

ORIGINAL ARTICLE

Altering intertidal sediment topography: effects on biodiversity and ecosystem functioning

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Conflicts of interest

The authors declare no conflicts of interest.

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Abstract

Sedimentary marine systems are often highly productive and perform important nutrient regeneration functions as they efficiently decompose organic material. In recent years the role of habitat effects and of species composition in ecosystem functioning has become of interest. Estuarine environments are frequently subject to considerable anthropogenic pressures whilst supporting a variety of habitats ranging from well sorted soft muds through biogenically stable sediments to highly mobile coarse sands. There is therefore considerable spatial complexity in habitat type and faunal composition. This study set out to observe the effects of altering the topographical habitat features of an estuarine mudflat on a range of porewater nutrient concentrations (NH_4^+ , NO_3^- , NO_2^- , PO_4^{3-} and SiO) collected from four depths (3, 5, 9, and 12 cm) and on faunal composition. Two treatments (Shelled Nets and Net Controls) were used to alter the topography from simple mud to a mussel shell crumble and were compared to un-manipulated Control areas. Sediment granulometry and organic matter content analyses alongside biological traits analysis of the fauna were also conducted.

Differences were observed in porewater nutrient concentrations between the Control and both netted treatments at 5 cm depth only; the species diversity and abundance were also different in the netted treatments compared to the Controls, although no difference between the two manipulated treatments were observed. The changes in faunal composition were attributed solely to the altered topography and the observed nutrient changes were attributed to the faunal alteration rather than the topographical manipulation.

Introduction

Recent concern over the alteration and degradation of the environment has led to speculation about the consequences for the provision of ecosystem services (*i.e.* ecological processes with a value to humanity such as climate regulation) and those ecological functions (*e.g.* nutrient regeneration) that directly or indirectly underpin these services (*e.g.* see Bolger 2001; Naeem 2002; Giller *et al.* 2004; Hooper *et al.* 2005 and references therein; Stachowicz *et al.* 2007). Ecosystem functions result from the biological, chemical and physical processes carried out by the species inhabiting an area (Naeem *et al.* 1994) and

they are determined by the life habits of these species. Life habits (also known as functional traits) can range from mode of locomotion, trophic group to the type of reproductive strategy exhibited.

Several theories have been proposed to explain the relationship between biodiversity and ecosystem functioning (Ehrlich & Ehrlich 1981; Lawton *et al.* 1993; Mooney *et al.* 1995; Naeem 2002). The redundant species hypothesis recognizes that species contribute to a number of 'ecological functions' and different species contribute different mixes of functions, overlapping and giving the system some redundancy. The idiosyncratic hypothesis argues that as individual species roles are varied and complex,

the effects on ecosystem functions of the loss of any one species are unpredictable (Naeem 2002; Solan *et al.* 2004). Therefore consideration must be given to the multiple roles of each species to understand their relationship with ecosystem functioning.

Several studies have found that reduced species diversity impaired the ability of an ecosystem to provide certain services (Naeem *et al.* 1994; Emmerson *et al.* 2001) and that changes in functional diversity have a greater impact on ecosystem services than changes in species diversity, although both have an effect (Tilman *et al.* 1997). More recently, research has focused on the composition of functional traits in an assemblage and how these traits affect ecosystem functions and services. Studies have been concerned with the definition of traits and their effects on the environment (Bremner *et al.* 2003; Welsh 2003; Wolanski *et al.* 2004), how the composition of traits within an area alters after a disturbance and the subsequent effects on ecosystem functioning and delivery of services (Tillin *et al.* 2006; De Juan *et al.* 2007; Savage *et al.* 2007) and the effect of different species classified with the same functional trait(s) on an ecosystem function, *e.g.* whether two 'bioturbators' affect nutrient cycling in the same way (Matisoff & Wang 1998; François *et al.* 1999; Michaud *et al.* 2005, 2006). The latter studies have found that species classified by their functional traits as biodiffusers, but inhabiting different depths in the sediment, affect the depth penetration of oxygenated water differently, thus affecting nutrient cycling in different ways (*e.g.* Michaud *et al.* 2006; Karlson 2007), indicating that species identity may be just as important as the traits they represent.

Within the marine environment most studies have been conducted using intertidal estuarine species (*e.g.* Banta *et al.* 1999; Christensen *et al.* 2000; Emmerson *et al.* 2001) as the species assemblages are typically small (10–20 species), the fauna have been relatively well studied compared to many sub-tidal species and they are usually present in large numbers over a small spatial range, allowing sufficient specimens to be collected for laboratory studies.

The effects of nutrient regeneration and flux within intertidal areas due to diffusive and advective porewater flows, along with changes to oxygen depth penetration, have been studied with regard to both biological and physical factors (Huettel & Gust 1992; Aller & Aller 1998; Kristensen 2000; Kuwae *et al.* 2003, 2006; Mermillod-Blondin *et al.* 2004; Billerbeck *et al.* 2006). Biological factors such as polychaete tubes, burrowing and bio-irrigation by infauna affect nutrient regeneration by altering porewater flow (Huettel & Webster 2001) and the sediment surface area available for oxygen exchange (Mortimer *et al.* 1999; Aller 2001). Physical factors investigated have

included observing the effects of varying topographical features on porewater movement and oxygen penetration (Ziebis *et al.* 1996; Huettel & Webster 2001; Billerbeck *et al.* 2006). It was found that singular protrusions as little as 700 μm from the sediment surface can cause increased advective porewater flow at overlying water flows of 3 cm s^{-1} , pulling porewater from deep within to the surface sediments (Huettel & Gust 1992) and increasing oxygen penetration twofold in muddy, low permeability sediments (Ziebis *et al.* 1996).

The effects of large species that are also habitat modifiers (*e.g.* *Cerastoderma edule* Linnaeus) have been investigated with regard to nutrient flux and impact on faunal communities (Rossi *et al.* 2008; Cesar & Frid 2009), as have the effects of mussel aggregations and macroalgal growth on infauna (*e.g.* Günther 1996; Raffaelli 2000; Jones & Pinn 2006). The influence of substratum heterogeneity on epibenthic community structure (Bourget *et al.* 1994) and the effects of polychaete tubes on infaunal communities and overlying water flow have been studied (Luckenbach 1986; Friedrichs *et al.* 2000; Callaway 2003). However, the combined effects of topographical variation and subsequent alterations to species composition on nutrient regeneration have not been. As the ecological functions of an area are dependent on the species found within it (Hooper *et al.* 2005), it may be the case that the composition of functional traits and the delivery of ecosystem functions will vary as the species assemblage does.

Due to the nature of estuarine environments a variety of habitats ranging from well sorted soft muds through biogenically stable sediments to highly mobile coarse sands can exist in close proximity to each other. The sedimentary characteristics and the changing effects of tidal flow on these habitats can vary on a small spatial scale, potentially affecting the faunal assemblages present within an area. The present study aims to alter the physical features of an estuarine mudflat area to observe the effects on faunal assemblages, biological trait composition and nutrient regeneration in the sediment to answer the questions:

- 1 Do different micro-habitats in intertidal mudflats contain significantly different faunal assemblages and, if they do, are the trait compositions of the assemblages different?
- 2 If the traits present are different between the two assemblages does this affect nutrient regeneration?

Method

On the Dee Estuary, at Tinkers Dell Steps ($53^{\circ}20'16''\text{N}$, $03^{\circ}08'31''\text{W}$) (Fig. 1), patches of poorly mixed shell debris and muddy sand, termed 'crumble', occur adjacent to areas of firm, muddy sand. The 'muddy sand', had little

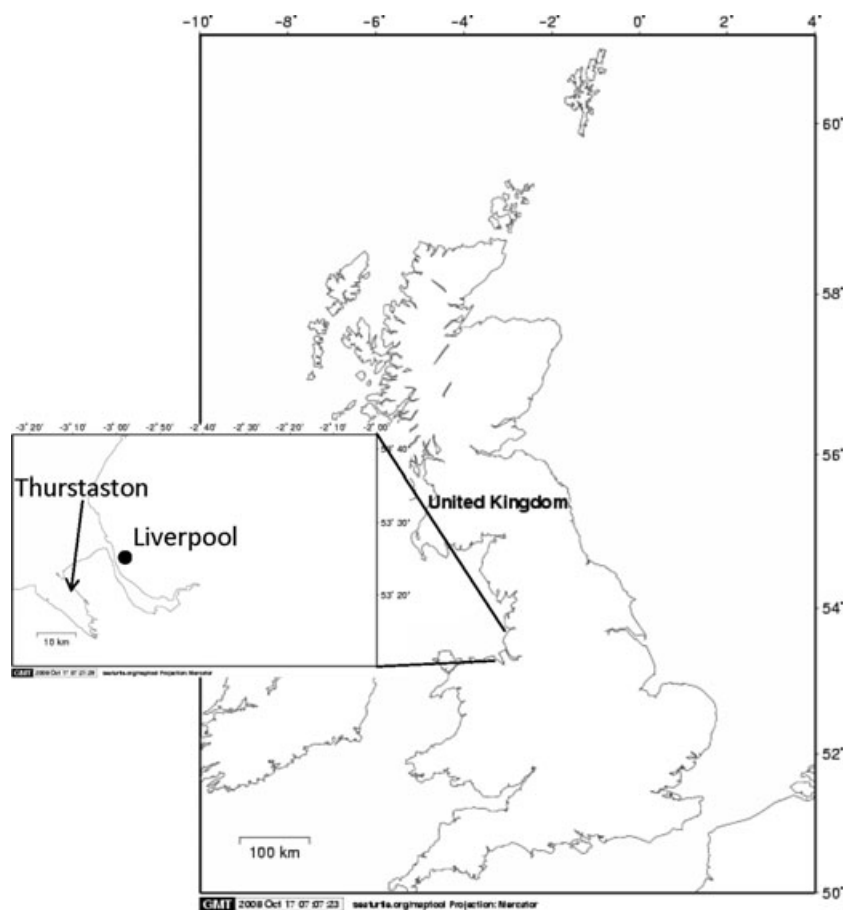


Fig. 1. Geographical location of Thurston (53°20'16"N, 03°08'31"W) study site in relation to Liverpool, North-West England. Map created using MAPTOOL, <http://www.seaturtle.org>.

surface relief, without obvious stones or shell debris consisting of an average 50% sand (63–150 μm), 40% silt (<63 μm) content and little coarse material ($\sim 1\% \geq 1000 \mu\text{m}$). In contrast the crumble sediment consisted of 25% sand, 36% silt content with a larger percentage of coarse material ($\sim 16\% \geq 1000 \mu\text{m}$) comprising stones (mostly encrusted with barnacles), shell debris (mostly mussel shells) and byssus threads from live mussels, creating a rough surface. The faunal assemblage of the muddy sand was characterized by a large abundance of small crustaceans (*Corophium* sp.), spionid polychaetes and species which show a preference for sandy sediments over silty ones (*i.e.* *Owenia fusiformis* Delle Chiaje). The crumble fauna, in contrast, contained surface dwelling bivalves, their associated epifauna, a higher abundance of oligochaetes and several opportunistic deposit-feeding taxa (*i.e.* *Capitella* sp. Fabricius). Organic matter content, determined by loss on ignition, for the two sediments averaged 1% for the muddy sand and 2% for the crumble. These two areas of differing topography provided a 'natural' experimental site in which to compare the influence of boundary layer topography on benthic assemblage composition and ecosystem functioning. Nutrient concentra-

tions (mg L^{-1}) were used as a proxy of nutrient regeneration in this study, as it would be expected that concentrations of nutrients in the sediment would increase as regeneration increased. The investigation was carried out from 15 August 2006 until 15 November 2006.

To isolate the influence of the physical environment on ecosystem functioning, the muddy sand surface was manipulated to mimic the crumble using PVC mesh nets in $1 \times 1 \text{ m}$ plots. Five nets were produced composed of two layers of mesh, a 50 mm mesh bottom layer and a 20 mm mesh top layer. The 20 mm mesh was cut into $25 \times 25 \text{ cm}$ panels and empty mussel shells were attached to this using an epoxy resin. Sixteen of these panels (giving $228 \pm 3.38 \text{ m}^{-2}$ mussel shell density) were attached to the larger 50 mm mesh using cable ties to create an imitation of the crumble surface. Five $1 \times 1 \text{ m}$ nets were also created in the same manner but without attached shells, to control for any netting effect. On each net, nine holes were cut in the 50 mm mesh, at the intersections of the smaller mesh panels, to allow for subsequent porewater sampling. These were randomly allocated to one of two groups of four; group one was used on the 1st, 3rd and

5th sampling occasion and group two on the 2nd, 4th and 6th, leaving one hole spare for sediment sampling at the conclusion of the study. On 15 August 2006, 15 plots were marked out and each was randomly assigned one of the three treatments [five shelled nets (treatment), five blank nets (net control) and five sediment plots (control)]. The nets were secured in place with 30 cm plastic pegs at each corner.

Using a modified Poreextractor (see Nayar *et al.* 2006 for operational details) sampling of sediment porewaters was conducted, the shallowest depth attainable without surface water contamination being 3 cm. Porewater sampling began on 29 August 2006, 2 weeks after initial set-up, when samples from four depths (3, 5, 9 and 12 cm) were obtained for nutrient analysis. On each sampling occasion a Poreextractor (one for each depth) was inserted into the sediment through one of the pre-cut holes in the mesh. Sampling of porewater was repeated on a fortnightly basis during the neap tide cycle and the samplers were deployed ~3 h after high tide (when the site first became exposed).

The Poreextractors were set according to the method described in Nayar *et al.* (2006), a vacuum was applied using a syringe and the membrane pierced using a plastic rod, after which the device was left in the sediment for 1 h to allow the flow of porewater into the sampling chamber. Once this time had elapsed a plastic pipette was pushed through the membrane and water from the sampling chamber was collected using a 20 ml syringe. For each sample a minimum extraction of 5 ml of water from the sediment was attempted; where more water was available the syringes were filled to capacity. The syringes were placed in cool-boxes and kept in the cold and dark for later filtration and analysis; samples were always returned to the laboratory and filtered within 4 h of collection.

Water samples were filtered using 25 μm Millipore syringe filters and analysed using standard colorimetric methods for ammonia (NH_4^+), total N (nitrate/nitrite), silicate (SiO_2) and phosphate (PO_4^{3-}) on a Bran+Lubbe AA3 continuous flow Autoanalyser. A minimum 1 ml of water (after filtration) was required for high-range nutrient analysis by the Autoanalyser, and 5 ml was required for low-range analysis. For separate nitrate/nitrite analyses, twice this amount (*i.e.* 2 or 10 ml) was required, as the Autoanalyser consisted of a combined nitrate/nitrite channel and separate analyses would be required to obtain data for each. Samples for ammonia analysis were occasionally diluted 1:2 as the levels detected were over-range for the colorimetric method utilized by the Autoanalyser (4 mg L^{-1} maximum detectable limit).

Porewater collection was completed on 15 November 2006 and the nets were collected from the shore on 29th November 2006, at which time core samples for

faunal analysis and sediment granulometry were also obtained.

Three sediment samples per plot were obtained from the area underneath the netting using a 0.01 m^2 diameter corer for faunal analysis. The samples were returned to the laboratory where they were washed through a 0.5 mm sieve and fixed in 4% buffered formaldehyde solution. Fauna were extracted and enumerated by taxa, generally species, although some problematic groups were not identified to species level.

The nets were placed in plastic bags on site and returned to the laboratory where accumulated surface sediment was washed off, collected, sieved and preserved using the same method as for the infauna samples. Any fauna that had attached to the netting were collected at this time and added to the overall surface net sample. After allowing the fauna to be fixed the samples were again washed through a series of sieves. Any fauna larger than 20 mm (*e.g.* *Cerastoderma edule*) were retained for identification as this was the minimum mesh size of the experimental nets. Those fauna recognized as surface dwellers (*i.e.* littorinids) or that had been attached to the netting were also retained.

Sediment samples were collected on 29 November for particle size analysis (PSA) and loss on ignition (LOI) using a small (3 cm i.d., 9 cm length) core. The samples were frozen on return to the laboratory for later analysis. When thawed the samples were wet weighed, dried at 60 °C for 24 h and re-weighed to ascertain the water content. Following the method described in Eleftheriou & McIntyre (2005), PSA and LOI were carried out on the dried sediment. For LOI approximately 7 g (± 1.27) of the dried sediment was homogenized using a pestle and mortar and placed in a pre-weighed crucible before being weighed again. The crucibles were then fired in a muffle furnace at 450 °C for 5 h after which time they were re-weighed. The remainder of the dried sediment was weighed and then passed through a series of graduated sieves (63 μm –2000 mm) on a sieve shaker for 15 min and each fraction weighed for the PSA.

Data analysis

Faunal data were collated and the average abundance per experimental plot (core sample data and net surface data) was calculated for final analysis, thus avoiding pseudo-replication (Hurlbert 1984). Bray–Curtis similarity was calculated on square root-transformed abundance data in the statistical package PRIMER (v6). This reduces the influence of the dominant taxa and allows variation in the rarer taxa to influence the pattern. Following examination of the resultant cluster analysis, ANOSIM and SIMPER tests were also carried out.

Biological traits analysis (BTA) was carried out on the combined faunal data from the core and net surface samples using five biological traits that relate to processes affecting nutrient regeneration. Although the inclusion of more traits would provide additional information on ecosystem functioning (Bremner *et al.* 2006), the traits used were chosen as potential factors relating to nutrient regeneration effects of the fauna. Three of these represented behaviour (bioturbation type, feeding type and depth found in sediment) and the remaining two represented life history (longevity and body size). The five traits were further sub-divided into several modalities to better represent the spread of variation for each, e.g., bioturbation was separated into biodiffuser, gallery-diffuser, regenerator, upward-conveyor, downward-conveyor and bio-irrigator (Table 1).

Fuzzy coding (Chevenet *et al.* 1994), with a scoring range of 0–3, was used to code individual taxa for the degree to which they exhibited the different modalities of each trait. No affinity for a trait was coded as 0 and complete affinity as 3, e.g. *Corophium volutator* Pallas can be a deposit-feeder but also actively suspension-feed, and so were coded 2 (Deposit-feeder) and 1 (Suspension-feeder) and 0 for the remaining modalities within the feeding type trait. Information for each of the biological traits was gathered from the literature where there was a direct reference and was also based on autecology of the taxa and descriptions of particular traits, e.g. *Pygospio elegans* Claparède is a tube-dwelling head-up deposit-feeder, and from the descriptions of bioturbation categories in François *et al.* (1997) this species can be classed as a downward-conveyor (2), due to its feeding method of moving sediment from the surface to deeper areas, and as a biodiffuser (1), as it will cause some passive diffusion of oxygen along its tube-length. Taxa that were not identifiable to genus were not included in the BTA.

Trait modality affinity scores per taxon were multiplied by the abundance of each taxon for every sample and subsequently summed to provide an overall value for each trait modality per sample. The trait by sample table was analysed using nMDS in the statistical package PRIMER (v6). Various transformations were performed on the data (including no transformation) to compare patterns on the nMDS ordinations that were plotted. SIMPER analysis was also carried out on the data to observe the effects of the individual traits.

The nutrient data collection followed a repeated measures design and was analysed using a linear mixed model (LMM) in the statistical package SPSS (v15). LMM were used as some data were missing, the data collected at different times were not independent of each other and the Hyunh-Feldt assumption of sphericity was unlikely to be met (Rowell & Walters 1976). Additionally, although data

Table 1. Biological trait variables and modalities used to describe fauna identified in the study.

trait	no.	modality
bioturbation	1	none
	2	biodiffuser fauna which move sediment in a random manner over short distances causing diffusive mixing (François <i>et al.</i> 1997)
	3	gallery diffuser biodiffusion and active, intermittent irrigation of tubes in sediment-containing gallery systems (e.g. those created by <i>Hediste diversicolor</i>) (François <i>et al.</i> 2002)
	4	regenerator fauna which dig in the sediment, transferring material from depth to the surface (Gardner <i>et al.</i> 1987)
	5	upward-conveyor head-down oriented fauna which cause active movement of sediment from depth to the surface (François <i>et al.</i> 1997)
	6	downward-conveyor Head-up oriented fauna which cause active movement of sediment from the surface to depth through their gut (François <i>et al.</i> 1997)
	7	bio-irrigator fauna which actively irrigate burrows by drawing down surface water past their gills
feeding Mode	1	deposit-feeder
	2	suspension: active
	3	suspension: passive
	4	opportunistic/scavenger
	5	grazer
	6	predator
depth	1	surface
	2	0–3 cm
	3	3–8 cm
	4	8–15 cm
	5	15–25 cm
body size (mm)	1	≤5
	2	5 < >10
	3	10 < >20
	4	20 < >0
	5	40 < >80
	6	80 < >160
longevity	1	≤1 year
	2	1–2 years
	3	3–5 years
	4	6–10 years
	5	>10 years

were collected every 2 weeks, the collection dates were not exactly 14 days apart due to tidal variations and therefore the temporal spacing was not equal; LMM can accommodate this inequality (Wang & Goonewardene 2004). Of the 16 covariance structures available in LMM

in SPSS (v15.0) only the seven appropriate to a repeated measures design were retained (see Wang & Goonewardene 2004 for further information). These covariance structures were examined for the best fit using the Bayesian information criteria (BIC) where smaller is better, *i.e.* the covariance structure which returned the smallest BIC was used to analyse the data. Data for each nutrient at each depth were analysed separately using the appropriate covariance structure. Maximum likelihood (ML) estimation was used to run the model, as the analysis contained the fixed effects of treatment, which restricted maximum likelihood (REML) estimation is unable to handle (Diggle 2008; Garson).

As LMM does not carry out contrast analysis to separate out differences between individual treatments, the data were coded to indicate the presence (+) and/or absence (–) of shell and net. This method allowed any statistical differences between the treatments to be apparent and made the assumption that the combination of ‘Shell’ and ‘Net’ (*i.e.* Shelled Net treatment) did not alter any effects that ‘Net’ alone may have had.

Results

Environment

Comparison of the sand fraction ($>63\ \mu\text{m}$, arcsin-transformed) from the experimental plots showed a significant difference between the three treatments (one-way ANOVA $F = 16.26$, $P = 0.001$), with both netted treatments differing from Controls. Overall there was a decrease in the proportion of sand present in the Shelled Net and Net Control treatments and an increase in the proportion of larger sediment particles (Fig. 2), indicating an alteration towards a coarser overall sediment composition in both the netted treatments.

One-way ANOVA of the sand fraction from the crumble and muddy sand (long-term monitoring data) showed no difference between the crumble and either netted treatment, indicating an alteration mimicking that of the crumble. Nor was any difference seen between the Control and muddy sand, indicating the Controls were good representations of the wider muddy habitat. Loss on ignition (LOI) data were not significantly different between the three experimental treatments or in comparison with the LOI data from the long-term monitoring.

Fauna

A total of 29 taxa were identified from the experimental core samples. Of these, five were found only in Shelled Net treatments (*Streblospio shrubsolii* Buchanan, *Capitella* sp., *Manayunkia aesturina* Bourne, *Paranais littoralis* Mul-

ler and *Elminius modestus* Darwin) and two were found only in Control treatments (*Corophium arenarium* Crawford and *Arenicola marina* Linnaeus). Of the taxa found in the Shelled Net, *Capitella* sp., *M. aesturina* and *P. littoralis* are opportunistic, deposit-feeding annelids not previously recorded from the muddy sand sediment (D. Jones, unpublished data). However, all three taxa have previously been identified from crumble samples, indicating a shift in the taxonomic composition of the Shelled Net treatments towards that of the natural crumble over the 12-week study period.

One-way ANOVA performed on Shannon–Weiner diversity indices indicated that the netted treatments were significantly different to the Controls ($F = 4.77$, $P = 0.032$). Pair-wise comparisons from ANOSIM analysis showed significant differences between the Control/Net Control and the Control/Shelled Net treatments ($R = 0.881$, 0.548 , respectively, $P = 0.8\%$ for both), and nMDS ordination (Fig. 3A), plotted from Bray–Curtis similarities, clearly shows a grouping of the Net Control separate from the Control treatment group. The Shelled Net treatments are scattered to the right of the plot, away from the Controls but around the Net Controls, with no significant difference observed between the two netted treatments.

The treatment effects on the eight taxa most common in muddy sand and crumble (as indicated by long-term monitoring data) were further analysed using Kruskal–Wallis tests (Table 2). Four had significantly different abundances (*Pygospio elegans*, $H = 9.11$, $P = 0.011$; *Eteone longa* agg. Fabricius, $H = 9.54$, $P = 0.008$; *Heterochaeta costata* Claparède, $H = 7.16$, $P = 0.028$; *Corophium volutator*, $H = 10.38$, $P = 0.008$); examination of Kruskal–Wallis ranks indicate that the differences observed were between the net treatments and the Controls in every case. The remaining four (*Hydrobia ulvae* Pennant, *Macoma balthica* Linnaeus, *Hediste diversicolor* Müller and Nematoda) were not significantly different. Abundances of the polychaetes *P. elegans* and *E. longa* agg. and the amphipod *C. volutator* were higher in the Control treatment compared to the two net treatments, whereas abundance of the tubificid oligochaete *H. costata* were lower in the Control.

SIMPER analysis showed that differences between the netted treatments and the Controls were attributable to six taxa (5% or greater contribution to dissimilarity), *P. elegans*, *C. volutator*, Nematoda, *H. ulvae*, Collembola and *E. longa* agg. The cumulative percentage difference for these taxa was $\sim 60\%$, indicating that abundances of these six taxa were having a significant effect on the taxonomic differences observed between the treatments, with *P. elegans* making the greatest contribution (Table 3A,B).

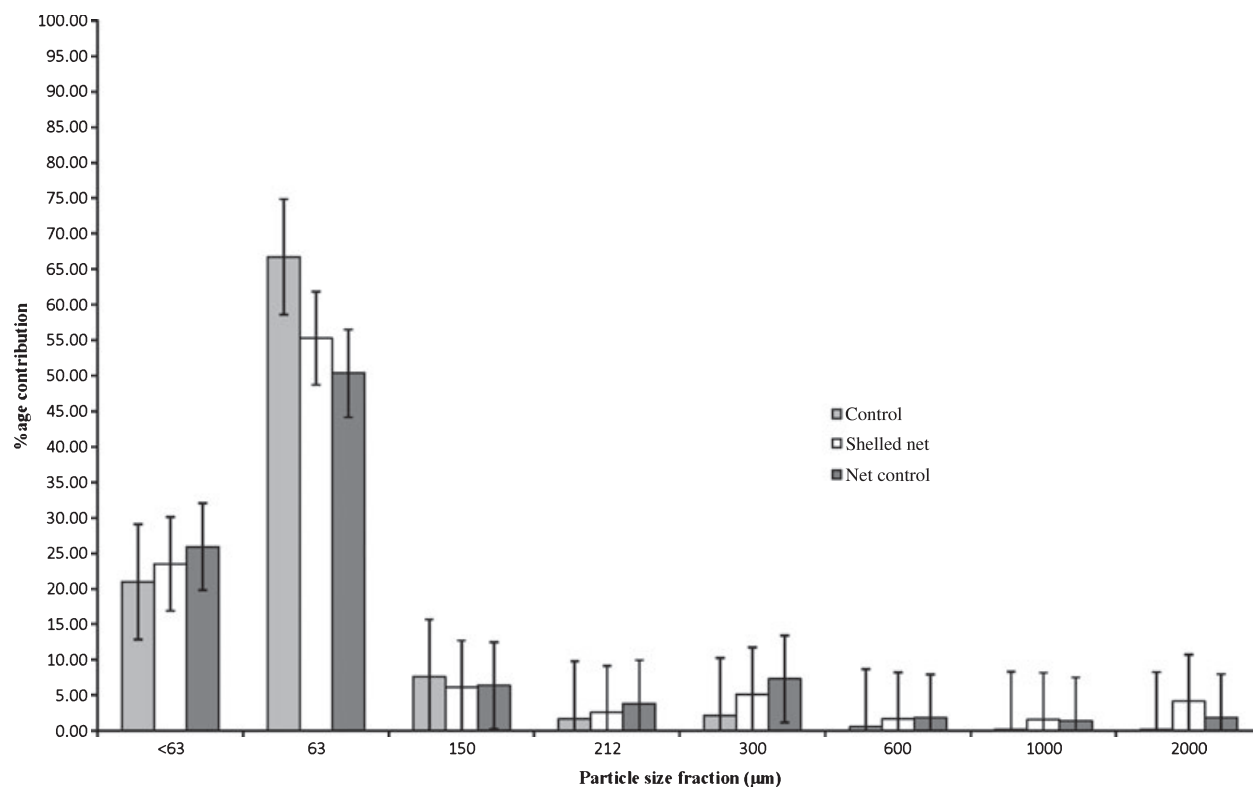


Fig. 2. Sediment particle size analysis for each treatment showing the percentage contribution of sediment to each size fraction.

Nine taxa were identified from the net surface samples. The common mussel *Mytilus edulis* Linnaeus established small aggregations on all net surfaces, although no significant difference between the Net Control and Shelled Net treatments was found for their abundance, or for the abundance of the associated barnacle *Elminius modestus*. Overall abundance of *M. edulis* (combined core sample and net surface) was significantly different between the netted treatments and Controls (Kruskal–Wallis, $H = 11.33$, $P = 0.003$), although no difference was observed for the core data alone. The gastropod *Littorina littorea* Linnaeus was also present in both netted treatments, although no significant difference in abundance was found. This species was not seen in the experimental cores but had been previously identified from the crumble samples.

Overall, several opportunistic taxa common in the crumble appeared only in the Shelled Net treatments and the overall abundance of oligochaete species in the netted treatments increased. There was a decline in the tube-dwelling polychaete *P. elegans* in the netted treatments, with an associated decline of its predator, *E. longa* agg. There was a decline in abundance of the amphipod genus *Corophium*, with *C. volutator* decreasing in number whilst *C. arenarium* disappeared altogether from the netted treatments. Small aggregations of *M. edulis* also appeared on the netted treatments, increasing the overall surface

area of the sediment, and providing settlement areas for the barnacle *E. modestus*.

Biological traits analysis (BTA)

Of the 29 trait modalities used in the analysis, two ('upward-conveyor' bioturbator modality and '15–25 cm' habitat depth) were not represented in the Net Control, one ('15–25 cm' habitat depth) was not present in the Shelled Net and one ('grazer' feeding modality) was not represented in the Control. *Arenicola marina* and *Capitella* sp. were the only two species to represent the two trait modalities lost from the Net Control. The lack of *A. marina* in the Shelled Net treatment also explains the loss of the habitat depth modality '15–25 cm'.

The bioturbator trait modalities 'None', 'gallery-dif-fuser' and 'regenerator' were represented to a greater extent in both netted treatments than in the Control. The same was observed for the 'opportunist/scavenger' feeding modality, 'surface' and '8–15 cm' habitat modalities, and the '3–5 years' longevity. The 'deposit-feeder', '≤5 mm' body size modality and '1–2 years' longevity were more highly represented in the Shelled Net treatment than in either Net Control or Control.

The nMDS ordination (Fig. 3B) showed a similar pattern of groupings to that seen in the faunal abundance

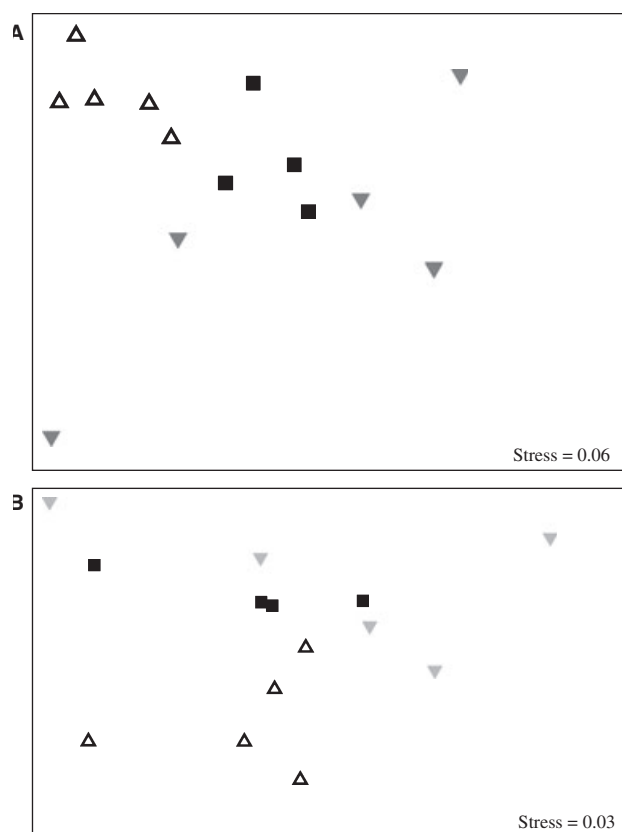


Fig. 3. MDS ordinations of A) faunal assemblages and B) biological trait distribution for the combined core sample and net surface sample faunal assemblages. (Δ) Control, (■) Net Control, (▼) Shelled Net.

Table 2. Kruskal–Wallis analysis from core sample data for the eight most abundant taxa as indicated from long-term monitoring data.

taxon	rank			H	P-value
	control	shelled Net	net control		
Nematoda	10.60	6.00	5.50	4.30	0.116
<i>Tubificoides benedii</i>	6.60	6.80	9.50	1.29	0.526
<i>Hydrobia ulvae</i>	5.3	9.6	7.6	2.65	0.248
<i>Macoma balthica</i>	10.00	6.00	6.30	2.79	0.266
<i>Pygospio elegans</i>	12.00	5.20	4.80	9.11	0.011
<i>Eteone longa</i> agg	12.00	4.20	6.00	9.54	0.008
<i>Heterochaeta costata</i>	4.30	11.20	6.90	7.16	0.028
<i>Corophium volutator</i>	12.00	6.20	3.50	10.38	0.006

Significant p values in **bold**.

ordination (Fig. 3A). Control treatments formed a distinct group, with Net Control forming a second grouping and the Shelled Net treatment scattered over the ordination, whilst being closer to the Net Control than the Control treatments. The ordination was plotted using several transformations and no deviation from the pattern of clustering was observed, indicating the overall groupings

Table 3. (A,B) SIMPER analysis showing faunal percentage contribution to average dissimilarity* between treatments from core sample data. *Control & Shelled net = 40% dissimilarity; Control & Net Control = 29% dissimilarity; Net Control & Shelled Net = 30% dissimilarity.

taxon	contrib%
(A) Control & Shelled Net	
<i>Pygospio elegans</i>	14.49
Nematoda	13.66
Collembola	11.94
<i>Hydrobia ulvae</i>	10.25
<i>Corophium volutator</i>	9.44
<i>Eteone longa</i> agg	5.29
total	65.07
(B) Control & Net Control	
<i>Pygospio elegans</i>	21.55
<i>Corophium volutator</i>	14.7
Nematoda	12.01
<i>Hydrobia ulvae</i>	8.69
<i>Eteone longa</i> agg	6.1
total	63.05

were stable. ANOSIM carried out on the data showed a significant difference between the Control and both netted treatments ($R = 2.92$, $P = 1.6\%$ for Shelled Net; $R = 0.356$, $P = 4.8\%$ for Net Control) and no significant difference between the netted treatments.

Similarity of percentages (SIMPER) analysis showed differences between the treatments were attributable to 10 of the trait modalities (5% or greater contribution to dissimilarity) (Table 4A,B). Of these, five were common to all comparisons (deposit-feeder, surface dwellers, 'none' for bioturbation, 1–2 year longevity and <5 mm body size), three were observed in a single comparison (downward conveyor bioturbation modality, 10–20 mm body size and <1 year longevity in the Control/Net Control comparison) and two were observed in two of the three comparisons (0–3 cm depth in the comparison of Control with both net treatments; biodiffuser in the comparison of Shelled Net to both Control and Net Control treatments).

Control and Shelled Net comparison

Seven trait modalities contributed 5% or greater to the dissimilarity between Shelled Net and Control treatments (Table 4A) with Deposit-feeding (DF) being common to many of the taxa identified, therefore a degree of redundancy could be expected. The abundance of DF taxa in the Shelled Net decreased overall compared to the control, indicating a decrease in this trait modality.

The same was true of the ≤5 mm body size and shallow depth (0–3 cm) habit modalities; abundance of the taxa exhibiting these traits (both *Corophium* species, *Pygospio elegans*, *Capitella* sp., *Manayunkia aesturina*, *Para-*

Table 4. (A,B) SIMPER analysis showing trait percentage contribution to average dissimilarity* between treatments. Fauna data from core samples and net surface samples were combined for use in this comparison. *Control & Shelled net = 34% dissimilarity; Control & Net Control = 25% dissimilarity; Net Control & Shelled Net = 27% dissimilarity.

trait	contrib%
(A) Control & Shelled Net	
deposit-feeder	12.23
surface	11.59
none	11.56
1–2 years	11.37
≤5 mm	7.96
0–3 cm	7.08
biodiffuser	5.94
total	67.73
(B) Control & Net Control	
0–3 cm	10.61
1–2 years	9.83
surface	9.62
none	9.6
deposit-feeder	8.97
10< >0 mm	6.58
≤5 mm	6.28
downward-conveyor	5.83
≤1 year	~5
total	72.32

nais littoralis and *Streblospio shrubsolii*) was greater in the Control treatment than the Shelled Net. The change in surface dwelling and 'None' for bioturbation can be attributed to the increased abundance of *Mytilus edulis* and *Carcinus maenas* juv Linnaeus in the Shelled Net treatments along with the appearance of *Littorina littorea*, *Eliminius modestus* and *P. littoralis*. A lower abundance of Biodiffuser (BD) taxa (*Corophium arenarium*, *Corophium volutator*, *P. elegans*, *Eteone longa* agg) present in the Shelled Net treatment compared to the Control indicates an overall decrease in this bioturbation trait modality.

Control and Net Control comparison

Nine trait modalities contributed 5% or more of the dissimilarity between Net Control and Control treatments, six of which (Deposit-feeders, 0–3 cm depth habit, Surface dwellers, 1–2 years longevity, no bioturbation and ≤5 mm body size) were the same as found in the Shelled Net and Control comparison. Deposit feeders decreased in abundance in the Net Control and no additional species (*i.e.* *Paranais littoralis*, *Streblospio shrubsolii*) were present to add to their overall abundance, indicating a lack of redundancy for this trait in the Net Control treatment. The trait modalities surface dweller, 'none' for bioturbation and ≤5 mm body size showed the same pattern of change as in the Shelled Net comparison and were attributable to the same taxa.

Three other trait modalities (bioturbation modality downward-conveyor, ≤1 year longevity and 10–20 mm body size) contributed 5% or more to the dissimilarity between the Net Control and Control treatments. The only taxa exhibiting the downward-conveyor trait in the two treatments was *Pygospio elegans*, which decreased in abundance in the Net Control compared to the Control. This decrease in the downward-conveyor modality is solely attributable to this species, indicating a lack of redundancy with respect to this trait modality.

Four taxa exhibit the ≤1 year longevity (*Tubificoides benedii* Udekem, *Heterochaeta costata*, *Corophium volutator* and *Corophium arenarium*). There was an overall decrease in this trait modality from Control to Net Control treatments attributable to the lower *Corophium* abundance observed in the Net Control. *Tubificoides benedii* abundance was similar between the two treatments, therefore the representation of this trait modality by this species would have remained similar. The increase in *H. costata* was not as great as the decrease in *Corophium* and may not have compensated for this loss with regard to this trait modality. The 10–20 mm body size was attributable to several taxa common in both Control and Net Control treatments and there was an overall decrease in the combined abundance of those taxa, and thus a decrease in this trait modality.

Overall there were more surface dwelling, and no bioturbating or medium life span (1–2 years) taxa in the Net Control and Shelled Net treatments, and fewer deposit-feeding, biodiffuser, shallow depth habit (0–3 cm), short-lived (<1 year) and small (<5 mm) taxa than in the Control treatments.

Nutrients

Nutrient levels (mg L⁻¹) over time were plotted for each depth separately (Fig. 4). Missing data points are due to a lack of water being collected in the porewater device, no sample being available or anomalous data being returned from the analysis, *i.e.* a negative value. Total N (nitrate/nitrite) was below the detection limit of the Autoanalyser whenever sufficient water could be collected and so is not considered further.

An initial increase in silicate and ammonia levels was observed at the 9 and 12 cm depths (also 5 cm for ammonia) and a decrease was noted starting at the 4th sampling time. Levels of ammonia in both netted treatments were generally greater than in Controls at 3 and 5 cm depths. At 9 and 12 cm depth the ammonia levels were highly variable over time and differences between the treatments were not obvious. Phosphate levels over time were more variable but slight increases are seen in the 3, 9 and 12 cm depth charts (Fig. 4I,K,L) for Controls. Both Shelled Net and Net

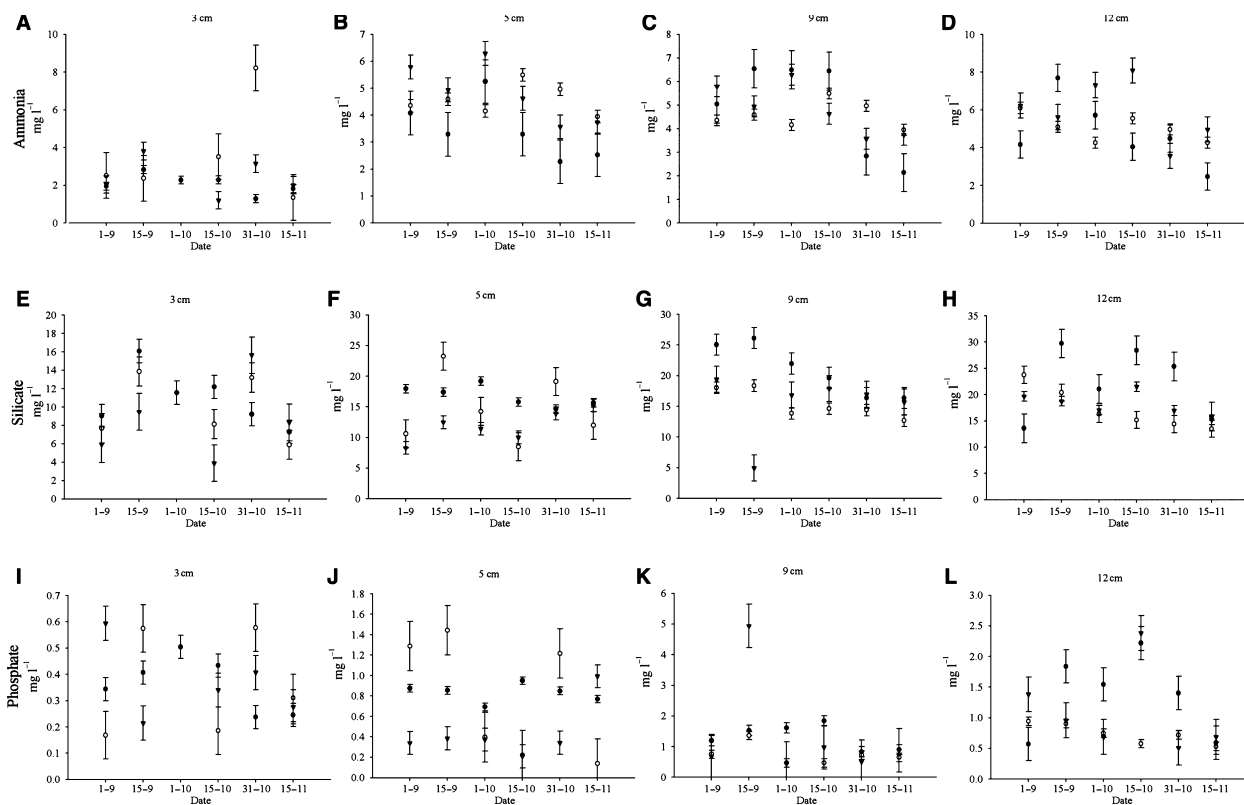


Fig. 4. Nutrient levels (mg L^{-1}) over time for ammonia (A–D), silicate (E–H) and phosphate (I–L), plotted according to collection depth. • Control; ▼ Net Control; ○ Shelled Net.

Control phosphate levels at 12 cm decreased over time. Phosphate levels were generally lower in Net Control compared to Control at 5 cm depth ($0.2\text{--}0.7 \text{ mg L}^{-1}$) and at 12 cm depth phosphate levels in both netted treatments were lower than in the Controls ($\approx 1 \text{ mg L}^{-1}$). Silicate levels were generally lower in the netted treatments at 3 and 5 cm depths by $4\text{--}10 \text{ mg L}^{-1}$ compared to the Control and a steady decrease in silicate levels over time was observed at 9 and 12 cm depths.

Linear mixed model (LMM) analysis of the nutrient data was carried out for each depth separately over time using the appropriate covariance structure (Table 5A,B); Auto-regressive-1 (AR1) was used for all analyses apart from 12 cm Silicate (Toeplitz) and 12 cm Phosphate (AR1-heterogeneous). At 3 cm depth Time was the only significant factor for both ammonia and silicate and no significant difference was found for phosphate. 'Net' was a significant factor for all three nutrients at 5 cm depth, as was Time for silicate and phosphate. Also, the interaction of 'Shell*Time' was significant for phosphate at this depth. At 9 cm depth only ammonia was significantly different (factor 'Time' and 'Net*Time'). At 12 cm depth the interaction 'Net*Time' was significant for all three

nutrients and Time was significant on its own for silicate. Overall there was a treatment effect for all nutrients at 5 cm depth, and Net*Time was significant for all nutrients at 12 cm depth. Effects observed at other depths were mostly due to variation over time.

Discussion

This study set out to examine the extent to which the biotic changes that accompany habitat change affect ecosystem functioning. Changes to the topography were expected to alter the overlying water flow dynamics and affect upwelling of nutrient-rich porewaters from deep sediment layers, causing an increase in nutrient concentrations in the near-surface sediments. (Booij *et al.* 1991; Huettel & Gust 1992; Vitousek & Hooper 1993; D'Andrea *et al.* 2002) Further alterations to the habitat caused by accretion of sediment and deposition of detrital material were also expected, affecting nutrient concentrations and faunal composition (*e.g.* McLachlan 1996; Rossi & Underwood 2002; Bishop & Kelaher 2007). Although significant changes to the species diversity and abundance were observed, there were no significant alterations to nutrient

Table 5. (A–D) Mixed Model analysis results of nutrient levels mg L⁻¹ per depth for each nutrient analysed.

	ammonia		phosphate		silicate	
	F	P	F	P	F	P
(A) 3 cm depth						
Shell	1.594	0.215	0.001	0.981	0.217	0.646
Net	0.206	0.653	0.001	0.972	1.515	0.234
Time	3.097	0.020	1.142	0.359	3.538	0.012
Shell*Time	2.439	0.070	1.666	0.182	0.756	0.562
Net*Time	0.375	0.824	1.101	0.375	1.926	0.131
(B) 5 cm depth						
Shell	0.000	0.988	2.571	0.122	3.224	0.081
Net	5.875	0.023	4.646	0.042	11.099	0.002
Time	1.209	0.317	3.687	0.007	3.038	0.017
Shell*Time	1.317	0.272	3.569	0.009	1.998	0.094
Net*Time	0.795	0.559	0.773	0.574	1.077	0.383
(C) 9 cm depth						
Shell	2.176	0.154	0.740	0.789	1.394	0.248
Net	0.824	0.373	0.498	0.488	2.087	0.160
Time	5.151	0.001	0.836	0.531	2.213	0.069
Shell*Time	1.777	0.133	0.238	0.944	0.117	0.988
Net*Time	2.706	0.029	0.692	0.632	0.878	0.502
(D) 12 cm depth						
Shell	1.703	0.203	2.372	0.137	0.775	0.394
Net	3.205	0.086	0.680	0.419	2.569	0.133
Time	2.073	0.083	2.496	0.054	24.957	≤ 0.001
Shell*Time	1.469	0.216	0.999	0.436	0.804	0.555
Net*Time	3.170	0.015	4.485	0.005	24.020	≤ 0.001

Significant p values in **bold**.

concentrations in either the near-surface or deeper (>9 cm) sediments sampled. The net treatments caused a significant change in the faunal composition and nutrient concentrations at 5 cm depth compared to the Control and both treatments showed an increased accretion of sediment, further altering the habitat by raising the sediment surface above that of the surrounding area and by altering the particle grain size composition. This indicates that the influence of the netting on faunal composition was similar regardless of additional 'roughness' due to the mussel shell debris and it may therefore be the subsequent alteration in species composition that influenced observed nutrient concentrations rather than the altered topography.

The observed biotic shift in the faunal composition reduced the abundance of individuals that actively irrigated burrows (*Corophium volutator* and *Corophium arenarium*) and species inhabiting permanent, or semi-permanent, tubes within the sediment (*Pygospio elegans*). The lower abundances of these bioturbators would have reduced the surface area available for solute exchange (Kristensen 2000; Pearson 2001; Volkenborn *et al.* 2007) and had an effect on microbial community composition in the near-surface sediments that had utilized the

burrows and tubes as oxygenated habitats (Marinelli *et al.* 2002; Mermillod-Blondin *et al.* 2004). As such, an increase in nutrient levels in the near-surface sediments may have been expected, as less oxidation of reduced substances from deeper layers was carried out. This was not the case, suggesting that (i) the nutrients were utilized either by microbial or by micro-phytobenthos communities, (ii) some redundancy with regard to the traits represented by these three species was present in the system.

The burrowing and movement of benthic macrofauna can impact on the sediment structure by causing compaction of sediment grains and increasing rigidity of the sediment layers via tube construction (Jones & Jago 1993; Mermillod-Blondin & Rosenberg 2006; Guillén *et al.* 2008). The oligochaetes present in the study area increased in abundance in the manipulated sediment moving nutrient-rich yet oxygen-poor material towards the surface and resulting in lower levels of nutrients than would have been observed if oxygen had not been available.

The altered species composition in the net treatment was accompanied by a shift in the range of biological traits exhibited by the fauna. This provides further, indirect, evidence of a change in ecological functioning being mediated by the biotic response. Alterations in the bioturbatory modes exhibited in the different treatments may have been enhanced by changes in the horizontal water flow and contributed to differences in the transport of oxygen, nutrients and particles from the sediment–water interface to areas below the redox zone (Biles *et al.* 2003). The combination of a shift in the depth at which the majority of burrowing fauna were residing and the changes to bioturbation, alongside the potential alterations to the sediment caused by the biotic shift, may have accounted for the significant differences observed in nutrient levels at 5 cm depth.

The analysis of the traits did not show a simple relationship with the altered nutrient dynamics. This suggests that whilst BTA may offer a means of predicting/quantifying ecological functioning (Usseglio-Polatera *et al.* 2000; Bremner *et al.* 2003), it relies on the selection of traits used. Bremner *et al.* (2006) have shown that the number of traits used can alter the ability of the analysis to describe the relationships between assemblages. They concluded that the greater the number of traits utilized in an analysis, the clearer any relationships between the traits and faunal assemblages will appear. Although the traits chosen in this study (bioturbatory mode, feeding mode, habitat depth, body size and longevity) were those considered to have an influence on nutrient regeneration, it may have been the case that more traits would have provided a clearer picture. However, the time constraints inherent with collecting trait-based data for any species assemblage force a compromise, causing those traits con-

sidered to be of importance to the ecosystem function of interest to be favoured over those that are not (Bremner *et al.* 2006).

The influence of functional diversity and composition on productivity and resource use has been well documented in terrestrial ecosystems (Hooper & Vitousek 1997; Tilman *et al.* 1997), concluding that alterations to functional group composition can have greater effects on ecosystem functions than functional diversity can (Hooper & Vitousek 1997). Also, changes to habitats via disturbance, species invasions or nutrient enrichment affect ecosystem functions (Tilman *et al.* 1997) and the loss or addition of various traits can have varying impacts on different ecosystem functions (Naeem *et al.* 1994; Tilman *et al.* 1997; Heemsbergen *et al.* 2004; Hooper *et al.* 2005; Rossi *et al.* 2008). The alteration of the topography in this study did cause a significant change to the faunal diversity and the biological traits represented. In particular, the 5 cm data indicated that the microbial and geochemical environment had been altered. However, the relationship of the traits to alterations in nutrient regeneration was less clear.

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References

- Aller R.C. (2001) Transport and reactions in the bioirrigated zone. In: Boudreau B.P., Jørgensen B.B. (Eds), *The Benthic Boundary Layer: Transport Processes and Biogeochemistry*. Oxford University Press, New York: 269–301.
- Aller R.C., Aller J.Y. (1998) The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *Journal of Marine Research*, **56**, 905–936.
- Banta G.T., Holmer M., Jensen M.H., Kristensen E. (1999) Effects of two polychaete worms, *Nereis diversicolor* and *Arenicola marina*, on aerobic and anaerobic decomposition in a sandy marine sediment. *Aquatic Microbial Ecology*, **19**(2), 189–204.
- Biles C.L., Solan M., Isaksson I., Paterson D.M., Emes C., Raffaelli D.G. (2003) Flow modifies the effect of biodiversity on ecosystem functioning: an in situ study of estuarine sediments. *Journal of Experimental Marine Biology and Ecology*, **285**, 165–177.
- Billerbeck M., Werner U., Polerecky L., Walpersdorf E., DeBeer D., Huettel M. (2006) Surficial and deep pore water circulation governs spatial and temporal scales of nutrient recycling in intertidal sand flat sediment. *Marine Ecology Progress Series*, **326**, 61–76.
- Bishop M.J., Kelaher B.P. (2007) Impacts of detrital enrichment on estuarine assemblages: disentangling effects of frequency and intensity of disturbance. *Marine Ecology Progress Series*, **341**, 25–36.
- Bolger T. (2001) The functional value of species biodiversity – A review. *Proceedings of the Royal Irish Academy – Section B Biology and Environment*, **101**(3), 199–224.
- Booij K., Helder W., Sundby B. (1991) Rapid redistribution of oxygen in a sandy sediment induced by changes in the flow velocity of the overlying water. *Netherlands Journal of Sea Research*, **28**(3), 149–165.
- Bourget E., DeGuise J., Daigle G. (1994) Scales of substratum heterogeneity, structural complexity, and the early establishment of a marine epibenthic community. *Journal of Experimental Marine Biology and Ecology*, **181**(1), 31–51.
- Bremner J., Rogers S.I., Frid C.L.J. (2003) Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series*, **254**, 11–25.
- Bremner J., Rogers S.I., Frid C.L.J. (2006) Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators*, **6**(3), 609–622.
- Callaway R. (2003) Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks. *Journal of Experimental Marine Biology and Ecology*, **283**(1–2), 115–132.
- Cesar C.P., Frid C.L.J. (2009) Effects of small-scale cockle (*Cerastoderma edule* L.) fishing on ecosystem function. *Marine Ecology – An Evolutionary Perspective*, **30**(Suppl. 1), 123–137.
- Chevenet F., Doledec S., Chessel D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, **31**(3), 295–309.
- Christensen B., Vedel A., Kristensen E. (2000) Carbon and nitrogen fluxes in sediment inhabited by suspension-feeding (*Nereis diversicolor*) and non-suspension-feeding (*N. virens*) polychaetes. *Marine Ecology Progress Series*, **192**, 203–217.
- D'Andrea A.F., Aller R.C., Lopez G.R. (2002) Organic matter flux and reactivity on a South Carolina sandflat: the impacts of porewater advection and macrobiological structures. *Limnology and Oceanography*, **47**(4), 1056–1070.
- De Juan S., Thrush S.F., Demestre M. (2007) Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Marine Ecology Progress Series*, **334**, 117–129.
- Diggle P.J. (1988) An approach to the analysis of repeated measurements. *Biometrics*, **44**(4), 959–971.
- Ehrlich P.R., Ehrlich A.H. (1981) *Extinction: the Causes and Consequences of the Disappearance of Species*. Random House, New York.
- Eleftheriou A., McIntyre A. (2005) Sediment analysis and seabed characterisation. In: Eleftheriou A., McIntyre A. (Eds),

- Methods for the Study of the Marine Benthos*. Blackwell Publishing, Oxford, Malden: 418 pp.
- Emmerson M.C., Solan M., Emes C., Paterson D.M., Raffaelli D. (2001) Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature*, **411**(6833), 73–77.
- François F., Poggiale J.C., Durbec J.P., Stora G. (1997) A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheoretica*, **45**(3–4), 295–319.
- François F., Gerino M., Stora G., Durbec J.-P., Poggiale J.-C., Stora G. (2002) Functional approach to sediment reworking by gallery-forming macrobenthic organisms: modeling and application with the polychaete *Nereis diversicolor*. *Marine Ecology Progress Series*, **229**, 127–136.
- Friedrichs M., Graf G., Springer B. (2000) Skimming flow induced over a simulated polychaete tube lawn at low population densities. *Marine Ecology Progress Series*, **192**, 219–228.
- Gardner L.R., Sharma P., Moore W.S. (1987) A regeneration model for the effect of bioturbation by fiddler crabs on ²¹⁰Pb profiles in salt marsh sediments. *Journal of Environmental Radioactivity*, **5**, 25–36.
- Garson G.D. (2008) Linear mixed models: random effects, hierarchical linear, multilevel, random coefficients, and repeated measures models. *Statnotes: Topics in Multivariate Analysis*. <http://www2.chass.ncsu.edu/garson/pa765/statnote.htm> (last accessed 10 June 2009).
- Giller P.S., Hillebrand H., Berninger U.G., Gessner M.O., Hawkins S., Inchausti P., Inglis C., Leslie H., Malmqvist B., Monaghan M.T., Morin P.J., O'Mullan G. (2004) Biodiversity effects on ecosystem functioning: emerging issues and their experimental test in aquatic environments. *Oikos*, **104**(3), 423–436.
- Guillén J., Soriano S., Demestre M., Falqués A., Palanques A., Puig P. (2008) Alteration of bottom roughness by benthic organisms in a sandy coastal environment. *Continental Shelf Research*, **28**(17), 2382–2392.
- Günther C.P. (1996) Development of small *Mytilus* beds and its effects on resident intertidal macrofauna. *Marine Ecology*, **17**, 117–130.
- Heemsbergen D.A., Berg M.P., Loreau M., Van Hal J.R., Faber J.H., Verhoef H.A. (2004) Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science*, **306**, 1019–1020.
- Hooper D.U., Vitousek P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**(5330), 1302–1305.
- Hooper D.U., Chapin F.S. III, Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setaälä H., Symstad A.J., Vandermeer J., Wardle D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3.
- Huetzel M., Gust G. (1992) Impact of bioturbation on interfacial solute exchange in permeable sediments. *Marine Ecology Progress Series*, **89**, 253–267.
- Huetzel M., Webster I.T. (2001) Porewater flow in permeable sediments. In: Boudreau B.P., Jørgensen B.B. (Eds.), *The Benthic Boundary Layer: Transport Processes and Biogeochemistry*. Oxford University Press, New York: 144–179.
- Hurlbert S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Jones S.E., Jago C.F. (1993) In situ assessment of modification of sediment properties by burrowing invertebrates. *Marine Biology*, **115**, 133–142.
- Jones M., Pinn E. (2006) The impact of a macroalgal mat on benthic biodiversity in Poole Harbour. *Marine Pollution Bulletin*, **53**, 63–71.
- Karlson K. (2007) Diurnal bioturbating activities of *Monoporeia affinis*: effects on benthic oxygen and nutrient fluxes. *Marine Ecology Progress Series*, **331**, 195–205.
- Kristensen E. (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia*, **426**, 1–24.
- Kuwaie T., Kibe E., Nakamura Y. (2003) Effect of emersion and immersion on the porewater nutrient dynamics of an intertidal sandflat in Tokyo Bay. *Estuarine, Coastal and Shelf Science*, **57**, 929–940.
- Kuwaie T., Kamio K., Inoue T., Miyoshi E., Uchiyama Y. (2006) Oxygen exchange flux between sediment and water in an intertidal sandflat, measured in situ by the eddy-correlation method. *Marine Ecology Progress Series*, **307**, 59–68.
- Lawton J.H., Naeem S., Woodfin R.M., Brown V.K., Gange A., Godfray H.J.C., Heads P.A., Lawler S., Magda D., Thomas C.D., Thompson L.J., Young S. (1993) The Ecotron: a controlled environmental facility for the investigation of population and ecosystem processes. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences*, **341**, 181–194.
- Luckenbach M.W. (1986) Sediment stability around animal tubes: the roles of hydrodynamic processes and biotic activity. *Limnology & Oceanography*, **31**, 779–787.
- Marinelli R.L., Lovell C.R., Wakeham S.G., Ringelberg D.B., White D.C. (2002) Experimental investigation of the control of bacterial community composition in macrofaunal burrows. *Marine Ecology Progress Series*, **235**, 1–13.
- Matisoff G., Wang X. (1998) Solute transport in sediments by freshwater infaunal bioirrigators. *Limnology and Oceanography*, **43**, 1487–1499.
- McLachlan A. (1996) Physical factors in benthic ecology: effects of changing sand particle size on beach fauna. *Marine Ecology Progress Series*, **131**(1–3), 205–217.
- Mermillod-Blondin F., Rosenberg R. (2006) Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences*, **68**, 434–442.
- Mermillod-Blondin F., Rosenberg R., François-Carcaillet F., Norling K., Mauclair L. (2004) Influence of bioturbation by three benthic infaunal species on microbial communities and biogeochemical processes in marine sediment. *Aquatic Microbial Ecology*, **36**, 271–284.

- Michaud E., Desrosiers G., Mermillod-Blondin F., Sundby B., Stora G. (2005) The functional group approach to bioturbation: the effects of biodiffusers and gallery-diffusers of the *Macoma balthica* community on sediment oxygen uptake. *Journal of Experimental Marine Biology and Ecology*, **326**, 77–88.
- Michaud E., Desrosiers G., Mermillod-Blondin F., Sundby B., Stora G. (2006) The functional group approach to bioturbation: II. The effects of the *Macoma balthica* community on fluxes of nutrients and dissolved organic carbon across the sediment-water interface. *Journal of Experimental Marine Biology and Ecology*, **337**, 178–189.
- Mooney H.A., Lubchenco J., Dirzo R., Sala O.E. (1995) Biodiversity and ecosystem functioning: basic principles. In: Heywood V.H. (Ed.), *Global Biodiversity Assessment*. Cambridge University Press, Cambridge: 275–326.
- Mortimer R.J.G., Davey J.T., Krom M.D., Watson P.G., Frickers P.E., Clifton R.J. (1999) The effect of macrofauna on porewater profiles and nutrient fluxes in the intertidal zone of the Humber estuary. *Estuarine, Coastal and Shelf Science*, **48**(6), 683–699.
- Naeem S. (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology*, **83**, 1537–1552.
- Naeem S., Thompson L.J., Lawler S.P., Lawton J.H., Woodfin R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734–737.
- Nayar S., Miller D., Bryars S., Cheshire A.C. (2006) A simple, inexpensive and large volume pore water sampler for sandy and muddy substrates. *Estuarine Coastal and Shelf Science*, **66**, 298–302.
- Pearson T.H. (2001) Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanography and Marine Biology: An Annual Review*, **39**, 233–267.
- Raffaelli D. (2000) Interactions between macro-algal mats and invertebrates in the Ythan estuary, Aberdeenshire, Scotland. *Helgoland Marine Research*, **54**, 71–79.
- Rossi F., Underwood A.J. (2002) Small-scale disturbance and increased nutrients as influences on intertidal macrobenthic assemblages: experimental burial of wrack in different intertidal environments. *Marine Ecology Progress Series*, **241**, 29–39.
- Rossi R., Gribsholt B., Middelburg J.J., Heip C. (2008) Context-dependent effects of suspension feeding on intertidal ecosystem functioning. *Marine Ecology Progress Series*, **354**, 47–57.
- Rowell J.G., Walters D.E. (1976) Analysing data with repeated observations on each experimental unit. *Journal of Agricultural Science*, **87**, 423–432.
- Savage V.M., Webb C.T., Norberg J. (2007) A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. *Journal of Theoretical Biology*, **247**, 213–229.
- Solan M., Cardinale B.J., Downing A.L., Engelhardt K.A.M., Ruesink J.L., Srivastava D.S. (2004) Extinction and ecosystem function in the marine benthos. *Science*, **306**, 1177–1180.
- Stachowicz J.J., Bruno J.F., Duffy J.E. (2007) Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology, Evolution and Systematics*, **38**, 739–766.
- Tillin H.M., Hiddink J.G., Jennings S., Kaiser M.J. (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, **318**, 31–45.
- Tilman D., Knops J., Wedin D., Reich P., Ritchie M., Siemann E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.
- Usseglio-Polatera P., Bournaud M., Richoux P., Tachet H. (2000) Biomonitoring through biological traits of benthic macroinvertebrates: how to use species trait databases? *Hydrobiologia*, **422**, 153–162.
- Vitousek P.M., Hooper D.U. (1993) Biological diversity and terrestrial ecosystem biogeochemistry. In: Schulze E.D., Mooney H.A. (Eds), *Biodiversity and Ecosystem Function*. Springer-Verlag, New York: 3–14.
- Volkenborn N., Polerecky L., Hedtkamp S.I.C., van Beusekom J.E.E., de Beer D. (2007) Bioturbation and bioirrigation extend the open exchange regions in permeable sediments. *Limnology and Oceanography*, **52**, 1898–1909.
- Wang Z., Goonewardene L.A. (2004) The use of MIXED models in the analysis of animal experiments with repeated measures data. *Canadian Journal of Animal Science*, **84**, 1–11.
- Welsh D.T. (2003) It's a dirty job but someone has to do it: the role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. *Chemistry and Ecology*, **19**, 321–342.
- Wolanski E., Richmond R.H., McCook L. (2004) A model of the effects of land-based, human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia. *Journal of Marine Systems*, **46**, 133.
- Ziebis W., Huettel M., Forster S. (1996) Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. *Marine Ecology Progress Series*, **140**, 227–237.