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# Distribution, diversity and abundance of epibenthic fauna in the North Sea

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The assemblages of attached and freeliving epibenthic species in the North Sea are described, based on analysis of samples collected with a small beam trawl. Clustering of survey sites based on the presence or absence of attached species indicated that three regions had characteristic assemblages: the northern North Sea, the central North Sea from 55 to 57°N and the southern North Sea. Clustering of sites based on counts of free-living epibenthic species also revealed that the sites formed three major groups but these corresponded to regions in the north-east North Sea, the northern and western central North Sea and the southern and eastern central North Sea. Species which contributed most to the similarity within and dissimilarity between groups were identified. The environmental factors which best accounted for the grouping of sites were depth, winter temperature and the temperature difference between winter and summer for attached species and depth and the temperature difference between winter and summer for free-living species. The species richness of attached and free-living epibenthic species was higher in the central and northern North Sea than in the south. The number of abundant (Hill's $N_1$) and very abundant (Hill's $N_2$) free-living species also increased from south to north.

## INTRODUCTION

The North Sea is one of the most environmentally diverse regions in the north-east Atlantic (Glémarec, 1973; Lee, 1980). The southern North Sea is characterized by shallow water, large seasonal temperature fluctuations, relatively low salinity, strong tidal currents and mobile substrata whereas the north is characterized by deep-water, small seasonal temperature fluctuations, relatively high salinity, low tidal currents and stable substrata (Lee, 1980; Lee & Ramster, 1981). Physical processes, in conjunction with the impact of anthropogenic activities are expected to have a profound influence on the distribution, diversity and abundance of epibenthic fauna (Anon., 1993; Basford et al., 1996; Bergman & Santbrink, 1994; Daan & Richardson, 1996; de Groot, 1984; Gislason, 1994).

Spatial patterns in some North Sea benthic communities were described over 50 y ago (Stephen, 1933, 1934). Glémarec (1973) reviewed the early literature and proposed that there were three distinct benthic regions in the North Sea, separated by the 0–60 m, 60–100 m and 100–200 m depth strata. The spatial scale and taxonomic resolution of early studies was rather limited but the distribution of both meiofauna and macrofauna was subsequently described at sites throughout the North Sea (Dyer et al., 1982, 1983; Frauenheim et al., 1989; Heip et al., 1992; Heip & Craeymeersch, 1995; Huys et al., 1992; Künitzer et al., 1992; Rees et al., 1999). Heip et al. (1992) and Heip & Craeymeersch (1995) sampled benthic macrofauna (retained by 1-mm sieve) using corers and grabs. The diversity and biomass of many taxonomic groups increased with increasing latitude. However, the data from this survey did not provide information on many of the larger free-living and attached epibenthic species because they were too scarce to be sampled effectively with corers or grabs.

The larger macrofauna have assumed increasing research importance because they are good indicators of fishing effects, may be sensitive to pollution and other anthropogenic impacts and because they provide much of the food for commercial fishes (Bergman & van Santbrink, 1994; Bromley & Kell, 1993; de Groot, 1984; de Groot & Lindeboom, 1994; Graham, 1955; Jennings & Kaiser, 1998). Larger macrofauna form a significant proportion of the by-catch in trawl fisheries (Camphuysen et al., 1993; Kaiser & Spencer, 1994) and the first large scale studies of macrofaunal distribution relied on examination of invertebrates retained as by-catch during fishery surveys (Dyer et al., 1982, 1983). These studies broadly supported the biogeographic zonation proposed by Glémarec (1973), showing a major split between the northern and southern North Sea fauna with further subdivisions in these regions. However, the large trawls used were poor for quantitative sampling, the majority of rare species were placed in broad taxonomic groups and even abundant groups such as the hermit crabs were not identified to species. Moreover, there was limited emphasis on attached groups such as hydroids and bryozoa despite their role in creating habitat complexity. Subsequently, Frauenheim et al. (1989) used a small beam trawl to sample the epibenthos. This was an important development because these trawls sampled the larger and rarer species more effectively and integrated small-scale patchiness. They also provided better quantitative abundance estimates than the larger otter trawls which

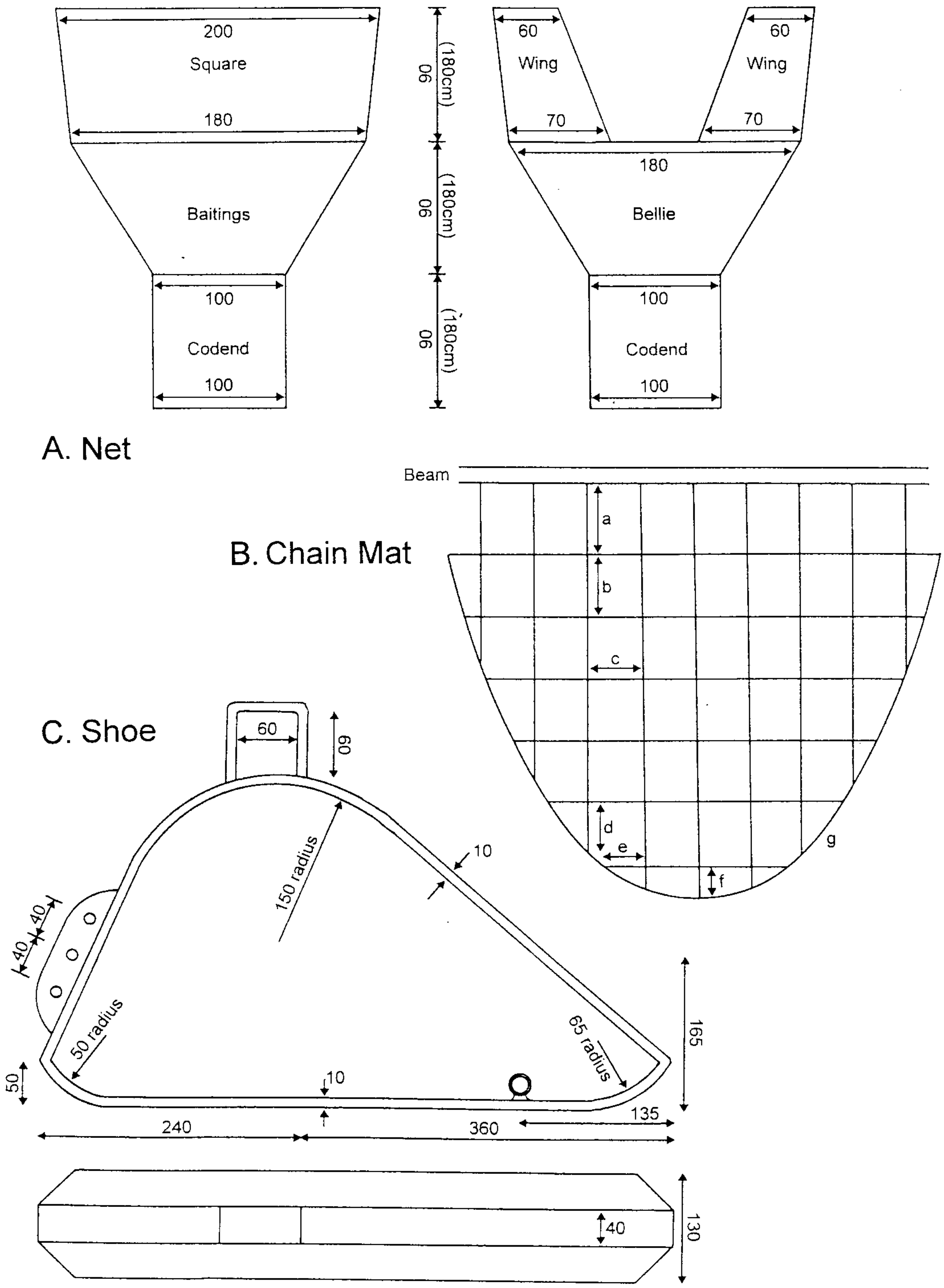


**Figure 1.** Design of 2 m beam trawl used for collection of epibenthic samples in the North Sea. The net (A) is constructed of 20-mm mesh and the measurements are given as number of meshes. The chain mat (B) is constructed of 3/8″ long-link galvanized chain and 3/8″ shackles. The first drop 'a' is 13 links, the second 'b' and subsequent drops are 11 links, the cross pieces 'c' are seven links and the groundchain is 156 links. Interdrops 'd', end cross pieces 'e' and bosom drops 'f' were all adjusted for the smoothest curve. The beam shoes (C) are constructed of galvanized mild steel and are welded to a 2 m beam of 60 mm square section.

have variable ground contact, sweep different areas when fished at different depths and catch so much benthos that subsampling is essential. However, the analyses of Frauenheim et al. (1989) were based on incomplete taxonomy (species grouped into genera or families) and few attached species were studied.

The aims of the present study were to describe assemblages of freeliving and attached epibenthic species in the North Sea based on a complete taxonomic analysis and to determine which species characterize these assemblages and the differences between them. In addition, we seek to identify those environmental variables which best account

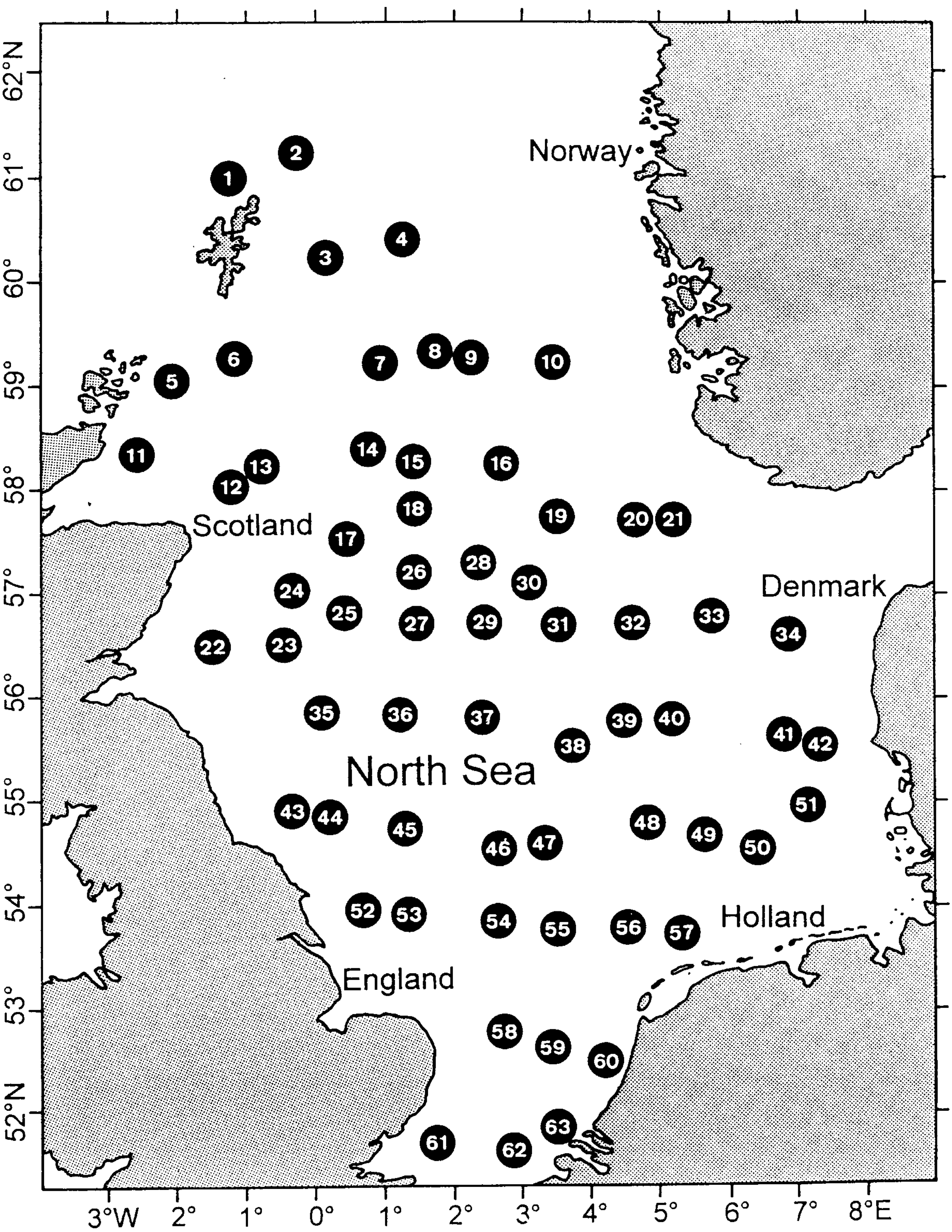


**Figure 2.** The location of sampling stations in the North Sea. The positions (as latitude–longitude) of these stations are given in Appendix 1.

for the distribution patterns of the epibenthos and to describe latitudinal trends in a range of diversity measures.

## MATERIALS AND METHODS

### *Sampling*

Epibenthic species were sampled using a 2 m beam trawl. The design was based on that developed by Riley et al. (1986) and Kaiser et al. (1994), but was modified to permit fishing in deeper water on a range of substrates from large RV and in rough seas. The wooden beam was replaced with a steel beam of 60 mm square section and a chain mat was added to exclude boulders from the net. Beam shoes were widened and strengthened and attached to the 2.9 m bridles using the central towing eyes (Figure 1). A 4 mm knotless mesh liner was fitted inside the net. The complete net weighed approximately 50 kg in air.



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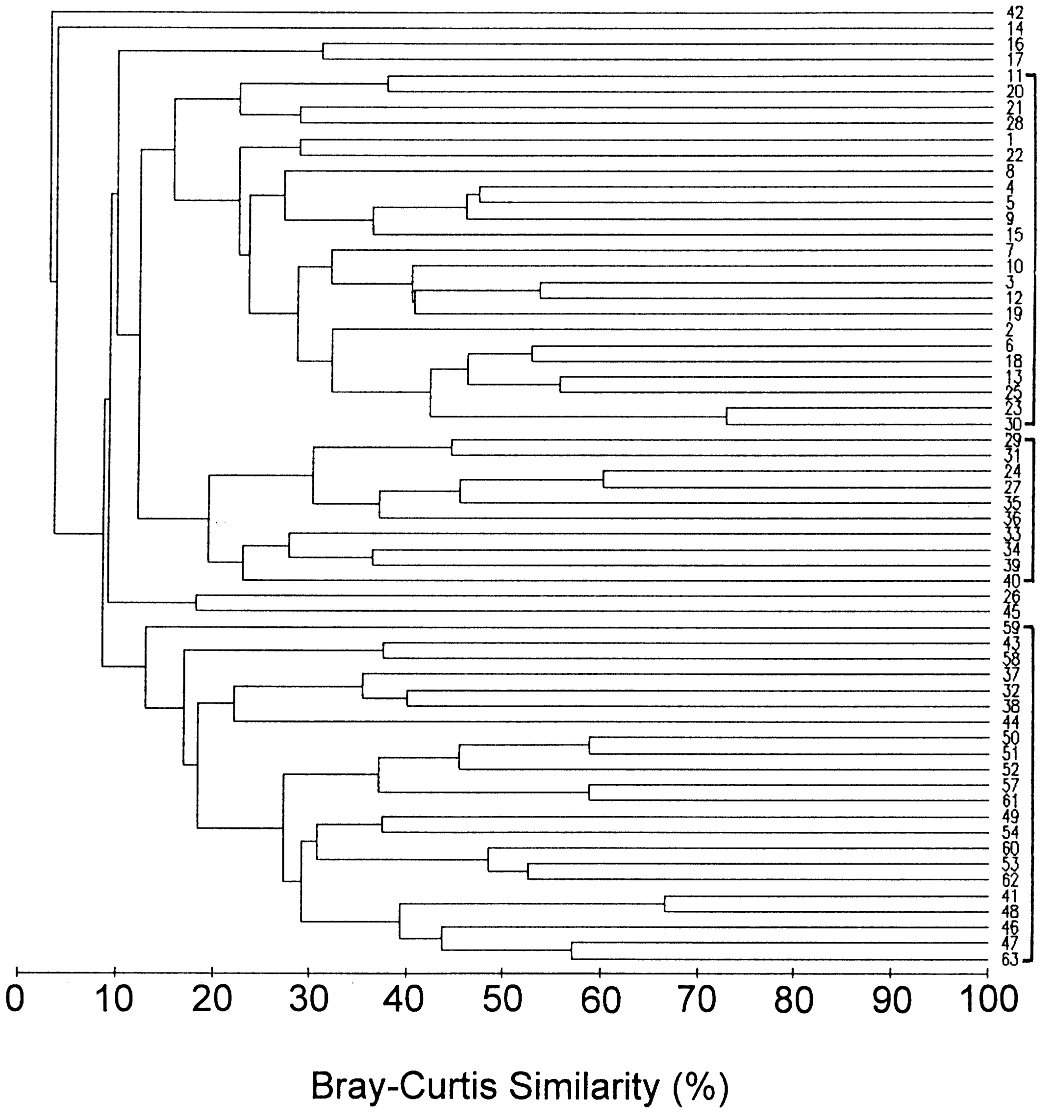


**Figure 3.** A dendrogram showing the grouping of sites formed by hierarchical classification analysis of presence–absence data for attached epibenthic species. The three main clusters are marked.

Tows were completed throughout the North Sea from 10 August to 20 November 1996. The beam trawl was fished from the stern ramp or starboard quarter of the RV 'Cirolana', using a warp length of three times the water depth. Each tow was 5 min in duration at a speed of 1 kn. The 5 min period was timed from the moment that the net contacted the seabed until the moment of hauling. Operational constraints meant that the distance covered had to be measured retrospectively, using sextant software linked to the ship's Differential Global Positioning System (DGPS).

Catches were sieved through 10 and 5 mm square mesh (internal measurement) and epibenthic species were sorted from the catch at each sieving. Those animals which could be identified to species level were counted at sea. All other material was preserved in 4% seawater formalin buffered with $3\,g\,l^{-1}$ sodium acetate and retained for identification at the University of Wales, Swansea. Encrusting taxa were only included if the area of the encrustation or colony exceeded $5\,mm^2$. Since it was impossible to meaningfully count or weigh many of the attached species they were recorded as present or absent.

### *Data analysis*

Species recorded during the survey were classified as infauna, attached epifauna (species which are anchored to shell, stone, rock or sand), free-living epifauna and fishes. The analyses were restricted to attached and free-living epifauna, and abundances of free-living epifauna were expressed as no. $m^{-2}$. Fishes were not included because many species are too fast and mobile to be sampled effectively by a small and slow moving beam trawl (Wardle, 1993). Infauna were not included because the extent to which the trawl samples within the substrate is highly dependent on the type of seabed.

An agglomerative hierachical clustering procedure was used to group sites on the basis of their attached and



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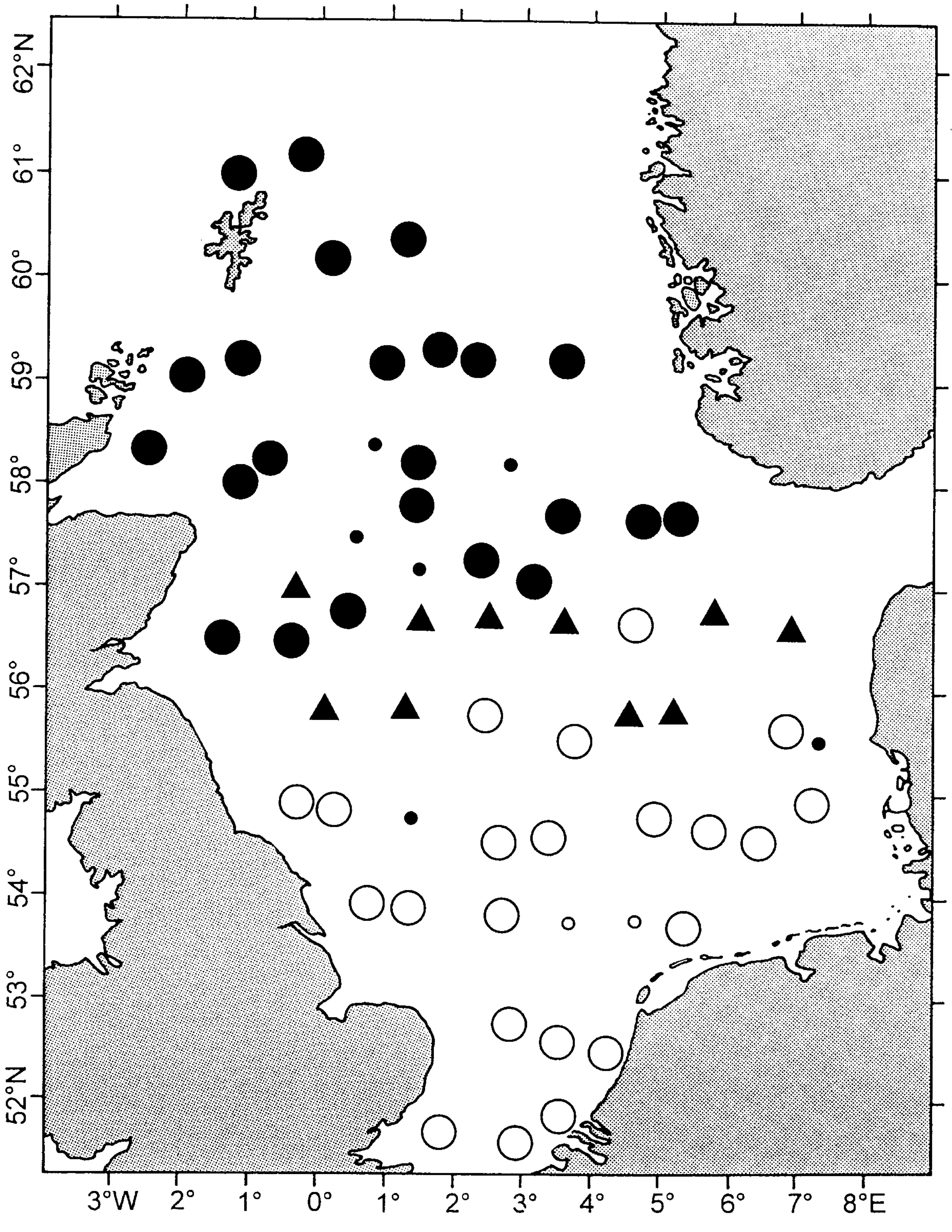


**Figure 4.** The location of sites which belong to northern (filled circles), central (triangles) and southern (open circles) clusters as identified by hierarchical classification analysis of presence–absence data for attached epibenthic species. Outlying sites are indicated with small fill circles and small open circles indicate the two sites where no attached species were caught.

free-living epifaunal communities. Count data for the free-living species were root-root transformed. The Bray–Curtis similarity measure was used to produce the similarity matrix and the similarity percentages test of Clarke (1993) was used to determine the contribution of each species to the similarity within, and dissimilarity between, groups identified by the cluster analysis. When the Bray–Curtis measure is applied to the

**Table 1.** *Attached species accounting for similarity within the North, Central and Southern North Sea clusters as identified by hierarchical classification analysis with presence–absence data. The terminology North, South and Central follows the location of site clusters shown in Figure 4 (North, fill circles; Central, triangles; South, open circles). Mean similarity is the mean similarity within the group and contribution is the contribution of individual species to the total similarity within the group.*

| Cluster Group | Mean Similarity (%) | Species | Contribution (%) |
|---|---|---|---|
| North | 15.8 | *Flustra foliacea* | 14.6 |
| | | *Hydrallmania falcata* | 12.2 |
| | | *Lafoea dumosa* | 8.2 |
| | | *Suberites ficus* | 7.4 |
| | | *Ciona intestinalis* | 6.0 |
| | | *Alcyonidium diaphanum* | 4.7 |
| Central | 25.5 | *Hydractinia echinata* | 34.2 |
| | | *Suberites ficus* | 13.5 |
| | | *Flustra foliacea* | 11.6 |
| | | *Alcyonidium diaphanum* | 11.0 |
| | | *Alcyonium digitatum* | 7.1 |
| | | *Epizoanthus papillosus* | 4.6 |
| South | 30.5 | *Hydractinia echinata* | 76.4 |
| | | *Electra pilosa* | 8.2 |
| | | *Hydrallmania falcata* | 4.8 |
| | | *Alcyonium digitatum* | 3.0 |
| | | *Flustra foliacea* | 2.7 |
| | | *Sertularia argentea* | 1.2 |

presence–absence data it collapses to the Czechanowski measure (e.g. Clifford & Williams, 1980).

The mean temperatures and current speeds at each site were calculated from Lee & Ramster (1981), depths were recorded at the time of the survey and 1995 international trawling effort in the ICES rectangle (boxes of 0.5° latitude by 1° longitude) into which each site fell was taken from Jennings et al. (1999). Sites were then clustered on the basis of the environmental characteristics: mean bottom temperature in winter, mean bottom temperature in summer, temperature stability (difference between summer and winter bottom temperatures), depth, maximum current speed during mean spring tides and fishing effort. In order to determine the extent to which abiotic variables were responsible for the observed groupings of the epibenthic communities from different sites, similarity matrices underlying biotic (epibenthic) and abiotic (environment) ordinations were compared using the 'Bioenv' procedure of Clarke & Ainsworth (1993). All multivariate analyses were conducted using 'Primer' software (Clarke & Warwick, 1994).

**Table 2.** *The six attached species which account for most of the total dissimilarity between North, Central and Southern North Sea clusters identified by hierarchical classification analysis. The terminology North, South and Central follows the location of site clusters shown in Figure 4 (North, fill circles; Central, triangles; South, open circles). Species are ordered according to their average contribution to the total average dissimilarity. Cluster names in parentheses indicate the cluster in which a given species was more abundant.*

| Group | Central | Dissimilarity (%) | South | Dissimilarity (%) |
|---|---|---|---|---|
| North | *Hydractinia echinata* (Central) | 6.1 | *Hydractinia echinata* (South) | 8.0 |
| | *Flustra foliacea* (Central) | 4.2 | *Flustra foliacea* (North) | 4.8 |
| | *Suberites ficus* (Central) | 4.1 | *Hydrallmania falcata* (North) | 4.7 |
| | *Alcyonidium diaphanum* (Central) | 4.1 | *Ciona intestinalis* (North) | 3.7 |
| | *Hydrallmania falcata* (North) | 3.5 | *Electra pilosa* (South) | 3.3 |
| | *Alcyonium digitatum* (Central) | 3.3 | *Alcyonium digitatum* (South) | 3.2 |
| Central | | | *Flustra foliacea* (Central) | 6.9 |
| | | | *Suberites ficus* (Central) | 6.8 |
| | | | *Alcyonidium diaphanum* (Central) | 6.7 |
| | | | *Hydractinia echinata* (Central) | 5.1 |
| | | | *Electra pilosa* (South) | 5.1 |
| | | | *Alcyonium digitatum* (Central) | 5.0 |

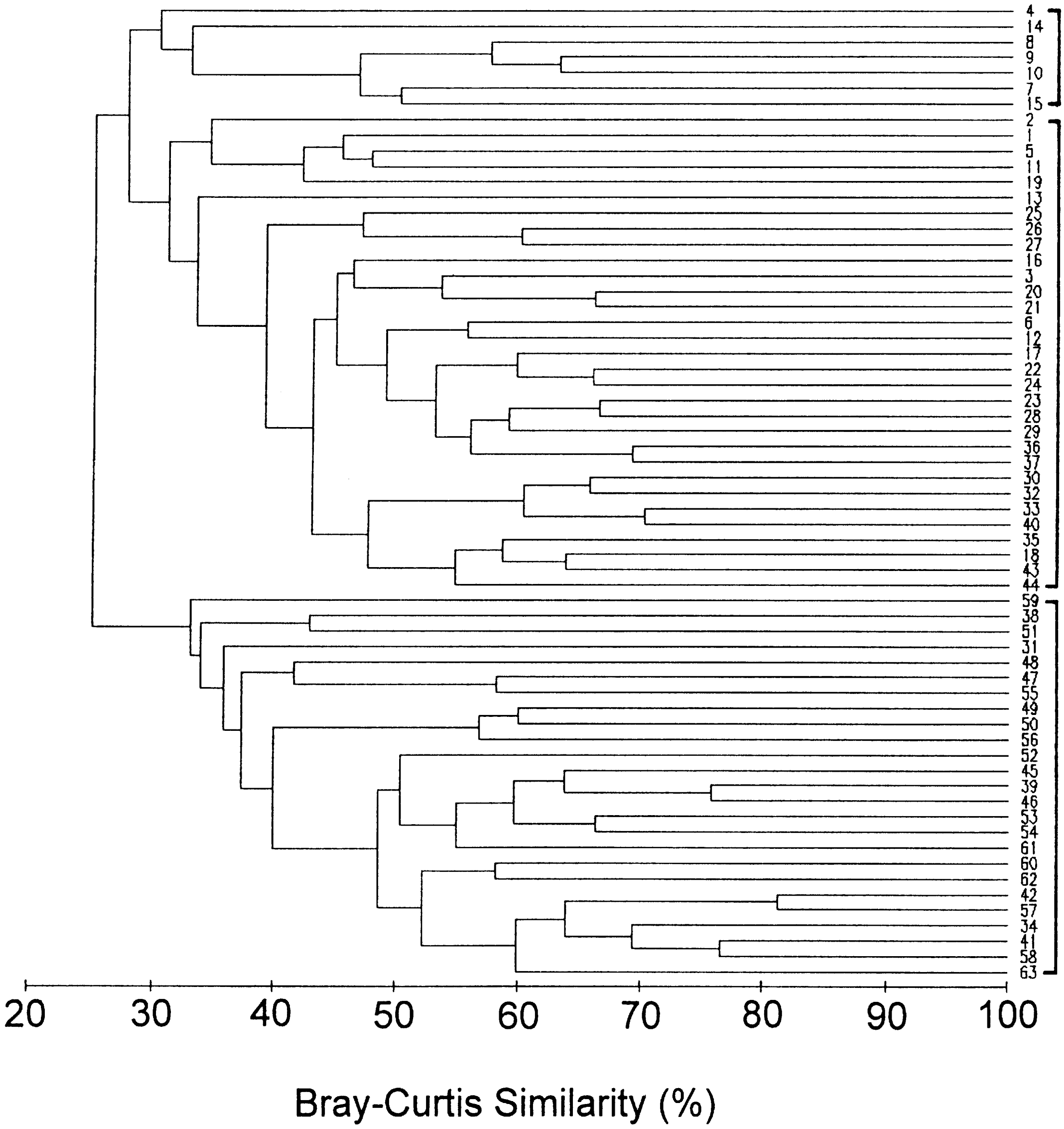


**Figure 5.** A dendrogram showing the grouping of sites formed by hierarchical classification analysis of root-root transformed counts of freeliving epibenthic species. The three main clusters are marked.

The diversity of the attached benthos at each site was expressed as species richness and the diversity of free-living epibenthos as the Hill numbers $N_1$ and $N_2$ (Hill, 1973). $N_1$ is effectively a measure of the number of abundant species in the sample and $N_2$ a measure of the number of very abundant species. Linear regression was used to test the significance of relationships between latitude and measures of diversity.

## RESULTS

Sixty-three sites were sampled (Appendix 1, Figure 2) and a total of 334 species were recorded. Ninety-four species were classified as attached and 120 as free-living epibenthos. Sixty-four attached and 76 free-living species were recorded at two or more sites (Appendices 2 & 3). The full dataset is too large to reproduce here, but copies may be obtained directly from S.Jennings@cefas.co.uk.

Clustering of sites based on the presence/absence of attached species (Figure 3) revealed that the sites formed three major groups. These corresponded to regions in the northern North Sea, the central North Sea from 55 to 57°N and the southern North Sea (Figure 4). No attached species were recorded at sites 55 and 56 (Figure 2). The similarity percentages analysis indicated those species that contributed to the similarity within (Table 1) and dissimilarity between (Table 2) groups. The abiotic variables which best grouped the sites in accordance with the biotic grouping were depth, winter temperature and the temperature difference between winter and summer ($p_w = 0.26$).

Free-living epibenthic species were clustered after removing the 33 species which accounted for $<1\%$ total abundance (Appendix 3). Clustering of sites based on counts of free-living epibenthic species (Figure 3) also revealed that the sites formed three major groups (Figure 5). These groups corresponded with regions in



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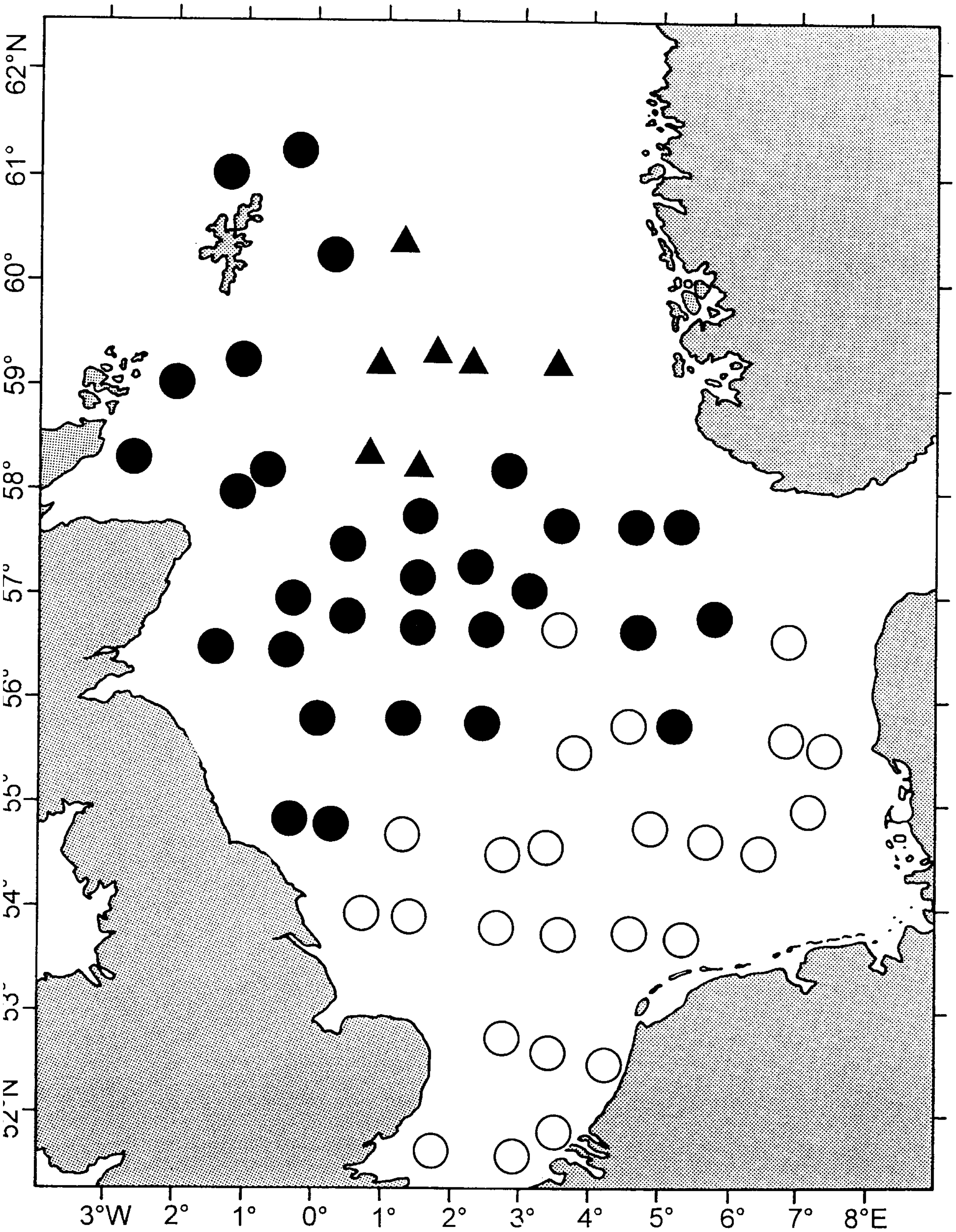


**Figure 6.** The location of sites which belong to northern (triangles), central (filled circles) and southern (open circles) clusters as identified by hierarchical classification analysis of root-root transformed counts of free-living epibenthic species.

the north-east North Sea, the northern and western central North Sea and the southern and eastern Central North Sea (Figure 6). It is clear that the location of these groupings is rather different from that based on the attached species. The similarity percentages analysis indicated those species that contributed to the similarity within (Table 3) and dissimilarity between (Table 4) groups. The abiotic variables which best grouped the



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**Table 3.** *The six free-living epibenthic species which account for most of the similarity within the North, Central and Southern North Sea clusters identified by hierarchical classification analysis with root-root transformed abundances. The terminology North, South and Central follows the location of site clusters shown in Figure 6 (North, triangles; Central, fill circles; South, open circles). Mean similarity is the mean similarity within the group and contribution is the contribution of individual species to the total similarity within the group.*

| Cluster Group | Mean Similarity (%) | Species | Contribution (%) |
|---|---|---|---|
| North | 40.7 | *Astropecten irregularis* | 30.5 |
| | | *Echinus acutus* | 20.0 |
| | | *Crangon allmanni* | 13.0 |
| | | *Aphrodite aculeata* | 5.2 |
| | | *Nephrops norvegicus* | 4.9 |
| | | *Pagurus pubescens* | 4.2 |
| Central | 40.5 | *Asterias rubens* | 14.8 |
| | | *Crangon allmanni* | 14.1 |
| | | *Pagurus bernhardus* | 11.4 |
| | | *Hyas coarctatus* | 10.3 |
| | | *Astropecten irregularis* | 7.3 |
| | | *Anapagurus laevis* | 6.9 |
| South | 42.7 | *Ophiura ophiura* | 23.5 |
| | | *Pagurus bernhardus* | 22.8 |
| | | *Asterias rubens* | 22.2 |
| | | *Liocarcinus holsatus* | 10.5 |
| | | *Astropecten irregularis* | 8.5 |
| | | *Psammechinus miliaris* | 2.6 |

sites in accordance with the biotic grouping were depth and the temperature difference between winter and summer ($p_w = 0.53$).

The species richness of attached and free-living epibenthic species was higher in the central and northern North Sea than in the south (Figure 7; $F=21.91$, df$=1,61$, $P<0.001$). The number of abundant (Hill's $N_1$) and very abundant (Hill's $N_2$) free-living species also increased significantly from south to north (Figure 7; Hill's $N_1$ $F=5.86$, df$=1,61$, $P=0.019$; Hill's $N_2$ $F=3.90$, df$=1,61$, $P=0.053$). Clearly, variations in tow length may affect measures of diversity and community structure. Mean tow length, although variable, was not significantly related to latitude ($F=0.24$, df$=1,61$, $P=0.628$).

**Table 4.** *The six species which account for most of the dissimilarity between North, Central and Southern North Sea clusters as identified by hierarchical classification analysis with root-root transformed abundances of free-living epibenthos. The terminology North, South and Central follows the location of site clusters shown in Figure 6 (North, triangles; Central, fill circles; South, open circles). Species are ordered according to their average contribution to the total average dissimilarity. Cluster names in parentheses indicate the cluster in which a given species was more abundant.*

| Group | Central | Dissimilarity (%) | South | Dissimilarity (%) |
|---|---|---|---|---|
| North | *Echinus acutus* (North) | 10.8 | *Echinus acutus* (North) | 11.5 |
| | *Astropecten irregularis* (North) | 6.2 | *Astropecten irregularis* (North) | 7.0 |
| | *Asterias rubens* (Central) | 5.2 | *Ophiura ophiura* (South) | 6.8 |
| | *Pagurus bernhardus* (Central) | 4.0 | *Asterias rubens* (South) | 6.1 |
| | *Anapagurus laevis* (Central) | 3.2 | *Pagurus bernhardus* (South) | 5.0 |
| | *Pandalus borealis* (North) | 3.2 | *Crangon allmanni* (North) | 4.9 |
| Central | | | *Ophiura ophiura* (South) | 7.6 |
| | | | *Astropecten irregularis* (South) | 5.5 |
| | | | *Crangon allmanni* (South) | 5.0 |
| | | | *Anapagurus laevis* (Central) | 4.6 |
| | | | *Hyas coarctatus* (Central) | 4.2 |
| | | | *Liocarcinus holsatus* (South) | 4.1 |

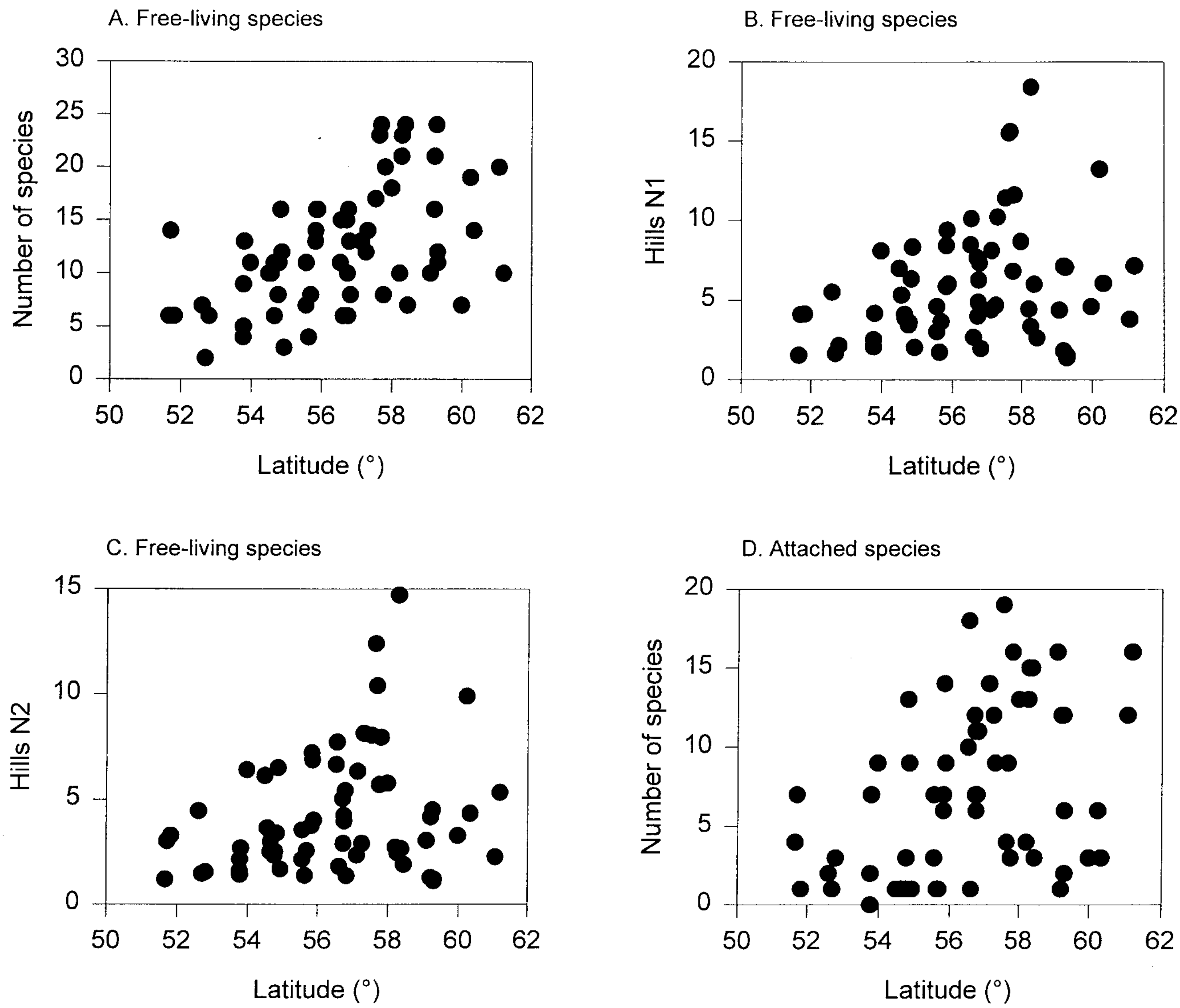


**Figure 7.** Relationships between the latitude of sampling and (A) number of free-living species, (B) Hill's $N_1$ for free-living species, (C) Hill's $N_2$ for free-living species and (D) the number of attached species.

## DISCUSSION

Previous large-scale studies of the North Sea macro-invertebrate fauna have tended to aggregate free-living and attached species and work with incomplete taxonomy. Frauenheim et al. (1989), for example, also sampled with a small beam trawl and recorded 95 species (all groups) at two or more of their 90 stations in a summer survey and 117 species at 109 stations in a winter survey. During the present survey we recorded 64 attached species and 76 epibenthic species at two or more sites, while using shorter tows at fewer stations than Frauenheim et al. (1989). Moreover, the shorter tow lengths used in the present survey ensured that catches did not need to be subsampled. Frauenheim et al. (1989) used very long tows of 1 nautical mile and the need to subsample would have biased presence–absence data. Given that so little is currently known about the distribution and ecology of many species recorded in our samples (P.J. Hayward, personal communication), the data provides a valuable indication of the distribution, and in some cases abundance, of many benthic species.

The analyses revealed gross differences between southern and northern North Sea assemblages, though it is hard to make direct comparisons with previous studies because our clusters were based on separate analyses for free-living and attached species. The Frauenheim et al. (1989) summer clusters and those of Dyer et al. (1983) also indicated a major north–south split. For free-living epibenthos, the species which characterise the southern North Sea assemblage are the sand dwelling *Ophiura ophiura*, *Pagurus bernhardus*, *Asterias rubens* and *Liocarcinus holsatus*. It is notable that the southern North Sea is intensively fished (Jennings et al., 1999) and that these species scavenge on animals damaged by beam trawls and discarded by trawlers (e.g. Kaiser & Spencer, 1996). In the central North Sea assemblage, the southern species are still present, but the shrimp *Crangon allmanni* and hermit crab *Anapagurus laevis* are increasingly dominant, in accordance with the findings of Dyer et al. (1983). In the northern North Sea, subarctic species such as the prawn *Pandalus borealis* and deep-water species such as the urchin *Echinus acutus* account for similarity within the assemblage. These species account for much of the dissimilarity between the northern North Sea fauna and that of the central and southern regions; another result that is largely in accordance with Dyer et al. (1983) and Frauenheim et al. (1989).

The occurrence of cold water species north of the Dogger bank and warm water species to the south has also been reported by Ursin (1960), Petersen (1977) and Heip & Craeymeersch (1995). However, our investigation of the environmental factors which account for the faunal distributions suggest that temperature variation and depth are better descriptors of this separation than absolute temperature. The stable temperatures in the deep areas of the northern North Sea result from the influx of deep Atlantic water. The southern regions, conversely, are affected by the variable influx of water from the English Channel (Lee, 1980). The relationship with depth is clearly not expected to be causal, rather, depth will correlate with other environmental factors that have not been measured. These could include light availability, nutrient supply, turbidity and stability of the substrate, all of which are known to affect the distribution and community structure of marine benthic species (e.g. Rhoads, 1974; Hall 1994).

A number of long-term changes in the North Sea macrobenthos have been reported and these have been attributed to fishing effects and environmental changes (Kroncke, 1990; Bergman & Hup, 1992; Bergman & van Santbrink, 1994). Benthic species have differential susceptibility to the effects of trawling. For example, on hard sandy substrates, *Asterias rubens* and *Pagurus bernhardus* survive after being trawled and discarded while sea urchins and some molluscs do not (review Jennings & Kaiser, 1998). Descriptions of changes in the macrofauna in the south-eastern North Sea from 1991–1994 (Holtmann et al., 1995) and longer term comparisons on the Dogger Bank between 1950–1954 and 1985–1987 (Kroncke, 1990) suggest that opportunistic short lived species have increased in abundance while the abundance of long living mollusca decreased. Trawling intensity has increased in the same period. However, spatial variations in trawling effort did not account for the distribution of benthos reported in the present study. This may reflect the overiding effect of broad oceanographic and depth effects on the structure of benthic communities or result from differences in the scale at which community and fishing effort data were recorded. The effort data included in the analysis represent the most complete data set for the North Sea and yet they are only recorded by ICES rectangle (boxes of 0.5° latitude by 1° longitude) (Jennings et al., 1999). Although differences in effort between rectangles exceed two orders of magnitude, it is not known whether the small area of seabed from which the benthic sample was taken has actually been fished. Addressing the large-scale impacts of fishing on benthic assemblages will not progress until fished areas can be accurately and reliably identified by, for example, the satellite tracking of all trawling vessels.

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**Appendix 1.** *Locations, biological and environmental data for the sampling sites in the North Sea. Temperature is the mean bottom temperature in February (winter) and August (summer). Effort is international trawl fishing effort in 1995 for the ICES statistical rectangle (boxes of 0.5° latitude by 1° longitude) in which the sampling site falls and current is the maximum tidal current speed during mean spring tides.*

| | Location | | Number of species | | | Temperature | | | |
|---|---|---|---|---|---|---|---|---|---|
| Site | Latitude | Longitude | Attached | Free-living | Depth (m) | Winter (°C) | Summer (°C) | Effort ($1000\ h\ y^{-1}$) | Current ($m\ s^{-1}$) |
| 1 | 061°03.41′N | 001°20.18′W | 12 | 20 | 150 | 7.5 | 10 | 2.82 | 0.51 |
| 2 | 061°11.21′N | 000°22.31′W | 16 | 10 | 162 | 7.5 | 9 | 12.09 | 0.51 |
| 3 | 060°13.99′N | 000°12.26′E | 6 | 19 | 146 | 7 | 8 | 9.07 | 0.32 |
| 4 | 060°19.57′N | 001°12.35′E | 3 | 14 | 149 | 7 | 7.5 | 4.96 | 0.32 |
| 5 | 059°05.50′N | 002°06.35′W | 16 | 10 | 78 | 7 | 11.5 | 4.12 | 1.03 |
| 6 | 059°15.78′N | 001°09.13′W | 12 | 24 | 120 | 7 | 8.5 | 3.47 | 0.51 |
| 7 | 059°12.69′N | 000°55.95′E | 12 | 21 | 117.5 | 6.5 | 7 | 8.39 | 0.32 |
| 8 | 059°18.14′N | 001°39.12′E | 2 | 11 | 116 | 6.5 | 7 | 1.59 | 0.26 |
| 9 | 059°17.89′N | 002°07.73′E | 6 | 12 | 126.5 | 6.5 | 7 | 3.27 | 0.19 |
| 10 | 059°12.63′N | 003°23.84′E | 1 | 16 | 185 | 7 | 7 | 2.48 | 0.19 |
| 11 | 058°22.12′N | 002°34.57′W | 15 | 24 | 48.5 | 6.5 | 11.5 | 5.58 | 0.51 |
| 12 | 057°59.33′N | 001°04.48′W | 13 | 18 | 119 | 6.5 | 10 | 15.87 | 0.51 |
| 13 | 058°12.85′N | 000°34.30′W | 4 | 10 | 106 | 6.5 | 9 | 19.25 | 0.39 |
| 14 | 058°26.89′N | 000°43.96′E | 3 | 7 | 149.5 | 6.5 | 7 | 30.15 | 0.32 |
| 15 | 058°16.07′N | 001°28.47′E | 13 | 21 | 110 | 6.5 | 6.5 | 9.23 | 0.26 |
| 16 | 058°16.87′N | 002°43.66′E | 15 | 23 | 73.5 | 6.5 | 6.5 | 4.69 | 0.26 |
| 17 | 057°32.24′N | 000°26.49′E | 19 | 17 | 93 | 6.5 | 8 | 15.25 | 0.32 |
| 18 | 057°48.22′N | 001°11.85′E | 16 | 20 | 90 | 6.5 | 7 | 2.35 | 0.32 |
| 19 | 057°45.32′N | 003°34.20′E | 3 | 8 | 66 | 6 | 7 | 7.99 | 0.19 |
| 20 | 057°40.72′N | 004°43.21′E | 9 | 24 | 86 | 6 | 7 | 2.81 | 0.13 |
| 21 | 057°38.33′N | 005°03.71′E | 4 | 23 | 91.5 | 6 | 7 | 2.62 | 0.13 |
| 22 | 056°31.44′N | 001°22.11′W | 10 | 11 | 68.5 | 6 | 11 | 3.42 | 0.51 |
| 23 | 056°33.00′N | 000°25.10′W | 18 | 15 | 75 | 6.5 | 9 | 5.4 | 0.39 |
| 24 | 057°07.03′N | 000°20.80′W | 14 | 13 | 90 | 6.5 | 10 | 5.4 | 0.39 |
| 25 | 056°49.15′N | 000°19.37′E | 11 | 8 | 85.5 | 6.5 | 8 | 7.6 | 0.32 |
| 26 | 057°15.41′N | 001°33.50′E | 12 | 12 | 97 | 6.5 | 7 | 1.36 | 0.32 |
| 27 | 056°45.88′N | 001°24.63′E | 6 | 16 | 97.6 | 6.5 | 7 | 1.63 | 0.26 |
| 28 | 057°18.66′N | 002°28.88′E | 9 | 14 | 82 | 6 | 6.5 | 1.82 | 0.26 |
| 29 | 056°42.69′N | 002°27.10′E | 12 | 15 | 74 | 6 | 6.5 | 2.25 | 0.19 |
| 30 | 057°08.41′N | 003°08.59′E | 14 | 13 | 66.5 | 6 | 7 | 4.91 | 0.19 |
| 31 | 056°44.67′N | 003°40.23′E | 11 | 6 | 59 | 5.5 | 7 | 2.8 | 0.19 |
| 32 | 056°43.92′N | 004°33.60′E | 7 | 10 | 57 | 5.5 | 7.5 | 3.07 | 0.13 |
| 33 | 056°47.44′N | 005°43.51′E | 7 | 13 | 57 | 5 | 9 | 7.12 | 0.13 |
| 34 | 056°36.54′N | 006°49.15′E | 1 | 6 | 40 | 4.5 | 11 | 10.28 | 0.13 |
| 35 | 055°53.26′N | 000°05.17′E | 9 | 16 | 87 | 6.5 | 7.5 | 3.73 | 0.39 |
| 36 | 055°50.96′N | 001°09.03′E | 14 | 16 | 77.9 | 6 | 7 | 2.82 | 0.39 |
| 37 | 055°49.80′N | 002°26.72′E | 7 | 14 | 82 | 5 | 7 | 2.17 | 0.32 |
| 38 | 055°33.31′N | 003°45.16′E | 3 | 7 | 36 | 5.5 | 11 | 6.27 | 0.32 |
| 39 | 055°33.45′N | 004°31.70′E | 7 | 11 | 33 | 5.5 | 10 | 9.44 | 0.32 |
| 40 | 055°49.29′N | 005°17.43′E | 6 | 13 | 55 | 5 | 10 | 4.16 | 0.32 |
| 41 | 055°40.87′N | 006°45.31′E | 1 | 8 | 37 | 4 | 13.5 | 8.13 | 0.39 |
| 42 | 055°37.79′N | 007°10.65′E | 1 | 4 | 30 | 3 | 15 | 13.26 | 0.39 |
| 43 | 054°51.85′N | 001°16.38′W | 9 | 12 | 73 | 6.5 | 9 | 40.93 | 0.77 |
| 44 | 054°49.63′N | 000°13.72′E | 13 | 16 | 83 | 6 | 8.5 | 18.06 | 0.51 |
| 45 | 054°46.66′N | 001°17.41′E | 3 | 11 | 37 | 5.5 | 12 | 7.34 | 0.51 |
| 46 | 054°29.23′N | 002°42.45′E | 1 | 10 | 27.5 | 5 | 14 | 9 | 0.45 |
| 47 | 054°39.38′N | 003°20.35′E | 1 | 6 | 42 | 5.5 | 13 | 8.01 | 0.45 |
| 48 | 054°45.40′N | 004°53.72′E | 1 | 8 | 44.6 | 5.5 | 13 | 19.12 | 0.39 |
| 49 | 054°38.47′N | 005°37.31′E | 1 | 11 | 44 | 5 | 13.5 | 16.3 | 0.45 |
| 50 | 054°33.29′N | 006°22.67′E | 1 | 10 | 40 | 5 | 14.5 | 46.19 | 0.51 |
| 51 | 054°55.64′N | 007°06.02′E | 1 | 3 | 32 | 3.5 | 15 | 13.26 | 0.51 |
| 52 | 053°59.05′N | 000°50.07′E | 3 | 7 | 51 | 6 | 14 | 17.75 | 1.03 |
| 53 | 053°58.35′N | 001°16.14′E | 9 | 11 | 41 | 6 | 14 | 6.2 | 0.77 |
| 54 | 053°48.29′N | 002°34.06′E | 7 | 13 | 32.5 | 5 | 14.5 | 17.3 | 0.51 |
| 55 | 053°46.23′N | 003°33.71′E | 0 | 4 | 38.5 | 5 | 15 | 17.3 | 0.51 |
| 56 | 053°46.55′N | 004°29.68′E | 0 | 9 | 41.4 | 4.5 | 15.5 | 44.62 | 0.51 |
| 57 | 053°46.53′N | 005°22.48′E | 2 | 5 | 32.2 | 5 | 16 | 27.91 | 0.77 |
| 58 | 052°47.96′N | 002°43.51′E | 3 | 6 | 40.3 | 5.5 | 16.5 | 18.72 | 1.03 |
| 59 | 052°42.10′N | 003°24.99′E | 1 | 2 | 28.5 | 5.5 | 17 | 31.52 | 0.77 |
| 60 | 052°36.31′N | 004°12.61′E | 2 | 7 | 24 | 5 | 17 | 36.01 | 0.77 |
| 61 | 051°42.84′N | 001°44.25′E | 7 | 14 | 30.4 | 6 | 17 | 22.75 | 1.03 |
| 62 | 051°39.67′N | 002°50.96′E | 4 | 6 | 35.5 | 5.5 | 17 | 33.17 | 0.77 |
| 63 | 051°49.15′N | 003°38.98′E | 1 | 6 | 23.3 | 5 | 17 | 65.94 | 1.03 |

**Appendix 2.** *Attached species recorded in survey. Ubiquity indicates the proportion of sites at which the species was recorded. Species are listed in taxonomic order.*

| Species | Ubiquity (%) | Species | Ubiquity (%) |
|---|---|---|---|
| *Suberites ficus* (Linnaeus, 1767) | 30.2 | *Caryophyllia smithii smithii* (Stokes & Broderip, 1828) | 4.8 |
| *Axinella infundibuliformis* (Linnaeus, 1758) | 1.6 | *Ditrupa arietina* (O.F. Mueller, 1776) | 4.8 |
| *Stelligera stuposa* (Ellis & Solander, 1786) | 1.6 | *Hydroides norvegica* Gunnerus, 1768 | 9.5 |
| *Haliclona oculata* (Pallas, 1766) | 3.2 | *Filograna implexa* Berkeley, 1827 | 1.6 |
| *Tubularia indivisa* Linnaeus, 1758 | 14.3 | *Scalpellum scalpellum* (Linnaeus, 1767) | 4.8 |
| *Tubularia larynx* Ellis & Solander, 1786 | 4.8 | *Verruca stroemia* (O.F. Mueller, 1776) | 12.7 |
| *Eudendrium rameum* (Pallas, 1766) | 3.2 | *Balanus crenatus* Brugiere, 1789 | 3.2 |
| *Bougainvillia britannica* (Forbes, 1841) | 3.2 | *Modiolula phaseolina* (Philippi, 1844) | 1.6 |
| *Dicoryne conybeari* (Allman, 1864) | 6.4 | *Anomia ephippium* Linnaeus, 1758 | 6.4 |
| *Dicoryne conferta* (Alder, 1857) | 3.2 | *Turtonia minuta* (Fabricius, 1780) | 1.6 |
| *Hydractinia echinata* (Fleming, 1828) | 50.8 | *Tubilipora liliacea* (Pallas, 1766) | 3.2 |
| *Podocoryne* spp.'M. Sars, 1846 | 1.6 | *Lichenopora verrucaria* (Fabricius, 1780) | 3.1 |
| *Podycoryne borealis* (Mayer, 1900) | 1.6 | *Alcyonidium albidum* Alder, 1857 | 4.8 |
| *Podocoryne carnea* M. Sars, 1846 | 3.2 | *Alcyonidium diaphanum* (Hudson, 1762) | 27.0 |
| *Obelia bidentata* Clarke, 1875 | 1.6 | *Alcyonidium parasiticum* (Fleming, 1828) | 4.8 |
| *Obelia longissima* (Pallas, 1766) | 1.6 | *Alcyonidium* sp.nov. Lamouroux, 1813 | 9.5 |
| *Filellum serpens* (Hassall, 1848) | 9.5 | *Eucratea loricata* (Linnaeus, 1758) | 17.5 |
| *Lafoea dumosa* (Fleming, 1828) | 19.1 | *Electra pilosa* (Linnaeus, 1767) | 14.3 |
| *Halecium beanii* (Johnston, 1838) | 1.6 | *Flustra foliacea* (Linnaeus, 1758) | 38.1 |
| *Halecium labrosum* Alder, 1859 | 3.2 | *Carbasea carbasea* (Ellis & Solander, 1786) | 1.6 |
| *Halecium muricatum* (Ellis & Solander, 1786) | 6.4 | *Securiflustra securifrons* (Pallas, 1766) | 11.1 |
| *Halecium tenellum* Hincks, 1861 | 1.6 | *Callopora craticula* (Alder, 1856) | 1.6 |
| *Abietinaria abietina* (Linnaeus, 1758) | 17.5 | *Callopora dumerilii* (Audouin, 1826) | 1.6 |
| *Abietinaria filicula* (Ellis & Solander, 1786) | 7.9 | *Tegella unicornis* (Fleming, 1828) | 3.2 |
| *Amphisbetia operculata* (Linnaeus, 1758) | 1.6 | *Amphiblestrum auritum* (Hincks) | 1.6 |
| *Diphasia pinaster* Hincks, 1868 | 1.6 | *Amphiblestrum flemingii* (Busk, 1854) | 1.6 |
| *Hydrallmania falcata* (Linnaeus, 1758) | 34.9 | *Dendrobeania fruticosa* (Packard, 1863) | 1.6 |
| *Sertularella gayi* (Lamouroux, 1821) | 3.2 | *Dendrobeania murrayana* (Johnston, 1847) | 9.5 |
| *Sertularella polyzonias* (Linnaeus, 1758) | 1.6 | *Scrupocellaria scrupea* Busk, 1852 | 1.6 |
| *Sertularia argentea* Linnaeus, 1758 | 11.1 | *Tricellaria ternata* (Ellis & Solander, 1786) | 9.5 |
| *Sertularia cupressina* Linnaeus, 1758 | 3.2 | *Cellaria fistulosa* (Linnaeus, 1758) | 3.2 |
| *Tamarisca tamarisca* (Linnaeus, 1758) | 3.2 | *Escharella ventricosa* (Hassall, 1842) | 1.6 |
| *Thuiaria thuja* (Linnaeus, 1758) | 3.2 | *Porella compressa* (Sowerby, 1805) | 1.6 |
| *Halopteris catharina* (Johnston, 1833) | 1.6 | *Porella concinna* (Busk, 1854) | 1.6 |
| *Nemertesia antennina* (Linnaeus, 1758) | 1.6 | *Palmiskenea lorea* (Alder, 1864) | 1.6 |
| *Nemertesia ramosa* Lamouroux, 1816 | 4.8 | *Stomachetosella sinuosa* (Busk, 1860) | 1.6 |
| *Clytia hemisphaerica* (Linnaeus, 1758) | 9.5 | *Schizomavella linearis* (Hassall, 1841) | 3.2 |
| *Clytia paulensis* (Vanhoffen, 1910) | 1.6 | *Turbicellepora avicularis* (Hincks, 1860) | 11.1 |
| *Alcyonium digitatum* Linnaeus, 1758 | 28.6 | *Omalosecosa ramulosa* (Linnaeus, 1767) | 3.2 |
| *Pennatula phosphorea* Linnaeus, 1758 | 11.1 | *Buskea dichotoma* (Hincks, 1868) | 4.8 |
| *Epizoanthus papillosus* (Dueben & Koren, 1847) | 25.4 | *Reteporella beaniana* (King, 1846) | 3.2 |
| *Actinauge richardi* (Marion, 1882) | 7.9 | *Ciona intestinalis* (Linnaeus, 1767) | 12.7 |
| *Bolocera tuediae* (Johnston, 1832) | 7.9 | *Ascidiella aspersa* (O.F. Mueller, 1776) | 3.2 |
| *Metridium senile* (Linnaeus, 1761) | 3.2 | *Ascidiella scabra* (O.F. Mueller, 1776) | 20.6 |
| *Sagartia elegans* (Dalyell, 1848) | 1.6 | *Ascidia virginea* O.F. Mueller, 1776 | 9.5 |
| *Hormathia digitata* (O.F.Mueller, 1776) | 11.1 | *Polycarpa pomaria* (Savigny, 1816) | 1.6 |
| *Adamsia carciniopados* (Otto, 1823) | 7.9 | *Caryophyllia smithii clavus* (Stokes & Broderip, 1828) | 3.2 |

**Appendix 3.** *Free-living species recorded in the survey. Ubiquity indicates the proportion of sites at which the species was recorded. Species contributing to >1% of the total abundance, and included in the classification analysis, are indicated with an asterisk. Species are listed in taxonomic order.*

| Species | Ubiquity (%) | Abundance (* if >1%) |
|---|---|---|
| *Aphrodita aculeata* Linnaeus, 1758 | 33.3 | * |
| *Laetmonice filicornis* Kinberg, 1855 | 1.6 | * |
| *Eunoe nodosa* (M. Sars, 1861) | 3.2 | * |
| *Gattyana cirrosa* (Pallas, 1766) | 1.6 | |
| *Harmothoe impar* (Johnston, 1839) | 3.2 | * |
| *Lepidonotus squamatus* (Linnaeus, 1758) | 1.6 | |
| *Lophogaster typicus* M. Sars, 1857 | 1.6 | * |
| *Schistomysis ornata* (G.O. Sars, 1864) | 1.6 | |
| *Epimeria cornigera* (Fabricius, 1779) | 3.2 | |
| *Menigrates obtusifrons* (Boeck, 1861) | 1.6 | |
| *Tmetonyx cicada* (Fabricius, 1780) | 4.8 | |
| *Ampelisca macrocephala* Liljeborg, 1852 | 3.2 | |
| *Ampelisca spinipes* Boeck, 1861 | 3.2 | * |
| *Maera loveni* (Bruzelius, 1859) | 1.6 | * |
| *Melita dentata* (Kroyer, 1842) | 3.2 | * |
| *Rocinela damnoniensis* Leach, 1815 | 1.6 | |
| *Cirolana borealis* Liljeborg, 1851 | 11.1 | * |
| *Astacilla longicornis* (Sowerby, 1806) | 3.2 | * |
| *Spirontocaris lilljeborgi* (Danielssen, 1859) | 25.4 | * |
| *Processa canaliculata* Leach, 1815 | 7.9 | * |
| *Dichelopandalus bonnieri* Caullery, 1896 | 3.2 | * |
| *Pandalina brevirostris* (Rathke, 1837) | 4.8 | * |
| *Pandulus borealis* Kroyer, 1838 | 7.9 | * |
| *Pandalus montagui* Leach, 1814 | 30.2 | * |
| *Crangon allmanni* Kinahan, 18577 | 1.4 | * |
| *Crangon crangon* (Linnaeus, 1758) | 4.8 | * |
| *Crangon bispinosus neglecta* (Hailstone, 1835) | 3.2 | * |
| *Crangon echinulatus* (M. Sars, 1861) | 1.6 | |
| *Pontophilus spinosus* (Leach, 1815) | 11.1 | |
| *Crangon trispinosus* (Hailstone, 1835) | 3.2 | * |
| *Crangon sculptus* (Bell) | 1.6 | |
| *Nephrops norvegicus* (Linnaeus, 1758) | 9.5 | * |
| *Anapagurus chiroacanthus* (Liljeborg, 1856) | 1.6 | |
| *Anapagurus hyndmanni* (Bell, 1845) | 3.2 | * |
| *Anapagurus laevis* (Bell, 1845) | 39.7 | * |
| *Pagurus alatus* Fabricius, 1775 | 3.2 | |
| *Pagurus bernhardus* (Linnaeus, 1758) | 79.4 | * |
| *Pagurus prideauxi* Leach, 1815 | 19.1 | * |
| *Pagurus pubescens* Kroyer, 1838 | 30.2 | * |
| *Galathea* sp. Fabricius, 1793 | 1.6 | |
| *Galathea dispersa* Bate, 1859 | 9.5 | |
| *Galathea squamifera* Leach, 1814 | 1.6 | * |
| *Munida rugosa* (Fabricius, 1775) | 1.6 | * |
| *Ebalia cranchii* Leach, 1817 | 11.1 | * |
| *Ebalia tuberosa* (Pennant, 1777) | 4.8 | * |
| *Inachus dorsettensis* (Pennant, 1777) | 1.6 | * |
| *Macropodia linaresi* Forest & Z Alvarez, 1964 | 3.2 | * |
| *Macropodia rostrata* (Linnaeus, 1761) | 12.7 | * |
| *Macropodia tenuirostris* (Leach, 1814) | 9.5 | * |
| *Hyas coarctatus* Leach, 1815 | 55.6 | * |
| *Corystes cassivelaunus* (Pennant, 1777) | 20.6 | * |
| *Atelecyclus rotundatus* (Olivi, 1792) | 6.4 | * |
| *Liocarcinus arcuatus* (Leach, 1814) | 1.6 | |
| *Liocarcinus pusillus* (Leach, 1815) | 1.6 | * |
| *Liocarcinus depurator* (Linnaeus, 1758) | 9.5 | * |
| *Liocarcinus holsatus* (Fabricius, 1798) | 47.6 | * |
| *Pilumnus hirtellus* (Linnaeus, 1761) | 1.6 | |
| *Nymphon gracile* Leach, 1814 | 3.2 | * |
| *Pycnogonum littorale* (Strom, 1762) | 11.1 | * |
| *Emarginula fissura* (Linnaeus, 1758) | 1.6 | |
| *Calliostoma zizyphinum* (Linnaeus, 1758) | 1.6 | |
| *Turritella communis* Risso, 1826 | 7.9 | * |
| *Aporrhais pespelecani* (Linnaeus, 1758) | 3.2 | * |
| *Aporrhais serresianus* (Michaud, 1828) | 1.6 | * |
| *Trivia arctica* (Pulteney, 1799) | 1.6 | |
| *Velutina velutina* (O.F. Mueller, 1776) | 6.4 | * |
| *Polinices pulchellus* (Risso, 1826) | 1.6 | * |
| *Euspira catenas* (da Costa, 1778) | 11.1 | * |
| *Polinices fuscus* (de Blainville, 1825) | 3.2 | * |
| *Polinices montagui* (Forbes, 1838) | 1.6 | * |
| *Colus gracilis* (da Costa, 1778) | 34.9 | * |
| *Colus islandicus* (Mohr, 1786) | 6.4 | * |
| *Colus jeffreysianus* (Fischer, 1868) | 4.8 | * |
| *Acteon tornatilis* (Linnaeus, 1758) | 3.2 | * |
| *Neptunea antiqua* (Linnaeus, 1758) | 22.2 | * |
| *Buccinum undatum* Linnaeus, 1758 | 36.5 | * |
| *Dendronotus frondosus* (Ascanius, 1774) | 1.6 | |
| *Archidoris pseudoargus* (Rapp, 1827) | 1.6 | * |
| *Aeolidia papillosa* (Linnaeus, 1761) | 1.6 | |
| *Facelina bostoniensis* (Couthouy, 1838) | 1.6 | * |
| *Nucula nitidosa* Winckworth, 1930 | 6.4 | * |
| *Heteranomia squamula* (Linnaeus, 1758) | 3.2 | * |
| *Aequipecten opercularis* (Linnaeus, 1758) | 3.2 | * |
| *Pecten maximus* (Linnaeus, 1758) | 1.6 | |
| *Palliolum tigerinum* (O.F. Mueller, 1776) | 1.6 | |
| *Palliolum striatum* (O.F. Mueller, 1776) | 1.6 | |
| *Pseudamussium septemradiatum* (O.F. Mueller, 1776) | 7.9 | * |
| *Astarte sulcata* (da Costa, 1778) | 12.7 | * |
| *Arctica islandica* (Linnaeus, 1767) | 1.6 | |
| *Corbula gibba* (Olivi, 1792) | 4.8 | * |
| *Hiatella arctica* (Linnaeus, 1767) | 4.8 | * |
| *Cuspidaria cuspidata* (Olivi, 1792) | 1.6 | * |
| *Sepiola atlantica* Orbigny, 1840 | 7.9 | * |
| *Rossia macrosoma* (delle Chiaje, 1830) | 1.6 | * |
| *Eledone cirrhosa* (Lamarck, 1798) | 1.6 | |
| *Astropecten irregularis* (Pennant, 1777) | 65.1 | * |
| *Luidia sarsi* Dueben & Koren, 1846 | 23.8 | * |
| *Pontaster tenuispinus* (Dueben & Koren, 1846) | 1.6 | * |
| *Hippasteria phrygiana* (Parelius, 1768) | 1.6 | |
| *Porania pulvillus* (O.F. Mueller, 1776) | 1.6 | |
| *Henricia sanguinolenta* (O.F. Mueller, 1776) | 6.4 | * |
| *Stichastrella rosea* (O.F. Mueller, 1776) | 3.2 | * |
| *Asterias rubens* Linnaeus,1758 | 82.5 | * |
| *Ophiura albida* Forbes, 1839 | 3.2 | * |
| *Ophiura ophiura* (Linnaeus, 1758) | 61.9 | * |
| *Ophiura robusta* (Ayres, 1851) | 1.6 | |
| *Ophiura sarsi* Luetken, 1858 | 4.8 | * |
| *Ophiura affinis* Luetken, 1858 | 9.5 | * |
| *Ophiothrix fragilis* (Abildgaard, 1789) | 12.7 | * |
| *Ophiopholis aculeata* (Linnaeus, 1766) | 4.8 | * |
| *Amphiura brachiata* (Montagu, 1804) | 1.6 | |
| *Amphiura chiajei* Forbes, 1845 | 3.2 | * |
| *Amphiura filiformis* (O.F. Mueller, 1776) | 1.6 | |
| *Psammechinus miliaris* (Gmelin, 1778) | 14.3 | * |
| *Echinus acutus* Lamarck, 1816 | 15.9 | * |
| *Echinus elegans* Dueben & Koren, 1843 | 7.9 | * |
| *Strongylocentrotus droebachiensis* (O.F. Mueller, 1776) | 9.5 | * |
| *Leptopentacta elongata* (Dueben & Koren, 1844) | 1.6 | |
| *Ocnus lacteus* (Forbes & Goodsir, 1839) | 1.6 | * |
| *Pseudothyone raphanus* (Dueben & Koren, 1845) | 1.6 | * |

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