

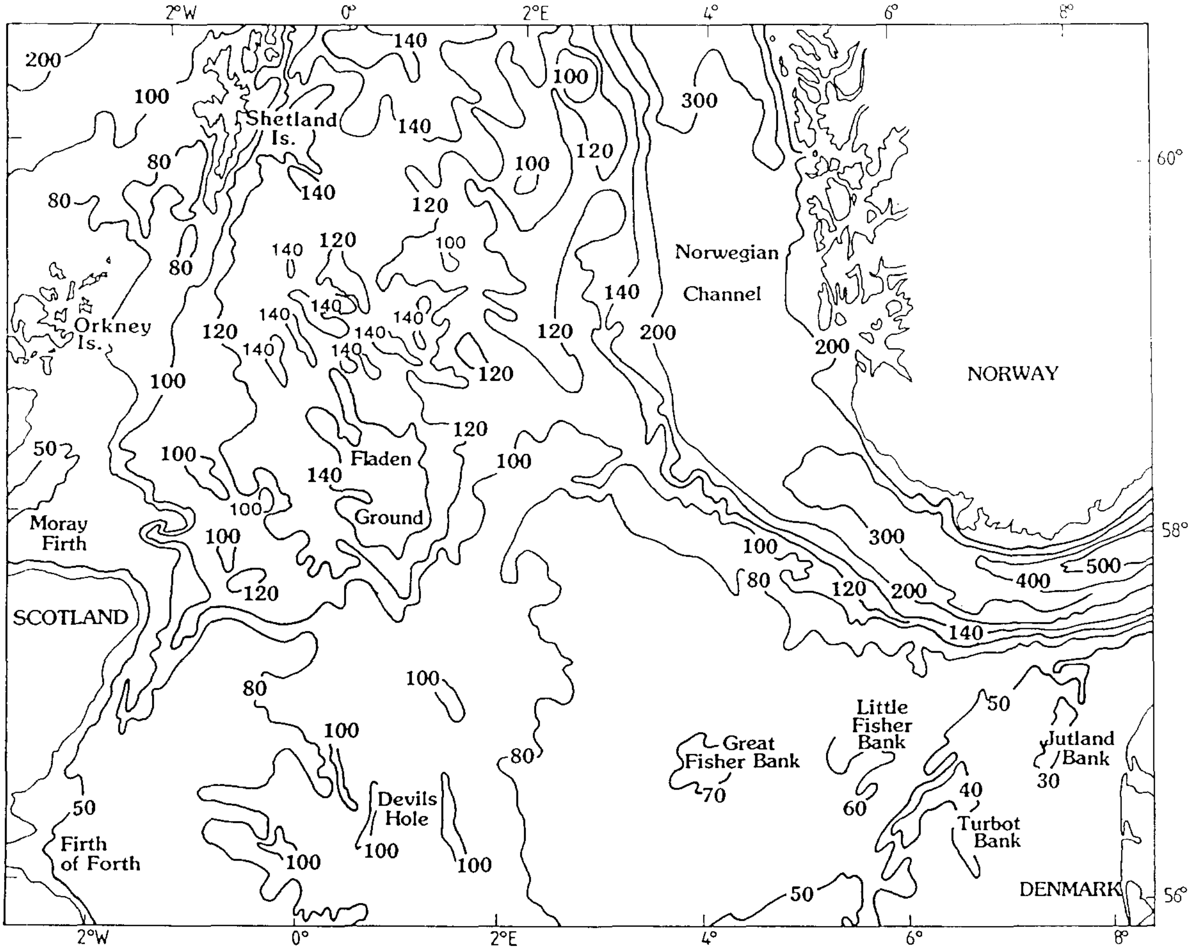

Fig. 3. Map showing bathymetry of the northern and central North Sea (map redrawn from CASTON, 1979; BASFORD & ELEFTHERIOU, 1988).

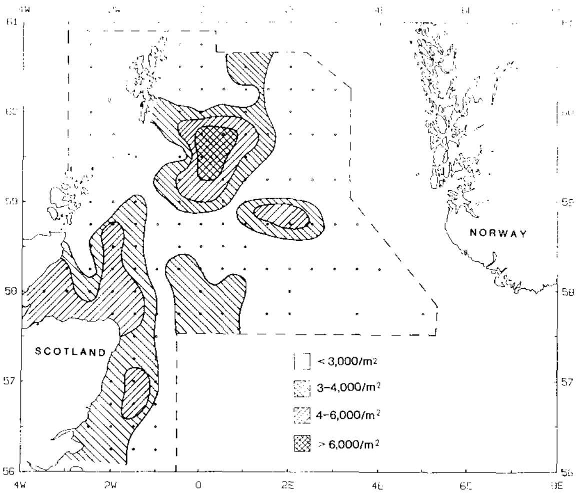

Fig. 4. Contour map of infaunal densities in the northern North Sea between 1980 and 1985.

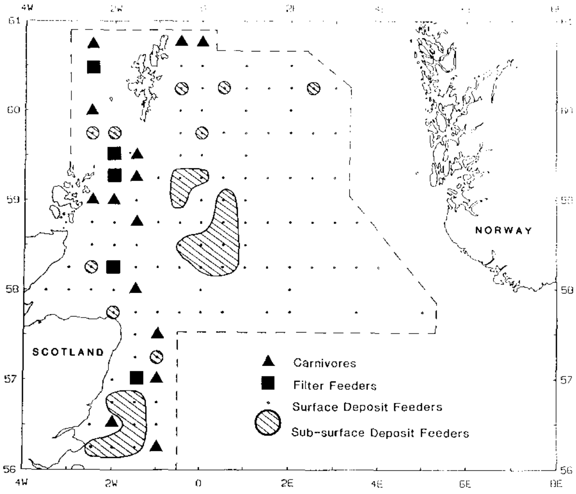

Fig. 6. Predominant feeding types of the five most abundant infaunal species at each station.

were in general low with few stations recording over 200 individuals per 1000 m^2 (Fig. 8). High abundances (>500 per 1000 m^2) were recorded at widely separated stations (the smoothing process of the computer programme SURFACE, used to contour the maps, only displays one station in this category) where large numbers of Echinoderms particularly the starfish *Luidia sarsi* (Duben & Koren), the brittle star *Ophiothrix fragilis* (Abildgaard), the urchins *Echinus acutus* (Lamarck) and *Brissopsis lyrifera* (Forbes) and, on one occasion, a large number of sponges occurred. Because specimens were not retained no biomass data are available.

Ordination of the infaunal assemblages revealed that axis 1 (eigenvalue = 0.68) was highly correlated with all the environmental parameters measured, except for sediment sorting (Table 1). The highest correlations of axis 1 were with sediment parameters, *viz.* silt content, median diameter and organic carbon, with depth having a slightly lower correlation coefficient. Axis 2 (eigenvalue = 0.49) was also significantly correlated with all the measured environmental variables, but the correlation coefficients were somewhat smaller than for axis 1 (Table 1). Axis 3 (eigenvalue = 0.39) was not significantly correlated with any of the measured variables. By contrast, axis 1 (eigenvalue = 0.76) of the epibenthos ordination (Table 1) was most correlated with depth and sediment sorting whilst axis 2 (eigenvalue = 0.61) was correlated only with depth ($P<0.05$).

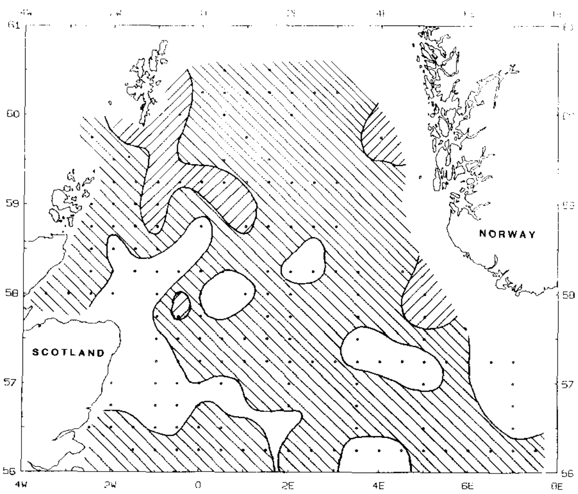

Fig. 5. Contour map of infaunal biomass in the northern North Sea between 1980 and 1985.

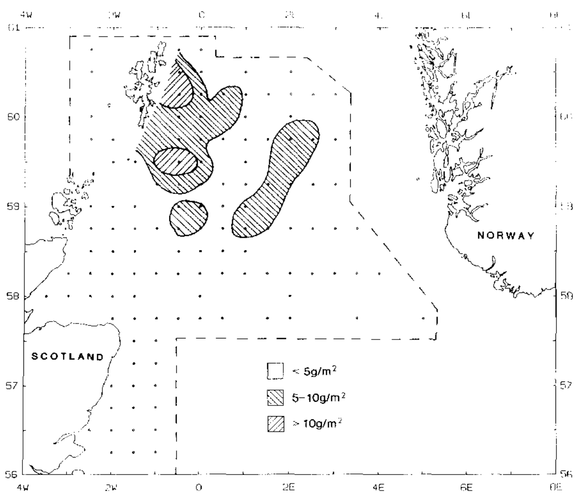

Fig. 7. Contour map of epifaunal species richness in the northern North Sea between 1980 and 1985. <10 species (□); 10-20 species (▨); >20 species (▨).

TABLE 1

Spearman's Rank Correlations between infaunal (A) and epifaunal (B) ordination axis scores and environmental parameters ($r=0.254$, $p<0.01$; $r=0.321$, $p<0.001$)

	Axis 1		*Axis 2*		*Axis 3*	
	A	*B*	*A*	*B*	*A*	*B*
Sorting (Folk)	0.276	0.448	-0.452	-0.058	-0.037	0.016
Carbon (µg g^{-1})	-0.740	-0.377	-0.454	0.008	-0.098	-0.151
Silt (%)	-0.792	-0.399	-0.452	-0.043	0.035	-0.011
Total pigment (µg g^{-1})	-0.598	-0.269	-0.268	0.145	-0.014	-0.161
Median diameter (ø)	-0.763	-0.249	-0.359	0.078	0.179	0.146
Depth (m)	-0.648	-0.531	-0.341	-0.247	-0.140	0.098

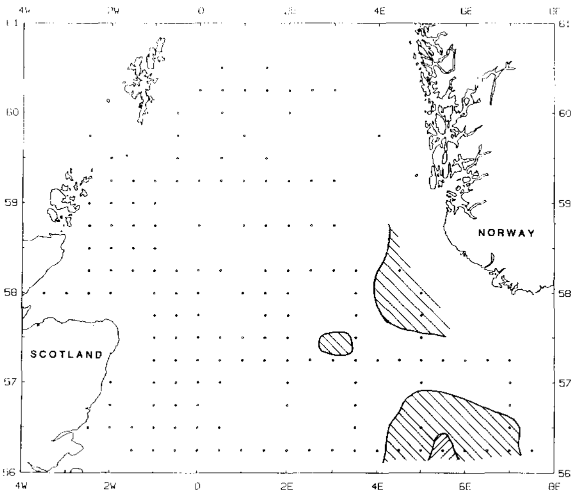

Fig. 8. Contour map of epifaunal densities. <200 individuals (□); >200 individuals (▧); >500 individuals per 1000 m^2(▨).

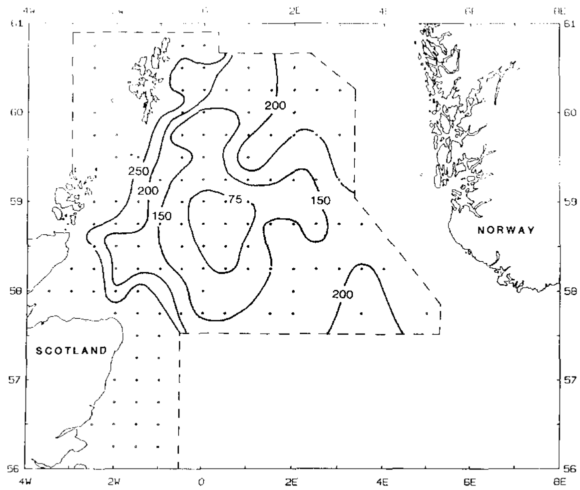

Fig. 9. Contour map of infaunal station scores on axis 1 of ordination.

Axis 3 (eigenvalue = 0.38) was not significantly correlated with any of the variables. This can also be seen in the contour plots of axis 1 where the programme SURFACE has been used to draw contours around stations with different axis scores (Figs. 9 and 10). Areas on the same contour have similar infaunal assemblages. For the infauna, high axis 1 contours are associated with the shallow and coarser sediment regions of the surveyed area (Fig. 9). The lowest axis scores appear to describe the finer sediments of the deeper Fladen Ground. The axis 1 contours for the epifauna also show an association with depth and sediments, with low scores at greater depth and on more poorly sorted sediments (Fig. 10). However, comparison of Fig. 9 and 10 indicate that the epifauna and infauna assemblages do not change over the area in precisely the same way. In other words the epifauna and infauna do not respond in a similar way to the major environmental gradients of depth and sediment.

At the first dichotomy of the TWINSPAN classification (Table 2), the infaunal stations were divided according to their species composition into two groupings, one containing coastal stations only and the other made up of offshore stations along with 12 coastal stations mainly from the Moray Firth (Fig. 11). However, within the offshore group, these 12 stations are ranked nearest the coastal group in terms of species composition.

The coastal group included the shallower areas with coarse deposits, low in organic carbon and silt, and was characterised by the indicator species *Ophelina neglecta* (Schneider), *Sphaerosyllis bulbosa* (Southern) and the echinoid *Echinocyamus pusillus*(O.F. Müller) (Table 2). Characteristic species are those defined by Twinspan as indicators or strong preferentials sensu GAUCH (1982). These coastal stations were further subdivided into two subgroups. The first of these (subgroup 1) included stations with the coarsest sediments which were inhabited by a diverse fauna characterised by the polychaete *Pisione remota* (Southern) and also the polychaetes *Exogone hebes* (Webster & Benedict) and *Glycera lapidum* (Quatrefages), along with the oligochaete *Pro-*

todrilus sp., ophiuroid juveniles and the echinoid *Echionocyamus pusillus* (Table 2). The second of these subgroups (subgroup 2) was characterised by the bivalve *Nucula tenuis* (Montagu) with additional species such as the polychaetes *Ophelina neglecta*, *Exogone verugera* (Claparède), *E. hebes*, *Scoloplos armiger* (O.F. Müller), and the echinoderms, *Echinocyamus pusillus* and *Amphiura filiformis* (O.F. Müller).

The offshore grouping included a large number of the deeper stations with finer sediments and higher organic carbon content and was characterised by the bivalve *Thyasira* spp. complex and the polychaete *Prionospio multibranchiata* (Fauvel) (Table 2). The coarser and distincly less silty sediments were characterised by the polychaete *Spiophanes bombyx* (Claparède) (subgroup 3). The deeper siltier parts of this area were characterised by the polychaetes *Lumbrineris gracilis* (Ehlers), *Heteromastus* sp., *Phylo norvegica* (Sars), *Ceratocephale loveni* (Malmgren), the amphipod *Eriopisa elongata* (Bruzelius) and the *Thyasira* spp. bivalve complex (subgroup 4).

The complex relationship between depth and sedimentary parameters is also seen in the epifaunal TWINSPAN analysis (Table 3) described in greater detail in BASFORD *et al.* (1989). At the first dichotomy the stations have been divided into: a) those with moderately sorted, coarse sediments with relatively low silt and organic carbon levels characterised by Porifera, *Flustra foliacea* (L.), the anemone *Bolocera tuediae* (Johnston) and the decapod *Hyas coarctatus* (Leach); and b) a second, deeper group with contrasting sedimentary characteristics which had a fauna typified by the echinoderms *Asterias rubens* (L.), *Astropecten irregularis* (Pennant) and *Brissopsis lyrifera*. Further divisions of these stations separates the deeper Fladen Ground and Norwegian Trough samples from the shallower Fisher Bank and some coastal stations

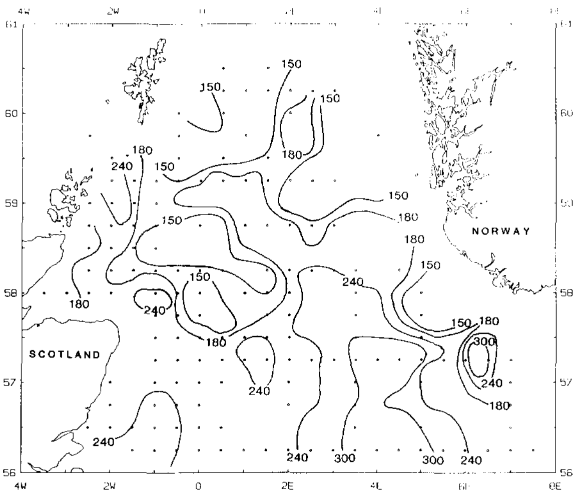

Fig. 10. Contour map of epifaunal station scores on axis 1 of ordination.

TABLE 2

Summary of infaunal TWINSPAN analysis showing taxa characteristic of the major station groupings and mean environmental parameters of the four station groups described at the second dichotomy.

First TWINSPAN dichotomy	COASTAL STATIONS *Ophelina neglecta* *Sphaerosyllis bulbosa* *Echinocyamus pusillus*		MAINLY OFFSHORE STATIONS *Thyasira* spp. *Prionospio multibranchiata*	
Second TWINSPAN dichotomy	Group 1 *Pisione remota*	Group 2 *Nucula tenuis*	Group 3 *Spiophanes bombyx*	Group 4 *Eriopisa elongata* *Thyasira* spp. *Lumbrineris gracilis* *Ceratocephale loveni*
Mean environmental parameters of station groups				
Sorting (Folk)	3.2	4.2	3.9	2.9
Carbon ($mg.g^{-1}$)	1.23	1.8	3.0	5.9
Silt (% weight)	4.6	1.0	8.5	40.7
Total pigment ($\mu g.g^{-1}$)	0.9	1.8	3.5	3.9
Median diameter (φ)	1.17	2.1	2.6	3.8
Depth (m)	88	77	106	131

(groups 4 and 3 respectively, Table 3). It should be noted that the average environmental characteristics used to describe each of the station groupings in Tables 2 and 3 are merely indicative of the benthic environment of those groupings. The DECORANA analysis more appropriately identifies the environmental gradients underlying the distributions of the assemblages.

4. DISCUSSION

The results in this paper have demonstrated that the major factors underlying the distribution and abundance of the infauna and epifauna are related to depth and sedimentary characteristics. On the basis of the magnitude of the correlation coefficients shown in Table 1, it would appear that the sediment is more important for the infaunal, and depth for the epifaunal distributions, although sediment and depth interact in a complex way to determine distributions patterns.

In this respect it should be noted that the graphical presentation of the multivariate analyses of the infaunal assemblages (Fig. 9) is more easily interpreted visually than that of the epifauna (Fig. 10). There could be several reasons for this. The grab sampling technique for infauna is much more quantitative and precise than the Agassiz trawl used for the study of the epifauna, even though the area sampled by trawl may be 10,000 times as large as that sampled by grab. Moreover, the large area sampled by trawl may contain material from a wider range of habitats and this may obscure the analyses. Perhaps more importantly, the infauna have, by definition, a much closer association with the sediment than the epifauna and it might be expected that any statistical relationships between sediment and biological characteristics would be clearer for infaunal than for epifaunal assemblages.

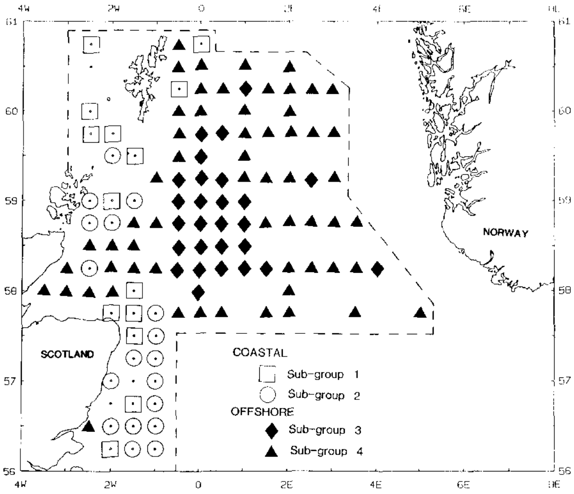

Fig. 11. Distributions of major infaunal TWINSPAN groupings defined at the first dichotomy (see text).

TABLE 3

Summary of epifaunal TWINSPAN analysis, showing taxa characteristic of the major station groupings at the first and third dichotomy and the mean environmental parameters of the four station groups defined at the third dichotomy.

First TWINSPAN dichotomy	Porifera *Flustra foliacea* *Hyas coarctatus* *Bolocera tuediae*		*Asterias rubens* *Astropecten irregularis* *Brissopsis lyrifera*	
Third TWINSPAN dichotomy	Group 1 Porifera	Group 2 Tunicates *Spirontocaris lilljeborgi*	Group 3 *Pagurus bernhardus* *Crangon allmanni* *Spatangus purpureus* *Colus gracilis*	Group 4 *Pennatula phosphorea*
Mean environmental parameters of station groups				
Sorting (Folk)	5.0	4.2	4.0	3.4
Carbon (mg.g^{-1})	1.8	3.15	3.0	5.7
Silt (% weight)	3.3	8.5	10.4	50.7
Total pigment (μg.g^{-1})	2.1	3.0	3.6	14.7
Median diameter (φ)	2.5	2.8	3.7	4.1
Depth (m)	72	100	92	144

The infaunal assemblages from the survey area fall broadly into the two regions which coincide with the north British Coastal and Offshore Northern sectors as described by ADAMS (1987). However, the use of the 100 m depth contour to demarcate the northern and central parts of the North Sea (GLÉMAREC, 1973; ADAMS, 1987) would not seem to be justified on the basis of the infaunal data presented here. A significant proportion of northern British Coastal sector stations is faunistically similar to that of the Offshore Northern sector, being placed in the same TWINSPAN grouping and reflecting their similar scores on axis 1 of the ordination (Fig. 9). In particular, the stations in the north east of the survey area would seem to have similar infaunal assemblages to the Moray Firth stations (Fig. 11). Thus infaunal assemblage distributions are not entirely coincident with either ADAMS'(1987) or GLÉMAREC'S (1973) schemes. This is perhaps not surprising since both of these schemes placed great emphasis on bathymetry and temperature, whereas the infauna respond primarily to sediment parameters, which do not always show a close association with depth. Because of the greater influence of depth on epifaunal assemblages, these seem to more closely reflect the hydrographic subdivisions suggested by Glémarec (DYER *et al.*, 1983). The latter authors concluded that some of their benthic regions coincided with those proposed by Glémarec although they distinguished at least two subgroups within Glémarec's 'étage du large'. By means of a more intensive survey the present authors were able to subdivide this region even further (BASFORD *et al.*, 1989).

Since the major influence on the epibenthos appears to be depth, whilst sediment characteristics are more important for the infauna, it is clear that the more comprehensively sampled epibenthos should not be used to predict the geographical distribution and boundaries of the infaunal assemblages. Further, the geographical distribution of communities which probably grade one into another (BASFORD *et al.*, 1989; ELEFTHERIOU & BASFORD, 1989) cannot be understood without intensive grid surveys of both faunal and environmental parameters. Also, since the fauna is likely to vary both annually and seasonally all the stations should be surveyed in the same season of the same year. However, this was not possible here and this may, in part, obscure the faunal boundaries but such small variations are unlikely to alter the general relationship between the fauna and environmental factors. Just as it was impossible to map infaunal communities from the initial transect surveys of STEPHEN (1923) it is implicit that more could be understood about the subtle changes in both the fauna and the environment from a more intensive survey than has been reported on here.

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