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Macro-infaunal biodiversity and analysis of associated feeding guilds in the Greater Minch area, Scottish west coast

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Survey work was carried out in the Greater Minch area on the west coast of Scotland in 1997. The survey covered an area of 17,000 km^2, extending from Kinlochbervie in the north-east to the Stanton Banks in the south-west. Acoustic and ground-truth surveys were conducted using the seabed discrimination system RoxAnn© and underwater television cameras. This paper examines the macro infaunal component of the benthic community from 28 stations sampled throughout the region. From these, 198 taxa were identified, while species per station ranged from 11 to 69 with a maximum abundance of 2100 individuals per m^2. Biomass ranged from 2.3 $g\,m^{-2}$ to 103.1 $g\,m^{-2}$, with a mean value of 21.0 $g\,m^{-2}$. Multivariate statistical analysis of the infaunal data revealed the presence of three benthic assemblages, which were closely related to habitat type. An investigation into the dominant feeding guilds or isotrophic groups from each assemblage revealed that surface deposit feeding dominated the very fine sand habitats while both surface and subsurface deposit feeding were very common in the silt communities. A combination of feeding types (namely carnivorous, suspension and surface-deposit feeding) was associated with the sand habitats. The findings of this study are discussed in relation to those in similar habitat types.

INTRODUCTION

In recent years, several large scale benthic diversity surveys have been undertaken in the seas surrounding the UK. The North Sea benthos was extensively examined by Eleftheriou & Basford (1989); Basford et al. (1990); Heip et al. (1992) and Künitzer et al. (1992) while work was carried out in the Irish Sea by Swift (1993), Mackie et al. (1995), Hensley (1996) and Ellis et al. (2000). In addition, Rees et al. (1999) have investigated the biodiversity of the North Sea, English Channel and Celtic Seas. By comparison however, the benthic faunal diversity of the offshore Scottish west coast has received comparatively little attention. Farrow et al. (1979) investigated the benthic communities found between Colonsay, Islay and Jura while Mitchell (1983) investigated the shallow subtidal communities of the Inner Hebrides. Survey work was also conducted in the littoral zones throughout the Greater Minch area by Bishop & Holme (1980) and by Smith (1983). More recently, the Joint Nature Conservancy Council's (JNCC) Marine Nature Conservation Review (MNCR) team surveyed all the sea lochs in this region (see Howson et al., 1994, and references therein, and Irving 1997).

From the work of the JNCC, 14 Marine Consultation Areas were sited in the Greater Minches (Irving, 1997). These were non-statutory designated sites identified by Scottish Natural Heritage (SNH) as being of particular natural importance because of their quality and sensitivity to change. Six further areas were also proposed as being special areas of conservation (SAC) containing benthic communities of special interest (Irving, 1997).

However, despite the work mentioned above, there remain large stretches of mainland coast from which little data have been collected. It is the aim of this study therefore to provide more information on the offshore environment and on the local distributions of the fauna from throughout the Greater Minch.

The area

The dramatic glacial landscape of the region seen above sea level is continued below, with the presence of drowned fjords and other isolated deeps, many of which are >100 metres in depth and a few >200 metres (Ellett & Edwards, 1983). The waters in these valleys are cut off from lateral exchange and their properties are only altered by vertical mixing with the overlying water. There are also widespread shallows, straits, points and other topographical features which cause increased current speeds, turbulence and eddies in the surface waters of the Greater Minch. Some geographical variation can be seen in these features, the north coasts generally descend deeply into the sea so that there is little water shallower then 50 metres while in the south there are extensive areas within the 50 metre contour which strongly influence patterns of water mixing and stratification. These effects are particularly noticeable between Canna and Islay.

The waters are derived from three sources: oceanic or Atlantic, the Clyde/Irish Sea and coastal water derived from the land. These waters mix as they proceed northwards through the Minch and across the Hebridean Shelf at speeds of up to several kilometres per day. However, of these three masses, the Atlantic water dominates limiting differences between summer and winter temperatures (Ellett & Edwards, 1983).

The seabed sediments encountered are largely derived from reworked glacial deposits and shell fragments (British Geological Survey, 1997). A wide range of sediment types have been described from the region including rocky outcrops, sand ribbons and sandwaves from the main tidal streams and highly burrowed muds in the deeper, low energy areas (e.g. Pinn et al., 1998b).

MATERIALS AND METHODS

Five cruises were undertaken during 1997 in the Greater Minch between Kinlochbervie (58°26.00′N 05°15.00′W) and the Stanton Banks (56°00.00′N, 07°33.00′W), an area of approximately 17,000 km^2, during which acoustic, photographic and faunal surveys were carried out (Figure 1).

Acoustic data from throughout the experimental area were collected from east–west transects, with a spacing of two miles, using the RoxAnn© seabed discrimination system. The equipment used was similar to that described by Pinn et al. (1998b). On return to the laboratory, data were treated by an unsupervised cluster analysis (peak histogram technique) following the methods described by Greenstreet et al. (1997) and by Pinn et al. (1998b). These methods allowed for differentiation between areas on the basis of their acoustic response and avoided the subjectivity of delimiting areas by user defined 'box sets'.

Ground truthing was accomplished by photographic techniques and, where soft sediments were encountered, by employing a 0.1 m^2 Day Grab. Sediments thus collected were stored in 70% alcohol, returned to the laboratory and analysed using a Malvern Multisizer/E laser sediment particle sizer. Data from these analyses were then related to the plots obtained from the acoustic information.

Investigations into the benthic communities were carried out at a total of 95 sites (Figure 1). The station positions were determined from the ground truthed acoustic data set by stratified random sampling so ensuring that all the sediment types identified were sampled where possible. However, positions to the south-west of Coll and Tiree were not investigated because of adverse weather conditions. Data on the composition and distribution of the epifaunal and burrowing megafaunal communities have been published elsewhere (Pinn et al., 1998b) and will not be further discussed here.

The benthic macrofauna were sampled at 28 sites. Five replicate samples were collected from each station using a 0.1 m^2 Day Grab and sieved through a 0.5-mm mesh, the retained portion being preserved in 5% formal-saline until analysis could be undertaken. Rumohr et al. (2001) reported that five replicate samples were sufficient to obtain $<40\%$ error in estimates of average abundance and the Shannon index. Over 30 replicates were, however, required to reduce this error to $<10\%$ (Rumohr et al., 2001). Increasing the number of replicates beyond five was not considered feasible in the present study in view of the time available and the broad nature of this study.

The macro-infauna were identified to species level where possible. Species names and authorities are taken from Hartmann-Schröder (1996) and Howson & Picton (1997). Biomass was assessed by wet weight measurement. Standard multivariate techniques, such as cluster analysis, were then applied to the data generated using the PRIMER statistical package (Plymouth Marine Laboratory). Margalef's index (d), the Shannon index (H′) and Pielou's evenness index (J) were calculated and compared for each of the benthic assemblages identified by the initial cluster analysis. In addition, Spearman's rank correlations were undertaken to assess the relationships between biological and physical parameters measured.

Investigation of feeding type can provide useful information on the structural complexity of a community and also the surrounding environment (Ghertsos et al., 2000; Tselepides et al., 2000). The ten most abundant organisms in each community grouping were allocated to four isotrophic groups or feeding guilds i.e. surface deposit, subsurface deposit, carnivorous and suspension feeders. These guilds were assigned according to Pearson (1971), Fauchald & Jumars (1979), Eleftheriou & Basford (1989) and Pinn et al. (1998a). In addition, similar isotrophic grouping was undertaken for the ten most important species in each community in terms of biomass. However, if the biomass of a single large organism dominated a station, as in the case of a single specimen of the bivalve mollusc *Glossus humanus* (L.) found at Station 49, it was excluded from the allocation to feeding guilds.

RESULTS

Acoustic results

Unsupervised cluster analysis of the acoustic data revealed the presence of five different clusters or broad substratum types (Figure 2). Comparisons between ground truthing and the acoustic data supported these divisions. The most common sediment type encountered, covering 4721.5 km^2 or 29.8% of the area surveyed, was silt mud (Cluster 1) while Cluster 2, accounting for 28.8% or 4561.8 km^2 of the area, represented a mixture of sand and mud. The third cluster comprised a mixed substratum dominated by sands and gravels and accounted for 21.0% or 3320.8 km^2 of the area surveyed while Cluster 4 (17.8% or 2820.3 km^2) again represented mixed sediments but was dominated by boulders and bedrock. The final cluster recognized (Cluster 5) comprised a second mud grouping, accounting for 2.6% or 416 km^2 of the surveyed area.

Infaunal results

Appendices I and II present a complete listing of the 198 species recognized from the Greater Minch area. The total number of species observed at each site ranged from 11 to 69 while total numbers of individuals varied from 122 m^{-2} to 2100 m^{-2} with the highest numbers of individuals being observed at sites associated with very fine sands with a relatively high silt/clay content. Of the enumerable taxa, 56.6% were polychaetes, 18.7% crustaceans, 13.6% molluscs, 4.5% echinoderms while 6.6% belonged to minor phyla. Infaunal biomass ranged from 2.3 g m^{-2} to 103.1 g m^{-2} per station with a mean value of 21.0 g m^{-2}. The highest biomass levels were recorded from coarser sediment.

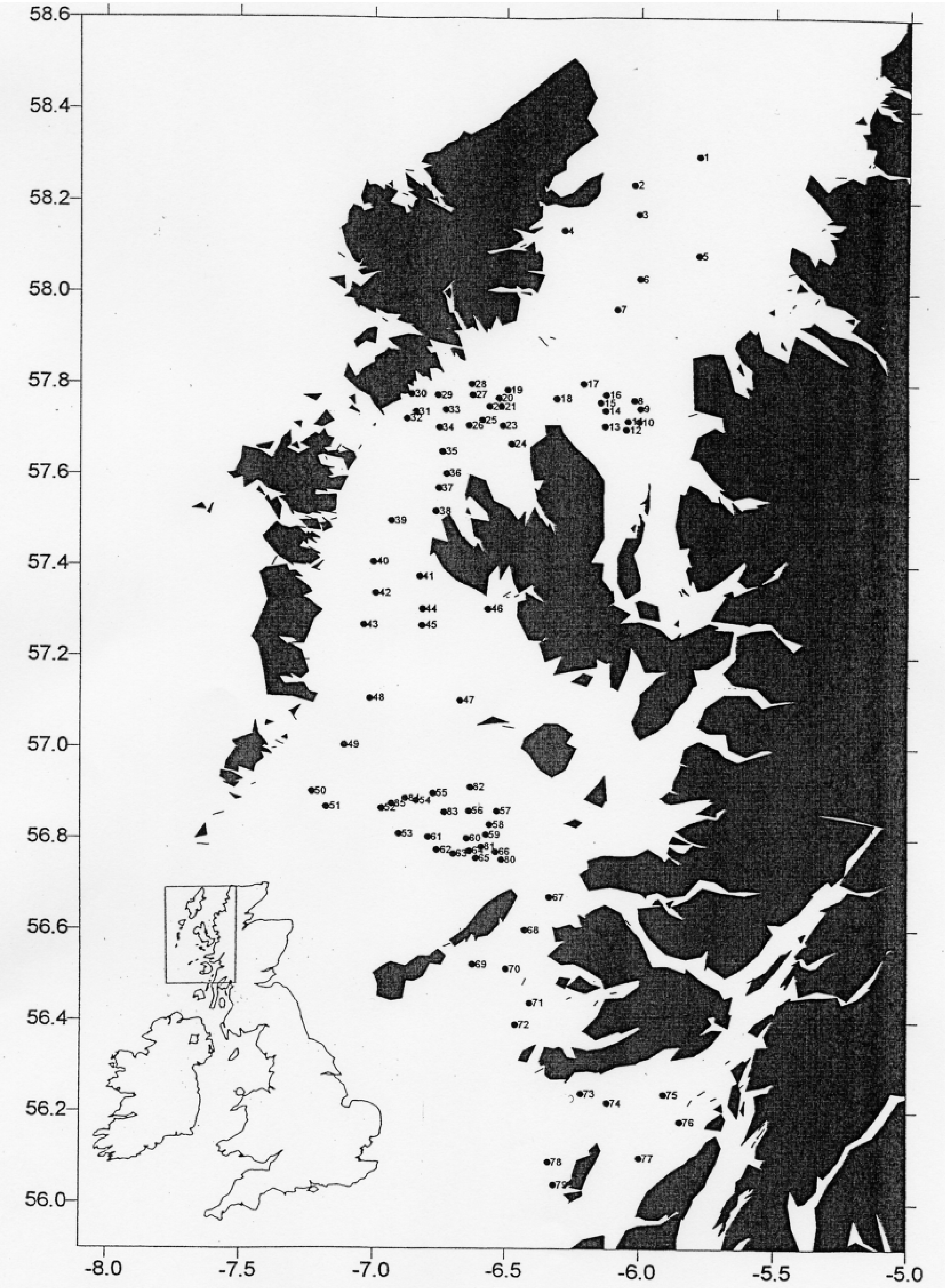

Figure 1. Sampling positions.

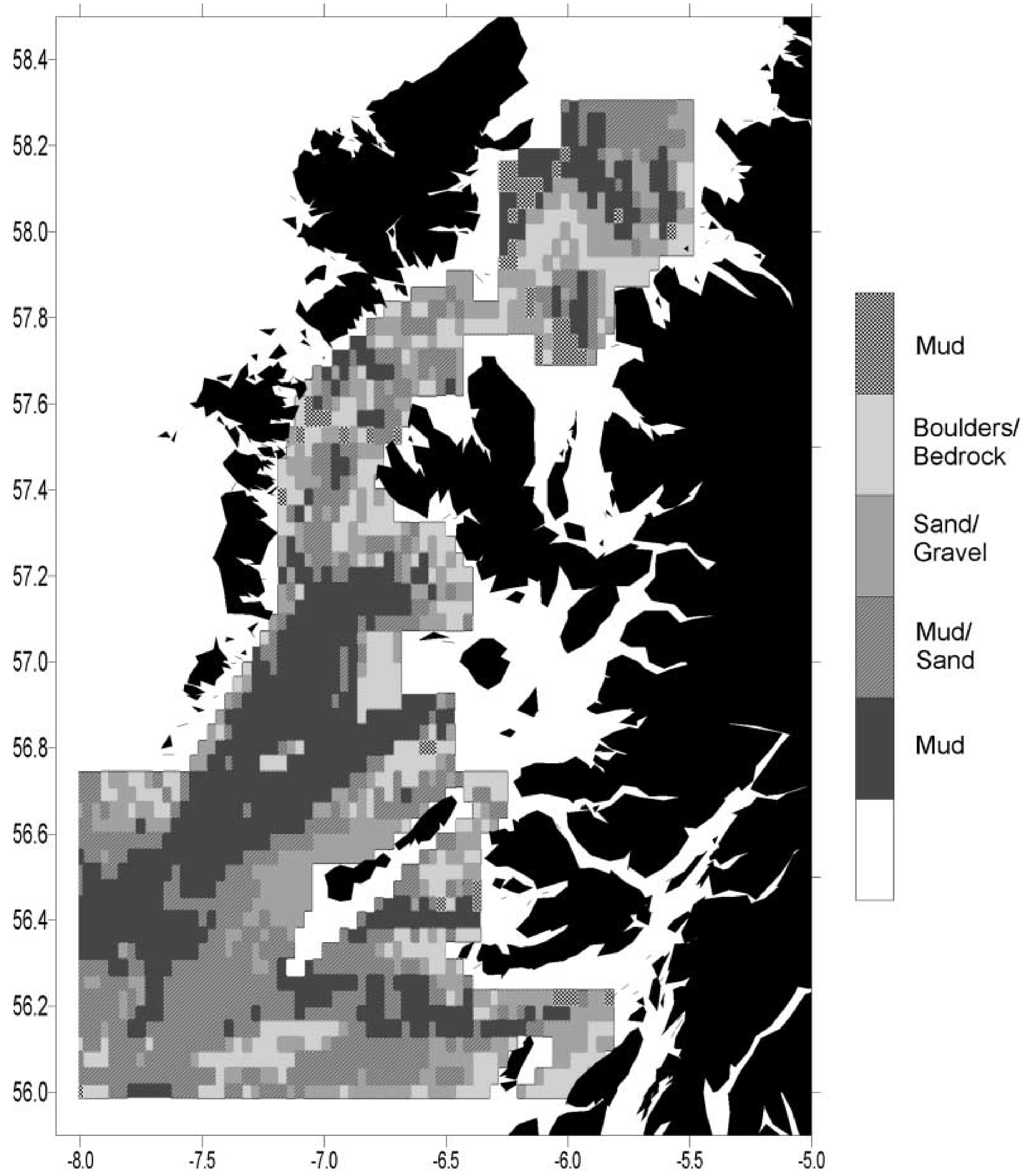

Figure 2. Acoustic survey results from the Greater Minch area.

Statistical analysis of the abundance data

Cluster analysis of the infaunal abundance data identified the presence of three community groupings at a similarity level of 35% (Figure 3).

Community A was represented by two sites and occurred over sand. The mean median grain size for these sites was 0.782 mm with 16.9% of the grains being defined as silt/clay, i.e. <63 μm (Table 1). The sediment was very poorly sorted and strongly fine skewed (Table 1). This community was derived by the presence of the polychaetes *Spiophanes kroeyeri*, *Glycera* sp., *Aonides paucibranchiata*, *Mediomastus fragilis*, *Lumbrineris* sp., the bivalve mollusc *Mysella bidentata*, the polychaetes *Sphaerosyllis hystrix* and *Goniada maculata*, Nemertea and Ampharetidae (unidentified).

Community B was recognized from eight of the sites investigated and occurred over very fine sand with a mean median grain size of 0.139 mm; 41.8% of the grains analysed were <63 μm in diameter (Table 1). The sediment was also very poorly sorted and strongly fine skewed

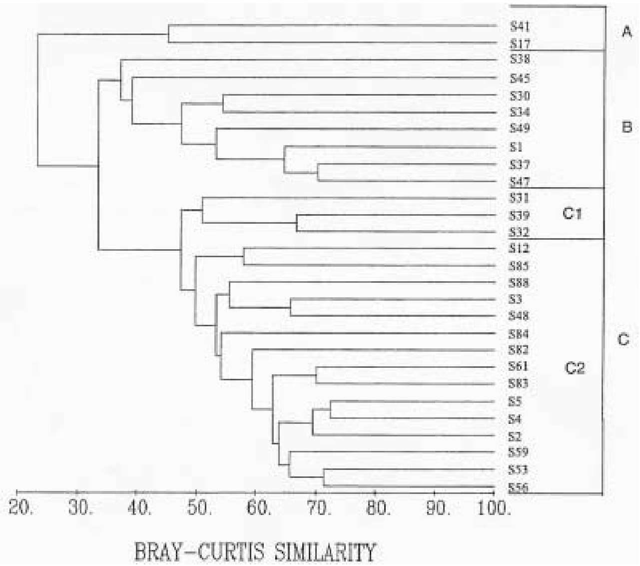

Figure 3. Cluster analysis of faunal abundance data.

(Table 1). Sites exhibited a variable benthic community with 13 species or groups accounting for 50% of the similarity between sites. These were, in order of importance, the polychaete *Aphelochaeta filiformis*, Nemertea, the polychaetes *Lumbrineris* sp., *Glycera rouxii* and *Chaetozone setosa*, the echinoderm *Amphiura chiajei*, the polychaetes *Minuspio cirrifera*, *Mediomastus fragilis*, *Notomastus latericius*, Hesionidae (unidentified) and *Goniada maculata*, the bivalve mollusc *Abra nitida* and the polychaete *Aricidea simonae*.

Community C, the most heavily sampled in this study, was found over 18 of the sites examined and occurred on silt mud with a median grain size of 0.023 mm and with 79.5% of the grains encountered $<63\,\mu$m in diameter (Table 1). Again the sediment was found to be very poorly sorted, but symmetrically distributed (Table 1). The benthic fauna observed in this grouping was less variable than the fauna encountered in Community B with six species accounting for approximately 50% of the similarity between sites. These species were the polychaetes *Aphelochaeta filiformis*, *Glycera rouxii*, *Lumbrineris* sp., *Cirrophorus branchiatus*, the decapod *Calocaris macandreae* and the bivalve mollusc *Nucula sulcata*.

Two subgroups were identified from within Community C. The first contained three sites from which sediments exhibited a higher median grain size (0.043 mm) and lower silt/clay content (63.1%) than the figures recorded for the main community. Species and groups important to this subgroup and in addition to the six recorded above were Solenogastres, and the polychaetes *Nephtys incisa*, *Minuspio cirrifera*, *Chaetozone setosa* and *Spio filicornis*. The second subgroup contained the remaining 15 sites from Community C and exhibited a lower median grain size (0.019 mm) and a higher silt/clay fraction (82.7%) than the subgroup described above. This subgroup dominated the community and its defining species were therefore similar to those determining the overall benthic

Table 1. *Summary of the biological and physical characteristics of the three communities derived by cluster analysis.*

	Rank	Community A	Community B	Community C
Top 5 ranked taxa in terms of density	1	*Spiophanes kroeyeri*	*Aphelochaeta filiformis*	*Aphelochaeta filiformis*
	2	*Glycera* sp.	*Caulleriella zetlandica*	*Cirrophorus branchiatus*
	=3	*Mediomastus fragilis*	*Chaetozone setosa*	*Minuspio cirrifera*
	=3	*Aonides paucibranchiata*		
	4	*Lumbrineris* sp.	Nemertea	*Nucula sulcata*
	5	*Mysella bidentata*	*Abra nitida*	*Spio filicornis*
Number of taxa		53.50 ±7.78	51.5 ±18.30	20.94 ±5.84
Number of individuals		544.50 ±14.85	848.87 ±566.59	352.94 ±159.29
Margalef's index		13.15 ±2.05	10.96 ±3.28	5.74 ±1.36
Shannon index		3.66 ±0.13	3.16 ±0.40	2.09 ±0.50
Pielou index		0.92 ±0.00	0.82 ±0.08	0.69 ±0.15
Depth (m)		90.0 ±0.0	121.3 ±42.7	135.5 ±26.8
Median grain size (mm)		0.782 ±0.054	0.139 ±0.082	0.023 ±0.02
% $<63\,\mu$m grain size		16.9 ±1.98	41.76 ±13.51	79.45 ±16.34
Sorting		2.82 ±0.03	2.54 ±0.21	2.02 ±0.29
Skewness		0.43 ±0.19	0.35 ±0.26	0.05 ±0.17
Habitat type		Sand	Very fine sand	Silt
Top 5 ranked taxa in terms of biomass	1	*Spatangus purpureus**	*Amphiura chiajei*	*Glossus humanus**
	2	Porifera	*Labidoplax digitata**	*Calocaris macandreae*
	3	*Tridonta elliptica*	*Glycera rouxii*	*Nucula sulcata*
	4	*Pista cristata*	*Nucula sulcata*	*Glycera rouxii*
	5	*Terebellides stroemi*	*Calocaris macandreae*	*Nephtys incisa*
	6	*Nephtys hombergii*	*Donsinia lupinus**	*Notomastus latericeus*
	7		*Abra nitida*	

*, Single individual.

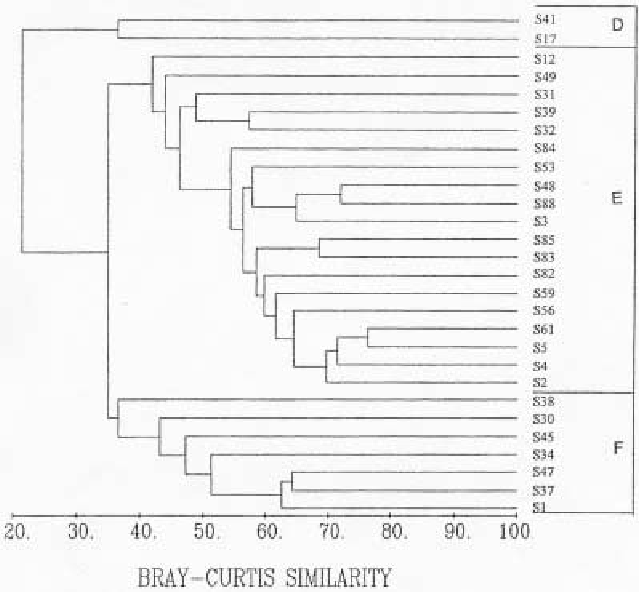

Figure 4. Cluster analysis of faunal biomass data.

assemblage of Community C but with the additions of the polychaetes *Praxillella affinis*, *Notomastus latericius*, *Levinsenia gracilis* and the phylum Nemertea.

Statistical analysis of the biomass data

A cluster analysis of the infaunal biomass data again identified the presence of three communities similar to those seen in the analysis of the abundance data (Figure 4).

Community D was similar to that seen in Community A in terms of the habitat type (sediment distributions) and the sites included. However, the species with the highest biomass recorded here was the echinoderm *Spatangus purpureus*. Also important was the bivalve mollusc *Tridonta elliptica* and the polychaetes *Pista cristata*, *Terebellides stroemi* and *Nephtys hombergii* as well as an unidentified poriferan.

Community E closely resembled Community C, which was described using the faunal abundance data, with the exception of Station 49 which was not included in the abundance data grouping. The decapod *Calocaris macandreae* dominated the biomass at these sites although the polychaete *Glycera rouxii*, the bivalve mollusc *Nucula sulcata* and the polychaete *Aphelochaeta filiformis* were also important.

Community F was similar to the Community B faunal abundance grouping with the exception of Station 49 which was included in the Community E faunal biomass grouping (see above). However, the number of species seen in this assemblage were more variable than those observed for Community E. The ophiuroid echinoderm *Amphiura chiajei* accounted for the greatest proportion of the biomass recorded here. Also important were the polychaetes *Glycera rouxii*, *Lumbrineris* sp., *Notomastus latericeus* and *Aphelochaeta filiformis*, the bivalve mollusc *Abra nitida* and Nemertea.

Hereafter, the benthic communities discussed in this study will be referred to as Communities A, B and C as identified by the multivariate statistical analysis of the abundance data presented above.

Analysis of biological and physical parameters of the communities

The benthic communities of the sand and very fine sand grounds (Communities A and B, respectively) supported the most diverse fauna having an average of 53.5 and 51.5 species respectively while Community C, occurring over silt, supported an average of 20.9 species (Table 1). However, on average, Community B supported substantially more individuals per site than did either Communities A or C (848.9, 544.5 and 352.9 individuals m^{-2} respectively). Margalef's species richness index were highest for Community A and lowest for Community C (Table 1). A similar trend was observed in the results obtained for the Shannon index and for Pielou's evenness index (Table 1).

A strong positive relationship was found between median grain size and species richness, number of individuals m^{-2}, Margalef's index and Shannon index (Table 2). No relationship was found between the median grain size and Pielou's index (Table 2). As would be expected, there was a strongly negative correlation between median grain size and % silt/clay content, whilst there is a strong positive correlation between median grain size and sorting and skewness (Table 2). The % silt/clay was found to be strongly positively correlated to species richness and strongly negatively correlated to the number of individuals m^{-2}, Margalef's index and Shannon index (Table 2). Sediment sorting was found to be strongly positively correlated to species richness, and Margalef's and Shannon indices (Table 2). It was also positively correlated to the number of individuals m^{-2}, but less strongly (Table 2).

Table 2. *Correlation matrix for biological and physical parameters (N=28).*

	Median grain size (mm)	% <63 µm	Sorting	Skewness	Species richness	No. of individuals (m^{-2})	Margalef's index	Shannon index
% <63 µm	−0.99***							
Sorting	0.87***	−0.89***						
Skewness	0.67***	−0.64***	0.44*					
Species richness	0.73***	−0.71***	0.62***	0.52**				
No. individuals (m^{-2})	0.56**	−0.56**	0.45*	0.38*	0.59**			
Margalef's index	0.63***	−0.62***	0.55**	0.47*	0.95***	0.45*		
Shannon–Weiner index	0.59**	−0.60***	0.54**	0.47*	0.79***	0.47*	0.79***	
Pielou's index	n.s.	n.s.	n.s.	n.s.	0.38*	n.s.	0.41*	0.85***

n.s., not significant; *, 0.05–0.01; **, 0.01–0.001; ***, <0.001.

Sediment skewness was strongly positively correlated with species richness, and less strongly correlated to the number of individuals m^{-2}, and the Margalef and Shannon indices (Table 2). Again as expected there were positive relationships between many of the biological parameters, e.g. species richness and the diversity indices.

Feeding guilds

Using the abundance data, it was estimated that surface deposit feeding was the most common strategy adopted by organisms observed in Community A with 42.0% of individuals employing this method. Additionally, 29.8% were found to be carnivores, 21.7% suspension feeders and only 6.3% subsurface deposit feeders. However, analysis of the biomass data revealed that the suspension feeders dominated with 38.3% of individuals adopting this method. Surface deposit feeding was employed by 29.4% of the animals observed while 18.6% were carnivores and 13.7% were subsurface deposit feeders.

Community B was dominated by surface deposit feeders in terms of abundance and biomass with 77.1% and 65.8% of the total animals observed adopting this method respectively. Carnivores accounted for 13.5% in terms of abundance and 15.2% in terms of biomass while subsurface deposit feeders accounted for 9.4% in terms of abundance and 13.4% in terms of biomass. No suspension feeders were observed in the ten highest ranked abundant species while only 5.7% of the top ten ranked biomass species were allocated to this feeding guild.

Allocation of animals from Community C to feeding guilds revealed that, in terms of abundance, surface deposit feeders dominated with all others considered to be carnivores. However, the biomass data revealed a different distribution with 41.9% being subsurface deposit feeders, 37.1% surface deposit feeders and 21.0% carnivores.

DISCUSSION

From the descriptions given by Jones (1950, 1951), it can be seen that Community A belongs to the offshore boreal muddy sand association. Further to this, the presence of *Glycera* sp., *Mysella bidentata* and *Goniada maculata* in this community indicate that this is a community similar to that reported on by Buchanan & Moore (1986) from off the Northumberland coast. This was described as belonging to the classical Petersen *Amphiura filiformis–Echinocardium cordatum* community. Similar communities have been described from deep, coarser sediments in the northern North Sea where the presence of *Spiophanes kroyeri*, *Mysella bidentata* and *Nephtys hombergii* were considered indicative of this assemblage (Künitzer et al., 1992).

Community B (very fine sand skewed towards silt/clay particle size range) and Community C (silt) correspond in general to the *Amphiura* communities described from soft sediments throughout the boreo-Mediterranean region (see Thorson 1957 for a summary of the characteristics of such a community). However, Community B exhibits some of the characteristics described by Jones (1956) and Mackie et al. (1995) for faunal associations occurring in the Irish Sea. This is particularly noticeable with the recording of the polychaetes *Terebellides stroemi*, *Chaetozone setosa* and *Glycera rouxii* from Community B. Community C appears analogous with Buchanan's (1963) deeper sub-community of *Amphiura chiajei* associated with *Glycera rouxii* and *Calocaris macandreae*. This also corresponds to the offshore boreal mud association described by Jones (1950). Similar communities have been described by Pearson (1971) from two Scottish lochs, by Josefson (1981) from the Skagerrak and by Mackie et al. (1995) and Hensley (1996) from the Irish Sea.

The Shannon index has become a standard measure of faunal diversity in marine benthic studies. This is despite much criticism, e.g. see Magurran, 1988. Buchanan & Moore (1986) reported Shannon index values of between 4.86–5.64 in muddy sands from off the Northumberland coast while Kingston (1987) reported values of 4.4–5.8 from similar sediments in the North Sea. Mackie et al. (1995) recorded even higher values for sites in the southern Irish Sea, ranging from 5.54–5.5. In the present study, a lower mean diversity index value of 3.66 was recorded for Community A, found on muddy sand. No comparable diversity indices could be found in the literature with those recorded here for Community B. However, Community C, observed over silt, exhibited faunistic similarities to assemblages described by Buchanan & Warwick (1974), Buchanan & Moore (1986) and by Mackie et al. (1995) from off the Northumberland coast and in the southern Irish Sea. These authors reported diversity values greater (ranging from 3.34 to 5.17) than those observed in the present study (mean of 2.09).

The differences observed in the diversity may be attributed to several factors. Hensley (1996) proposed that sampling method would have an influence on the diversity observed at a site. The main difference in the approach of the current study and that of previous ones, was the type of grab utilized (Day and van Veen respectively). This may account to some extent for the differences observed. However, it is unlikely that this is the main reason for the large differences in diversity observed.

Alternatively, the difference may be attributed to supply of organic material to the benthic environment. Creutzberg et al (1984) suggested that organic matter derived from primary production in the vicinity of a seasonal front or that certain hydrographic conditions lead to an accumulation of organic matter and benthic enrichment. Such findings have been reported by Holme & Rees (1986) and Hensley (1996). It is possible that the supply of organic material is lower at sites in the current study than at the other sites investigated. This, however, was not investigated.

Vanosmael et al. (1982) reported that in stressed conditions the diversity of benthic assemblages in sandy substrata was reduced. The low diversity of Communities A and C may indicate that they are under some kind of stress when compared to similar habitats elsewhere. This could possibly be attributed to the overall bathymetry of the Greater Minch, which restricts lateral water flow at deeper locations. This would result in stressed conditions, such as a reduced oxygen supply, which could lead to a reduction in the species able to survive in such a habitat type. However, it was not possible to ascertain if this was the case.

Rees et al. (1999) reported that particle size was a good static descriptor of habitat type, whilst sediment sorting and tidal current strengths gave a good indication of the dynamic nature of the local physical environment. As found by Rees et al. (1999), a strong relationship was observed between physical parameters, such as median grain size and sediment sorting, and the biological parameters, such as species richness, number of individuals m^{-2} and various diversity indices.

The prevailing hydrographic features which are responsible for the supply of organic matter to the benthos will also affect community structure (Pearson & Rosenberg, 1987; Tselepides et al., 2000). Consequently, an investigation of feeding types can provide useful information on the structural complexity of a community (Tselepides et al., 2000). Distribution of different isotrophic communities has been linked primarily to particle size distributions, to sediment organic carbon levels and to local current speeds (Pearson, 1971; Eleftheriou & Basford, 1989; Tselepides et al., 2000). Hartley (1984) reported that there was a significant negative correlation between the abundance of surface deposit feeders and filter feeders with sediment silt/clay content while the abundance of mud swallowers (equivalent to subsurface deposit feeders in the present study) was positively correlated. Pearson (1971) found that surface deposit feeding predominated in areas of deep mud and, to a lesser extent, sandy muds while suspension feeders dominated in areas of diminishing current speeds where the levels of suspended particles just above the sediments was greatest. Eleftheriou & Basford (1989) observed that subsurface deposit feeding communities dominated in silt sediments while carnivores dominated coarse substrata. More recently, Desrosiers et al. (2000) found that irregular inputs of organic matter and the subsequent decrease in food supply tends to favour sub-surface deposit feeding.

In line with these previous findings, a link was observed between feeding type and particle size in the present study. In areas of coarser sediments with higher current speeds, no single feeding guild is seen to dominate the fauna. For example, for Community A, associated with sand, a combination of carnivorous, suspension and surface deposit feeding types were observed. As the median grain size and current speeds reduce, levels of sediment organic matter increase and deposit feeding becomes the dominant feeding mode. For example surface deposit feeding dominates the very fine sand habitats (Community B). Desrosiers et al. (2000) suggested that communities dominated by surface deposit feeders had a regular, but relatively low-level supply of particulate matter. When median particle size is still further reduced, the sediment provides an ideal environment for burrowing and tube-building species, subsurface deposit feeding becomes common, as observed for Community C, a silt habitat type. Desrosiers et al. (2000) also suggested that where particulate inputs are irregular, subsurface deposit feeding tends to dominate.

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Appendix I. *Molluscan, crustacean, echinoderms and other species identified from the grab samples.*

Mollusca
Tonicella rubra (L.)
Solenogastres
Gastropoda
Turritella communis Risso
Polinices montagui (Forbes)
Cylichna cylindracea (Pennant)
Pelecypoda
Nuculidae
Nucula sulcata Bronn
Nuculoma tenuis (Montagu)
Myrtea spinifera (Montagu)
Thyasira ferruginea (Locard)
Mysella bidentata (Montagu)
Tridonta elliptica (Brown)
Tridonta montagui (Dillwyn)
Parvicardium scabrum (Philippi)
Spisula sp.
Phaxas pellucidus (Pennant)
Abra sp.
Abra alba (W. Wood)
Abra nitida (O.F. Müller)
Glossus humanus (L.)
Dosinia lupinus (L.)
Corbula gibba (Olivi)
Thracia convexa (W. Wood)
Thracia villosuiscula (Macgillivray)
Rissoa sp.

Crustacea
Ostracoda
Perioculodes longimanus (Bate & Westwood)
Leucothoe incisa Robertson
Leucothoe lilljeborgi Boeck
Urothoe elegans (Bate)
Phoxocephalidae
Harpinia antennaria Meinert
Harpinia crenulata (Boeck)
Harpinia pectinata G.O. Sars
Acidostoma nodiferum Stephensen
Guernea coalita (Norman)
Ampelisca sp.
Ampelisca gibba G.O. Sars
Ampelisca spinipes Boeck
Ampelisca tenuicornis Liljeborg
Eriopisa elongata (Bruzelius)
Gammaropsis maculata (Johnston)

Crustacea (cont.)
Erichthonius spp.
Photis longicaudata (Bate & Westwood)
Leptocheirus hirsutimanus (Bate)
Leptocheirus pectinatus (Norman)
Corophium affine Bruzelius
Phtisica marina Slabber
Hyperia galba (Montagu)
Eurydice pulchra Leach
Tanaidae
Iphinoe trispinosa (Goodsir)
Eudorella emarginata (Krøyer)
Eudorella truncatula (Bate)
Campylaspis sulcata G.O. Sars
Diastylis tumida (Liljeborg)
Decapod Larvae
Hippolytidae
Processidae
Nephrops norvegicus (L.)
Calocaris macandreae Bell
Anapagurus laevis (Bell)
Atelecyclus rotundatus (Olivi)

Echinodermata
Ophiuroidea
Ophiothrix fragilis (Abildgaard)
Amphiura chiajei Forbes
Echinoidea
Spatangus purpureus O.F. Müller
Brissopsis lyrifera (Forbes)
Holothuroidea
Leptosynapta inhaerens (O.F. Müller)
Labidoplax digitata (Montagu)

Other
Porifera
Anthozoa
Virgularia mirabilis (O.F. Müller)
Pennatula phosphorea L.
Cerianthus loydii Gosse
Platyhelminthes
Nemertea
Sipuncula
Golfingia vulgaris vulgaris (de Blaineville)
Oligochaeta
Phoronidae
Ascidiacea

Appendix II. *Polychaete species identified from the grab samples.*

Pisione remota (Southern)
Aphroditidae
Gattyana cirrosa (Pallas)
Malmgrenia sp.
Malmgrenia castanea (McIntosh)
Panthalis oerstedi Kinberg
Pholoe inornata Johnston
Eteone flava (Fabricius)
Eteone longa (Fabricius)
Hesionura elongata (Southern)
Anaitides maculata (L.)
Eulalia bilineata (Johnston)
Eulalia viridis (L.)
Glycera sp.
Glycera rouxii Audouin & Milne Edwards
Glycinde nordmanni (Malmgren)
Goniada maculata Oersted
Sphaerodoropsis minuta (Webster & Benedict)
Nereidae
Hesionidae
Nereimya punctata (O.F. Müller)
Ophiodromus flexuosus (Chiaje)
Podarkeopsis helgolandica Hillbig & Dittmer
Ancistrosyllis groenlandica McIntosh
Glyphohesione klatti Friedrich
Pilargis verrucosa Saint-Joseph
Typosyllis cornuta (Rathke)
Syllides longocirrata Oersted
Exogone hebes (Webster & Benedict)
Exogone verugera Claparède
Sphaerosyllis hystrix Claparède
Nereis elitoralis Eliason
Nephtys sp.
Nephtys caeca (Fabricius)
Nephtys cirrosa Ehlers
Nephtys hombergii Savigny
Nepthys hystricis McIntosh
Nephtys incisa Malmgren
Aponuphis bilineata (Baird)
Hyalinoecia tubicola (O.F. Müller)
Eunicidae
Marphysa bellii (Audouin & Milne Edwards)
Nematonereis unicornis (Grube)
Lumbrineris sp.
Lumbrineris latreilli Audouin & Milne Edwards
Dorvilleidae
Ophryotrocha sp.
Orbinia sertulata (Savigny)
Scoloplos armiger (O.F. Müller)
Aricidea sp.
Aricidea cerrutii Laubier
Aricidea simonae Laubier & Ramos
Cirrophorus lyra (Southern)
Cirrophorus branchiatus Ehlers
Levinsenia gracilis (Tauber)
Paraonis fulgens (Levinsen)
Poecilochaetus serpens Allen
Aonides paucibranchiata Southern
Laonice cirrata (M. Sars)
Minuspio cirrifera (Wiren)
Polydora socialis (Schmarda)
Prionospio steensrupi Malmgren
Pseudopolydora pulchra (Carazzi)
Scolelepis foliosa (Audouin & Milne Edwards)
Scolelepis squamata (Abildgaard)
Scolelepis tridentata (Southern)
Spio filicornis (O.F. Müller)
Spiophanes bombyx (Claparède)
Spiophanes kroeyeri Grube
Magelona alleni Wilson
Magelona minuta Eliason
Cirratulidae
Aphelochaeta sp.
Aphelochaeta filiformis Keferstein
Aphelochaeta vivipera (Christie)
Caulleriella caputesocis (Saint-Joseph)
Caulleriella zetlandica (McIntosh)
Chaetozone gibber Woodham & Chambers
Chaetozone setosa Malmgren
Tharyx killariensis (Southern)
Diplocirrus glaucus (Malmgren)
Pherusa flabellata (M. Sars)
Capitella capitata (Fabricius)
Capitomastus minimus (Langerhans)
Mediomastus fragilis Rasmussen
Notomastus latericeus M. Sars
Maldanidae
Praxillella affinis (M. Sars)
Nicomache sp.
Ophelina acuminata Oersted
Scalibregma inflatum Rathke
Myriochele danielsseni Hansen
Owenia fusiformis Chiaje
Pectinaria auricoma (O.F. Müller)
Petta pusilla Malmgren
Ampharetidae
Amage adspersa (Grube)
Ampharete falcata Eliason
Ampharete finmarchica (M. Sars)
Ampharete lindstroemi Hessle
Amphicteis sundevallii Malmgren
Amphicteis gunneri (M. Sars)
Anobothrus gracilis (Malmgren)
Terebellides stroemi M. Sars
Trichobranchus roseus (Malmgren)
Terebellidae
Pista cristata (O.F. Müller)
Pistella lornensis (Pearson)
Polycirrus sp.
Jasmineira elegans Saint-Joseph
Laonome kroyeri Malmgren
Hydroides norvegica Gunnerus