J. Mar. Biol. Ass. U.K. (2001), **81**, 1–9
Printed in the United Kingdom

Animal:sediment relationships in coastal deposits of the eastern English Channel

R.C. Newell*, L.J. Seiderer* and J.E. Robinson*†

*Marine Ecological Surveys Limited, Trewood Cottage, Steeple Lane, St Ives, Cornwall, TR26 2PF.
E-mail: seasurvey@aol.com. †Benthic Ecology Research Group, Department of Biological Sciences, University of Plymouth, Drake Circus, Plymouth, Devon, PL4 8AA

The purpose of the present study was to assess the relationship between sediment composition and biological community structure in mixed sands and gravel deposits of the eastern English Channel. Although some species are clearly associated with particular sediment types, the results confirm the lack of correspondence between community composition of the benthos and particle size distribution in unconsolidated sand and gravel deposits. The results also suggest that sample-to-sample variability commonly recorded in the species composition of macrofauna may reflect significant under-sampling by conventional grab sampling techniques. The implications of this for environmental monitoring and impact studies is discussed.

INTRODUCTION

Surveys of the nature and distribution of benthic communities that inhabit sand and gravel deposits of the English Channel include those of Holme (1961, 1966) and Cabioch (1968). More recent work in the eastern English Channel includes that of Holme & Wilson (1985), Rees (1987), Sanvicente-Anorve et al. (1996) and Kenny (1998).

The relationship between sediment characteristics and community structure has also been widely studied in other coastal deposits including the Bristol Channel (Warwick & Davies, 1977), the Irish Sea (Rees & Walker, 1991; Mackie et al., 1995; Hensley, 1996), and western English Channel (Parry et al., 1999). These studies, as well as those in the North Sea and elsewhere, show that in deep waters or sheltered areas there is a good correlation between sediment type and community composition (Dankers & Buekema, 1981; Salzwedel et al., 1985; Künitzer et al., 1992; Mackie et al., 1995; van Dalfsen et al., 2000). In other studies, however, there is little correspondence (Buchanan, 1963; Day et al., 1971; Duineveld & van Noort, 1990; Kenny, 1998; Seiderer & Newell, 1999).

Holme & Wilson (1985) suggested that in shallow waters of the English Channel the nature of faunal assemblages was related to the degree of disturbance by tidal scour and seasonal events, rather than directly to sediment composition itself. Tidal current speed has also been implicated in control of community structure elsewhere in coastal deposits including the English Channel (Cabioch, 1968), the Bristol Channel (Warwick & Uncles, 1980), and coastal deposits of the North Sea and eastern Irish Sea by Rees et al. (1999). Such factors are likely to account for the lack of close correspondence between biological communities and particle size composition in shallow water deposits on the Hastings Shingle Bank by Kenny (1998) or in sands and gravels of the southern North Sea (Seiderer & Newell, 1999) where intermittent disturbance by storms prevents the establishment of a long-term equilibrium between sediment composition and biological community structure.

The following study was carried out to determine the relationship between benthic biological community composition and sediment composition in mixed sands and gravels that characterize seabed deposits of the eastern English Channel. The results are used to assess the extent to which the well-known sample-to-sample variability in the species composition of the macrobenthos of gravels and sands is a reflection of under-sampling by standard grab sampling techniques.

MATERIALS AND METHODS

Sampling strategy and extraction of the benthos

Samples of sediment were taken by means of a 0.2 m^2 Hamon grab at a series of 44 sampling stations to the north and west of the Varne shoal, approximately 9 km south of Folkestone, Kent in April 1996. The sampling method is that used in many studies of the benthos of gravels and sands, and has the advantage that loss of material that commonly occurs through the jaws of other types of grabs is minimized (Holme & MacIntyre, 1984; Sips & Waardenburg, 1989). Use of a conventional 0.2 m^2 Hamon grab in our survey of the benthos of gravels and sands allows strict comparison of the data with those obtained in other surveys of coastal deposits elsewhere.

Positions were fixed with a Sercel NR103 Differential Global Positioning System (dGPS). Samples were released from the grab into a plastic tray, from which sub-samples of sediment were removed and placed in sealed plastic bags for subsequent analysis of particle size. Sediment samples were wet-sieved to estimate the percentage of $<63\,\mu m$ (silt+clay) fraction. The coarser fractions were dry-sieved over the range 16,000 μm down to 64 μm.

The volume of the residual sediment (generally approximately 14 litres) was then measured and the material

https://doi.org/10.1017/S0025315401003344 Published online by Cambridge University Press

preserved in formalin for subsequent elution through a 1-mm mesh sieve, and the fauna was separated for subsequent identification and analysis. This process of elution was repeated three times, and the residual sand, stones and shell were sorted by inspection. Any samples with encrusting biota were then removed and placed in alcohol together with the material separated by elution through the 1-mm mesh sieve.

This separation process was repeated for all samples and the material analysed for taxonomic composition (number of species, S), for number of individuals of each taxon (N) and for biomass (B) of the main faunal groups. Biomass was estimated from the blotted wet weight using conversion factors for the major faunal groups from Eleftheriou & Basford (1989), and expressed as grams ash-free dry weight (AFDW).

The complete data set, including a list of taxa recorded, the numbers of individuals of each taxon and the biomass of macrofauna recorded at each sampling site is available on the following web site:- www.marineecologicalsurveys.co.uk

Statistical analysis

Non-parametric multivariate analysis of community structure as described by Field et al. (1982) and by Clarke & Warwick (1994) has been used for both the sediment and biotic data obtained in our survey of the benthos of sands and gravel deposits of the eastern English Channel. This procedure is available in the software package PRIMER (Plymouth Routines in Multivariate Ecological Research) and has been widely used in other studies of benthic community structure in European waters. In all a total of 44 stations was used for multivariate analysis of community structure.

Biotic data were linked to particle size composition of the sediments using the approach of Clarke & Ainsworth (1993; see also Clarke & Warwick, 1994). The BIO-ENV procedure within the PRIMER program allows matching of community structure of the biota with environmental factors, in this case particle size composition of the sediments. Different combinations of sediment variables were considered at increasing levels of complexity (i.e. k variables at a time, where $k=1,2,3\ldots v$) to obtain best matches of biological and environmental similarity matrices for each k as measured by weighted Spearman rank correlation (ρ_{ω}).

RESULTS

Nature and distribution of the sediments

Most of the stations sampled were found to have a relatively high proportion of medium sand, with coarser deposits occurring in the central and north-eastern parts of the survey area. The near shore sediments, in contrast, had a high proportion of fine sand and in the case of station 5 were dominated by mobile silts. A group average sorting dendrogram showing the percentage similarity of the particle size composition of the sediments at each of the 44 stations in the survey area at which sediment samples were obtained is shown in Figure 1. The corresponding two-dimensional multidimensional scaling (MDS) ordination is shown in Figure 2.

Both of these methods of analysis show that the sediments in the survey area are best regarded as comprising four main groups. The groups are quite distinct from one another, and stations within each group are linked by a high level of internal similarity of approximately 80%. This high level of similarity within groups of coastal sediments is similar to that reported for the Hastings Shingle Bank to the west of our survey area by Kenny (1998). Similar results have been obtained in a survey that we carried out in the southern North Sea off Orford Ness, Suffolk (Seiderer & Newell, 1999). The distinction between the four sediment groups in the survey area is emphasized by the clear separation in the MDS ordination shown in Figure 2.

Figure 3 shows that sediments belonging to group 1 occupy the central part of the survey area. Group 2 sediments lie in isolated patches to the east. Group 3 sediments comprise fine silty sands in the near shore part of the survey area whilst group 4 sediments border the deeper waters on the east of the survey area.

Abundance and variety of macrofauna

The macrofauna (>1 mm) was dominated by Cnidaria, Polychaeta, Crustacea, Mollusca and Bryozoa. The species variety recorded from the survey area as a whole was rich compared with a similar survey that we carried out in the southern North Sea off Orford Ness, Suffolk. A total of as many as 343 taxa, representing at least 150 Families was recorded from the sediments off Folkestone compared with only 222 taxa comprising 121 Families in the southern North Sea off Orford Ness (Seiderer & Newell, 1999).

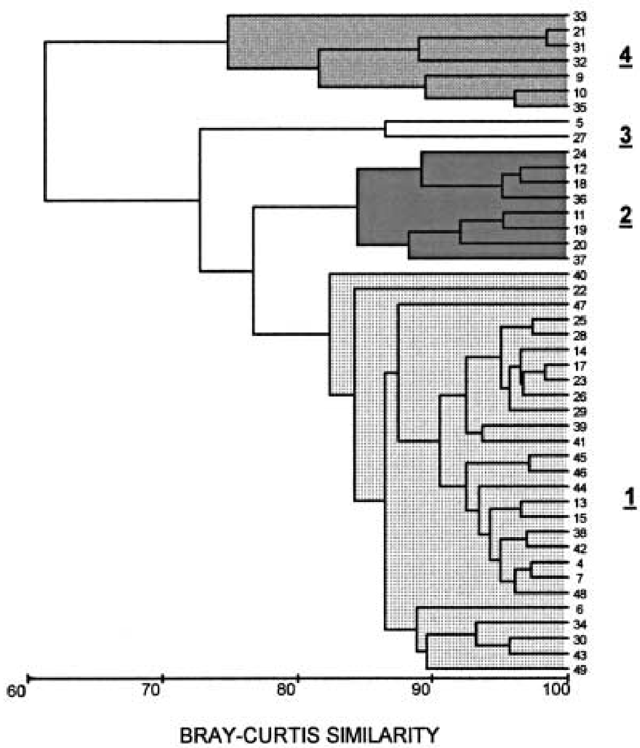

Figure 1. Group average sorting dendrogram showing the percentage similarity of the particle size composition at each of 44 stations sampled in April 1996.

https://doi.org/10.1017/S0025315401003344 Published online by Cambridge University Press

Relatively low values for species variety have also recently been recorded for macrofaunal assemblages in muddy sands and gravels of the western English Channel near Plymouth by Parry et al. (1999). They recorded a total of 185 taxa at sites that included coastal deposits and the Eddystone. The relatively high species variety of 343 taxa that we have recorded in coastal deposits of the eastern English Channel in the West Varne survey supports the results of Kenny (1998) who recorded as many as 303 taxa from sediments of the Hastings Shingle Bank.

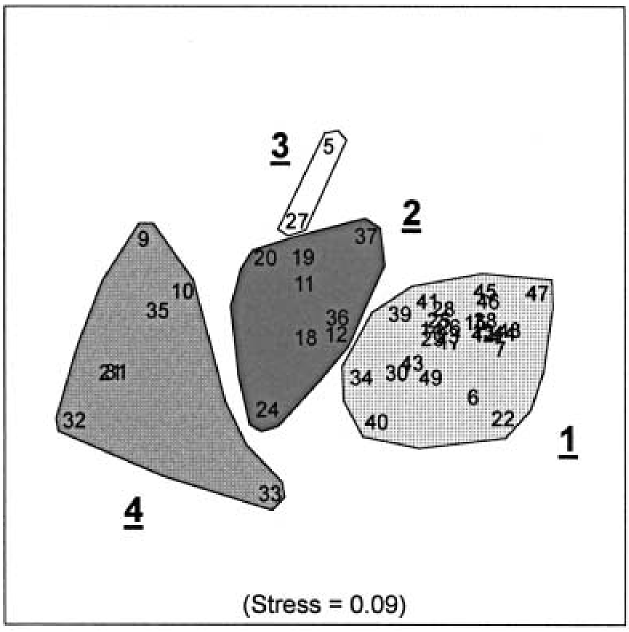

Figure 2. Two dimensional MDS-ordination for the particle size composition at each of the 44 stations sampled in April 1996.

The population density and species variety recorded from the grab samples was very variable throughout the survey area. The maximum population density was as high as 3425 individuals per 0.2 m^2 at station 6, and the minimum was only five individuals per 0.2 m^2 at station 10. The mean population density (P) for the survey area as a whole was 610.2 individuals (SD 777.6) per 0.2 m^2 Hamon grab sample. Similarly the number of species (S) showed considerable variation from a maximum of as many as 94 species at station 7, to a minimum of five species at station 10. The average taxonomic diversity for the survey area as a whole was 37.6 (SD 24.8) species, a value that compares with 39–49 species per replicate grab sample of 0.1 m^2 recorded for coastal deposits to the west of Plymouth (Parry et al., 1999).

Values for the biomass (B) also showed considerable variations. A maximum of 23.51 g AFDW per 0.2 m^2 was recorded from station 50 and a minimum of 0.01 g AFDW from station 10. The average for the survey area as a whole was 2.2 g AFDW (SD 3.78) per 0.2 m^2.

Community composition

A group average sorting dendrogram showing the percentage similarity of the macrofauna at 44 of the stations sampled is shown in Figure 4. The corresponding two-dimensional MDS ordination is shown in Figure 5.

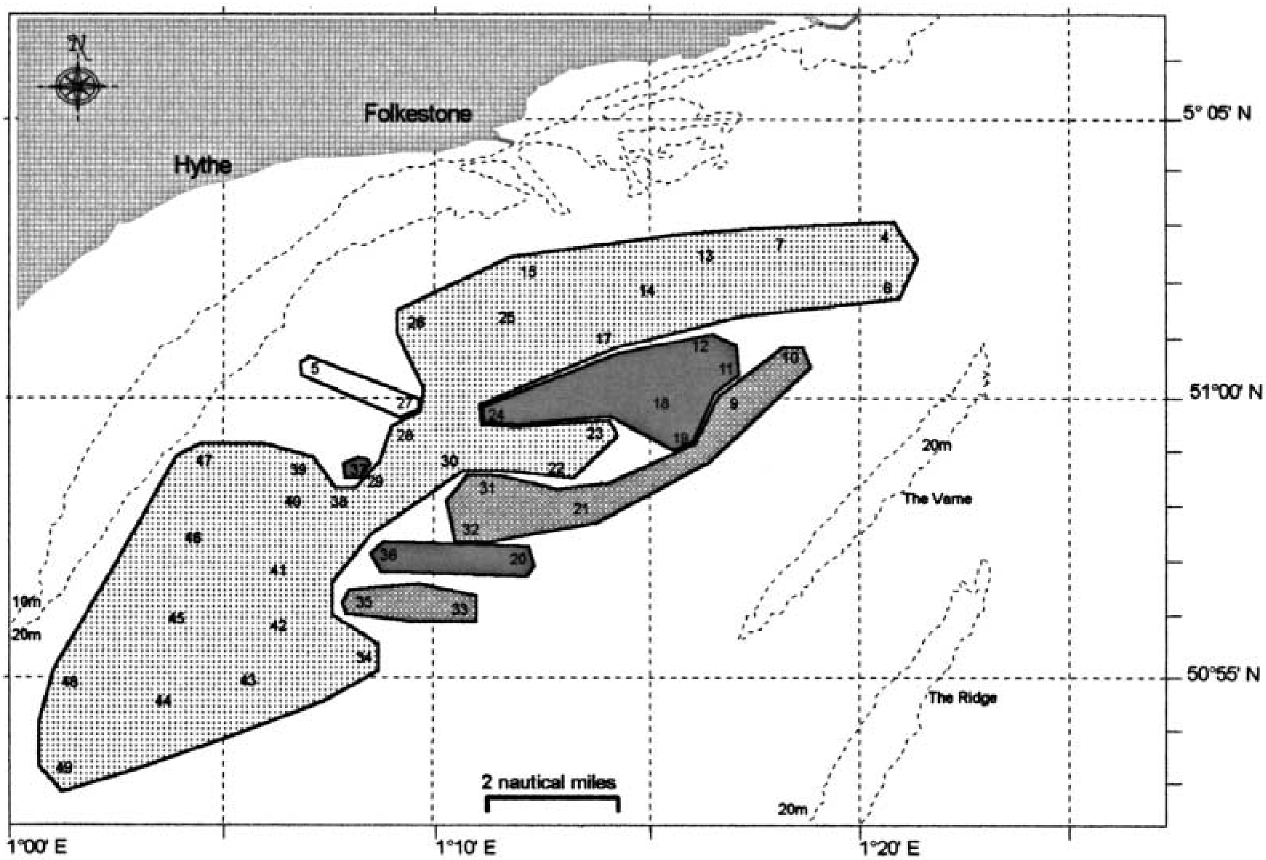

Figure 3. Map of the survey area showing the distribution of the sediment groups identified by multivariate techniques. Based on Figures 1 & 2.

https://doi.org/10.1017/S0025315401003344 Published online by Cambridge University Press

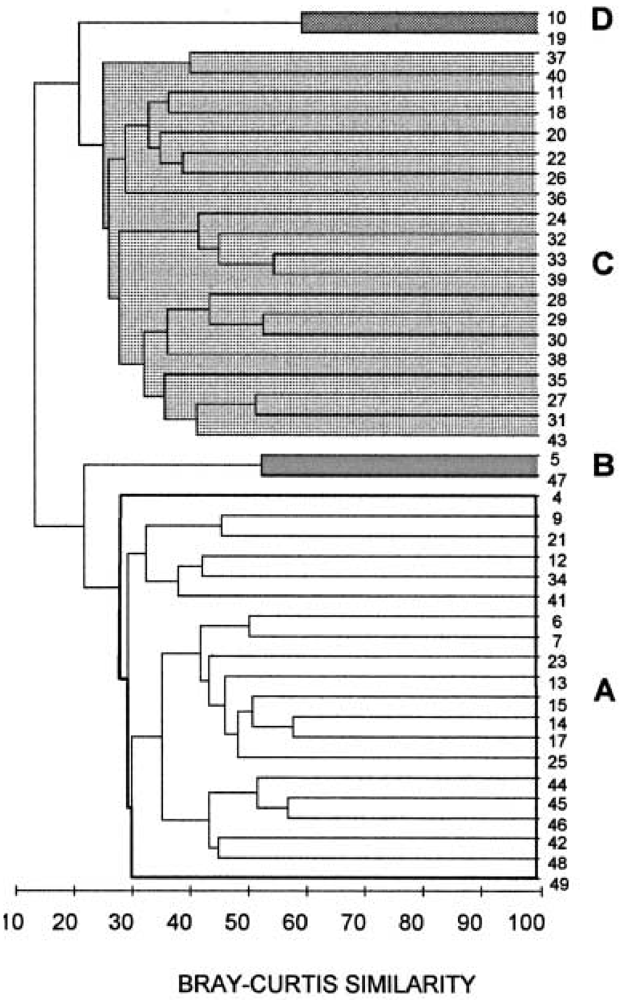

Figure 4. Group average sorting dendrogram showing the percentage similarity of the macrofauna at each of 44 stations sampled in April 1996.

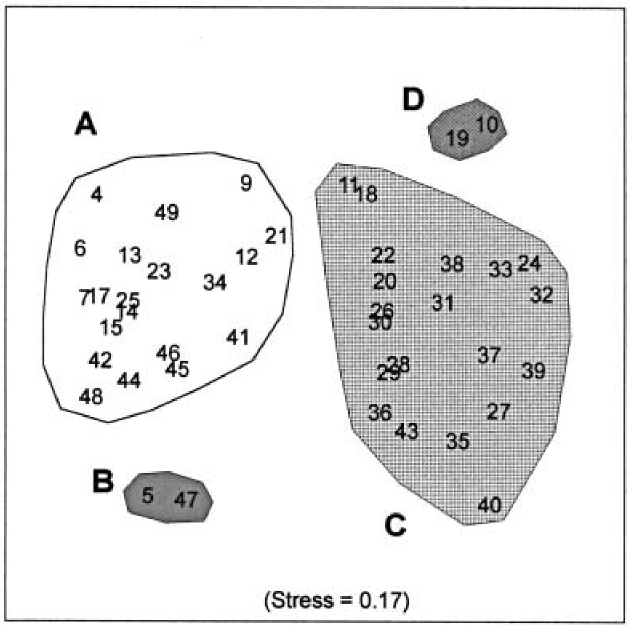

Figure 5. Two dimensional MDS-ordination for the macrofauna at each of the 44 stations sampled in April 1996.

Essentially the biological communities comprise a major group A, a small group B community, a large group C community and a small group D community. These faunal groups, or communities are well-separated on the MDS ordination which shows a stress level of only 0.17. This suggests that the faunal groups are highly distinct.

It is clear from the similarity dendrogram shown in Figure 4, however, that the internal similarity between the faunal assemblages at each of the sampling stations was low. Variability between community composition of macrobenthos samples has also been recorded in deposits of the Hastings Shingle Bank by Kenny (1998) and in a survey of the benthos of sands and gravels in the southern North Sea off Orford Ness by Seiderer & Newell (1999). A probable explanation for this station-to-station variability is discussed below.

The distribution of the main communities of macrobenthos in the survey area is shown in Figure 6. From this it is clear that the group A community occurs in deposits at the north-east and south-west of the survey area. Community B inhabits the fine deposits of near shore stations whilst the group C community occupies the deposits of the central part of the survey area. Finally the small Group D community occupies deposits on the eastern boundary of the survey area.

Relation between particle size composition and distribution of benthos

The relation between sediment composition and the four main faunal groups identified by multivariate analysis is summarized in Figure 7. This shows values for the relative percentages of large particles $>16{,}000\,\mu$m, gravel, sand and silt in the samples. These data have been superimposed on to the MDS plots for macrobenthic communities in the deposits. It is clear that there is some general correspondence between the type of deposit and the biological communities recorded in our survey. There is also a clear association between particular species and deposit type.

Figure 7 shows that the group A macrobenthic community is associated with sands, gravels and pebbles. In contrast, the group B community is associated mainly with deposits that contain significant proportions of sand and silt. The group C community is associated with sandy gravels whilst the group D community is associated mainly with sands. Figure 7 also shows that the polychaete *Sabellaria spinulosa* is mainly confined to the group A community and is associated with coarse gravels and sands. In contrast, the amphipod *Ampelisca tenuicornis* is confined to the group B community and is associated with fine silty deposits.

Despite the general association between the fauna in the survey area and coarseness of the deposits, the distribution of macrobenthic communities shown in Figure 6 and that for the sediments (Figure 3) show no clear correspondence. The relationship between sediment composition and biological community structure is summarized in Table 1. This shows the combinations of sediment particle size distribution that yield the best matches of faunal and sediment similarity matrices. The weighted Spearman rank correlation (ρ_ω) for the group A faunal community and coarser particles from 250–2000 μm was 0.441, but all other groups of macrobenthos showed a much lower correlation with particle

https://doi.org/10.1017/S0025315401003344 Published online by Cambridge University Press

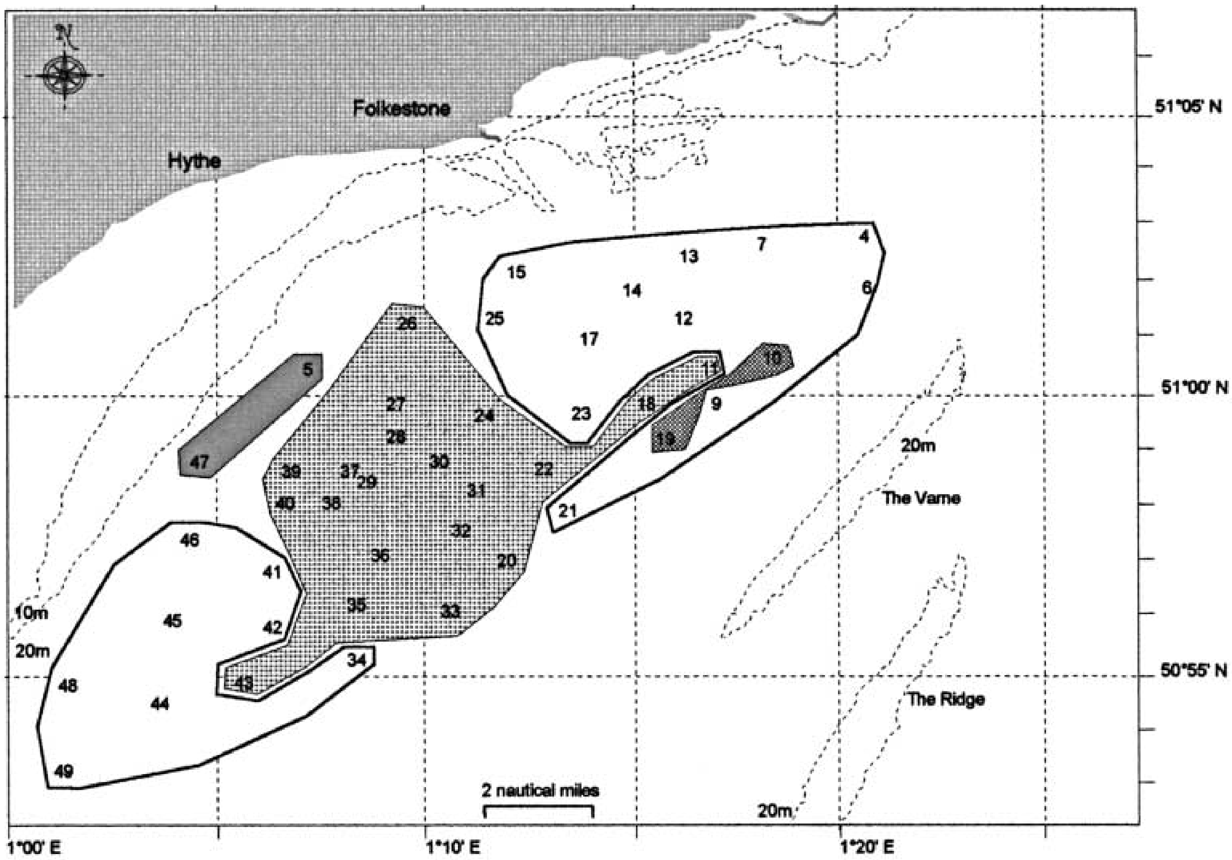

Figure 6. Map of the survey area showing the distribution of the macrofaunal communities identified by multivariate techniques. Based on Figures 4 & 5.

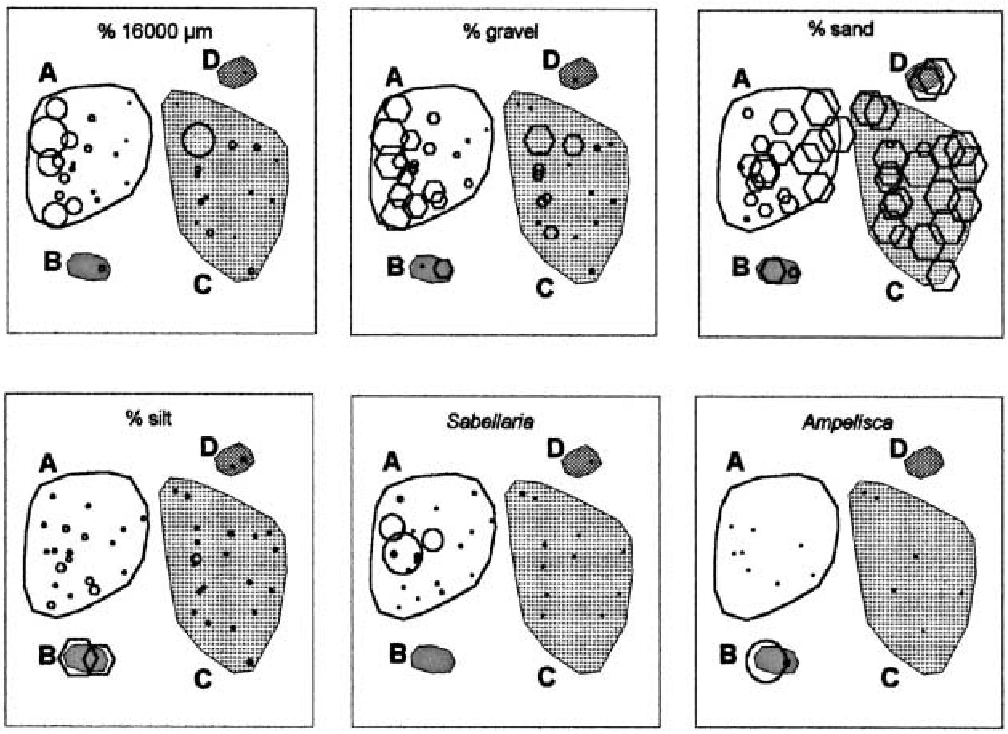

Figure 7. Relationship between the four major macrofaunal groups and type of deposit. The occurrence of *Sabellaria* sp. and *Ampelisca* sp. within the main faunal communities identified in Figures 4 & 5 is also shown.

https://doi.org/10.1017/S0025315401003344 Published online by Cambridge University Press

Table 1. *The optimum combinations of environmental variables yielding the best matches of environmental similarity matrices for benthic faunal groups and sediment composition, as measured by weighted Spearman rank correlation* ρ_{ω}.

Faunal groups	Variables	Optimum variable combinations	ρ_{ω}
A+B+C+D	Particle size class	8000 μm, 250 μm, 125 μm	0.175
	Per cent composition	% silt, % sand, % gravel	0.156
A	Particle size class	2000 μm, 1000 μm, 500 μm, 250 μm	0.441
	Per cent composition	% sand	0.227
B	(Too few stations)		
C	Particle size class	<63 μm	0.174
	Per cent composition	% silt	0.174
D	(Too few stations)		

Particle size classes: >16,000 μm, 16,000–8000 μm, 8000–4000 μm, 4000–2000 μm, 2000–1000 μm, 1000–500 μm, 500–250 μm, 250–125 μm, 125–63 μm, <63 μm; percentage composition: % silt, % sand, % gravel.

size distribution of 0.156–0.227. This implies that factors other than particle size composition are mainly responsible for macrobenthic community composition in the sands and gravels of the survey area.

Biological community structure

Differences in distribution of numbers of individuals among the species that comprise benthic communities can be illustrated by means of distribution plots such as *k*-dominance curves (see Lambshead et al., 1983; Warwick, 1993). Figure 8 shows a series of *k*-dominance curves plotted for the macrofauna in the four sediment groups identified by multivariate analysis of particle size distribution in the deposits (Figures 1 & 2).

This shows that the gravels comprising group 1 deposits in the central part of the survey area support a large variety of macrofauna comprising almost 300 taxa. The relative contribution of each species to the overall population density is relatively even throughout the entire spectrum of species. Deposits in the group 2 sediments are characterized by a macrobenthic community that has fewer taxa in total, but the contribution of each species to the overall population density is also relatively even throughout the species spectrum.

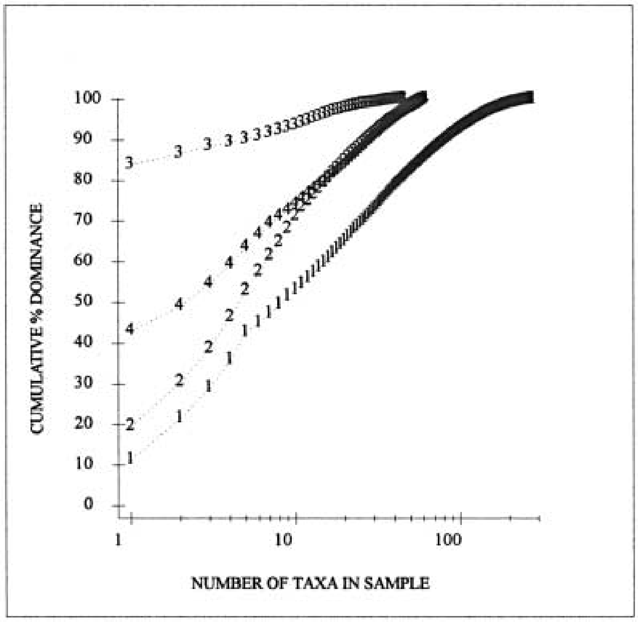

Figure 8. *k*-dominance curves for the macrofauna in the four sediment groups identified by multi-variate analysis of particle size distribution (see Figures 1 & 2).

The group 4 deposits have a similar species variety to the group 2 deposits, but in this case there is increasing dominance by a few species. Figure 8 shows that one species (*Balanus crenatus*) contributes >40% of the population of the group 2 deposits, three species (*Balanus crenatus*, *Nephthys cirrosa* and *Spiophanes bombyx*) >50% and over 70% of the population by less than ten of the total of the approximately 60 species present.

Finally, the fine silty sands represented by the near shore group 3 deposits also have a relatively high macrofaunal species complement of approximately 40 taxa. But in this case >80% of the population is represented by one species (*Ampelisca tenuicornis*) recorded at station 5. A high dominance by one or a few species is characteristic of mobile deposits and has been used as an index of both natural disturbance and the impact of man on benthic biological communities (see Warwick, 1993; Clarke & Warwick, 1994).

Implications for benthic sampling strategies

Figure 9 shows a series of 'species discovery curves' for the macrofauna in sediment groups 3, 4, 2 & 1. The species recorded have been plotted as a cumulative curve showing the additional taxa recorded in a series of samples that comprise each group of sediments shown in Figures 1 & 2. The samples have been arranged in decreasing order of additional species discovered in deposits comprising the fine silts and mud of the group 3 deposits, the mixed sands and stones of sediment groups 4 & 2 and the gravels of sediment group 1.

Figure 9 shows that the total number of species, as judged from the point at which no further taxa were discovered despite further replicate samples, is as high as 80 even in the muddy sands of the survey area. This is comparable with data recently reported for muddy coastal sediments at Jennycliff Bay and Cawsand Bay near Plymouth, Devon by Parry et al. (1999). The corresponding values in the sands and gravels of the groups 2 & 4 deposits was 60–70 taxa. In contrast, the coarser gravel deposits supported a total species complement of as many as 320 taxa, probably reflecting the increased habitat complexity of coarser gravel deposits.

https://doi.org/10.1017/S0025315401003344 Published online by Cambridge University Press

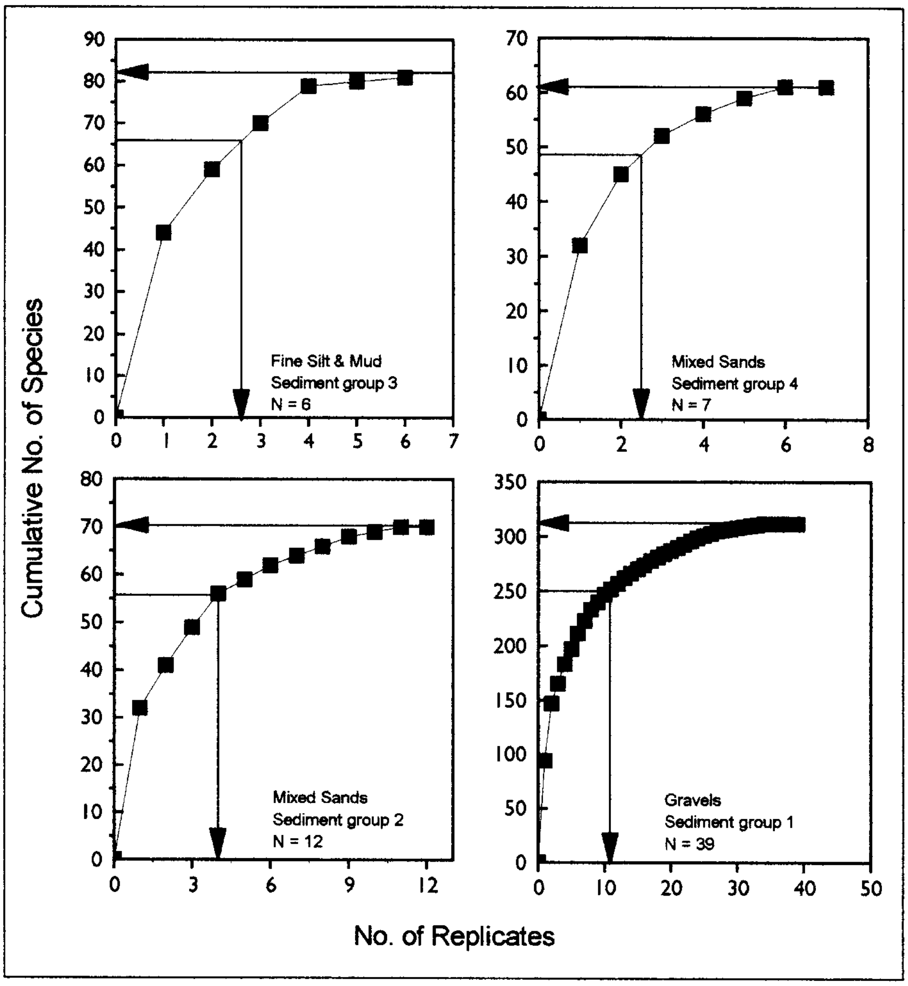

Figure 9. Cumulative 'species discovery curves' for the macrofauna in the four sediment groups identified by multi-variate analysis of particle size distribution (see Figures 1 & 2). Note that the curve for sediment group 3 has not reached an asymptote and is therefore an estimate.

The number of replicate samples required to identify 80% of the taxa that actually occur in the deposits is clearly related to sediment type. In the case of fine silts and muds that are dominated by one or a few taxa, only 2–3 replicate samples of 0.2 m^2 are required to discover at least 80% of the species present in the deposits even if the species complement is as high as 80 taxa. Recalculation of the data from Parry et al. (1999) suggest that approximately three replicate samples would also be required to define 80% of the species complement in muddy coastal deposits in the western English Channel.

Where the sediments support a community whose population has a more even species distribution, as in the case of sediment group 2 (see Figure 8), more replicate samples are required to establish 80% of the taxa in the sample, even though the total taxa recorded was lower than in either the muds or sands of groups 3 & 4 sediments. Clearly, both taxonomic diversity and the distribution of species within the population, affect the number of samples required to identify at least 80% of the taxa present in the deposits.

Finally, in sands and gravels comprising the group 1 sediments there is a combination of both a very high taxonomic diversity and a relatively even representation of the component species in the population. In this case at least ten replicates are evidently required to satisfactorily identify 80% of the taxonomic diversity in the sediments.

DISCUSSION

The results that have been cited above show that the data for particle size composition of the sediments fall into well-defined groups that show a high level of internal similarity between stations in any one group. In contrast, whilst the data for samples of macrobenthos also fall into well-defined groups or communities, there is considerable sample-to-sample variability in species numbers (S), population density (N) and biomass (B). Similar results have been obtained for gravel and sand deposits off Hastings, Kent by Kenny (1998) and off Orford Ness, Suffolk (Seiderer & Newell, 1999).

A probable explanation for the clear separation of the macrofaunal groups that occurs despite the variability of the samples used in the multivariate analysis of community composition, is that there is a high degree of 'redundancy' in the species that characterize community composition (Clarke & Warwick, 1998). Gray et al. (1988) showed, for example, that ordinations for macrobenthic community structure at six stations in Frierfjord, Norway, were similar to the results for the entire species complement even when only 20% of the species, selected at random, were used in the analyses. Each of the single samples taken evidently contains sufficient taxa to define the community from which the sample was taken, despite the under-sampling incurred by use of a 0.2 m^2 Hamon grab in the complex communities of macrobenthos that occur in coastal gravel deposits (see also Whitlatch, 1981; Morse et al., 1985).

Our results support the view that a high diversity of species that are uniformly represented in the population may lead to serious under-sampling of the macrofauna by conventional methods such as the 0.2 m^2 Hamon grab commonly used in benthic surveys of sands and gravels. Estimates of species numbers, population density, biomass and indices that depend directly on these are likely to be heavily dependent on the number of replicate samples taken, the type of deposit, the number of taxa present the distribution of species within the population and probably the size of grab sample taken (see also Warwick & Clarke, 1995, 1996).

The conclusion from our survey of the macrobenthos of sands and gravels off Folkestone, Kent is that multivariate analyses of community composition are evidently robust, and give a clear separation of faunal groups based on single samples, despite variability in the data between stations in the survey area. However, several subsamples are evidently required for assessment of indices that depend on species composition and distribution of species within the macrobenthic population. The results show that at least three replicate samples with a conventional 0.2 m^2 Hamon grab are required to obtain a satisfactory assessment of the species composition of the macrobenthos of sands and muds, but ten or more replicates are required for gravels.

We are grateful to Mr Graham Singleton of South Coast Shipping, Southampton, for permission to cite the data reported here.

REFERENCES

Buchanan, J.B., 1963. The bottom fauna communities and their sediment relationships off the coast of Northumberland. *Oikos*, **14**, 154–175.

Cabioch, L., 1968. Contribution a la conaissance des peuplements benthiques de la Manche occidentale. *Cahiers de Biologie Marine*, **9** (Supplement), 493–720.

Clarke, K.R. & Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, **92**, 205–219.

Clarke, K.R. & Warwick, R.M., 1994. *Change in marine communities: an approach to statistical analysis and interpretation*. Swindon: Natural Environment Research Council.

Clarke, K.R. & Warwick, R.M., 1998. Quantifying structural redundancy in ecological communities. *Oecologia*, **113**, 278–289.

Dalfsen, J.A. van, Essink, K., Toxvig Madsen, H., Birklund, J., Romero, J. & Manzanera, M., 2000. Differential response of macrozoobenthos to marine sand extraction in the North Sea and the western Mediterranean. *ICES Journal of Marine Science*, in press.

Dankers, N. & Beukema, J.J., 1981. Distributional patterns of macrozoobenthic species in relation to some environmental factors. In *Invertebrates of the Wadden Sea* (ed. N. Dankers et al.), pp 69–103. Rotterdam: A.A. Balkema.

Day, J.H., Field, J.G. & Montgomery, M.P., 1971. The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. *Journal of Animal Ecology*, **40**, 93–126.

Duineveld, G.C.A. & Noort, G.J. van, 1990. Geographical variation in the epifauna of the southern North Sea and adjacent regions. *International Council for the Exploration of the Sea (CM Papers and Reports)*, CM 1990/Mini, **9**, 11 pp.

Eleftheriou, A. & Basford, D.J., 1989. The macrobenthic infauna of the offshore northern North Sea. *Journal of the Marine Biological Association of the United Kingdom*, **69**, 123–143.

Field, J.G., Clarke, K.R. & Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**, 37–52.

Gray, J.S., Aschan, M., Carr, M.R., Clarke, K.R., Green, R.H., Pearson, T.H., Rosenberg, R. & Warwick, R.M., 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. *Marine Ecology Progress Series*, **66**, 285–299.

Hensley, R.H., 1996. Preliminary survey of benthos from the *Nephrops norvegicus* mud grounds in the north-western Irish Sea. *Estuarine, Coastal and Shelf Science*, **42**, 457–465.

Holme, N.A., 1961. The bottom fauna of the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **41**, 397–461.

Holme, N.A., 1966. The bottom fauna of the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **46**, 401–493.

Holme, N.A. & McIntyre, A.D., 1984. *Methods for the study of marine benthos*. International Biological Programme Handbook no. 16, 2nd ed. Oxford: Blackwell Scientific Publications.

Holme, N.A. & Wilson, J.B., 1985. Faunas associated with longitudinal furrows and sand ribbons in a tide-swept area in the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 1051–1072.

Kenny, A.J., 1998. A biological and habitat assessment of the sea-bed off Hastings, southern England. Report of the Working Group on the Effects of the Extraction of Marine Sediments on the Ecosystem. Annex IV, Item 6. *International Council for the Exploration of the Sea (CM Papers and Reports)*, CM 1998/E:5, 10 pp.

Künitzer, A. et al., 1992. The benthic infauna of the North Sea: species distribution and assemblages. *ICES Journal of Marine Science*, **49**, 127–143.

Lambshead, P.J.D., Platt, H.M. & Shaw, K.M., 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History*, **17**, 859–874.

Mackie, A.S.Y., Oliver, P.G. & Rees, E.I.S., 1995. Benthic biodiversity in the southern Irish Sea. *Studies in marine biodiversity and systematics from the National Museum of Wales. BIOMAR Reports*, no. 1, 263 pp.

Morse, D.R., Lawton, J.H., Dodson, M.M. & Williamson, M.H., 1985. Fractal dimension of vegetation and the distribution of arthropod body length. *Nature, London*, **314**, 731–733.

Parry, D.M., Kendall, M.A., Rowden, A.A. & Widdicombe, S., 1999. Species body size distribution patterns of marine benthic macrofauna assemblages from contrasting sediment types. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 793–801.

Rees, E.I.S., 1987. Benthos. In *Irish Sea status report of the marine pollution monitoring management group* (ed. R.R. Dickson), pp. 29–31. Lowestoft: MAFF. [Aquatic Environment Monitoring Report, MAFF, Directorate of Fisheries Research, Lowestoft, no. 17.]

Rees, E.I.S. & Walker, A.J.M., 1991. Indications of temporal variability in the benthos of Liverpool Bay. In *Estuaries and coasts: spatial and temporal intercomparisons* (ed. M. Elliott and J.-P. Ducrotoy), pp. 217–220. Fredensborg, Denmark: Olsen & Olsen.

Rees, H.L., Pendle, M.A., Waldock, R., Limpenny, D.S. & Boyd, S.E., 1999. A comparison of benthic biodiversity in the North Sea, English Channel, and Celtic Seas. *ICES Journal of Marine Science*, **56**, 228–246.

Salzwedel, H., Rachor, E. & Gerdes, D., 1985. Benthic macrofauna communities in the German Bight. *Veröffentlichugen des Institüt Meeresforschungin Bremerhaven*, **20**, 199–267.

Sanvicente-Anorve, L., Lepretre, A. & Davoult, D., 1996. Large-scale spatial patterns of the macrobenthic diversity in the eastern English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **76**, 153–160.

Seiderer, L.J. & Newell, R.C., 1999. Analysis of the relationship between sediment composition and benthic community structure in coastal deposits: implications for marine aggregate dredging. *ICES Journal of Marine Science*, **56**, 757–765.

Sips, H.J.J. & Waardenburg, H.W., 1989. The macrobenthic community of gravel deposits in the Dutch part of the North Sea (Klaverbank). Ecological impact of gravel extraction. *Reports of the Bureau Waardenburg bv, Culemborg, The Netherlands*, 34 pp.

Warwick, R.M., 1993. Environmental impact studies on marine communities: pragmatical considerations. *Australian Journal of Ecology*, **18**, 63–80.

Warwick, R.M. & Davies, J.R., 1977. The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to the substrate. *Estuarine, Coastal and Marine Science*, **5**, 267–288.

Warwick, R.M. & Uncles, R.J., 1980. The distribution of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. *Marine Ecology Progress Series*, **3**, 97–103.

Whitlatch, R.B., 1981. Animal–sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. *Journal of Experimental Marine Biology and Ecology*, **53**, 31–45.

Submitted 13 March 2000. Accepted 23 October 2000.