PERGAMON Continental Shelf Research 18 (1998) 1347–1363

CONTINENTAL SHELF RESEARCH

Influence of benthic macrofauna on the geotechnical and geophysical properties of surficial sediment, North Sea

A.A. Rowden[a,b,*], C.F. Jago[c], S.E. Jones[c]

[a] *Department of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK*
[b] *CCMS Plymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK*
[c] *School of Ocean Sciences, University of Wales, Bangor, Marine Science, Laboratories, Menai Bridge, Gwynedd, LL59 5EY, UK*

Received 8 January 1993; received in revised form 3 March 1995; accepted 27 March 1998

Abstract

Spatial and temporal variations in the structure of an *Amphiura-Echinocardium* macrobenthic community were studied in relation to geotechnical and geophysical properties of the seabed at a muddy-sand site in the seasonally stratified region of the southern North Sea. Vertical profiles of geotechnical properties were recorded in sediments collected by box corer. Maxima in water, organic matter, and fine particle contents coincided with the presence of the burrowing brittle star *Amphiura filiformis* and the mud shrimp *Callianassa subterranea* in the upper and lower parts, respectively, of the cores. A significant relationship existed between the abundance of *A. filiformis* and the water content of the upper 0.05 m of the bed. There were important temporal variations in rigidity modulus, derived from acoustic shear wave propagation in freshly recovered cores, of the upper 0.06 m of the sediment. The rigidity modulus was 45% greater in January than in May and this has been related to the burrowing/feeding activity of the macrobenthic community; there was an inverse relationship between *A. filiformis* abundance and bed rigidity. Thus the bed had a lower bulk density and lower rigidity in summer due to biological modification of the sediment fabric. This implies that the bed was less resistant to erosion in the summer. Such an effect may be important during summer storms in the shallowest parts of the seasonally stratified zone (ie close to shelf fronts). © 1998 Elsevier Science Ltd. All rights reserved

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*Corresponding author.

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PII: S0278-4343(98)00047-8

1. Introduction

The influence of burrowing organisms on the properties of the substratum in which they reside has long been recognised (Darwin, 1881; Dapples, 1942). Previous studies have demonstrated the range, extent and mechanics of biogenic influence on the geotechnical properties of marine sediments,particularly cohesive sediments (Rhoads, 1974; Richards and Parks, 1976; Lee and Swartz, 1980; Rhoads and Boyer, 1982). Furthermore, laboratory and field studies have emphasised the importance of properties such as sediment shear strength, water and organic matter contents as predictive determinants of, for example, threshold shear stress and erosion rate (Postma, 1967; Gulararte et al., 1980). So there can be little doubt that macrobenthic fauna, especially deposit feeding species in high abundance, modify those properties that govern the erodibility of cohesive sediment beds by intensively reworking the upper few centimetres of the substratum (Rhoads and Young, 1970; Young, 1971; Myers, 1977; Yingst and Rhoads, 1978; Anderson, 1983, Meadows and Tait, 1989; Meadows and Meadows, 1991). A few studies have identified relationships between specific types of bioturbation and bed erodibility (Young and Southard, 1978; Nowell et al., 1981; Grant et al., 1982).

There is a lack of field data in the literature and this reflects the obvious difficulties of making non-destructive *in situ* measurements of biological effects. However, it has been shown that the geoacoustic properties of marine sediments are extremely sensitive to biological effects (Richardson, 1983; Richardson et al., 1983). Furthermore, individual burrowing habits produce changes to sediment properties that can be identified by both acoustic and electrical geophysical techniques (Jones and Jago, 1993).

The aims of this work were twofold: (1) to use geophysical techniques to assess the importance of biological controls of sediment properties; (2) to assess the temporal (seasonal) variability of biologically modulated sediment properties. This formed part of an interdisciplinary study of sediment resuspension in the southern North Sea (see Morris and Howarth, 1998). Our aim was to measure biological impacts on sediment properties at a site where the substratum was cohesive and the macrobenthic density was high. A companion study investigated in more detail the role of a single species (*Callianassa subterranea*) in sediment resuspension (Rowden et al., 1998).

2. Materials and methods

2.1. Experimental site

The chosen site was located in the southern North Sea at 54° 35′N, 04° 50′E in 47 m of water and was characterised by a seasonally stratified water column over a seafloor composed of muddy-sand (median grain size = 100 μm). This was Site B in Morris and Howarth (1998) and was close to the transition from tidally stirred to seasonally stratified waters. The site covered an area of one square sea mile and included a twenty-five point sampling grid from which five positions were randomly chosen for benthic studies (numbered 1, 5, 13, 23 and 25).

2.2. Shipboard sampling

Samples were taken during the three main cruises with R.R.S. Challenger in January, May, and September 1989, with an additional opportunistic visit being made in October 1989.

2.2.1. Sediment/macrobenthos sampling

A USNEL box corer (which recovers a portion of undisturbed seabed with a surface area of 0.25 m^2 to depths of 0.3–0.4 m) was used once at each of the five stations. For each core, sediment temperature at a depth of 0.1 m was recorded using a digital probe and a visual assessment of surface sediment conditions (relief and consistency, faecal matter, faunal burrows/traces, the presence of living or dead fauna) was made. Five subcores (0.1 m diameter, 0.3 m length) were then removed for macrofauna analysis, each being ‘puddled’ with sea water before being poured through a 0.5 mm sieve (only two in January). The material retained on the mesh was gently washed with sea water to remove excess sediment and the residue was stored in pots containing 4% buffered formaldehyde. Another subcore (0.65 m diameter, 0.25 m length) was taken for laboratory analysis of water content, organic matter content and particle size analysis. This was immediately frozen (−20°C). The remaining contents of the box were examined for signs of vertical distributions of fauna and sediment structure. Finally, the sediment was washed and sieved through a 1 mm mesh and the residue was stored in pots containing 4% buffered formaldehyde solution.

2.2.2. Acoustic measurements

Acoustic shear wave velocity was measured using piezo-electric ceramic bender transducers as both shear-wave source and receiver (see Jones and Jago (1993) for details of measurement techniques). The transducers were designed to produce minimal sediment disturbance as they are pushed into the sediment to a depth of 0.04 m. Using a transducer separation of 0.05 m, the shear wave propagation is influenced by sediment properties to a maximum depth of 0.6 m. Measurements were made in freshly recovered box cores before any subsampling; cores that were visibly disturbed (scour, slumping) were rejected. Four measurements were made in each box core, in complementary pairs in order to check for anisotropy. All measurements were made in water saturated sediments; this was essential as rigidity and shear strength rapidly increase as a sediment drains.

2.3. Laboratory sample treatment

Samples were transported by road to the Plymouth Marine Laboratory (frozen samples were stored in a box containing dry ice) and analysed as follows:

2.3.1. Macrofauna

A solution of Rose Bengal (a protein stain which aids the identification of organic matter) was added to the pots containing the macrofauna, and the contents washed and sieved (0.5 mm) to remove most of the sediment. Material retained was transferred to a white plastic tray and covered with freshwater. Faunal remains were hand sorted, placed in petri dishes of preservative (70% ethanol) and identified, counted, measured and sexed (where possible) using Wild binocular (×10) and Zeiss compound (×25, ×40) microscopes. The subcores were used to determine the densities of the smaller and more abundant species, whilst the remainder of the box-core sample was used to enumerate the larger and rarer members of the macrofauna.

2.3.2. Sediment

The five subcores for sediment analysis were partially defrosted, extruded and the upper 0.02 m was sliced into 0.01 m sections. Each section was divided into three approximately equal portions and the following determinations made: (1) water content – the sediment was first weighed to an accuracy of 4 decimal places, dried in an oven overnight (100°C) and reweighed to constant weight. Water content was assumed to be the weight loss as a percentage of the original wet weight of sediment; (2) organic content – a 4–6 g portion of dried sediment (100°C overnight) was ground using a mortar and pestle, weighed and transferred to a china crucible and placed in a muffle furnace for 4 h at 550°C, and reweighed to constant weight to an accuracy of 4 decimal places. Organic content was assessed as the weight loss on ignition as a percentage of the original dry weight of the sediment; (3) particle size – the dry sieving technique described by Buchanan (1984), was used with a series of sieves of mesh size 1.0, 0.5, 0.25, 0.125, 0.063 mm. This method provided the mean particle diameter and grading of the sediment on the Wentworth scale. Unfortunately, no analysis of sediment samples taken in January was possible because of loss during storage.

2.4. Statistical analysis of benthic community data

To clarify temporal changes in the macrobenthic community between the three main sampling times, species abundance data were subjected to multivariate statistical analysis. Differences in community structure were determined using multidimensional scaling ordination (MDS) of double square root-transformed species abundance data, using the Bray–Curtis similarity measure (Warwick and Clarke, 1991). This multivariate method was used in preference to univariate statistical techniques because it allows for a comparison of communities on the basis of the identity of the component species as well as of their abundance. The significance of any observed differences in macrobenthic community structure between sampling times was assessed by one-way 'analysis of similarities' (ANOSIM). This programme computes a statistic (R) reflecting the average rank dissimilarity between replicate samples collected at one time, subtracted from the average dissimilarity between samples collected at other times (Clarke and Green, 1988). Application of the 'similarity percentages program' (SIMPER) described by Warwick et al. (1990) identified those species making the greatest contribution to differences between sampling times observed in the ordination result.

3. Results

3.1. The macrobenthic community

The faunal compositions at the study site (Appendices A–C) indicate that the macrobenthic assemblage can be classified as an *Amphiura-Echinocardium* community. A two-dimensional configuration plot of the MDS ordination carried out on the macrofaunal abundance data from the study site is illustrated by Fig. 1. Such a plot is a visual representation of the dissimilarity measured by the MDS analysis between each sample (all stations, all months). Samples which are similar in macrofaunal composition will appear closer together, whilst samples which are dissimilar will be relatively further apart. Fig. 1 clearly illustrates the 'clustering' exhibited by samples from the same month. In essence, the plot suggests that the five samples taken in the same month are more similar to one another than are the samples taken from the same stations between months. A wider 'cluster spread' for samples taken in January probably reflects the fact that faunal abundance was calculated from two replicate subcores (rather than five) for this month. The results of the ANOSIM test (Table 1) show that there are indeed statistically significant differences in community structure between the three main study occasions ($P \leqslant 0.01$). The dissimilarity in community structure is greatest between the months of January and September ($R = 0.84$), whilst the macrobenthic assemblage is the least dissimilar between September and May ($R = 0.54$). The most notable difference in the study site's macrofauna community structure, evident between January and May/September, appears to be related to changes in the abundance of *Callianassa subterranea*. However, SIMPER identified

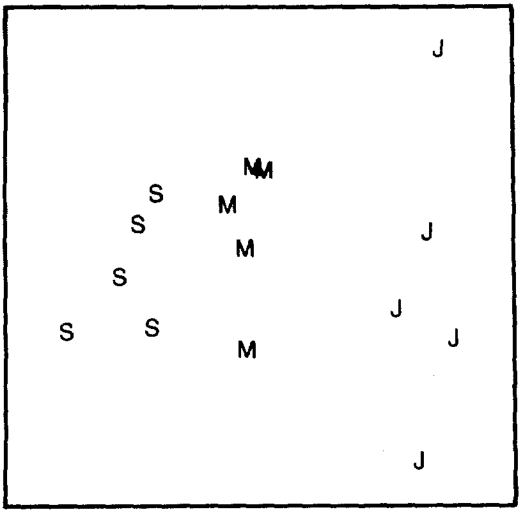

Fig. 1. Two-dimensional plot of Multi-Dimensional Scaling (MDS) configuration for macrofauna abundance (J = January, M = May, S = September, 1989).

Table 1
One-way ANOSIM test for differences between sampling occasions on the Bray–Curtis similarity matrix using double root transformed study site abundance data

Sample months compared	*R* statistic	*P*
May–January	0.61	<0.01
September–January	0.84	<0.01
September–May	0.54	<0.01

Table 2
Mean abundance (*a*) of study site macrofaunal species averaged between months

Species	*a*	*a*	δi	$\delta i\%$	$\Sigma\delta i\%$
	May	Jan.			
Callianassa subterranea	1.80	0.00	3.55	5.61	5.61
Harpinia antennaria	0.84	0.00	2.96	4.69	10.30
Aricidea minuta	0.80	0.00	2.83	4.48	14.78
Paraonis fulgens	0.00	0.35	2.15	3.39	18.17
Caulleriella caputesocis	0.48	0.10	2.07	3.27	21.44
Synelmis klatti	1.00	0.30	2.04	3.22	24.66
	Sept.	Jan.			
Callianassa subterranea	3.60	0.00	4.32	6.18	6.18
Ampharete juv. indet.	1.96	0.00	2.48	3.54	9.72
Paraonis fulgens	0.00	0.50	2.22	3.18	12.90
Corbula gibba	0.20	1.70	2.13	3.05	15.95
Pholoe minuta	0.36	0.00	2.07	2.96	18.91
Glycera rouxii	0.20	0.90	2.00	2.87	21.78
Harpinia antennaria	0.28	0.00	1.92	2.75	24.53
	Sept.	May			
Ampharete juv. *indet.*	1.96	0.00	1.83	3.52	3.52
Nephtys caeca	0.00	0.28	1.46	2.80	6.32
Philine scabra	0.40	0.00	1.43	2.75	9.07
Nermertean indet.	0.52	0.16	1.28	2.46	11.53
Mysella bidentata	1.04	3.24	1.27	2.44	13.97
Periculodes longimanus	0.36	0.00	1.24	2.38	16.35
Echinocardium cordatum	0.40	0.60	1.24	2.38	18.73
Corbula gibba	0.20	0.92	1.22	2.34	21.07
Glycera rouxii	0.20	0.44	1.20	2.30	23.37

Note: Species are ranked in order of their contribution (δi) to the average Bray–Curtis dissimilarity between months, also expressed as a percentage contribution ($\delta i\%$) and a cumulative percentage ($\Sigma\delta i\%$); a cut-off to the species list is applied at 25% [calculated using 'similarity percentages program' (SIMPER), of WARWICK et al. (1990)].

that those species most responsible (contributing to 25% of the difference) only accounted for 2–6% of the dissimilarity observed (Table 2). The latter analysis indicates that the temporal changes observed in community structure at the study site result from an overall change in the balance of relative species abundances, rather than substantial differences in just a few dominants.

3.2. Sediment properties

Vertical profiles of geotechnical properties in May and September exhibited very similar features (Fig. 2) with an upper region of relatively high values, below which discrete peaks punctuate a depth profile of otherwise lower magnitude. Average values of near-surface (0–0.05 m) water and organic contents were elevationed by of 24 and 11%, respectively, in comparison to mean values for the remaining 0.15 m of the core. A corresponding relationship was not shown by the fine fraction content of the sediment. The September near-surface value was slightly lower (2%) than that for the deeper region, though a comparable degree of difference (12%) was observed in May.

Geophysical properties of the upper 0.06 m of the sediment were generally consistent in all cores at any one time and the most significant differences occurred between

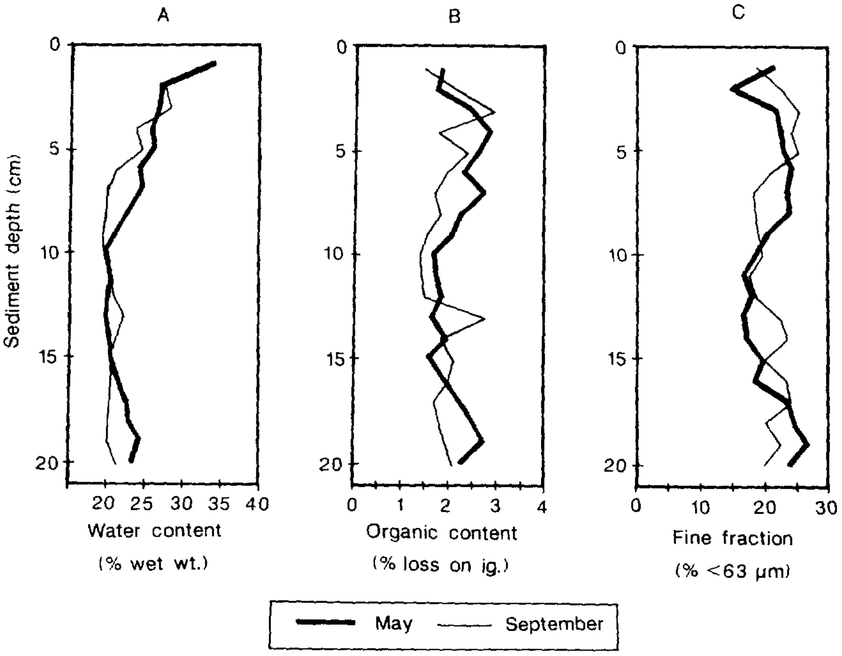

Fig. 2. Sediment geotechnical properties of the study site (example station 25): A. Water content, B. Organic content, C. Particle fine fraction.

sampling periods (Table 3). Shear wave velocities were very similar in May and September (26 and 27 $\mathrm{m\,s^{-1}}$, respectively) but were significantly greater in January (34 $\mathrm{m\,s^{-1}}$).

3.3. Faunal influence on bed properties

Correlation analyses of sediment water contents (0–0.05 m) and macrobenthic faunal abundances produced a highly significant positive relationship ($P \leqslant 1\%$) for the burrowing brittle star *Amphiura filiformis* (Fig. 3). *A. filiformis* resides in small burrows a few centimetres below the sediment surface and uses extended arms to feed on suspended and deposited material. Burrowing and feeding activities modify the fabric and increase mean particle size of the substrata by aggregation of fine particles into faecal pellets (indicated by an increased percent fine fraction when sediment is analysed by dry sieving; unpublished data). Such actions create a more open fabric with a higher water content. Hence it is probable that the observed correlation between *A. filiformis* abundance and water content is a causal relationship.

Table 3
Seasonal changes in abundance of *Amphiura filiformis* and associated sediment properties at the study site for sampling periods in 1989

Sample month	Station and site mean	*Amphiura* density (no. 78.5 $\mathrm{cm^2}$)	Sediment water content (% wet weight)	Sediment shear wave velocity ($\mathrm{m\,s^{-1}}$)
January	1	10.5	—	39.6
	5	7.0	—	34.1
	13	3.0	—	31.1
	23	4.5	—	35.0
	25	2.0	—	32.3
	mean (±SD)	5.4 (3.4)	—	34.4 (2.7)
May	1	14.4	24.8	26.4
	5	20.6	26.6	24.6
	13	9.6	25.7	25.4
	23	11.8	24.0	27.3
	25	17.4	27.6	—
	mean (±SD)	14.8 (4.4)	25.7 (1.4)	25.9 (1.7)
September	1	10.4	22.7	26.1
	5	7.0	25.0	25.8
	13	17.0	30.9	27.7
	23	8.6	24.8	26.6
	25	9.2	27.5	27.1
	mean (±SD)	10.4 (3.9)	26.2 (3.2)	26.7 (1.2)
October	1	13.0	25.2	—
	5	5.4	23.4	—
	13	6.2	21.6	—
	23	16.0	26.2	—
	25	7.8	24.1	—
	mean (±SD)	9.7 (4.6)	24.1 (1.8)	—

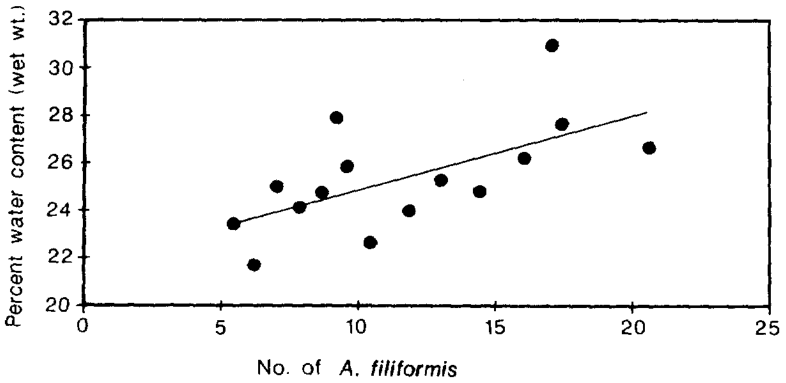

Fig. 3. Relationship between the abundance of the brittle star *Amphiura filiformis* and the water content of the upper 5 cm of sediment at the study site (May, September and October 1989, $n = 15$, $r = 0.642$, $P \leqslant 0.01$).

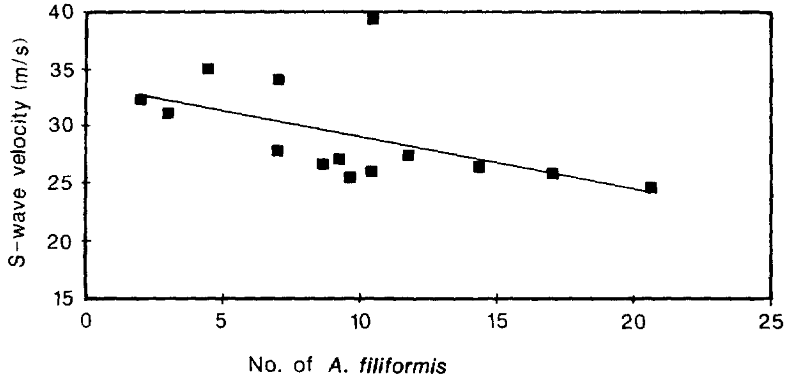

Fig. 4. Relationship between the abundance of the brittle star *Amphiura filiformis* and the shear wave velocity of the surface sediment at the study site (January, May and September 1989, $n = 14$, $r = 0.524$, $P \leqslant 0.05$).

Furthermore, there was a significant inverse relationship ($P \leqslant$ %) between shear wave velocity and *Amphiura filiformis* abundance in the box cores from all three cruise. V_s, and hence bed rigidity, decreased with increasing *A. filiformis* abundance (Fig. 4). Most of this observed variability in bed rigidity was temporal with the greatest change occurring between January and May/September. There were corresponding changes in faunal abundance. In particular, *A. filiformis* abundance increased dramatically in summer. Thus the seabed was most rigid in January when *A. filiformis* was least abundant, and least rigid in May when *A. filiformis* was most abundant (Fig. 5). The implication is that a biological effect controls the seasonal variability of bed rigidity and although we cannot be certain, the presence of *A. filiformis* is the most likely explanation.

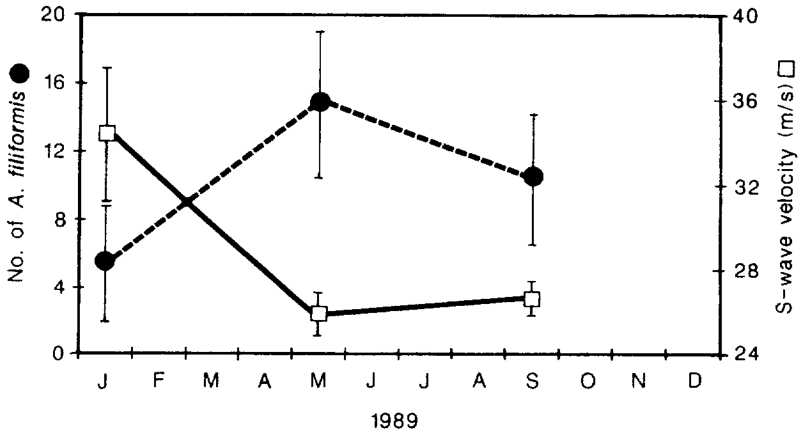

Fig. 5. Relative relationship between the mean abundance of the brittle star *Amphiura filiformis* (circles) and the mean shear wave velocity of the surface sediment (squares) during each of the three main sampling periods (error bars = ± 1SD).

The rapid vertical decrease in water content in the upper 0.01 m of the bed (Fig. 2) must be due, in part, to consolidation of the cohesive sediment. But the near-surface maxima in water, organic and fines contents are probably biologically controlled, presumably by *Amphiura filiformis*. The maxima at greater depths are attributable to the mud shrimp *Callianassa subterranea* which produces burrow tunnels at corresponding depths (Rowden and Jones, 1995).

4. Discussion

The properties of the upper few centimetres of the seabed at the experimental site were clearly modified by the presence/activities of the macrobenthic faunal community. *Amphiura filiformis* appeared to dominate in this respect. The measured temporal changes to bed properties, including acoustic properties, were substantial. The shear wave velocity (V_s) is controlled by the number and nature of particle contacts (i.e. the strength of interparticle forces) in the sediment. It is therefore qualitatively related to the same factors which determine sediment shear strength and it is quantitatively related to the sediment rigidity modulus (μ) by

$$\mu = d_s(V_s)^2 \tag{1}$$

where d_s is the bulk density of the sediment. The measured changes to V_s and d_s (derived from the moisture content) between January and May were equivalent to a 45% reduction in the rigidity modulus.

There is laboratory evidence using recently deposited muddy sediments that the critical erosion shear stress is related to an acoustically determined rigidity modulus of the upper centimetres of the bed (Jago et al., in prepn). If this result is applicable to seabed conditions then we can postulate that a reduction in rigidity modulus lowers the critical erosion shear stress. It follows that the bed at the experimental site should be eroded by a lower shear stress in summer than in winter. A comparable increased potential for erosion in summer was reported by Rhoads et al. (1978) at a shallow water cohesive sediment site and was shown to be due to bioturbation. Our results suggest that the effect of disruption of sediment fabric by bioturbation outweighed any effects of binding of the fabric by microorganisms (as reported by Nowell et al., 1981).

Nevertheless, the bed sediment itself was not significantly resuspended by tidal currents in either winter or summer (Jones et al., 1998). Indeed, it would not be to an organism's advantage for its activities to destabilize the bed during 'normal' weather conditions. However, it may be that resuspension of bed sediment occurs during infrequent storms in summer when the reduced resistance of the bed to erosion becomes critical. Since the seabed at this site is important to biogeochemical and metal fluxes in summer, especially after plankton blooms (Jones et al., 1998; Millward et al., 1998), summertime storms may produce important effects in these respects.

Many species of the *Amphiura-Echinocardium* community have the capacity to influence the physical nature of the muddy-sand of the seabed (Schafer, 1972) but only *Amphuira filiformis* seem to produce a major, measurable impact at our experimental site. Open burrows reduce bed rigidity; Jones and Jago (1993) report effects of comparable magnitude in intertidal sediments due to the burrowing amphipod *Corophium arenarium*. *Amphiura*-type communities are extremely common in the North Sea, covering most of its central and northern area (Kingston and Rachor, 1982). *Amphiura filiformis* occurred at 70% of the stations sampled by Kunitzer et al. (1992) during the ICES North Sea Benthos Survey. Biological modification of bed properties due to this organism alone are clearly important, but its impact on bed erodibility may be localised. Seabed stirring by waves is progressively less effective with depth, so that biological effects on erodibility by *A. filiformis* may well be restricted to regions where it occurs in shallow water. *A. filiformis* would be of most significance where it occurs at the boundary between well stirred and seasonally stratified waters – that is close to, and on the stratified side of, shelf fronts.

5. Conclusions

Geotechnical and geophysical properties of muddy-sands at a site in the southern North Sea with a mean water depth of 47 m were measurably variable in space and time. The properties of the upper 0.05 m of the bed were modified by the activities of the macrobenthic faunal community and, in particular, by the burrowing brittle star *Amphiura filiformis*. Increasing numbers of this organism were associated with increasing water content and decreasing velocity of acoustic shear wave propagation in the surficial sediments; we consider that these associations are causal. The result was significantly reduced sediment bulk density and bed rigidity in summer; hence the potential for resuspension of bed sediment was increased in summer. Such biological modification of the bed is considered to have important consequences for particle and particle-related benthic fluxes (e.g. metals), especially in the region of shelf fronts during summer storms.

Acknowledgements

The authors wish to express their gratitude to the Officers, crew and scientific staff of the R.R.S. Challenger. This work was supported by the Natural Environment Research Council within its North Sea Community Research Project. AAR was funded in part by the Department of the Environment under Contract No. PECD 7/8/141, CFJ and SEJ were supported by a NERC Special Topic Research Grant (GST/02/276).

Appendix A

Table 4
Macrofauna species composition in January 1989 (expressed as number per 0.25 m^2)

	Station				
Species	1	5	13	23	25
CNIDARIA					
Edwardsia claperedii	16				
Anthozoa indet.		16			
NERMERTEA					
Nermertean indet.		16			16
SIPUNCULA					
Golfingia vulgaris			16		
ANNELIDA					
Gattyana cirrosa			16		
Glycera rouxi		80	32	16	16
Synelmis klatti			16	32	
Exogone hebes			16	32	16
Nephtys caeca	32				
Lumbrinereis gracilis	16				48
Scoloplos armiger				16	
Paraonis fulgens	16		16	16	32
Magelona alleni				16	
Chaetopterus variopedatus		1	1	1	
Caulleriella caputesocis	16				
Amphictene auricoma					32
CRUSTACEA					
Copepoda indet.	16		16	48	32
Ampelisca brevicornis	16		16	48	32
Eudorella truncatula	16				
Upogebia stellata		1			
Corystes cassivelaunus			1		

Table 4. (*Continued*)

	Station				
Species	1	5	13	23	25
MOLLUSCA					
Cylichna cylindracea		16			16
Mysella bidentata	191	64	255	16	16
Gouldia minimum	16		16		
Corbula gibba			32	95	143
ECHINODERMATA					
Amphiura filiformis	334	223	95	143	64
Ophiura albida				1	
Echinocardium cordatum		3			
Brissopsis lyrifera		1			

Appendix B

Table 5
Macrofauna species composition in May 1989 (expressed as number per 0.25 m^2)

	Station				
Species	1	5	13	23	25
NERMERTEA					
Nermertean indet.			6	19	
PLATYHELMINTHES					
Turbellaria indet.			1		
SIPUNCULA					
Golfingia vulgaris			5		1
Golfingia procera				1	
ANNELIDA					
Gattyana cirrosa		1	4		
Leanira juv. indet.		6			
Pholoe minuta	13	6	6		19
Sthenelais limicola			6	6	
Glycera rouxi		13	6		19
Glycinde nordmanni	6		6		6
Goniada maculata					13
Ophiodromus flexuosus		13			
Synelmis klatti	64	19	26	26	26
Exogone hebes	19	19	13	13	26
Nephtys incisa	6	13		6	19
Lumbrinereis gracilis		6			6
Scoloplos armiger	6	6	6	19	6
Aricidea minuta	38	26	26	6	32

Table 5. (*Continued*)

	Station				
Species	1	5	13	23	25
Polydora caeca			32		
Spiophanes bombyx	6		6	6	
Magelona alleni	6	6			
Magelona filiformis		6		6	
Magelona mirabilis	6				
Chaetopterus variopedatus	1		8		3
Caulleriella caputesocis	19	26	6	6	19
Diplocirrus glaucus	6				
Heteromastus filiformis			6		
Notomastus latericeus			26		
Ophelia limacina				6	
Ophelina acuminata				6	
Amphictene auricoma			6		19
Amphictene belgica					6
Ampharete baltica					6
Echytraeidae indet.					19
CRUSTACEA					
Nebalia bipes			77		
Copepoda indet.	6		134	6	32
Harpinia antennaria	32	26	19	26	32
Ampelisca brevicornis	6	6			
Priambus typicus			6		
Ione thoracica	1				
Leptognathia gracilis					6
Eudorella emarginata					6
Eudorella truncatula		13	13		6
Euderellopsis deformis		6			
Diastylis laevis			6		
Callianassa subterranea	5	7	2	2	2
Corystes cassivelaunus		2			
MOLLUSCA					
Turritella communis		1		1	
Eulimidae indet.		6			13
Cylichna cylindracea			6		
Nuculoma (Nucula) tenuis					6
Mysella bidentata	122	269	26	19	83
Artica islandica	1				
Chamelea gallina		1			
Venus fasciata			13		
Gouldia minimum	6				
Corbula gibba	26	19	38	19	45
ECHINODERMATA					
Amphiura filiformis	461	659	307	378	557
Ophiura albida					2
Echinocardium cordatum		1		2	1
Brissopsis lyrifera	1	1			

Appendix C

Table 6
Macrofauna species composition for September 1989 (expressed as number per 0.25 m^2)

	Station				
Species	1	5	13	23	25
CNIDARIA					
Edwardsia claperedii	6				
NERMERTEA					
Cerebratulus marginatus					6
Nermertean indet.	6	38	26	6	13
SIPUNCULA					
Golfingia elongata			2		
ANNELIDA					
Aphoridita aculeata	1		2		
Gattyana cirrosa	1		1		3
Pholoe minuta	6		6	26	19
Sthenelais limicola	6	6	19		
Glycera rouxi			6		26
Glycinde nordmanni	6		6	13	
Ophiodromus flexuosus	13			13	6
Synelmis klatti	13	19	13	32	6
Exogone hebes	19	6	26		19
Nephtys incisa			6		
Nephtys hombergii		6	13		6
Lumbrinereis gracilis		6			13
Scoloplos armiger	19				6
Aricidea minuta	6	6	6		6
Spiophanes bombyx	6	6		6	
Magelona alleni	6	13	6	19	
Chaetopterus variopedatus	1		1		4
Caulleriella caputesocis	6	6			6
Cossura longocirrata	6		6		6
Diplocirrus glaucus		6	6	6	
Owenia fusiformis			6		6
Amphictene auricoma	13	6	282	6	26
Amphictene belgica		6		6	
CRUSTACEA					
Copepoda indet.	38	6	45	32	32
Periculodes longimanus	13	6		38	
Westwoodilla caecula					6
Gitanopsis inermis			6		
Harpinina antennaria			19	13	6
Ampelisca brevicornis			6		6
Lembos longipes			13		
Cirolana borealis			2		1
Ione thoracica	1	1		1	
Eudorella emarginata	6		19		
Diastylis bradyi	6	6		6	
Diastylis laevis	6				

Table 6. (*Continued*)

	Station				
Processa canaliculata		6			
Callianassa subterranea	16	17	9	9	6
Upogebia stellata	1	4			1
Liocarcinus pusillus			6		
MOLLUSCA					
Turritella communis		1			
Pyramidellidae indet.	13				
Eulimidea indet.			19		
Cylichna cylindracea	19	6		6	
Philine scabra	19	6	32		6
Mysella bidentata	70	51	32		13
Artica islandica			1		
Chamelea gallina	1				
Venus fasciata	6				
Gouldia minimum	6				
Corbula gibba		6	19	6	
ECHINODERMATA					
Amphiura filiformis	320	224	544	288	288
Ophiura albida					2
Echinocardium cordatum	3	2	2	2	2

References

Anderson, F.E., 1983. The northern muddy intertidal: seasonal factors controlling erosion and deposition – a review. Canadian Journal of Fisheries and Aquatic Science 40, 143–159.

Buchanan, J.B., 1984. Sediment analysis. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell Scientific Publications, Oxford, pp 41–65.

Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a 'biological effects' study. Marine Ecology Progressive Series 46, 213–226.

Dapples, E.C., 1942. The effect of macro-organisms upon near-shore marine sediments. Journal of Sedimentary Petrology 12, 118–126.

Darwin, C., 1881. On the formation of vegetable mould through the action of worms. J. Murray, London, pp. 1–326.

Grant, W.D., Boyer, L.F., Sanford, L.P., 1982. The effects of bioturbation on the initiation of motion of intertidal sands. Journal of Marine Research 40, 659–677.

Gularte, R.C., Kelley, W.E., Nacci, V.A., 1980. Erosion of cohesive sediments as a rate process. Ocean Engineering 7, 539–551.

Jones, S.E., Jago, C.F., 1993. In situ assessment of modification of sediment properties by burrowing invertebrates. Marine Biology 115, 133–142.

Jones, S.E., Jago, C.F., Bale, A.J., Chapman, D., Howland, R.J.M., Jackson, J., 1998. Aggregation and resuspension of suspended particulate matter at a seasonally stratified site in the southern North Sea. Continental Shelf Research 18, 1283–1309.

Kingston, P.F., Rachor, E., 1982. North Sea level bottom communities. ICES Report C.M., 1982/L, 41, 1–16.

Kunitzer, A., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dorjes, J., Duineveld, G.C.A., Eleftheriou, A., Heip, C., Herman, P., Kingston, P., Niermann, U., Rachor, E., Rumohr, H., deWilde, P.A.J., 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES Journal of Marine Science 49, 127–143.

Lee, H., Swartz, R.C., 1980. Biological processes affecting the distribution of pollutants in marine sediments. Part II. Biodeposition and bioturbation. In: Baker, R.A. (Ed.), Contaminants and Sediments, vol. 2, Ann Arbor Science Publish. Inc. Ann Arbor. pp. 555–606.

Meadows, P.S., Meadows, A., 1991. The geotechnical and geochemical implications of bioturbation in marine sedimentary ecosystems. Symposia of the Zoological Society of London, No. 63. The Environmental Impact of Burrowing Animals and Animal Burrows, pp. 157–181.

Meadows, P.S., Tait, T., 1989. Modification of sediment permeability and shear strength by two burrowing invertebrates. Marine Biology 101, 75–82.

Millward, G.E., Morris, A.W., Tappin, A., 1998. Benthic biogeochemical processes and trace metal transport in the North Sea. Continental Shelf Research 18, 1381–1400.

Morris, A.W., Howarth, M.J., 1998. Bed stress induced sediment resuspension (SERE 88/89). Continental Shelf Research 18, 1203–1213.

Myers, A.C., 1977. Sediment processing in a marine subtidal sandy bottom community: I Physical aspects. Journal of Marine Research 35, 609–632.

Nowell, A.R.M., Jumars, P.A., Eckman, J.E., 1981. Effects of biological activity on the entrainment of marine sediments. Marine Geology 42, 133–153.

Postma, H., 1967. Sediment transport and sedimentation in the estuarine environment. In: Lauff, G.H. (Ed), Estuaries. American Association for Advancement of Science, Washington, D.C., pp. 158–179.

Rhoads, D.C., 1974. Organism-sediment relations on the muddy sea floor. Oceanography Marine Biology Annals Review 12, 263–300.

Rhoads, D.C., Boyer, L.F., 1982. The effects of marine benthos on physical properties of sediments; a successional perspective. In: McCall, P.L., Tevesz, M.J.S. (Eds.), Animal-Sediment Relations; the Biogenic Alteration of Sediments. Plenum Publishing Corporation, New York, pp. 3–52.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research 28, 150–178.

Rhoads, D.C., Yingst, J.Y., Ullman, W., 1978. Seafloor stability in central Long Island Sound. Part 1. Temporal changes in the erodibility of fine grained sediment. In: Wiley, M.L. (Ed.), Estuarine Interactions. Academic Press, New York, pp. 221–224.

Richards, A.F., Parks, J.M., 1976. Marine Geotechnology: average sediment properties, selected literature and review of consolidation, stability, and bioturbation – geotechnical interactions in the benthic boundary layer. In: McCave, I.N. (Ed.), The Benthic Boundary Layer. Plenum Press, New York and London, pp. 157–181.

Richardson, M., 1983. The effects of bioturbation of sediment elastic properties. Bulletin di la Societe Geologique de France 25, 505–513.

Richardson, M., Young, D.K., Briggs, K.B., 1983. Effects of hydrodynamic and biological processes on sediment geoacoustic properties in Long Island Sound, USA. Marine Geology 52, 210–226.

Schafer, W., 1972. Ecology and Palaeoecology of Marine Environments. Oliver and Boyd, Edinburgh, p. 568.

Rowden, A.A., Jones, M.B., 1995. The burrow structure of the mud shrimp *Callianassa subterranea* (Decapoda: Thalassinidea). from the North Sea. Journal of Natural History 29, 1155–1165.

Rowden, A.A., Jones, M.B., Morris, A.W., 1996. The role of *Callianassa subterranea* (Montagu) (THALASSINIDEA) in sediment resuspension in the North Sea. Continental Shelf Research 18, 1365–1380.

Warwick, R.M., Platt, H.M., Clarke, K.R., Agard, J., Gobin, J., 1990. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. Journal of Experimental Marine Biology and Ecology 138, 119–142.

Warwick, R.M., Clarke, K.R., 1991. A comparison of some methods for analysing changes in benthic community structure. Journal of Marine Biolological Association of United Kingdom 71, 225–244.

Yingst, J.Y., Rhoads, D.C., 1978. Seafloor stability in central Long Island Sound. II Biological interactions and their potential importance for seafloor erodibility. In: Wiley, M.J. (Ed.), Estuarine Interactions, Academic Press, New York, pp. 245–260.

Young, D.K., 1971. Effects of infauna on the sediment and seston of a sub-tidal environment. Vie et Milieu, (Suppl.) 22, 557–571.

Young, R.A., Southard, J.B., 1978. Erosion of fine-grained marine sediments: Sea-floor and laboratory experiments. Bulletin of the Geological Society of America 89, 663–672.