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A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas

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Two complementary surveys of the benthos around the United Kingdom coastline and offshore are described. The first sampled the macroinfauna by day grab at several stations around the England and Wales coastline as part of a wider interdisciplinary assessment of environmental quality by the regulatory authorities. The second sampled the epifauna with a small beam trawl at the grab stations, and at several additional stations, most of which were in the central and southern North Sea.

Similar infaunal assemblages were encountered on both the eastern and western UK coasts in comparable environmental conditions. Tidal current velocity and sediment characteristics accounted for a significant amount of the observed variability in species richness and densities. There was no evidence of any adverse effects on these measures of assemblage structure arising from trace metal contamination of sediments.

Coastal influences (proximity to large estuaries), depth, tidal current velocity, and temperature all helped to explain the distribution of epifaunal assemblages. However, sediment type appeared to be the main structuring force, with a coarser component to samples collected from the north and west of the survey area, i.e. especially around the UK coastline, supporting a much wider variety of sessile taxa.

Grab samples provide unambiguously quantitative data which can be easily linked with sediment type within the small unit area of the sample. Trawls provide integrated samples of the fauna over a much larger area. However, both the design of the trawl, and inherent uncertainties over its sampling efficiency, determine that the survey results are "operationally defined", and consistency in sampling procedures is essential, especially for the analysis of temporal trends.

There is a need to provide better working descriptions of the environment along trawl tows where sediments are variable; a combination of acoustic methods and underwater photograpy may be most suitable.

Key words: infauna, epifauna, North Sea, English Channel, Celtic Seas, quality status, biodiversity, assemblage type.

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Introduction

In 1990, several stations in the North Sea and English Channel were established by the North Sea Task Force (NSTF) for sampling water, sediments, and biota to generate new information on the concentrations of contaminants and the "well-being" of biological systems, as a contribution to a Quality Status Report for an international North Sea Conference held at ministerial level in 1995 (NSTF, 1993). In United Kingdom waters, this initiative was paralleled by the establishment of a National Monitoring Programme (NMP) which, to date, has involved the coordinated sampling of over 80 "estuarine", "intermediate", and "offshore" stations by the regulatory agencies (Anon., 1994; Marine Pollution Monitoring Management Group, 1998). Several NMP stations in the western North Sea area correspond with the earlier NSTF programme.

In studies funded by the UK Ministry of Agriculture, Fisheries, and Food (MAFF), the Centre for Environment, Fisheries, and Aquaculture Science (CEFAS) undertook sampling at NSTF stations along

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the English east coast and offshore, and at "intermediate" and "offshore" NMP stations around the coastline of England and Wales. As a component of these programmes, the benthic macrofauna was sampled by day grab. At all these and at some additional stations, samples of the epifauna were also collected using a small beam trawl. Although the latter group, which includes starfish, crabs, and shrimps, is likely to be the most familiar to non-specialists and has an important role in the marine food chain (e.g. Collie *et al.*, 1997), it has received much less scientific attention than the infauna, largely due to sampling difficulties. The present survey aimed to redress the balance by providing an insight into the distribution and relative abundance of epifaunal taxa over a much wider geographical range than has previously been attempted in surveys of benthic populations around the UK coastline.

Efforts to describe and interpret variability in the benthic fauna over large geographical areas date back to the classic studies of Petersen and co-workers in Danish waters (e.g. Petersen, 1918), though few have been conducted on scales approaching whole seas. In the North Sea, recent examples of the latter include, for the infauna, the work of Eleftheriou and Basford (1989) and Kunitzer *et al.* (1992) and, for the epifauna, Dyer *et al.* (1983), Frauenheim *et al.* (1989), Duineveld and van Noort (1990), and Jennings *et al.* (1999). The fauna of large sectors of the English Channel has been described by Holme (1961, 1966) and, on the French side, by Cabioch and co-workers (e.g. Cabioch, 1968). A more recent evaluation of diversity across the easternmost part of the English Channel, based upon data collected in the 1970s, is given by Sanvicente-Anove *et al.* (1996).

Compared with the North Sea, coverage of western sea areas is more limited. Hartley (1979) described mollusc distributions in the central and northern Celtic Sea, while a more extensive dredge survey in this region by French and Irish scientists between 1977 and 1983 presently remains largely unreported (B. Ball and L. Cabioch, pers. comm.). Warwick and Davies (1977) described the benthic communities of the Bristol Channel and Mackie *et al.* (1995) reported on infaunal and epifaunal surveys of a proportion of the southern Irish Sea. Rees (1987) and Mackie *et al.* (1995) provide maps of the infaunal communities of the Irish Sea as a whole, although these contain a significant element of interpolation as they were not derived from systematic sampling. Rees and Walker (1991) and Hensley (1996) have conducted surveys of the benthic fauna over extensive areas of the NE and NW Irish Sea, respectively.

A feature of most of the epifaunal surveys cited above, as well as a number of the infaunal surveys of coarser substrata, is the variety of sampling methods employed, which precludes a standardized synthesis of the available data. The present survey employed standard methods over a wider geographical area around the UK coastline than has hitherto been attempted, allowing a more informative statement to be made about spatial trends in the fauna in relation to environmental variability.

Methods

Field sampling

Day grabs

During April and May 1993, and in February and May 1994, samples of the benthic macrofauna were collected from MAFF research vessels at each of 25 "intermediate" and "offshore" stations around the England and Wales coastline, following the guidelines of the NMP (Anon., 1994; see also Fig. 1). One station in the SW Approaches (S48) was sampled in December 1992, i.e. outside the recommended February to May sampling window, but this offshore, deep-water environment was included as a clean-water "reference" point. (An attempt to sample S48 in February 1994 had to be abandoned due to bad weather.) An additional station off the Tees Estuary was sampled to provide information on the shallow coastal environment in this area.

At each location, five sediment samples for macrofauna analysis were collected using a 0.1 m^2 day grab from the central point of a 500 m grid of 9 stations, the latter being sampled for contaminant analyses only. The five replicates were collected from within a 100 m range ring, using SEXTANT software and DGPS position-fixing.

The depth of sediment in the closed jaws of the grab was determined, as an indication of sample volume. Very small samples (i.e. less than about 5 cm depth) were discarded. A visual description of the sediment type was recorded, together with the location and times at which the sample was collected, and the prevailing sea state, wind strength, and water depth. A small subsample for sediment particle size analysis was removed using a 2 cm diameter perspex corer inserted to a depth of about 5 cm. The contents of the grab were transferred to a hopper, and gently washed over a 1 mm mesh brass sieve. The retained material was preserved for analysis in 5% formaldehyde in seawater with added Rose Bengal.

Beam trawls

Samples were obtained by MAFF research vessels from 69 stations between 1992 and 1996 (Fig. 1).

A standard 2 m Lowestoft beam trawl (Riley *et al.*, 1986) with a 3 mm mesh codend liner was deployed for 5–10 min across each station at a speed of about 0.5 m s^{-1}. The "start" (locking of winch following seabed contact) and "end" (commencement of hauling) positions were recorded. Tow length averaged about 400 m, but varied substantially (s.d. = 290) depending on tidal current velocity and wind strength at the time of

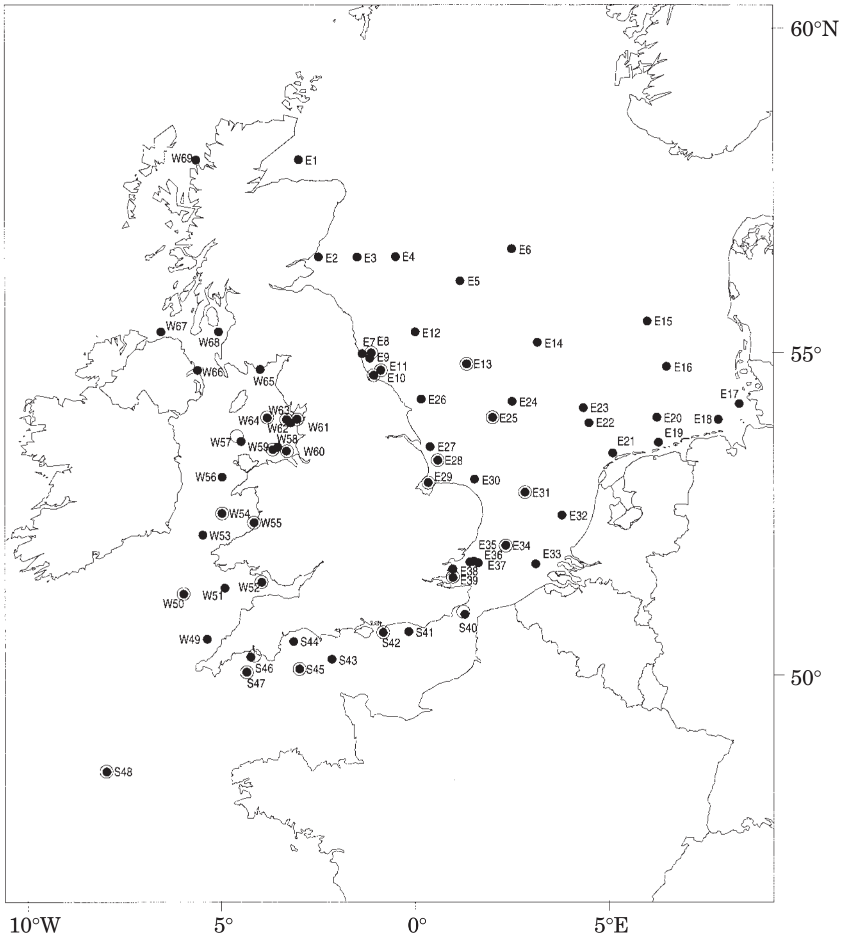

Figure 1. Location of 2-m beam trawl stations. Those also sampled by day grab off the England and Wales coastline as part of the UK National Monitoring Programme are encircled.

sampling. On retrieval of the trawl, an estimate of sample volume was made, along with a summary of the contents, noting especially the presence of stones, rock, etc. The sample was then sorted on deck over a 5 mm mesh sieve. Most specimens were identified and enumerated at sea. Any problematic specimens were preserved in formalin for identification on land.

The presence of infaunal organisms arising from the fouling of soft sediments was noted, as were occurrences of pelagic species such as jellyfish. However, these records were excluded from the final compilation of the data. The former included most polychaete worms (with the exception of encrusting forms such as *Sabellaria* and *Filograna*, and surface-dwelling specimens within the family Aphroditidae), bivalve molluscs (excepting taxa with a surface-dwelling habit such as *Chlamys* and *Modiolus*), and burrowing echinoderms such as *Echinocardium* and *Amphiura*. In the following account, the faunal data are reported as numbers per tow, i.e. unadjusted for tow length.

Laboratory analysis

Infauna and sediments

The macrofauna was identified to species level, as far as possible, with the use of a range of standard taxonomic keys. All animals were enumerated, with the exception of colonial organisms which were recorded on a presence/absence basis. Nomenclature followed that of Howson (1987). The biomass of each taxon was determined as wet blotted weight, and then expressed as ash-free dry weight using conversion factors mainly from Rumohr *et al.* (1987).

For particle size analyses, sediment subsamples were first wet sieved at 500 microns. The >500 micron fraction was then dry-sieved at half-phi intervals, and the <500 fraction analysed using a Coulter LS130 laser sizer.

Percentage organic carbon and nitrogen were determined using a CHN analyser, following exposure of sediment samples to fumes of concentrated HCl in order to dissolve carbonates.

Table 1. Ranked descriptor of substratum type.

Code	Description	Rank
M	Mud	1
M(S)	Sandy mud	2
S(M)	Muddy sand	3
S	Sand	4
S(Sh)	Shelly sand	5
G(S)	Sandy gravel	6
G(Sh)	Shelly gravel	7
G	Gravel	8

Concentrations of a range of trace metals were determined using an inductively-coupled plasma spectrometer or (for mercury) a cold-vapour atomic fluorescence spectrometer, following digestion of whole-sediment extracts (<2 mm) using hydrofluoric acid/nitric acid (Jones and Laslett, 1994).

As well as following "in-house" quality-control procedures, staff responsible for processing the NMP macrofauna and sediment samples also actively participated in the UK National Marine Biological and Chemical Analytical Quality Control Schemes, which were established to ensure consistency in the generation of NMP data from all sources.

Epifauna

Motile taxa not dealt with at sea were identified to species level, as far as possible, using a range of standard taxonomic keys. Nomenclature followed that of Howson (1987).

A ranked descriptor of the predominant substratum type along trawl tows was derived from a combination of records of trawl contents, particle size analyses of sediments from grabs where available, and information from Admiralty Charts (Table 1). Whilst useful as a crude indicator of sediment "coarseness", these summaries were inadequate to categorize some of the admixtures encountered, e.g. gravel and mud (see Discussion).

Data treatment

Statistical analyses of particle size distributions employed the formulae of Folk and Ward (1957).

Inter-relationships between the following variables (log-transformed, where necessary, to reduce skewness in the data) were examined using Pearson product moment correlation coefficients:

- Day grabs: maximum spring tidal current strength ($m\ s^{-1}$) from Admiralty data, depth (m), average winter surface-water temperature and salinity from Lee and Ramster (1981); latitude, longitude, median diameter (mm), sorting coefficient, % silt/clay, numbers of taxa $0.1\ m^{-2}$, numbers of individuals $0.1\ m^{-2}$, g AFDW biomass $0.1\ m^{-2}$, H'$\log_2$ (Shannon and Weaver, 1949), evenness (Pielou, 1966), % organic carbon and nitrogen, and concentrations in $mg\ kg^{-1}$ of a range of trace metals in sediments (As, Cd, Cr, Cu, Hg, Ni, Pb, and Zn). Biological and sediment variables were averaged across the five samples (nine in the case of trace metal determinations) taken at each station. No data were available on trace metal concentrations and organic content at two stations, and on organic content at a further four stations;
- Beam trawls: maximum spring tidal current strength ($m\ s^{-1}$), depth (m), average winter surface-water temperature and salinity, latitude, longitude, sediment type (1–8, see Table 1), tow length (m), numbers of taxa and numbers of individuals per trawl tow.

Average surface-water temperature and salinity in winter (February) were selected because only limited seabed data were available, especially for the western UK coast (Lee and Ramster, 1981). However, Lee and Ramster (1981) noted that differences in temperature between surface and bottom over most of the North and Irish Seas are minimal in winter. They also note the more conservative nature of salinity relative to temperature, with only very small differences in values between winter and summer both at the surface and at the seabed, and the similarity in distributional trends between surface and bottom, for the area covered by the present study.

Multivariate classification analysis was conducted on log-transformed quantitative infaunal data using the Bray–Curtis similarity measure (Bray and Curtis, 1957) and group-average sorting (Lance and Williams, 1967). Epifaunal data were analysed on a presence/absence basis. Relationships between the ranked dissimilarity matrices for the infaunal and epifaunal data and different combinations of environmental variables were examined using the method described by Clark and Ainsworth (1993): subsets which best explained the biological variability were identified by the highest correlation coefficients (ρ_w).

Results

Infauna from day grabs

Four-hundred and thirty taxa were identified, consisting of 186 polychaetes, 112 crustaceans, 76 molluscs, 19 echinoderms, and 37 in the category "other groups". Figure 2 provides an indication of spatial variability in the range and densities of taxa encountered at NMP stations, and in the prevailing sediment type. Stations in the easternmost part of the English Channel and southern North Sea off the Thames, and within the Bristol Channel, supported a very sparse fauna associated with medium sandy sediments. Highest diversities

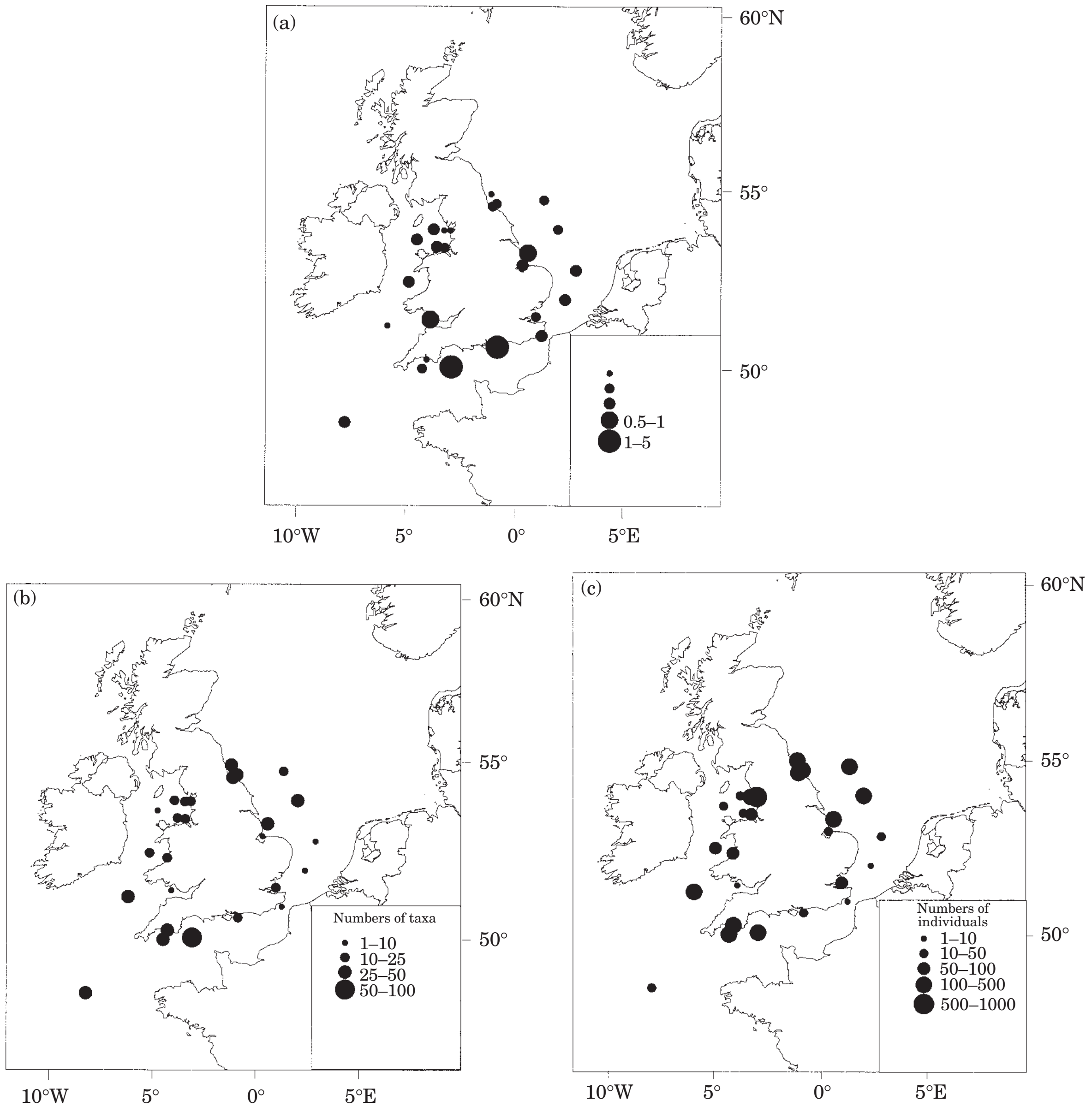

Figure 2. Median particle size of (a) sediments, (b) numbers of infaunal taxa, and (c) densities 0.1 m^{-2} at National Monitoring Programme stations.

were generally encountered off the NE and SW English coast, across a range of median particle sizes. Densities were also relatively high at most of these stations, and in coastal waters off Morecambe Bay, NW England.

A correlation matrix for a range of biological and environmental variables is given in Table 2. Concentrations of trace metals are all relatively low at the coastal and offshore stations examined here (Rowlatt and Lovell, 1994; Marine Pollution Monitoring Management Group, 1998). With the exception of As and Cd, the metals are strongly positively correlated with each other, with percentage organic carbon and nitrogen and, in turn, with measures of particle size (sorting coefficient and percentage silt/clay). Correlations between a number of metals, notably Cr and Pb, and biological measures (numbers of individuals and taxa 0.1 m^{-2}) are also positive. Trends in metal concentrations are therefore best explained by variation in sediment characteristics, or some other factors associated with this variation. The positive correlations between these concentrations and biological measures indicate that contamination by trace metals at the levels

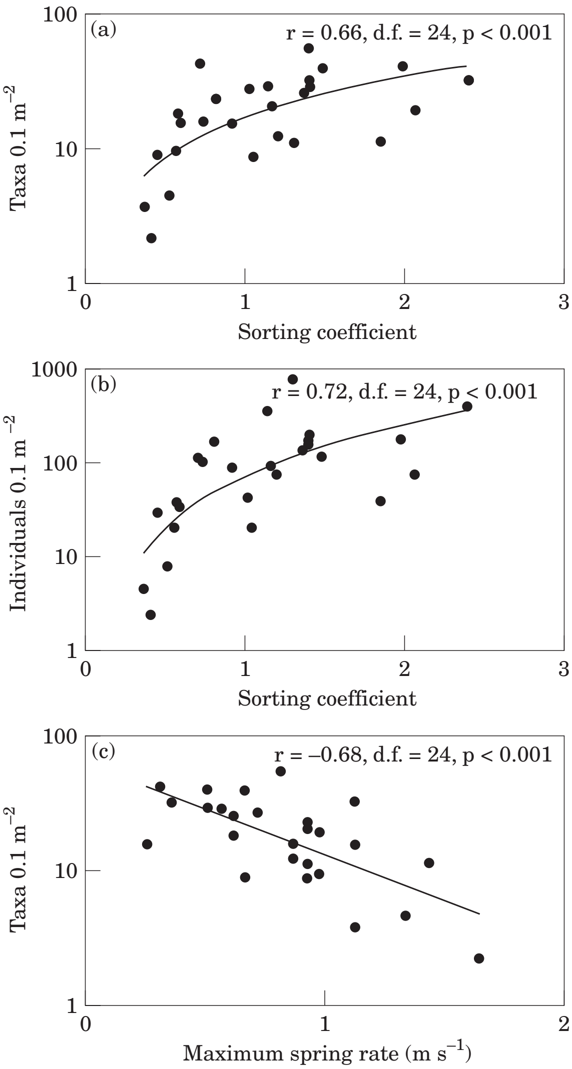

Figure 3. Plots of average numbers and densities of macrobenthic taxa 0.1 m^{-2} at National Monitoring Programme stations against sediment sorting coefficients (a, b), and average numbers of taxa 0.1 m^{-2} against the maximum spring rates at nearby locations, derived from Admiralty data (c).

encountered in the present survey has no adverse effects. There were no significant relationships between As, Cd, and biological measures.

Measures of particle size are significantly correlated with the primary biological measures, especially in the case of sorting coefficient vs. numbers and densities of taxa (Table 2). Power curves ($y=cx^b$) provided a better fit to these data [Fig. 3(a)(b)] largely on account of three very sparsely populated stations with well-sorted sediment near the origin of each plot. The characteristics of this group of stations are further described below, in relation to the outcome of cluster analysis. There are also relatively strong negative correlations between biological measures, particularly numbers of taxa, and current speed [Table 2 and Fig. 3(c)]. The latter is also correlated with the median diameter of sediments. Measures of diversity (H'$\log_2$ and evenness) were negatively correlated with longitude, i.e. diversity tends to increase in a westerly direction. This may be explained by coincident trends in depth, rather than suggesting any biogeographical influence (see Table 2). There were no significant relationships between biological variables and percentage organic carbon, winter temperature, and salinity.

Relationships between physical measures and biological variation were also explored using the method of Clarke and Ainsworth (1993). The highest correlation ($p_w=0.64$) arose from a combination of four variables: maximum spring tidal current strength (0.41), median diameter (0.40), longitude (0.18), and sorting coefficient (0.23). These are listed in rank order of their contributions to ascending best-variable combinations, and the figures in parentheses are correlation coefficients for each variable when tested singly against the biological data.

The correlation analyses therefore suggest that the predominant influence on benthic populations is that of tidal current strength (expressed in terms of maximum spring rate), mediated to a lesser degree through variation in sediment particle size.

Six assemblages were identified from cluster analysis of log-transformed quantitative data (Figs 4 and 5). It is evident from Figure 5 that, where environmental conditions are comparable, a similar benthic fauna can develop irrespective of geographical location. The faunal affinity of certain inshore and offshore sandy or muddy sand stations (e.g. groups C and E in Fig. 5) finds a parallel in the outcome of epifaunal analysis (below). Thus there is little evidence from this analysis of biogeographical constraints on the disposition of assemblage types A and C–E, or of a pronounced inshore/offshore dichotomy, although this is not to imply that all component species are cosmopolitan in their distribution within the survey area. Assemblage B, associated with coarser deposits, is confined to the English Channel and western approaches, while assemblage F comprises a discrete group of offshore medium sandy stations in the eastern Irish Sea (Fig. 5).

The main characteristics of these assemblages are summarized in Table 3. The groups have little in common in terms of the dominant taxa, reflecting the relatively low levels of similarity at which they are linked. Previously identified trends in relation to environmental variables are exemplified by the contrast between clusters A and D. Stations within the former, located in areas of relatively high tidal current velocity, support a very impoverished fauna characterized by the presence of the polychaete *Ophelia borealis*, a typical inhabitant of mobile sandy sediments (e.g. Vanosmael

Table 2. Correlation matrix for biological and environmental variables determined from day grab samples at National Monitoring Programme stations (n=26 except for trace metals where n=24, and percentage organic carbon and nitrogen, where n=20). Significance levels: *0.05–0.01; **0.01–0.001; ***<0.001.

	Current speed	Log depth	Temperature	Salinity	Latitude	Longitude	Log median	Sorting	% silt/clay	Log taxa	Log counts	Log biomass	$H'\log_2$	Evenness	% carbon	% nitrogen	Log As	Log Cd	Log Cr	Log Cu	Log Hg	Log Ni	Log Pb	Log Zn
Current speed																								
Log depth	n.s.																							
Temperature	n.s.	n.s.																						
Salinity	n.s.	n.s.	0.6**																					
Latitude	n.s.	n.s.	n.s.	n.s.																				
Longitude	n.s.	−0.45*	n.s.	n.s.	0.41*																			
Log median	0.54**	n.s.	−0.55**	n.s.	−0.4*	n.s.																		
Sorting	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.																	
% silt/clay	n.s.	n.s.	0.54**	n.s.	n.s.	n.s.	−0.77***	0.64***																
Log taxa	−0.68***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.57**	0.41*															
Log counts	−0.55**	n.s.	n.s.	n.s.	n.s.	n.s.	−0.39*	0.62***	0.51**	0.81***														
Log biomass	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−0.43*	n.s.	0.44*	0.47*	0.64***													
$H'\log_2$	−0.56**	0.45*	n.s.	n.s.	n.s.	−0.54**	n.s.	n.s.	n.s.	0.84**	n.s.	n.s.												
Evenness	n.s.	n.s.	n.s.	n.s.	n.s.	−0.43*	n.s.	n.s.	n.s.	n.s.	−0.73***	−0.5**	n.s.											
% carbon	n.s.	n.s.	0.54*	n.s.	n.s.	n.s.	−0.58**	0.58**	0.82***	n.s.	n.s.	n.s.	n.s.	n.s.										
% nitrogen	n.s.	n.s.	0.62*	n.s.	n.s.	n.s.	−0.63**	0.63**	0.85***	0.55*	0.47*	n.s.	0.47*	n.s.	0.93***									
Log As	0.61**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.								
Log Cd	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.							
Log Cr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−0.71***	0.55**	0.79***	0.49*	0.6**	0.52**	n.s.	n.s.	0.76***	0.8***	n.s.	n.s.						
Log Cu	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−0.56**	0.58**	0.71***	n.s.	0.43*	n.s.	n.s.	n.s.	0.68**	0.76***	n.s.	n.s.	0.79***					
Log Hg	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−0.48*	0.47*	0.54**	n.s.	0.51*	0.45*	n.s.	n.s.	0.61**	0.68**	n.s.	n.s.	0.77***	0.78***				
Log Ni	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.48*	0.57**	n.s.	n.s.	n.s.	n.s.	n.s.	0.81***	0.87***	n.s.	n.s.	0.45*	0.68***	0.55**			
Log Pb	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−0.64***	0.61**	0.73***	0.42*	0.5*	0.46*	n.s.	n.s.	0.83***	0.86***	n.s.	n.s.	0.86***	0.82***	0.77***	n.s.		
Log Zn	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−0.53**	0.62**	0.68***	n.s.	0.46*	n.s.	n.s.	n.s.	0.73***	0.79***	n.s.	n.s.	0.87***	0.82***	0.77***	n.s.	0.92***	

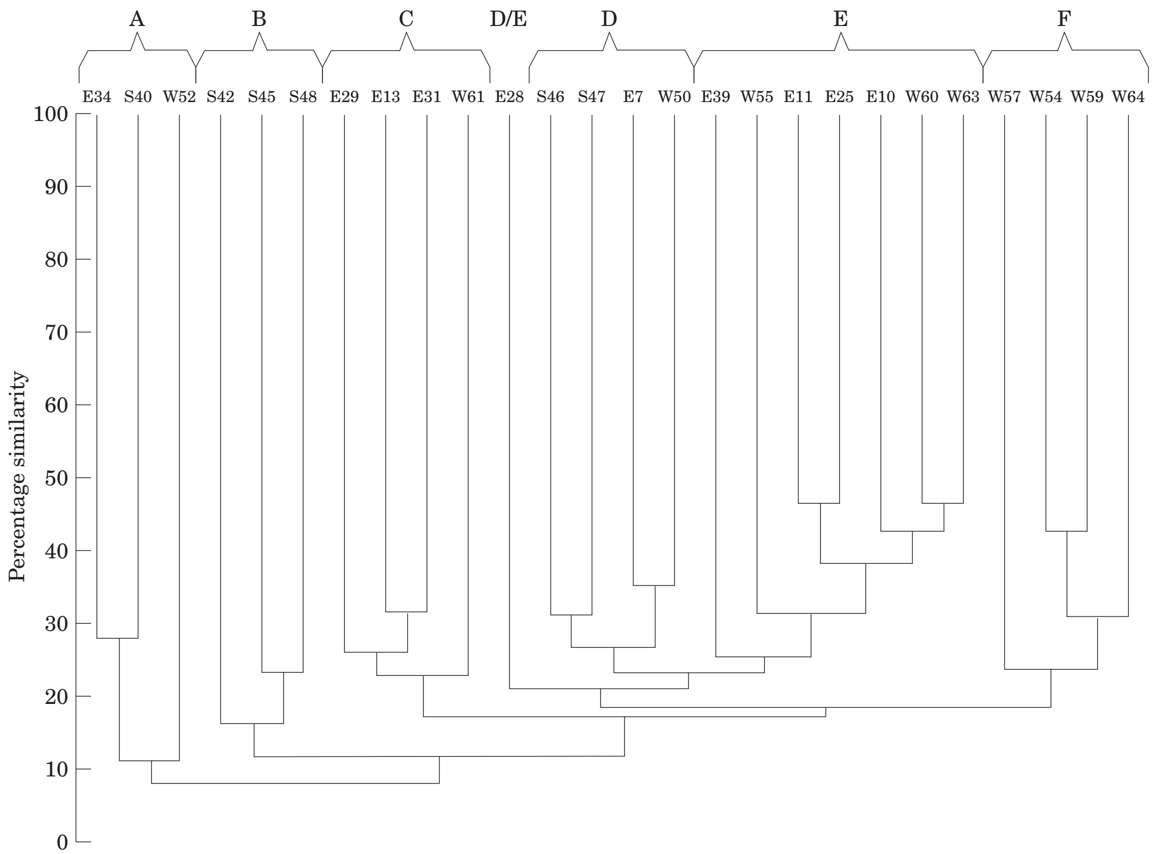

Figure 4. Dendrogram output from cluster analysis of the log-transformed macrofauna data at National Monitoring Programme stations. Six assemblage types have been identified, at various levels of similarity.

et al., 1982). Stations within the latter group, under conditions of lower tidal current velocity and generally deeper water, support a much higher diversity of species as well as enhanced densities and biomass, indicative of more stable substrata.

For other cluster groups in Table 3, it is clear that faunal affinities between stations can occur although environmental conditions may be very different. For example, the coarse sand assemblage within the English Channel, typified by the dominant taxa of group B, occurs at widely varying depths and under substantially different tidal current regimes which, in turn, is reflected in the range of total numbers of taxa encountered. Similar observations apply especially to group E, and help to explain why the relationships established between univariate measures of biological and environmental status at individual stations are not so readily identified from the output of cluster analysis.

A single station representative of coarser deposits off the Humber estuary (D/E in Table 3, since it has closest affinity with these groups: see Fig. 5), supported a rich and distinctive fauna characterized by the presence of the reef-building polychaete *Sabellaria spinulosa*. The development of such reefs, typically on gravelly substrata with strong tidal flow, provides a stable platform for colonization by a wide variety of species (see, e.g. George and Warwick, 1985). Strictly, such an assemblage could be defined as epifaunal, even though the habitat presented is clearly suitable for both "infaunal" and epifaunal colonizers (see Table 3).

Epifauna from beam trawls

Sediments

Sampling stations in the southern North Sea were characteristically sandy in nature [Fig. 6(a)]. Sand and mud in varying proportions were associated with stations in inner Liverpool and Morecambe Bays (northwest England) and off the Tyne (northeast England). Deeper-water samples in the northwestern North Sea had an appreciable gravel component (although the prevailing sediment type is, in parts, finer: see Discussion), as did those in coastal waters off eastern England, where coarse deposits are widespread. Samples

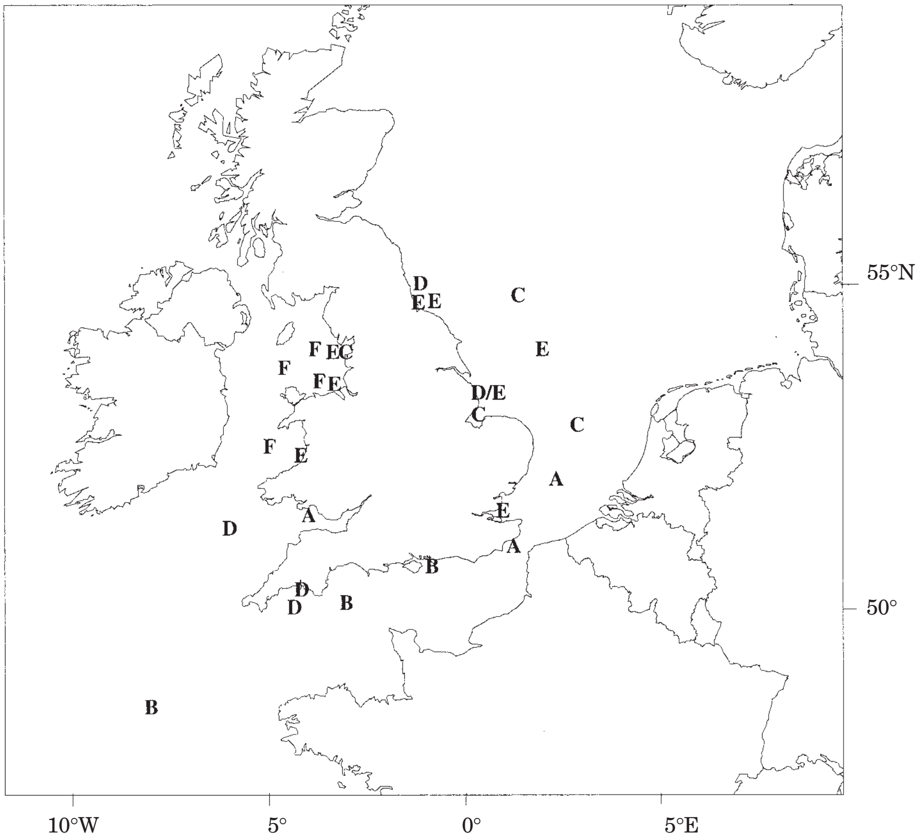

Figure 5. Grouping of National Monitoring Programme stations around the England and Wales coastline according to the outcome of cluster analysis of macrofauna data (see Fig. 4).

from the English Channel, Celtic, and Irish Seas were also predominantly gravelly in nature.

Fauna

The apportioning of taxa across major groups (Table 4a) showed that bryozoans, molluscs, and crustaceans were dominant, with hydroids and fish also being well represented. The total across all animal groups amounted to 414 taxa. The six most frequently encountered taxa (Table 4b) were Paguridae (hermit crabs), *Asterias rubens* (common starfish), *Ophiura* spp. (brittle-stars), *Liocarcinus holsatus* (swimming crab), *Crangon allmani* (brown shrimp), and Gobiidae (gobies). These are all motile, in contrast to the remaining four (the hydroid *Hydrallmania falcata*, the barnacle *Balanus crenatus*, and the bryozoans *Electra pilosa* and *Flustra foliacea*) which are sessile. Overall, relatively few taxa were widespread throughout the sampling area and 132 (about 30%) were single occurrences.

A comparison of Figure 6(a) and (b) shows that, in the North Sea, higher numbers of taxa tend to be associated with coarser substrata to the north of the survey area, and along parts of the eastern English coastline. Elsewhere, gravelly substrata in the English Channel and adjacent to the western UK coast also supported a generally high epifaunal diversity. The distribution of animal densities [Figure 6(c)] is more even across the survey area, although very high numbers were occasionally encountered at inshore locations. For example, in the German Bight, Liverpool Bay, and Solway Firth, dense populations of the brittle star *Ophiura* were sampled.

Statistical relationships between numbers of taxa and individuals per trawl and a range of environmental variables were explored through correlation analysis (Table 5). There was a significant positive correlation between sediment "coarseness" and log numbers of taxa, and a significant negative relationship with log densities. The former may be explained by the capacity of the mixed gravelly areas to provide more attachment points and refuges, compared with uniform muddy areas [see Fig. 6(b)]. The latter reflects a capacity for muddy sand or muddy deposits, especially close inshore near to major estuaries, to support very high densities of common species such as brittle-stars [see Fig. 6(c)] which, in turn, accounts for the significant negative

Table 3. Top five ranked taxa in terms of derived mean densities 0.1 m^{-2} $\bar{y}$, across station groups identified from cluster analysis. Means and ranges of total numbers of taxa, densities and biomass 0.1 m^{-2} across stations, along with particle size statistics, maximum spring tidal rates, depths, and habitat descriptions, are listed below.

	A	$\bar{y}$	B	$\bar{y}$	C	$\bar{y}$	D/E	$\bar{y}$
	Ophelia borealis	5.7	*Typosyllis* spp.	37.3	*Lagis koreni*	868.3	*Nucula hanleyi*	128.0
	Nephtys spp.	4.3	*Sphaerosyllis hystrix*	28.3	*Bathyporeia guilliamsoniana*	63.8	*Sabellaria spinulosa*	123.0
	Spisula elliptica	2.0	*Echinocyamus pusillus*	17.0	*Nephtys* spp.	42.8	*Pholoe* sp.	38.0
	Oligochaete sp.	1.3	*Polycirrus medusa*	15.0	*Fabulina fabula*	37.5	*Ophiura* spp.	20.0
	Bathyporeia elegans	1.3	*Glycera lapidum*	15.0	*Mysella bidentata*	22.5	*Ampelisca typica*	8.0
	Spio filicornis	1.0	Anthozoa sp.	12.3				
Numbers of taxa	3.5 (2.2–4.6)		31.1 (11.4–54.6)		11.2 (8.8–15.8)		32.4	
Numbers of individuals	5 (2–8)		67 (38–181)		83 (20–768)		394	
Biomass (g AFDW)	0.042 (0.001–0.425)		0.120 (0.061–0.326)		0.188 (0.053–2.580)		0.523	
Median diameter (mm)	0.44 (0.35–0.56)		1.56 (0.45–2.87)		0.23 (0.12–0.32)		0.63	
Sorting coefficient	0.43 (0.36–0.51)		1.42 (1.02–1.85)		0.88 (0.44–1.30)		2.4	
Maximum spring rate (m s^{-1})	1.4 (1.1–1.7)		1 (0.7–1.4)		0.7 (0.3–0.9)		1.1	
Depth (m)	34 (26–49)		84 (20–167)		30 (28–35)		20	
Habitat type	Mobile medium sand		Coarse sand		Fine sand		Muddy gravelly sand	
Location	S North Sea/Bristol Channel		English Channel		North Sea		Wash, E England	

	D	$\bar{y}$	E	$\bar{y}$	F	$\bar{y}$
	Maldanidae	57.5	*Chamelea gallina*	116.1	*Abra alba*	76.0
	Melinna palmata	46.3	*Amphiura filiformis*	96.1	*Scoloplos armiger*	16.3
	Abra alba	39.8	*Nucula nitidosa*	61.9	*Nephtys* spp.	13.8
	Echinocyamus pusillus	37.5	*Spiophanes bombyx*	57.9	*Spatangus purpureus*	11.0
	Abra nitida	30.3	*Abra alba*	47.4	*Spisula elliptica*	10.3
Numbers of taxa	35.1 (25.8–42.2)		24.7 (12.4–39.6)		14.9 (9.6–18.4)	
Numbers of individuals	147 (116–181)		136 (75–360)		40 (21–91)	
Biomass (g AFDW)	0.272 (0.096–0.564)		0.713 (0.220–3.068)		0.180 (0.095–0.303)	
Median diameter (mm)	0.12 (0.06–0.24)		0.14 (0.04–0.24)		0.40 (0.25–0.47)	
Sorting coefficient	1.36 (0.70–1.99)		1.32 (0.81–2.06)		0.65 (0.55–0.92)	
Maximum spring rate (m s^{-1})	0.5 (0.3–0.6)		0.8 (0.5–1)		0.9 (0.6–1.1)	
Depth (m)	69 (39–95)		33 (16–74)		57 (39–79)	
Habitat type	Stable muddy very fine sand		Mainly inshore muddy fine sand		Offshore medium sand	
Location	NE and SW coasts		E and W coasts		W coast	

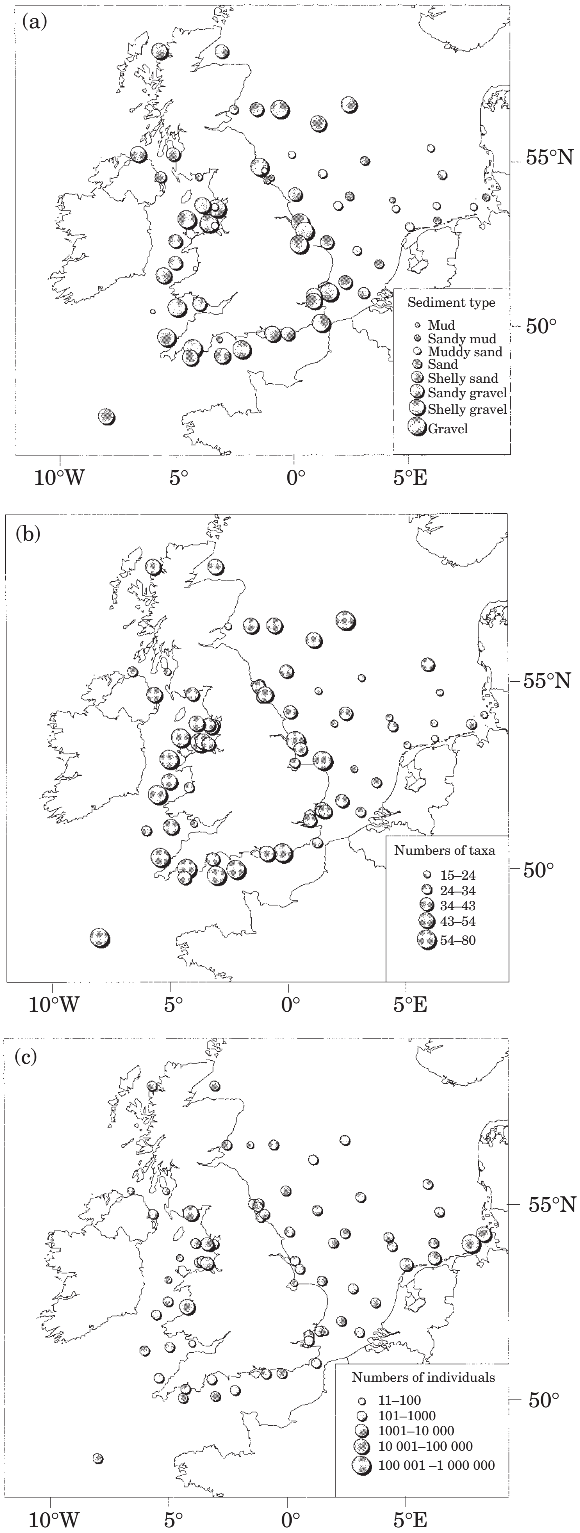

Figure 6. Predominant sediment type (a), numbers of epifaunal taxa (b), and densities (c) per trawl tow.

Table 4. Numbers of epifaunal taxa allocated to each major faunal group (a); top 10 ranked taxa in terms of frequency of occurrence in trawls (b).

(a) Group	No. of taxa
Bryozoa	80
Mollusca	66
Crustacea	62
Hydrozoa	43
Pisces	40
Porifera	36
Echinodermata	26
Anthozoa	24
Ascidiacea	23
Other groups	14
Total	414

(b) Taxon	Frequency (max=69)
Paguridae	64
Asterias rubens	57
Ophiura spp.	48
Liocarcinus holsatus	47
Crangon allmani	45
Gobiidae	45
Hydrallmania falcata	43
Balanus crenatus	43
Electra pilosa	42
Flustra foliacea	40

relationship between counts, water depths, and salinity (Table 5).

A significant negative correlation between numbers of taxa and longitude (i.e. numbers tend to increase in a westerly direction) appears to be largely a function of coincident trends in temperature, depth, and, to a degree, substratum type. There was also a discernible underlying trend towards increased winter surface-temperature in a north–south direction which, along with substratum type, might help to explain a comparable, but less pronounced, trend in numbers of taxa. There was no significant correlation between faunal measures and maximum spring tidal current strength, despite a significant positive correlation between this variable and sediment "coarseness", and a significant negative correlation with latitude. A weak (non-significant) positive relationship between numbers of taxa and current velocity ($p=0.054$) contrasts with a significant negative relationship between the two for infaunal data (see above).

Relationships between epifaunal and environmental data were further examined using the procedure of Clarke and Ainsworth (1993). Maximum correlation ($p_w=0.47$) arose from a combination of five variables: latitude (0.30), sediment type (0.29), log depth (0.27),

Table 5. Correlation matrix for biological and environmental variables at 2-m beam trawl stations (n = 69). Significance levels: *0.05–0.01; **0.01–0.001; ***<0.001.

	Current speed	Log depth	Temperature	Salinity	Latitude	Longitude	Sediment type	Log tow length	Log taxa	Log counts
Current speed										
Log depth	− 0.26*									
Temperature	n.s.	0.61***								
Salinity	n.s.	0.48***	0.61***							
Latitude	− 0.44***	n.s.	− 0.47***	n.s.						
Longitude	− 0.25*	− 0.41***	− 0.75***	n.s.	n.s.					
Sediment type	0.37**	n.s.	0.36**	n.s.	− 0.24*	− 0.29*				
Log tow length	n.s.	n.s.	n.s.	n.s.	n.s.	− 0.25*	n.s.			
Log taxa	n.s.	0.34**	0.51***	n.s.	− 0.25*	− 0.47***	0.51***	n.s.		
Log counts	n.s.	− 0.31*	n.s.	− 0.46***	n.s.	n.s.	− 0.44***	n.s.	n.s.	

maximum spring tidal current strength (0.14), and winter temperature (0.26). These are listed in rank order of their contributions to ascending best-variable combinations, and the figures in parentheses are correlation coefficients for each variable when tested singly against the biological data. As was the case with numbers and densities of taxa (Table 5), there was no significant influence of tow length ($p_w = -0.01$).

Multivariate classification analysis of presence/absence data identified eight faunal assemblages (Fig. 7). These broadly correspond with differences associated with substratum type, and are therefore most easily described in these terms (Fig. 8), although it is recognized that subclusters, especially within groups 7 and 8, will repay further investigation in relation to species distributions. A biogeographical influence is suggested by, e.g. the distinction between a "NW North Sea" group and a "W Channel/W Coast" group, both of which are characterized by a gravelly component to samples. However, other groupings (especially in coastal areas) comprised stations from widely separated geographical locations. Six stations remained "unclassified"; they are generally located inshore, typically contained relatively few taxa and, in four cases, were intermediate in character to other major cluster groups.

Average numbers of taxa for each cluster group (Table 6) show that there is a trend of increasing numbers with increasing sediment "coarseness", the major distinction arising from an appreciable gravelly component to samples in the four groups at the base of the Table. Lowest numbers were found in predominantly sandy areas of the southern North Sea (group 4) and highest numbers in a "stony ground" assemblage, mainly off the western UK coast (group 8). Cluster groups can be further characterized in terms of the most frequently occurring taxa (Table 6). The contributions of sessile and motile species to these lists again serves to highlight the importance of substratum type in determining the character of epifaunal assemblages.

Offshore stations in the North Sea are grouped into three regions. The southern part supports a relatively sparse epifauna characteristic of sandy substrata, with limited scope for the establishment of sessile species. Indeed, of the 12 most frequently occurring taxa (Table 6, group 4), the only sessile species is the hydroid *Hydractinia echinata*, which was recorded as an epigrowth on the shells of hermit crabs, which are themselves motile. The central part encompasses the relatively shallow Dogger Bank area. Sediments here are slightly muddier in nature and, while still lacking an appreciable gravel component, have the capacity to support marginally greater numbers of sessile taxa than sandy stations to the south. The epifauna shares similarities with comparable nearshore muddy sand substrata in the German Bight and eastern Irish Sea (Fig. 8 and Table 6, group 5). Finally, samples from the deeper northern parts were more gravelly in nature, allowing colonization by a wider array of attached species. As a result, higher numbers of taxa are found here, compared with offshore stations to the south [Fig. 6(b)], and there is a more equitable balance between sessile and motile species among the most frequently occurring taxa (Table 6, group 1).

Towards the NE English coast, muddier sediments prevail, and these are characterized by the presence of *Nephrops norvegicus*, and a reduced frequency of occurrence of sessile species (group 2 in Table 6). These conditions are mirrored in a station in the Celtic Deep off the western UK coast which was linked with the NE group.

Influences associated with estuarine efflux are evident at nearshore sites off the estuaries of the Elbe/Weser, Thames and Tees, within the Wash, Bristol Channel, and Morecambe Bay, and off Belfast Lough where a comparable "estuarine" fauna is encountered (Fig. 8). The assemblage is notable for the frequent occurrence of the brown shrimp *Crangon crangon* and the pink shrimp *Pandalus montagui* (Table 6, group 7), both of which are

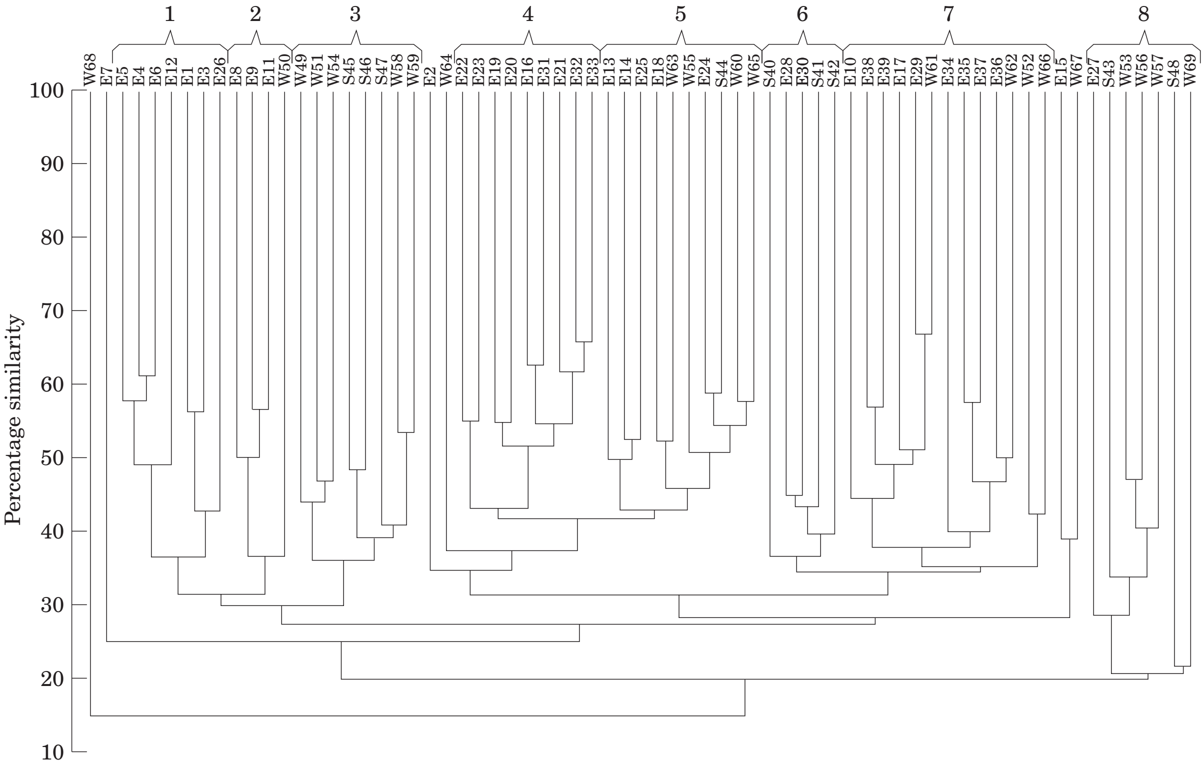

Figure 7. Outcome of cluster analysis of presence/absence data for the epifauna from 2-m beam trawls.

commonly encountered within estuaries as well as coastal waters. Numbers of taxa at these stations are similar to those in the Dogger Bank area.

Elsewhere, gravelly samples collected off the south and west coasts supported a similar fauna characterized by high numbers of taxa [Fig. 6(b)]. The frequent occurence of the echinoderm *Psammechinus miliaris*, and the rarity of the large gastropods *Neptunea antiqua* and *Colus gracilis* in the western assemblage helped to distinguish it from the "NW North Sea" assemblage (Table 6, groups 3 and 1, respectively). The higher frequencies (and densities) of *Pandalus montagui* and *Crangon allmani* in an "E Channel/E Coast" gravelly cluster (Table 6, group 6) suggested that these stations are more subject to coastal influences than the predominantly offshore stations on the western side. This was also supported by the close affinity of this group with the "estuarine" assemblage, in the dendrogram output from cluster analysis (Fig. 7).

Another coarse ground cluster (defined as "stony" in Fig. 8) comprises stations which are widely separated both geographically and in terms of depth. For example, it includes a station off the Humber at 20 m, a station off the Pembrokeshire coast of Wales at 100 m and one in the South West Approaches at 170 m, although these stations are linked at a low level of similarity. Highest numbers of taxa generally occurred within this group, the most frequently ocurring being largely sessile forms, especially hydroids and bryozoans (Table 6, group 8).

Discussion

This is the first time that a survey employing standard methods to sample the subtidal infauna and epifauna has been conducted over such a wide geographical scale around the UK coastline, and the data should therefore provide a valuable "baseline" for future work directed at these groups. The epifaunal survey has particular value for community classification, especially in offshore areas, where recent information is relatively sparse (e.g. Doody *et al*., 1993).

Multivariate analysis of the infaunal data showed that groups of similar stations associated with softer substrata were common to both the eastern and western UK coasts. Both sediment sorting and tidal current strengths are useful expressions of the dynamic nature of the local physical environment, and significant relationships with numbers and densities of taxa were evident (see Fig. 3). Thus the degree of *physical disturbance* of sediments expressed in these terms, as well as particle size alone as a "static" descriptor of habitat type,

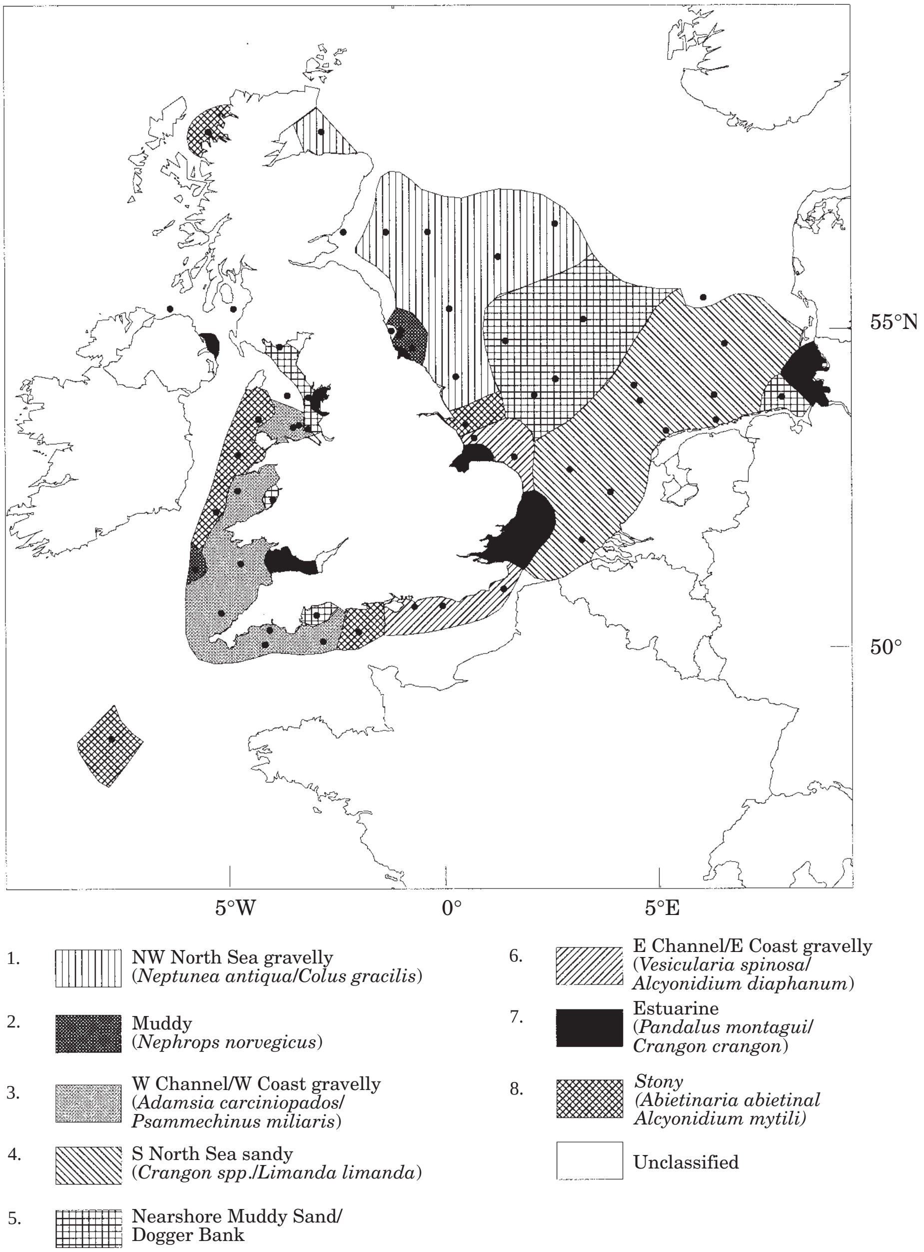

Figure 8. The distribution of epifaunal assemblages derived from cluster analysis of presence/absence data. Where possible, distinctive taxa (or combinations of taxa) among those most frequently occurring are also listed against cluster type.

provided a convincing explanation of broad trends in the data. This finding is comparable with that of Warwick and Uncles (1980) who linked variability in the fauna of the Bristol Channel to bed shear stresses arising from tidal current action. Cabioch (1968) also identified the critical importance of tidal influences on the distribution of benthic species in the English Channel, mediated through their effects on substratum characteristics, particulate transport and water mixing.

Too few stations were occupied in the North Sea to delineate patterns in the distribution of infaunal assemblage types comparable with those derived from the 1986 ICES North Sea benthos survey (Kunitzer *et al*., 1992), which also incorporated earlier data for the northern part (Eleftheriou and Basford, 1989). The survey design comprised a grid of stations across the whole North Sea, but the nearshore environment along the English east coast, where the majority of NMP

Table 6. Most frequently occurring taxa in cluster groups 1–8. Groups are ranked in sequence from top left to bottom right according to the contribution of sessile taxa, which are highlighted. In the column adjacent to each group, numbers of occurrences (n) appear above the total sample number.

	Group 4: "S North Sea sandy"	n	Group 2: "Muddy"	n	Group 5: "Nearshore muddy sand/Dogger Bank"	n	Group 7: "Estuarine"	n
	Paguridae	9	***Hydrallmania falcata***	4	*Paguridae*	10	*Paguridae*	13
	Liocarcinus holsatus	9	***Laomedea flexuosa***	4	*Asterias rubens*	10	***Electra pilosa***	13
	Gobiidae	9	*Aphrodita aculeata*	4	*Ophiura* spp.	10	*Asterias rubens*	13
	Hydractinia echinata	8	*Crangon allmani*	4	*Liocarcinus holsatus*	9	*Pandalus montagui*	12
	Arnoglossus laterna	8	*Nephrops norvegicus*	4	***Hydractinia echinata***	8	***Sertularia cupressina***	11
	Limanda limanda	8	*Paguridae*	4	***Hydrallmania falcata***	8	***Balanus crenatus***	10
	Buglossidium luteum	8	*Astropecten irregularis*	4	*Aphrodita aculeata*	8	*Crangon crangon*	10
	Crangon allmani	7			***Electra pilosa***	8		
	Crangon crangon	7			*Astropecten irregularis*	8		
	Asterias rubens	7			*Callionymus lyra*	8		
	Ophiura spp.	7			*Buglossidium luteum*	8		
	Callionymus lyra	7						
Number of samples		9		4		10		13
Average number of taxa (95% CL)	22 (19–25)		35 (20–51)		31 (25–37)		33 (27–39)	

	Group 6: "E Channel/E Coast gravelly"	n	Group 3: "W Channel/W Coast gravelly"	n	Group 1: "NW North Sea gravelly"	n	Group 8: "Stony"	n
	Hydrallmania falcata	5	***Serpulidae***	8	***Hydractinia echinata***	7	***Sertularia cupressina***	7
	Paguridae	5	*Paguridae*	8	***Alcyonium digitatum***	7	***Hydrallmania falcata***	6
	Macropodia spp.	5	*Hyas coarctatus*	8	***Serpulidae***	7	***Serpulidae***	6
	Alcyonidium diaphanum	5	*Ophiura* spp.	8	*Paguridae*	7	***Flustra foliacea***	6
	Vesicularia spinosa	5	***Alcyonium digitatum***	7	*Neptunea antiqua*	7	***Calycella syringa***	5
	Flustra foliacea	5	***Adamsia carciniopados***	7	*Colus gracilis*	7	***Abietinaria abietina***	5
	Gobiidae	5	***Balanus crenatus***	7	*Asterias rubens*	7	*Paguridae*	5
			Macropodia spp.	7	***Suberites domuncula***	6	*Calliostoma zizyphinum*	5
			Anomiidae	7	***Clytiahemisphaerica***	6	***Anomiidae***	5
			Psammechinus miliaris	7	***Epizoanthus incrustatus***	6	***Crisia eburnea***	5
					Hyas coarctatus	6	***Alcyonidium mytili***	5
							Escharella immersa	5
							Scrupocellaria scruposa	5
Number of samples		5		8		7		7
Average number of taxa (95% CL)	50 (29–71)		58 (46–70)		49 (43–55)		64 (53–75)	

stations were located, was not adequately covered. Nevertheless, some parallels are evident. For example, the two southern stations within group A of Figure 5 appear to represent extreme manifestations of the relatively species-poor assemblage Ia in this area (Fig. 4 in Kunitzer *et al*., 1992), characterized by coarser sediments in depths generally less than 30 m. The northernmost station within group D of Figure 5 has affinities with the finer-sediment assemblage IIIa of Kunitzer *et al*. (1992), occupying deeper water of 70–100 m adjacent to this coastline, which has also been described by Buchanan *et al*. (1978).

Parallels with groups C and E are less easy to draw, especially as stations within the latter group cross the latitudinal and depth boundaries for assemblage types identified by Kunitzer *et al*. (1992). Counterparts of North Sea assemblage types C and E are associated with inshore sediments of the Irish Sea, where they share attributes of the "shallow *Venus*" and *Abra* communities, described in these areas by Mackie *et al*. (1995). The description of an "*Abra alba–Pectinaria koreni*" community for the eastern Bay of Seine (Thiebaut *et al*., 1997) also matches the fauna frequently associated with inshore muddy sands of the Irish Sea. Offshore medium sandy stations in the Irish Sea (comprising group F in Fig. 5) fall within the zone of a "deep *Venus*" community interspersed among areas of hard ground, according to Mackie *et al*. (1995), and the species complement is broadly consistent with this definition. Elements of the fauna of group B stations in the English Channel and western approaches, for example, the presence of the green sea urchin *Echinocyamus pusillus*, are also indicative of coarser deposits, but there are few similarities with the work of Holme (1961, 1996), who employed an Anchor dredge for seabed sampling, and concentrated only on the larger mollusc and echinoderm species.

Concentrations of trace metals in sediments from the present study were relatively low, and there was no evidence of any adverse effects on the benthic fauna. Future work will include an evaluation of temporal trends in benthic populations at representative stations, which should facilitate the detection of any more subtle effects arising from anthropogenic activities. However, at present, it is evident that any contaminant effects are subsidiary to natural influences in accounting for the overall spatial distribution of assemblage types at intermediate and offshore NMP stations.

Multivariate analysis of the epifaunal data also revealed a number of similar assemblages inhabiting comparable environments across the large geographical range of the survey area. In other cases, biogeographical factors, such as increasing winter temperatures to the south and west, probably contributed to differences in the complement of species between assemblages, although intercorrelation among many of the environmental variables under consideration complicates the identification of causal influences. Nevertheless, substratum type appeared to be the main structuring force, with significantly enhanced diversity on coarser ground, as would be expected given the scope for colonization of this more complex habitat by a wider array of sessile species. Thus sandy areas of the southern North Sea were relatively impoverished, while samples with an enhanced gravelly or stony component generally supported the richest assemblages.

Inshore, the outflow from major estuaries was also an influential factor, with a distinctive assemblage type developing, irrespective of geographical location. Nearby muddy sand locations in the inner German Bight and NE Irish Sea were characterized by high densities of the brittle-star *Ophiura*, which matched the earlier findings of Riese and Bartsch (1990) and Rees *et al*. (1992), respectively, and indicates an enhanced food supply at these locations.

Within the English Channel, the distinction between a western and eastern gravelly fauna broadly corresponds with the boundary for "W Channel" species identified by Holme (1966), and may be linked to the west–east transition from deeper, stratified to shallower, mixed waters. From the results of photographic and acoustic surveys of the seabed, Holme and Wilson (1985) highlighted the importance of tidally-induced sand transport in determining the structure of benthic assemblages at a predominantly coarse-ground location SW of the Isle of Wight. Different successional states in the fauna encountered over short distances could be explained by the degree of abrasion or overburden. Species largely characteristic of "sub-climax" assemblage types were frequently encountered in Channel trawl samples during the present study, but the relatively large tow distances would be expected to integrate across small-scale patchiness and hence preclude finer-scale resolution.

Mackie *et al*. (1995) have recently reported on surveys of the macrobenthic infauna and epifauna of the southern Irish Sea. Multivariate analysis of the data revealed a similar species-rich offshore gravelly assemblage adjacent to the western Wales coastline (equivalent to the "stony" group of Fig. 8), trending to a muddy fauna in the Celtic Deep area. The sessile epifauna was relatively uniform in character throughout the survey area, with local topography and sediment type being more influential than geographical location.

For the North Sea area, comparable but more intensive surveys of the epifauna encompassing the region sampled in the present study have been reported by, for example, Dyer *et al*. (1983), Frauenheim *et al*. (1989), and Duineveld and van Noort (1990). Despite differences in sampling methodology, all three studies identified a broad division between a "northern" and "southern" fauna lying along the 50 m contour, i.e. the northern edge of the Dogger Bank, a finding paralleled by the outcome of the present survey. This division of the North Sea was similar to that proposed by Glemarec (1973), based upon thermal stability of the water column, and is supported by the recent work of Jennings *et al*. (1999) who identified a combination of depth and the differences between winter and summer bottom temperatures as factors which best explained trends in the North Sea epifauna sampled by 2 m beam trawl. In a more limited epifaunal survey of the southeastern and central North Sea, Kunitzer (1990) similarly distinguished between a northern and southern fauna, citing earlier observations on the boundary between stratified and mixed waters, and on the influence of different water masses (N Atlantic and Channel inflow to the northern and southern North Sea, respectively) in explanation. Kunitzer also identified a transitional assemblage, comparable with that of group 5 in Figure 8, occupying stations to the northeast of the Dogger Bank.

Duineveld and van Noort (1990) found no significant relationship between the distribution of epifaunal assemblages and that of sediment type, as measured by the percentage silt/clay content of grab samples. The authors speculated that the paucity of attached epifaunal species (such as anemones, ascidians, and sponges) in the southern North Sea might be due to the high intensity of commercial beam trawling. Collie *et al.* (1997) observed a reduction in bryozoans and hydroids at gravelly locations on Georges Bank (NW Atlantic) subject to disturbance by commercial dredging. While the present survey also found a low frequency of occurrence of sessile taxa in the southern North Sea, evidence of a causal relationship with fishing activity still remains inconclusive, since the prevailing sandy sediments would be expected to naturally restrict the occurrence of sessile taxa. On a wider scale, Jennings *et al*. (1999) found no relationship between epifauna distributions and fishing effort in the North Sea within ICES rectangles, but cautioned that the available information was too imprecise to establish whether or not commercial trawling had actually occurred across individual sampling stations.

Basford *et al*. (1989) sampled the epifauna of the northern North Sea using a 2 m Agassiz trawl with a 2 cm end-mesh, and identified depth and sediment characteristics as the principal determinants of assemblage type. Only the southernmost part of their grid overlapped with the present survey but, despite differences in sampling methodology, a number of larger taxa co-occurred, e.g. the anthozoans *Alcyonium digitatum*, *Hormathia digitata*, and *Bolocera tuediae*, the bryozoan *Flustra foliacea,* and ascidians, all indicative of a coarser sediment type in this area. In a comparison between the outcome of infaunal and epifaunal surveys in the northern North Sea, Basford *et al*. (1990) noted that the role of sediment type in determining the distribution of epifauna assemblages was apparently secondary to that of depth. However, they recognized the possibility that, at many stations, sediment samples from grabs may be inadequate to account for variation in the habitat along trawl tows.

International surveys of demersal fish have been conducted over a number of years under ICES auspices, and Rogers *et al*. (1998) report similar trends in species numbers to those of the epifauna (including fish) in the present study, namely lower species richness in the uniform sandy area of the SE North Sea, compared with the English Channel and the UK west coast, where a higher diversity is supported by the generally coarser substrata.

Infaunal and epifaunal surveys provide different, but complementary, perspectives on the benthic ecosystem. The benthic infauna can be reliably sampled by grabs, at least in soft sediment areas, and relationships with sediment type at the exact locality of grab penetration are easily explored through simultaneous subsampling of the material collected. However, the conventional sampling unit (0.1 m^2) is relatively small, and large numbers of samples may be required to adequately characterize a complex area. Trawl sampling of the epifauna has the advantage of providing an integrated sample over a much wider area than is feasible with ‘‘spot’’ sampling by grabs, and is an essential procedure for assessing the larger, rarer ‘‘megafaunal’’ taxa (McIntyre, 1978). Another advantage of trawling for larger organisms is that much of the material may be processed on deck immediately after collection. However, there are inherent uncertainties over the performance of the trawl at the seabed, especially across coarser substrata. Therefore, it is preferable to treat the data on a presence/absence or, at most, ‘‘semi-quantitative’’ basis in the absence of replication.

It must also be recognized that, as with demersal fish population surveys, the results from trawl sampling of the epifauna are ‘‘operationally determined’’, i.e. they are subject to systematic error or bias associated with the design specification (width of beam, mesh sizes of ‘‘belly’’ and ‘‘codend’’ and so on). Consistency in equipment design and in deployment practices is therefore essential, especially for the assessment of temporal trends.

One important operational problem is the tendency of the trawl to select for larger particles, where present. This may result in a bias toward the sampling of attached species, especially colonial hydroids and bryozoans. Thus the description of a ‘‘gravelly’’ fauna from a trawl tow may, in some circumstances, provide a misleading impression of the predominant sediment type (and faunal assemblage) along its entirety, especially when the data are treated on a presence/absence basis. Caution must therefore be exercised in drawing inferences about habitat type from the content of trawl tows, and an agreed procedure for describing faunal assemblages arrived at.

Useful working descriptions of the environment along trawl tows are difficult to establish, especially where a variety of sediment types are encountered. There is a need to assess the feasibility of developing an integrated and cost-effective measure of such variability, e.g. using combined acoustic and photographic techniques such as those employed by Holme and Wilson (1985), Sotheran *et al*. (1997), and Service and Magorrian (1997), as occasional "spot" samples of sediments using grabs may underestimate the complexity of the environment in many areas.

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