Ecological Monographs, 72(4), 2002, pp. 599–615

DIVERSITY, BIOMASS, AND ECOSYSTEM PROCESSES IN THE MARINE BENTHOS

S. G. BOLAM,[1] T. F. FERNANDES,[2] AND M. HUXHAM[2,3]

[1]*CEFAS, Burnham Laboratory, Remembrance Avenue, Essex, CMO 8HA United Kingdom*
[2]*School of Life Sciences, Napier University, Edinburgh, EH10 5DT United Kingdom*

Abstract. Recent studies in terrestrial, plant-dominated systems have shown that reductions in diversity can affect essential ecosystem processes, especially productivity. However, the exact form of the relationship between diversity and ecosystem functions remains unknown, as does the relevance of these studies to other systems. We studied the relationships between macroinvertebrate species richness and ecosystem functions in a soft-bottom, intertidal system. We also considered, as a separate variable, the effects of macroinvertebrate biomass on ecosystem functions. A field experiment was conducted at Blackness, a mudflat in the Firth of Forth, Scotland, United Kingdom, using cages with different mesh sizes (195, 300, and 3000 μm) to establish low, medium, and high species richness treatments through differential colonization of defaunated sediments. Low, medium, and high biomass treatments were established by enclosing differing amounts of ambient sediment in defaunated plots. Other treatments controlled for the effects of defaunation and caging. The experiment ran for six weeks in the summer of 1999. All treatments contained species within the same five main functional groups of macroinvertebrate, but species' identity varied both within and between treatments (thus species richness was considered a random, rather than fixed, variable). A total of 27 macroinvertebrate species were sampled across all treatments; 37% of these occurred in the low, 52% in the medium, and 74% in the high diversity treatments.

At the end of the experiment, the following physical variables were measured as indicators of ecosystem functions such as sediment stabilization and nutrient fluxes: sediment shear strength (a measure of sediment cohesiveness), water content, silt/clay content, organic content, redox potential (a measure of anoxia), nitrate, nitrite, phosphate and ammonium fluxes, and community respiration. Changes in biomass and species richness were found to have significant effects on oxygen consumption; these relationships were driven in particular by the presence of the largest species in our study, *Nephtys hombergii*. All other variables were not significantly affected by the treatments. These results support the null hypotheses of no relationship between ecosystem functions and diversity and biomass. However, our experiment was necessarily limited in both spatial and temporal scale; the implications of this when scaling up to larger scale generalizations are discussed. Our results suggest that diversity/biomass/ecosystem function relationships in the soft sediment benthos are likely to be very complex and may depend more on functional groups than species richness.

Key words: benthos; biomass; Blackness, Firth of Forth, Scotland, UK; diversity; ecosystem function; macrofauna; soft-sediment intertidal.

INTRODUCTION

Many ecosystems are currently experiencing a loss of biodiversity associated with human activities (Erhlich and Wilson 1991). Reasons for concern about this decline include the loss of aesthetic quality and of economic opportunity (Erhlich and Wilson 1991). However, most recent attention has focused on the potential effects of biodiversity loss on the adequate functioning of the Earth's ecosystems (Grime 1997), or more specifically, the ''services'' that ecosystems provide to humanity (Erhlich and Wilson 1991, Naeem et al. 1994, Snelgrove 1999).

Lawton (1994) and Naeem et al. (1995) proposed four main hypotheses that relate the responses of ecosystem processes to reductions in species richness (which is usually synonymous with diversity in the literature). First, the redundant species hypothesis suggests that there is a minimum diversity necessary for proper ecosystem function, but beyond that additional species are redundant (although may provide ''insurance'' against future disturbances). Second, the rivet hypothesis suggests that all species make a contribution to ecosystem performance. This hypothesis likens species to rivets holding a complex machine, and postulates that functioning will be impaired as rivets (species) fall out. Third, the idiosyncratic response hy-

Manuscript received 25 September 2000; revised 22 October 2001; accepted 23 October 2001; final version received 17 December 2001.

[3] Corresponding author: E-mail: m.huxham@napier.ac.uk

pothesis suggests that ecosystem function changes when diversity changes, but the magnitude and direction of change is unpredictable because the roles of individual species are complex. Fourth, the null hypothesis proposes that ecosystem function is insensitive to any changes in diversity.

There have been few empirical tests of these contrasting hypotheses. At present, most of the work in this area has focused on grassland ecosystems, and these studies have indicated that decreasing species richness impairs some ecosystem functions, particularly productivity (Naeem et al. 1994, 1995, 1996, Tilman and Downing 1994, Tilman et al. 1996, 1997, Symstad et al. 1998, Hector et al. 1999, Nilsson et al. 1999, Stocker et al. 1999, Wilsey and Potvin 2000). However, the experimental designs of many of these studies have been criticized (Andre et al. 1994, Givnish 1994, Aarssen 1997, Huston 1997, Hodgson et al. 1998, Wardle 1999). In particular, three main problems have been identified: (1) lack of controls for changes in plant biomass between plant diversity treatments, (2) nonrandom selection of species within diversity treatments, and (3) too small a range in manipulated diversity compared with real systems. Consequently, empirical evidence regarding the effects of biodiversity loss on the functioning of ecosystems remains equivocal. There is evidence however, that it is not the number of species which is important in ecosystems, but the functional characteristics of the species (Elmgren and Hill 1997, Grime 1997, Hooper and Vitousek 1997, Tilman et al. 1997, Symstad et al. 1998, Hector et al. 1999, Wardle 1999, Emmerson and Raffaelli 2000).

The marine benthos is arguably the largest ecosystem on Earth, and ecosystem processes occurring within it have important effects both locally and globally (Nixon 1982, Snelgrove et al. 1997, Snelgrove 1998, 1999); Costanza et al. (1997) recently suggested that the oceans account for approximately two-thirds of the value of global ecosystem services. Within the marine benthos, it is perhaps in shallow coastal habitats that the relationship between species richness and ecosystem processes needs most urgently to be ascertained. These habitats play a major role in biogeochemical cycles because they receive massive inputs of terrestrial organic matter and nutrients, and are among the most geochemically and biologically active areas of the biosphere (Gattuso et al. 1998). Coastal habitats tend to be disproportionately impacted worldwide, which often results in their macrofaunal communities having a reduced diversity (see review by Pearson and Rosenberg 1978).

The ecology and ecosystem processes of the marine benthos have been shown to be greatly affected by a few visually obvious species such as mangrove trees (Alongi et al. 1998, Kristensen et al. 1998) and seagrasses (Irlandi 1994, Irlandi et al. 1995, Fourqurean et al. 1997). However, such species are absent from most benthic systems, which are characterized instead by small invertebrate infauna. At the phylum level, marine macrofauna represent one of the most diverse assemblages on Earth with extremely high diversity at the species level (Snelgrove 1998, 1999). There is much literature indicating that the presence of particular species of macrofauna can significantly affect nutrient fluxes between the sediments and overlying water column (Aller 1982, 1988, Kristensen 1984, 1988, Kristensen and Blackburn 1987, Huttel 1990), sediment oxygenation (Rhoads 1974), and sediment stability (Rhoads and Young 1970, Daro and Polk 1973, Noji and Noji 1991, Morgan 1997). All these ecosystem processes are important in the management of coastal marine habitats, and changes in them are likely to have large economic and aesthetic costs.

The significance of biodiversity to ecosystem processes in marine sediments is poorly understood. Limited data suggest that there is substantial functional redundancy in macrofauna within functional groups, but whether this redundancy is sufficient to allow species loss without significantly affecting ecosystem processes is unknown (Snelgrove et al. 1997, Snelgrove 1998). In this paper, we describe a field experiment in which the species richness of a macroinfaunal community of a temperate intertidal mudflat is manipulated. The three main concerns about the experimental design of previous studies identified earlier are addressed in this experiment as follows: First, the effects of changes in macrofaunal biomass, which could confound the effects of changing diversity, are controlled for by performing a parallel experiment in which the macrofaunal biomass is manipulated independently of species richness. Our experiment was designed to explicitly examine the effects of changes in biomass, to allow the subsequent separation of this variable from species richness. Second, species composition within all diversity treatments is not fixed, but varies between replicates. Third, since temperate intertidal mudflats are relatively species poor, a substantial range of the species naturally present is represented in the experimental treatments. The main objectives of the present study were to experimentally test whether differences in macrofaunal species richness and biomass affect ecosystem processes. The two null hypotheses are that reductions in species richness and biomass have no effects on ecosystem processes.

Methods

Study site

The experiment was conducted at Blackness, a large intertidal mudflat located within the lower Forth Estuary (56°0′ N, 3°30′ W; Fig. 1), 25 km west of Edinburgh. The area is relatively unpolluted, being over eight kilometers downstream of the industrial effluents from Grangemouth (McLusky et al. 1983). On a large spatial scale, the sediments at Blackness vary from fine mud to sand (*personal observation*). Various soft-bot-

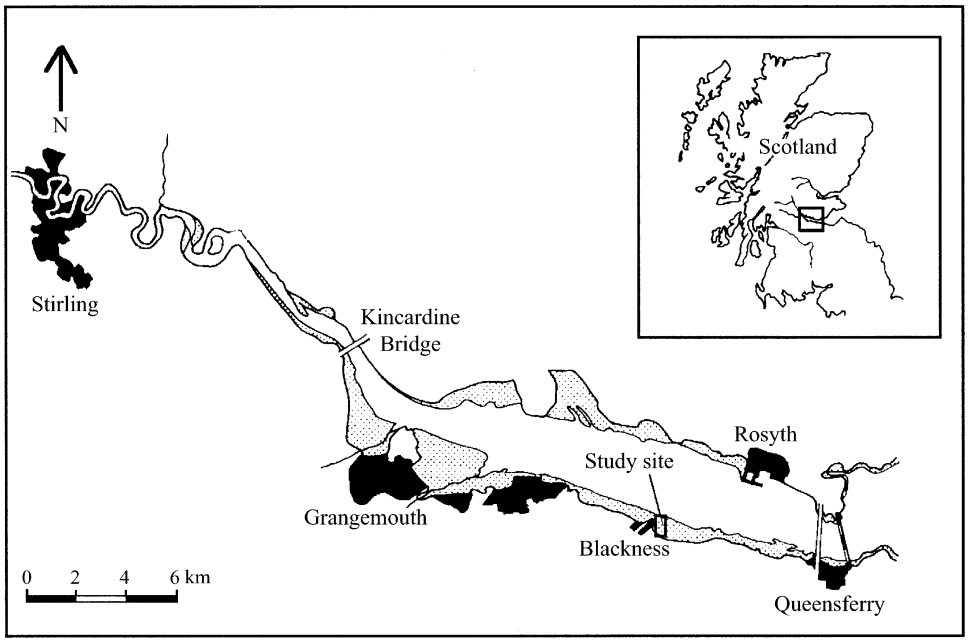

FIG. 1. Map of the Forth Estuary showing the position of the study site.

tom manipulation experiments have recently been conducted at Blackness (e.g., Fernandes et al. 1999, Richards et al. 1999, Huxham et al. 2000), and its benthic ecology is fairly well understood.

Macrofaunal community

In general, five trophic or functional groups are present on the mudflat: grazers, suspension-, surface-, and subsurface deposit feeders, and predators. The contrasting feeding, burrowing, and irrigation methods of these trophic groups have different effects on sedimentary processes (Aller 1988). For example, while grazers remove sediment-stabilizing diatoms, resulting in sediment destabilization, the irrigation activity of tube-dwelling deposit feeders increases oxygenation of subsurface sediments, changing the dominance and distribution of oxidation-reduction reactions.

The macrofaunal community of Blackness is numerically dominated by six species: the bivalves *Macoma balthica* (L.) and *Cerastoderma edule* (L.), the gastropod *Hydrobia ulvae* (Pennant), the amphipod *Corophium volutator* (Pallas), and the spionid polychaetes *Pygospio elegans* (Claparède) and *Streblospio benedicti* (Webster) (see Table 1). These species comprise ~95% of total infaunal density at Blackness. While *H. ulvae* actively migrates across the sediment surface grazing on benthic diatoms, the other five species are more-or-less sedentary, deposit and/or suspension feeders, feeding from semipermanent tubes or burrows. The other important species, although numerically less dominant, on Blackness is the predatory polychaete *Nephtys hombergii* (Savigny).

The relative sizes and biomasses of these main species vary greatly (Table 1). *H. ulvae* and *C. volutator*, and to a lesser extent *P. elegans* and *S. benedicti*, are the numerical dominants at Blackness; however, because of their small size they do not individually contribute greatly to the total biomass. In contrast, although less abundant, the two bivalve species *M. balthica* and *C. edule*, and the polychaete *N. hombergii*, are biomass dominants at Blackness. Similar numerical and biomass dominance has been observed for other temperate intertidal mudflats, e.g., the tidal flats of the Dutch Wadden Sea (Beukema 1976).

Experimental design

Three experimental blocks were established, perpendicular to tidal movement, within a relatively homogeneous area of Blackness (Fig. 2). The sediments within this area typically have an approximate loss on ignition of 6.4% and a silt/clay fraction of 29% (Fernandes et al. 1999). Within each block, two replicates of each of 11 treatments (as described in the section *Experimental treatments*) were randomly assigned to 22 plots (Fig. 2). These plots were 1×1 m, and 2 m apart from neighboring plots. Therefore, the experiment used a replicated block design with six replicates. For the diversity, biomass, and defaunated plot treatments, the sediments were first defaunated by placing wooden boards (90×70 cm) on the sediment surface. Concrete blocks were placed on each board to keep them in place. Regular sampling revealed that total macrofaunal defaunation occurred beneath the boards after five weeks, and sediment redox potentials were significantly reduced compared to nondefaunated sediments. Macrofaunal defaunation was initially delayed

TABLE 1. Description of the main invertebrate species at Blackness.

Species	Description	Maximum size
Hydrobia ulvae	Small, brackish-water gastropod mollusc, locally very abundant on the surface of mudflats. Grazes on benthic diatoms.	shell 6 mm long
Macoma balthica	Broadly oval-shaped bivalve mollusc. Locally abundant on estuarine intertidal mud- and sandflats. Inhabits top 2–3 cm of sediment, deposit and suspension feeding with siphons.	shell 25 mm long
Cerastoderma edule	Broadly oval-shaped bivalve mollusc. Present in sandy mud, sand, or fine gravel. Mid tide level to low water springs. Same feeding mechanism as *M. balthica*.	shell 50 mm long
Corophium volutator	Intertidal amphipod crustacean, locally abundant on mudflats. Lives in U-shaped, semipermanent burrows from which the animal deposit feeds.	length 8 mm
Pygospio elegans	Spionid polychaete, inhabits long, flexible tubes of fine sand grains embedded in mucus. Surface deposit feeds on intertidal mud- and sandflats and shallow sublittoral.	slender body, 10–15 mm long
Streblospio benedicti	Small, spionid polychaete abundant in muddy sediments inter- and subtidally. Inhabits muddy tube from which the animal deposit feeds.	slender body, 8–10 mm long
Nephtys hombergii	Common and widespread on sandy and muddy intertidal habitats and shallow sublittoral. Motile carnivores that prey on benthic molluscs, crustaceans, and polychaetes.	100–200 mm long

as the wooden boards did not sufficiently prevent water flow to the sediment surface. Extra concrete blocks were placed on top of each board after three weeks, and total defaunation was achieved two weeks later. On 14 July 1999, the experiment was initiated by removing the boards, and cages were placed onto 9 of the 11 treatments.

Cage design

Exclosure cages were used in this experiment to establish communities of different macrofaunal species richness based on individual size. To reduce treatment-specific artifacts, differences in the between-treatment cages were minimized. Therefore, any differences in the cages were confined to the 5 cm above and below the sediment surface (Fig. 3). Colonization of small-scale disturbances in soft-bottom habitats generally occurs via larval settlement (although passive and/or active adult immigration can also be important, both at this site and elsewhere; Smith and Brumsickle 1989, Gunther 1992, Thrush et al. 1992, Huxham et al. 2000).

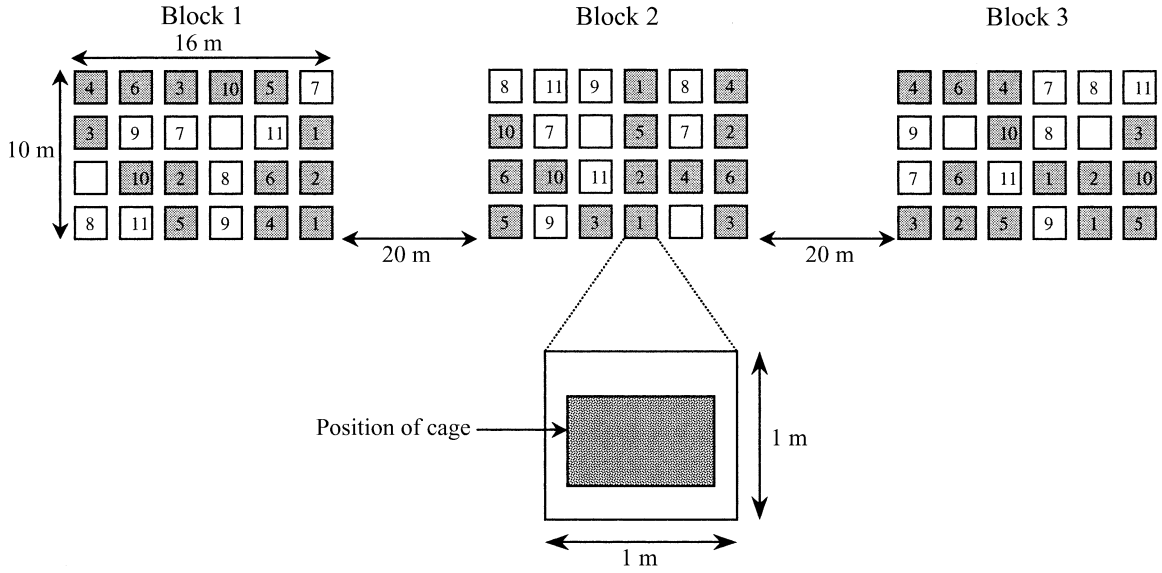

FIG. 2. Experimental layout showing the positions of treatment replicates within blocks 1–3. Treatments are: 1–3, low, medium, and high diversity; 4–6, low, medium, and high biomass; 7–9, low, medium, and high diversity cage control; 10, defaunated plot (defaunated treatment); and 11, unmanipulated control. Shaded plots were previously defaunated.

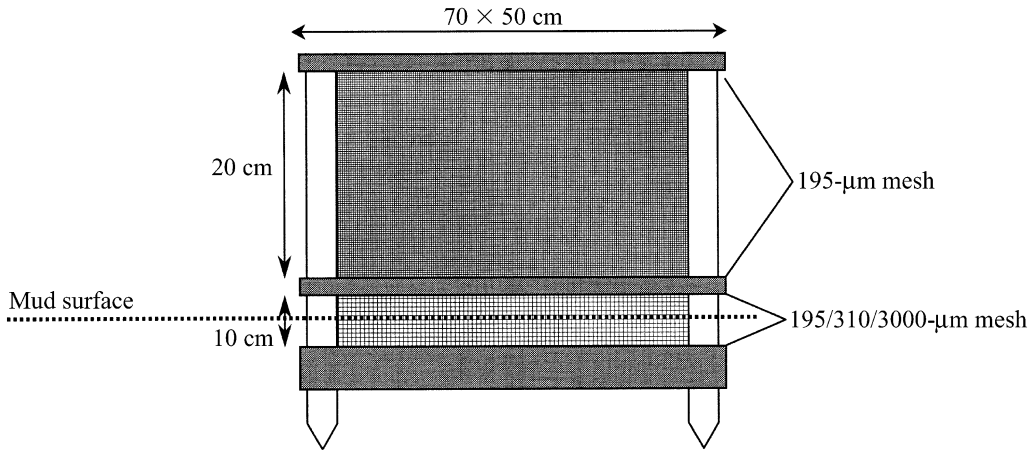

FIG. 3. The design of cages used to establish different macrofaunal diversities. The top portion was identical for all cage types, but treatments varied in the mesh used for the lower 10-cm region.

Consequently, the mesh size used in the cage design had to take account of the larval sizes of the species present. Preliminary experiments at Blackness revealed that the larval stages of a few species were able to colonize defaunated sediments through a 195-μm net mesh, while a larger proportion could colonize through a 310-μm net mesh. These mesh sizes were therefore used to establish the low and medium diversity communities respectively. A 3000-μm net mesh was used for the high diversity treatment cages. Although both the larval and adult stages of most macrofaunal species could pass through this mesh, epifaunal predators at Blackness, the shore crab *Carcinus maenas* (L.), and the shrimp *Crangon crangon* (L.) (Richards et al. 1999), were excluded, preventing the cages from offering a refuge for these predators. Neither of these species were found inside cages at the end of the experiment. Low diversity design cages were used to establish all the biomass treatments.

Experimental treatments

Eleven treatments, within five treatment groups, were used in this experiment:

1) Diversity treatments: low, medium, and high. The cages used for these treatments were placed onto defaunated sediments.

2) Biomass treatments: low, medium, and high. Low diversity design cages were used in establishing these communities. However, treatments differed in the extent of defaunation. For the low biomass treatments, 60% of the enclosed sediment had been previously defaunated, with 40% defaunation for the medium biomass treatment, while only 20% of the sediments had been defaunated within the high biomass treatments. This was achieved by varying the degree of overlap of the cages with the defaunated sediments. Previous work had indicated that the majority of the species at Blackness would be present within the undisturbed sediments of the low biomass treatments.

3) Cage controls: low, medium and high. These treatments were included to determine the presence of cage-specific artifacts. The three cage types were placed on nondefaunated sediments.

4) Defaunation control treatment. This treatment, in which the sediment was defaunated without the addition of a cage, was incorporated to determine the effect of defaunation, and to indicate the degree of recovery of the macrobenthic community at the end of the experiment.

5) Unmanipulated treatment. Controls to record the ambient macrobenthic community and ecosystem processes that occurred at Blackness at the end of the experiment.

Sampling

On 20 August, six weeks after the start of the experiment, samples were taken from all plots. Faunal recovery of the treatments had been monitored: changes in abundance and species richness were negligible after six weeks, suggesting that stable communities had established within each treatment. Macrofaunal, meiofaunal, and sediment samples were taken from each plot, together with redox potential measurements, sediment shear strength measurements, and cores of sediment for incubation in the laboratory. Macrofaunal samples were taken by three randomly positioned cores (6 × 6 cm, 6-cm depth), which were then pooled to avoid pseudoreplication (Hurlbert 1984). The fauna were preserved by the addition of saline, neutralized formaldehyde solution (10%) with a Rose Bengal stain. Meiofaunal samples were taken by four randomly located cores (1.4-cm internal diameter, 1.5-cm depth), pooled, and preserved with neutralized, saline formaldehyde solution (4%). Sediment samples were taken by three random cores (2.7-cm internal diameter, 3-cm depth), which were also pooled. These samples were analyzed in the laboratory for percentage water content (loss of mass at 80°C), percentage carbon (loss of mass

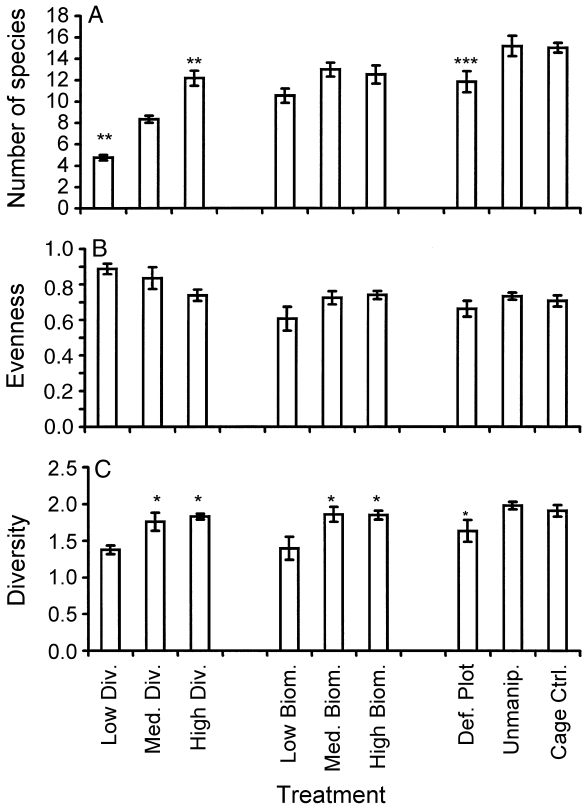

FIG. 4. (A) Mean numbers of macrofaunal species per sample for each treatment (mean ± 1 SE; $n = 4$ for low diversity treatment, 6 otherwise). In all figures, an asterisk (*) denotes statistical significance between treatments within the three treatment groups (i.e., diversity treatments, biomass treatments, and control treatments). In panel (A), asterisks indicate significant difference from the medium diversity treatment and the unmanipulated plot. (B) Mean Pielou's evenness (mean ± 1 SE; $n = 4$ for low diversity treatment, 6 otherwise). (C) Mean Shannon-Wiener diversity (mean ± 1 SE; $n = 4$ for low diversity treatment, 6 otherwise). In panel (C), asterisks indicate statistical significance from low diversity and low biomass treatments and unmanipulated plot. Abbreviations are: Div., diversity; Bio., biomass; Def., defaunated; Unmanip., unmanipulated; and Ctrl., control.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

at 450°C), and percentage silt (fraction retained on a 65-μm mesh). Redox potential values were taken at three depths; 1, 2, and 4 cm, readings being recorded after 60 s of the probe being inserted, or before if the reading had stabilized (Pearson and Stanley 1979). Sediment shear strengths were measured using a Geonor H-60 Vane Borer (Goenor A/S, Oslo, Norway).

Incubation procedure

One core for incubation was taken from each replicate within the diversity and biomass treatments using an 8-cm (internal diameter) core. The cores contained 10 cm of sediment and were filled with 30-cm depth of artificial seawater before incubation at 18°C (ambient sediment temperature) for 6 h in the dark. Before the incubation, initial water samples were taken for dissolved oxygen and nutrient analyses, then nitrogen gas was added to displace air remaining in the core, before the addition of a sealed lid. The water was constantly, slowly stirred to prevent stratification without resuspension of the sediment. Benthic respiration rates were determined by the difference in dissolved oxygen concentration between the start and the end of incubation. Dissolved oxygen was determined using a Micro-Winkler technique (Strickland and Parsons 1972). Nutrient fluxes between the sediment and the overlying water column were determined by changes in nitrate, nitrite, ammonium, and phosphate concentrations in the overlying water. Nutrient analysis was carried out on GF/C-filtered samples by the Scottish Environment Protection Agency using a colorimetric microplate method.

Data analysis

All data were checked for normality (Anderson-Darling test) and homogeneity of variance (Bartlett test). Data not meeting these criteria were appropriately transformed (Zar 1984). Mixed model two-way ANOVAs were used to assess treatment (fixed) and block (random) effects, and interactions between them. All tests were balanced, except for those within the diversity treatment group due to the loss of two low diversity cages during the experiment. Where necessary, Tukey multiple comparison tests were carried out to indicate which treatments were significant at the 5% level of significance. To provide further information on the effects of the treatments on community structure, Pielou's evenness and Shannon-Wiener diversity measures were calculated. A posteriori power analyses were performed to determine the minimum detectable differences between means given 90% power (Zar 1984). Correlation analyses were carried out between macrofaunal species richness, macrofaunal biomass, and meiofaunal abundance with all the measured variables using a Pearson product-moment correlation after the data were normalized. Scatterplots of macrofaunal species number and biomass against ecosystem processes were produced to aid interpretation of correlation results. To separate out the effects of biomass and species richness, these two variables were used as predictors in multiple regression analyses of significant relationships. To investigate the influence of individual species on those variables identified as having a significant relationship with macrofaunal biomass or diversity, multiple regressions (stepwise, forward, and r^2 options, SAS software) were performed with the abundances of individual species as the predictor variables. Variance inflation was used to check for multicollinearity. To test for possible block-scale artifacts, bulk sediment variables from individual plots were regressed against plot location within the block (measured as relative distance from low water mark). Statistical analyses

TABLE 2. Species list showing total numbers of each species from each diversity and biomass treatment.

Taxon	Diversity			Biomass		
	Low	Medium	High	Low	Medium	High
Grazers						
Hydrobia ulvae (Mg)	2 (1)	70 (6)	320 (6)	273 (6)	232 (6)	260 (6)
Surface deposit feeders						
Pygospio elegans (Ap)	23 (4)	26 (5)	101 (6)	55 (6)	151 (6)	171 (6)
Streblospio benedicti (Ap)	3 (2)	18 (6)	48 (6)	22 (6)	165 (6)	209 (6)
Spio setosa (Ap)	0	0	1 (1)	0	0	0
Polydora ligni (Ap)	4 (3)	5 (3)	7 (3)	8 (3)	2 (2)	3 (3)
Chaetozone setosa (Ap)	0	0	1 (1)	0	0	0
Manayunkia sp. (Ap)†	1 (1)	0	3 (3)	1 (1)	17 (4)	42 (2)
Cossura longocirrata (Ap)	0	0	0	0	2 (2)	2 (2)
Tharyx sp. (Ap)	0	0	0	0	8 (4)	4 (3)
Tellina fabula (Mb)	0	0	1 (1)	0	0	0
Macoma balthica (Mb)†	2 (1)	20 (6)	200 (6)	26 (5)	31 (6)	54 (6)
Cerastoderma edule (Mb)†	22 (4)	29 (6)	111 (6)	40 (6)	41 (4)	63 (6)
Corophium volutator (Ca)	0	20 (6)	272 (6)	192 (4)	94 (3)	73 (4)
Subsurface deposit feeders						
Aricidea catherina (Ap)	0	0	0	1 (1)	2 (1)	2 (2)
Scoloplos armiger (Ap)	0	0	0	1 (1)	0	1 (1)
Notomastus sp. (Ap)	0	8 (3)	0	19 (4)	81 (6)	150 (5)
Capitella capitata (Ap)	0	1 (1)	6 (3)	19 (4)	19 (6)	20 (3)
Oligochaetes (Ao)	3 (2)	6 (2)	31 (6)	30 (5)	99 (6)	92 (5)
Predators						
Eteone flava (Ap)	0	1 (1)	2 (2)	1 (1)	2 (2)	4 (2)
Phyllodoce mucosa (Ap)	0	0	0	1 (1)	1 (1)	0
Nephtys hombergii (Ap)	0	0	8 (5)	2 (1)	15 (4)	19 (6)
Polynoid sp. (Ap)	0	2 (1)	2 (2)	0	1 (1)	0
Glycera convoluta (Ap)	0	0	1 (1)	0	1 (1)	0
Turbellaria sp. (P)	10 (2)	18 (5)	53 (6)	19 (5)	19 (5)	15 (5)
Retusa obtusa (Mg)	0	0	2 (2)	0	2 (2)	5 (2)
Sigalionid sp. (Ap)	0	0	1 (1)	0	0	0
Nemertea	0	0	0	1 (1)	0	0

Notes: Numbers in parentheses refer to the number of replicates in which each species was present for each treatment. Abbreviations: Mg = gastropod mollusc, Ap = polychaete annelid, Mb = bivalve mollusc, Ca = amphipod crustacean, Ao = oligochaete annelid, P = platyhelminth.

† Taxa that are simultaneously surface-deposit and suspension feeders.

were performed using Minitab version 10.1 (Minitab 1998) and SAS version 6.12 (SAS Institute 1997).

RESULTS

Macrofaunal species richness

Fig. 4A shows the mean number of species per sample for each treatment. There were significant differences between the mean number of species in all three diversity treatments ($P < 0.001$, with Tukey multiple comparison test); low diversity 4.75 ± 0.25 (mean ± 1 SE), medium diversity 8.33 ± 0.33, and high diversity 12.12 ± 0.17. There were no significant differences between the number of species in the three biomass treatments ($P = 0.081$). The mean number of species in the defaunated treatment was significantly lower than in the unmanipulated control plots ($P < 0.001$, t test). This could indicate that by the end of the experiment, defaunated communities had not recovered to background levels.

Fig. 4B and 4C show mean Pielou's evenness and Shannon-Wiener diversity for each treatment. There was a trend of decreasing evenness with increasing species richness in the diversity treatments, caused by a large influx of the five dominant species *Macoma balthica*, *Hydrobia ulvae*, *Corophium volutator*, *Pygospio elegans*, and *Streblospio benedicti* in the medium and high diversity treatments. However, this trend was not significant; there were no significant differences in evenness between diversity ($P = 0.13$), biomass ($P = 0.11$), or defaunated/unmanipulated ($P = 0.1$) treatments. Shannon-Wiener diversity differed significantly between the low diversity treatment and the other two diversity treatments ($P = 0.01$): low diversity 1.38 ± 0.06, medium diversity 1.76 ± 0.12, and high diversity 1.83 ± 0.04. Shannon-Wiener diversity also differed significantly between the low biomass treatment and the other two biomass treatments ($P = 0.02$): low biomass 1.4 ± 0.16, medium biomass 1.86 ± 0.1, and high biomass 1.85 ± 0.06, and between the defaunated and unmanipulated treatments ($P = 0.036$).

The species sampled during this experiment are listed for each of the diversity and biomass treatments in

TABLE 3. Total numbers of species in each trophic group sampled from each treatment.

Trophic group	Diversity			Low biomass
	Low	Medium	High	
Primary producer†	D	D	D	D
Number of species	10 (4.7 ± 0.3)	14 (8.3 ± 0.3)	20 (12.2 ± 0.7)	18 (10.2 ± 0.7)
Grazer	1 (1.0 ± 0.0)	1 (1.0 ± 0.0)	1 (1.0 ± 0.0)	1 (1.0 ± 0.0)
Surface deposit feeder	5‡ (3.8 ± 0.3)	5‡ (5.2 ± 0.3)	8‡ (6.5 ± 0.2)	7‡ (5.2 ± 0.3)
Suspension feeder	3‡ (1.5 ± 0.3)	2‡ (2.0 ± 0.0)	3‡ (2.5 ± 0.2)	3‡ (2.2 ± 0.2)
Predator	1 (0.5 ± 0.3)	3 (1.2 ± 0.4)	8 (3.3 ± 0.7)	5 (1.5 ± 0.4)
Subsurface deposit feeder	2 (0.3 ± 0.3)	2 (1.0 ± 0.3)	2 (1.5 ± 0.2)	4 (2.5 ± 0.6)

Note: Mean ± 1 SE are in parentheses.

† "D" indicates the presence of diatoms (I. Roberts, *unpublished data*).

‡ Includes one or more species with more than one feeding mode. Consequently, species number is less than the sum of the number of species in each trophic group, as some species are included in more than one group.

Table 2. This table indicates that while the numbers of species significantly increased from the low to medium to high diversity treatments (Fig. 4A), those present in the low diversity treatment were a subset of those in the medium, which were a subset of those comprising the high diversity treatment. Additionally, it is apparent that species composition between the low, medium, and high biomass treatments were very similar; biomass differences are predominantly due to differences in the abundances of those present.

Table 3 shows the mean and total number of species sampled from each of the treatments, together with the total and mean numbers of species from each trophic group. Feeding modes are those proposed by Fauchald and Jumars (1979). Since macrofaunal feeding mode determines how a species reworks the sediment, and therefore reflects its role within the benthic ecosystem, trophic mode is used to indicate species' functional roles in this study (Table 3). A total of five macrofaunal feeding modes were sampled, with some species, such as *Macoma balthica*, exhibiting more than one feeding mode. All feeding types were represented in all treatments.

A total of 27 species were sampled between all the treatments, while only 22 were sampled from the unmanipulated control plots. Although the low diversity replicates contained on average only 4.70 ± 0.30 species, a total of 10 species were present (37% of all species found). Fourteen (52% of total) and 20 (74% of total) species were sampled from the medium and high diversity treatments, respectively. Eighteen species were present within the low biomass treatment, compared to 21 and 19 species from the medium and high biomass treatments, respectively.

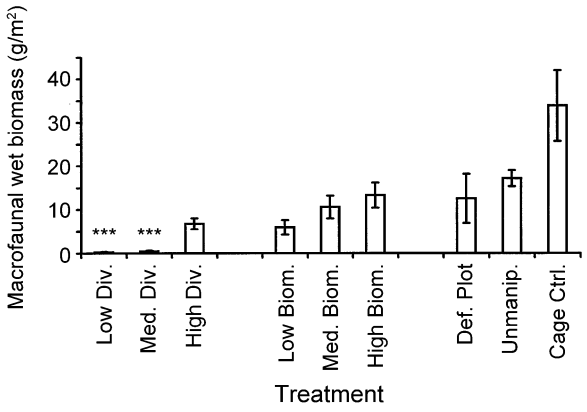

FIG. 5. Mean macrofaunal wet biomass (grams per square meter) for each treatment (mean ± 1 SE; $n = 4$ for low diversity treatment, 6 otherwise). See Fig. 4 for abbreviations. Asterisks denote statistically significant differences from high diversity treatment.

***$P < 0.001$.

Macrofaunal biomass

There were no significant differences in macrofaunal biomass between the low and medium diversity treatments, however, these two were significantly lower than that of the high diversity treatment ($P < 0.001$; see Fig. 5). Although there were no significant differences between the biomass treatments at the 5% level of significance ($P = 0.079$), there is a clear trend of increasing biomass within these treatments (Fig. 5). There was a dramatic increase in the macrofaunal biomass within the cage controls, mainly due to increases in the abundance of *Hydrobia ulvae*, which may have benefited from the refuge from predation provided by the cages.

Sediment properties and ecosystem processes

Cages in benthic environments can have large hydrodynamic effects, producing changes in bulk sediment characteristics. In the present experiment however, it was important that the effects of the cages were not significantly different between treatments. Table 4

TABLE 3. Extended.

Medium biomass	High biomass	Defaunation control	Unmanipulated	Cage control
D	D	D	D	D
21	19	20	22	19
(13.2 ± 0.7)	(12.5 ± 0.8)	(2.3 ± 0.4)	(15.2 ± 0.9)	(15.0 ± 0.4)
1	1	1	1	1
(1.0 ± 0.0)	(1.0 ± 0.0)	(1.0 ± 0.0)	(1.0 ± 0.0)	(1.0 ± 0.0)
8‡	9‡	9‡	9‡	8‡
(6.2 ± 0.5)	(6.3 ± 0.3)	(6.2 ± 0.5)	(7.0 ± 0.5)	(6.8 ± 0.3)
3‡	3‡	3‡	3‡	3‡
(2.3 ± 0.3)	(2.3 ± 0.2)	(2.2 ± 0.2)	(2.8 ± 0.2)	(2.6 ± 0.2)
7	4	4	6	5
(2.7 ± 0.3)	(2.5 ± 0.2)	(2.3 ± 0.2)	(3.7 ± 0.4)	(3.8 ± 0.5)
4	5	4	5	4
(3.3 ± 0.2)	(2.7 ± 0.6)	(2.3 ± 0.4)	(3.0 ± 0.4)	(3.4 ± 0.2)

displays the results of statistical testing within cage control, diversity and biomass treatment groups for sediment water, silt/clay and organic contents, together with all measured sediment properties and ecosystem processes for all treatments. There were no significant differences in bulk sediment properties between the cage control treatments. Therefore, we conclude that there were no treatment-specific artifacts in the present study and values for the low diversity cage control only are displayed in Figs. 4–6. Regressions of bulk sediment properties (percentage water, percentage silt, percentage organic content, and shear strength) against plot location within blocks showed no significant relationships ($P = 0.60$, 0.16, 0.58, and 0.80, respectively). Thus, there was no evidence of block-level artifacts in this study. Table 4 also reveals that macrofaunal species richness and biomass did not have significant effects on any of these sediment properties.

There were no significant differences or trends observed in the sediment shear strength values. The sediments within all treatments had mean shear strength values between 3 to 5 Pa. There were no significant differences between the low, medium, or high diversity treatments, or biomass treatments, for sediment redox potential at any sediment depth and no trend can be seen.

TABLE 4. Results of two-way ANOVAs (P values) within treatment groups of sediment properties and ecosystem processes.

Variable	Cage controls	Diversity treatments	Biomass treatments
Water content (%)	0.483	0.738	0.053
Silt/clay content (%)	0.634	0.900	0.331
Organic content (%)	0.441	0.346	0.527
Shear strength	···	0.685	0.527
1-cm redox potential	···	0.315	0.574
2-cm redox potential	···	0.473	0.493
4-cm redox potential	···	0.281	0.845
Total meiofauna	···	0.325	0.452
O_2 consumption	···	**0.015**	0.294
Nitrate flux	···	0.951	0.162
Nitrite flux	···	0.841	0.939
Ammonium flux	···	0.825	0.562
Phosphate flux	···	0.485	0.807

Notes: Sample size is $n = 6$ throughout except for the low diversity treatments ($n = 4$). Value in boldface type is statistically significant ($P < 0.05$).

Meiofaunal abundance

The meiofauna (those infaunal organisms passing through a 0.5-mm mesh but retained on a 63-μm mesh) were identified to phyla only. Over 99% of the total abundance was composed of only four groups; by far the most abundant were the nematodes, then the copepods, ostracods, and kynorynchs. Mean total meiofaunal abundance is displayed for each treatment in Fig. 6. There were no significant differences within the diversity or biomass treatment groups (Table 4), however, meiofauna were far more abundant in the unmanipulated control plots compared with any other plot type.

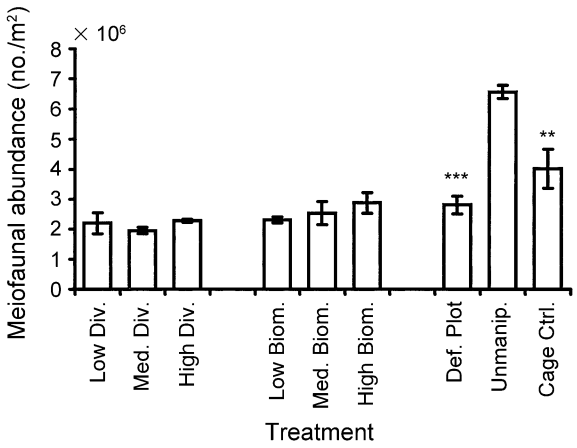

FIG. 6. Mean total meiofaunal abundance (number × 10^6 per square meter) for each treatment (mean ± 1 SE; $n = 4$ for low diversity treatment, 6 otherwise). See Fig. 4 for abbreviations. Asterisks denote statistical significance from unmanipulated plot.

$^{**}P < 0.01$; $^{***}P < 0.001$.

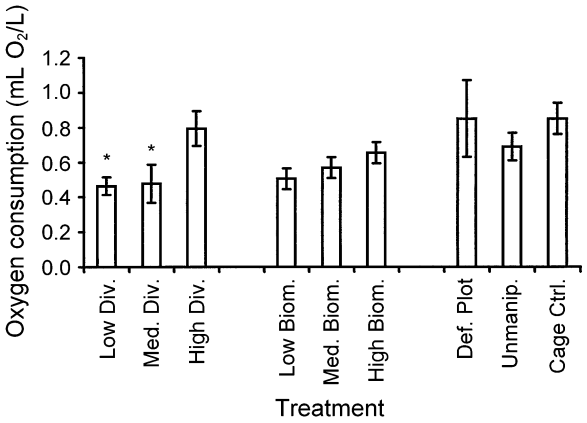

FIG. 7. Mean oxygen consumption (milliliters of oxygen per liter) of sediment cores after 6 h incubation in the dark (mean ± 1 SE; $n = 4$ for low diversity treatment, 6 otherwise). See Fig. 4 for abbreviations. Asterisks denote statistical significance from high diversity treatment.
*$P < 0.05$.

Oxygen and nutrient analyses

At the end of the 6-h incubation period, dissolved oxygen concentrations were between 80% and 90% of the original level, and, therefore, respiration was not affected by oxygen depletion towards the end of the incubation. There was no significant difference in oxygen consumption between the low and medium diversity treatments, but these were significantly lower than the high diversity treatment ($P = 0.015$; Table 4). There were no statistically significant differences between the three biomass treatments, however, a clear trend of increasing oxygen consumption can be seen with increasing macrofaunal biomass (Fig. 7). There were no significant differences for any nutrient between the diversity and biomass treatments (Table 4). No significant treatment × block effects were found in these or any of the other ANOVA tests performed.

Power analysis

Power analyses were performed on the results presented in Table 4; these are given as minimum detectable differences between means, assuming a power of 90%, in Table 5. Comparing these differences with the maximum differences actually recorded shows that the power of most of our ANOVA tests was low. The large amount of variability within treatments meant that in most cases much larger differences would have been required to give a high chance of detecting significant differences.

Correlation analysis

Pearson product-moment correlations between mean macrofaunal species number and biomass and ecosystem processes showed that only one of the measured ecosystem processes, benthic respiration, was significantly correlated at the 5% level; with macrofaunal species number ($P = 0.002$) and macrofaunal biomass ($P = 0.003$). All other correlations (including all those involving meiofauna) were not statistically significant (Table 6). Figs. 8A–M and 9A–M support the results of the correlation analyses, with the majority of sediment properties and ecosystem processes showing no obvious relationship with changes in species number and biomass.

Regression analysis

Including both species number and biomass as predictor variables for benthic respiration gave a regression equation of respiration = 0.05 + 0.003 species + 0.0008 biomass, ($r^2 = 0.18$, $F_{2,48} = 6.6$, $P = 0.003$). Most of the variability was explained by species richness; partial P values for species richness and biomass were 0.09 and 0.14, respectively. Hence respiration rates did not simply vary with total biomass, but responded independently to species richness. Variance inflation was 1.6, suggesting collinearity did not com-

TABLE 5. Power analysis of ANOVA results within treatment groups of sediment properties and ecosystem processes.

Variable	Cage controls	Diversity treatments	Biomass treatments
Water content (%)	10.4 (1.4)	13 (2.2)	12.4 (8.5)
Silt/clay content (%)	45 (7.3)	31 (6.5)	25 (5.8)
Organic content (%)	3.1 (1.4)	3.8 (1.4)	2.6 (0.7)
Shear strength	···	3.9 (0.68)	3 (0.94)
1-cm redox potential	···	71 (31)	108 (33)
2-cm redox potential	···	128 (41)	0.27 (0.07)
4-cm redox potential	···	355 (55)	71 (6)
Total meiofauna	···	729 657 (300 441)	1 646 329 (567 358)
O_2 consumption	···	0.066 (0.05)	0.03 (0.04)
Nitrate flux	···	11 (0.6)	3.3 (1.4)
Nitrite flux	···	0.71 (0.08)	0.88 (0.07)
Ammonium flux	···	27 (3.7)	17 (3.8)
Phosphate flux	···	6.0 (1.2)	9.6 (0.5)

Notes: Values are the minimum detectable differences between means given a power of 90% and $\alpha = 0.05$. Values in parentheses are the actual maximum differences between means. See Figs. 8 and 9 for relevant units.

TABLE 6. Pearson product-moment correlation coefficients (r_P) and r^2 values from scatterplots of macrofaunal species richness and biomass with sediment properties and ecosystem processes.

Variable	Macrofaunal species richness		Macrofaunal biomass	
	r_P	r^2	r_P	r^2
Water content (%)	0.036	0.054	0.226	0.104
Silt/clay content (%)	−0.271	0.012	0.033	0.007
Organic content (%)	0.132	0.014	0.426	0.010
Shear strength	0.445	0.041	0.485	0.022
1-cm redox potential	0.308	0.024	0.041	0.038
2-cm redox potential	0.419	0.002	0.365	0.016
4-cm redox potential	0.292	0.002	0.434	0.001
Total meiofauna	0.131	0.121	0.250	0.205
O_2 consumption	**0.501**	0.134	**0.547**	0.050
Nitrate flux	−0.174	0.013	−0.056	0.013
Nitrite flux	0.010	0.009	0.050	0.001
Ammonium flux	0.243	0.001	0.243	0.001
Phosphate flux	−0.218	0.004	−0.178	0.004

Note: Correlation coefficients in boldface represent those that are statistically significant ($P < 0.05$).

promise the interpretation of these results. To investigate the contribution of individual species of macrofauna to this relationship, abundance data for all taxa were log(x + 1) transformed and used as predictor variables. All multiple regression procedures used (stepwise, forward and r^2) suggested that the best model was one containing only the species *Nephtys hombergii* and *Tellina fabula* (respiration = 0.08 + 0.04 *Nephtys* + 0.6 *Tellina*; $r^2 = 0.5$, $F_{2,48} = 25$, $P = 0.0001$). Variance inflation was 1.01.

DISCUSSION

Tests of the relationships between ecosystem functions and species richness must be carefully planned to allow clear interpretation in the face of possible confounding variables and ''hidden treatments'' (Huston 1997, Hodgson et al. 1998, Emmerson and Raffaelli 2000). In the present study, low, medium, and high diversity macrofaunal communities on a temperate, intertidal mudflat were allowed to establish, with species richness ranging from 4 to 12. Each diversity treatment contained every trophic/functional group present within the system, and species composition was not a fixed factor; species' identities varied within, as well as between, treatments. Changes in macrofaunal biomass, inherently associated with changes in species richness in our diversity treatments, were controlled for using a separate group of treatments in which biomass was manipulated while species richness remained constant. We had anticipated using a regression approach to distinguish between these two possible predictor variables, but the lack of significant results made this unnecessary except for the relatively trivial case of benthic respiration. Ecosystem processes such as major nutrient fluxes between the sediment and the overlying water column, and sediment properties such as water, organic and silt/clay content, redox potential, and shear strength were not significantly affected by changes in macrofaunal species richness or biomass. Species richness and biomass significantly altered only oxygen consumption.

The regression analysis with oxygen consumption as the dependent variable and species' abundances as the predictors suggests that two species, *Nephtys hombergii* and *Tellina fabula*, had a disproportionately large impact on oxygen uptake. Only one, large individual *Tellina* was found in all of the samples, hence its apparent effects on oxygen uptake are the result of one outlier. This species is very rare at the field site (*personal observation*), and is unlikely to significantly influence ecosystem processes at Blackness. *Nephtys* was the largest species in our study (see Table 1). It was incapable of passing through the small and medium sized meshes, and was thus absent from low and medium diversity treatments. As a large species, it may be expected to have a significant impact on total respiration rates. However, the fact that *Nephtys* abundance is a better predictor of oxygen uptake than total biomass suggests that this effect is not simply because this large species contributes most to the biomass figures. For example, the sample with the single largest number of *Nephtys* (14), taken from a cage control treatment, had the lowest biomass recorded from the five-cage control replicates. *Nephtys* is an active predator, and is known to have a high energy demand (Weigelt 1991, Arndt and Schiedek 1997).

With the exception of benthic respiration, the results of the present study support the null hypotheses that state that changes in macrofaunal species richness and biomass have no significant effect on ecosystem processes within intertidal mudflats. However, this finding is contrary to previous work in soft-bottom habitats where the presence of certain species has been shown to have large effects on various aspects of ecosystem function. The ecosystem studied here is relatively species poor compared with most marine, soft-bottom systems, and consequently, the conclusions presented here may only be cautiously applied to those more diverse ecosystems. However, the demonstration of an apparent lack of relationship between ecosystem function and species richness in a species-poor ecosystem would imply that this phenomenon should carry for more diverse ecosystems where functional redundancy is likely to be higher.

There are four main possible explanations for the lack of significant results in the present study:

1) *Artifacts and Type II error*.—The use of cages in soft-bottom habitats is known to cause artifacts such as altered sedimentation and scouring rates. These artifacts can compromise the interpretation of experimental results when they are treatment specific. However, we found no evidence that our different cage designs caused differences in bulk sediment properties. Since our main ANOVA tests for differences between treatments were restricted to those treatments that had

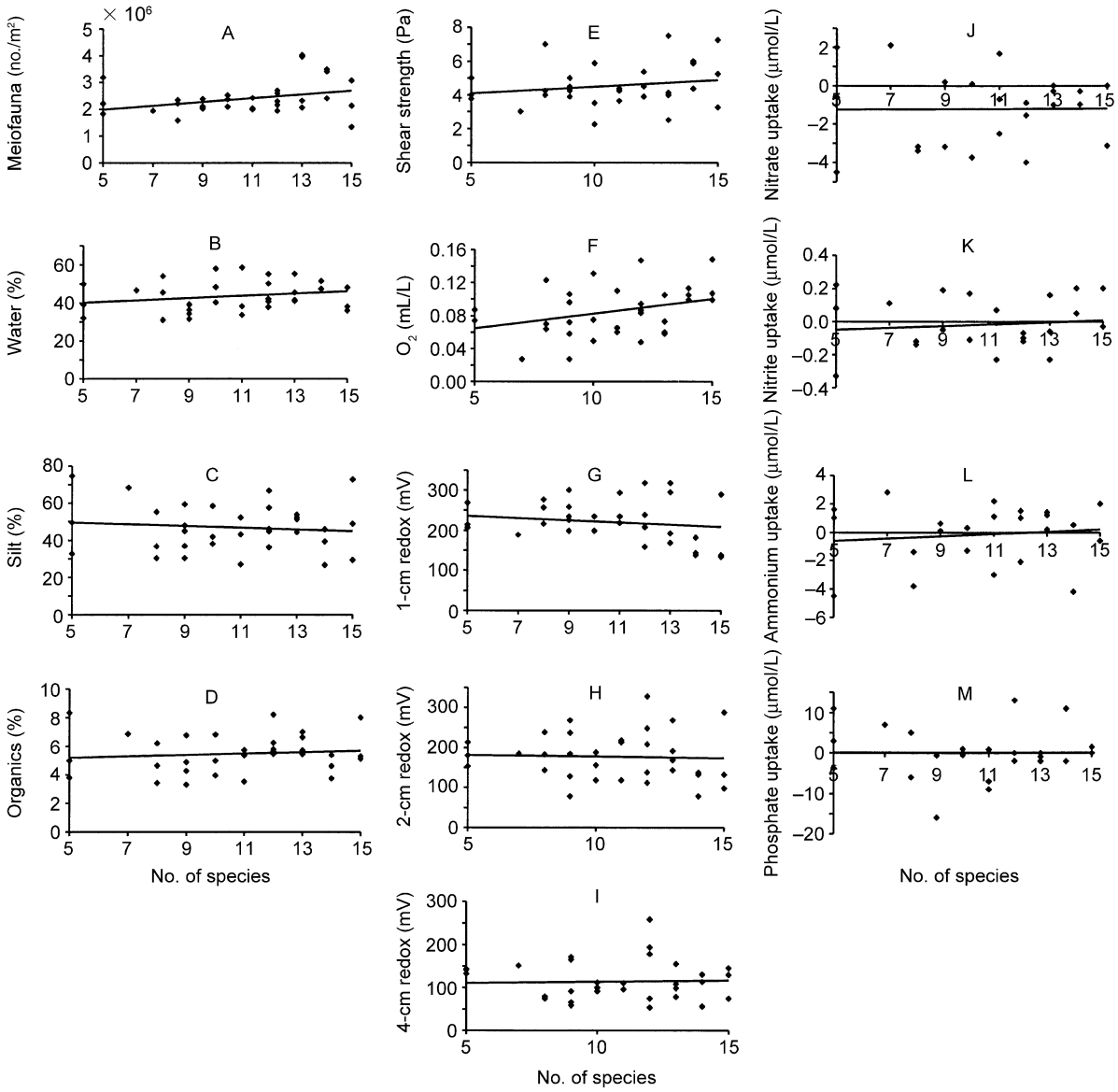

FIG. 8. Scatterplots showing relationships of ecosystem processes with macrofaunal species richness. Lines of best fit have been superimposed. Corresponding r^2 values are as follows: (A) 0.1, (B) 0.05, (C) 0.02, (D) 0.02, (E) 0.04, (F) 0.134, (G) 0.024, (H) 0, (I) 0, (J) 0, (K) 0.013, (L) 0.02, (M) 0.

been caged, we are confident that treatment-specific artifacts did not affect our results. Similarly, there was no evidence of block-scale artifacts. Our manipulation involved compression and de-oxygenation of the sediment, which would have caused physical and chemical changes regardless of any related changes in species richness or biomass. There was therefore a danger of artifactual results in our biomass treatments, which incorporated different proportions of defaunated sediment. However, the lack of significant differences (excepting oxygen) between these treatments suggests any such treatment-specific artifacts were unimportant after the six-week recovery period.

High within-treatment variability meant that the power of most of our tests was low (Table 5); any treatment effects would have needed to be much larger to allow a high chance of detection. So the lack of significant results in the present study could reflect Type II error. However, examination of the scatterplots in Figs. 8 and 9 shows little evidence of any trends in our response variables. It is unlikely, therefore, that greater replication would have resulted in more significant results. Any treatment effects that did occur must have been small compared with background variation, and are therefore unlikely to be important in natural systems.

2) *Critical species*.—The concept of a single species having a disproportionately large effect on ecosystem

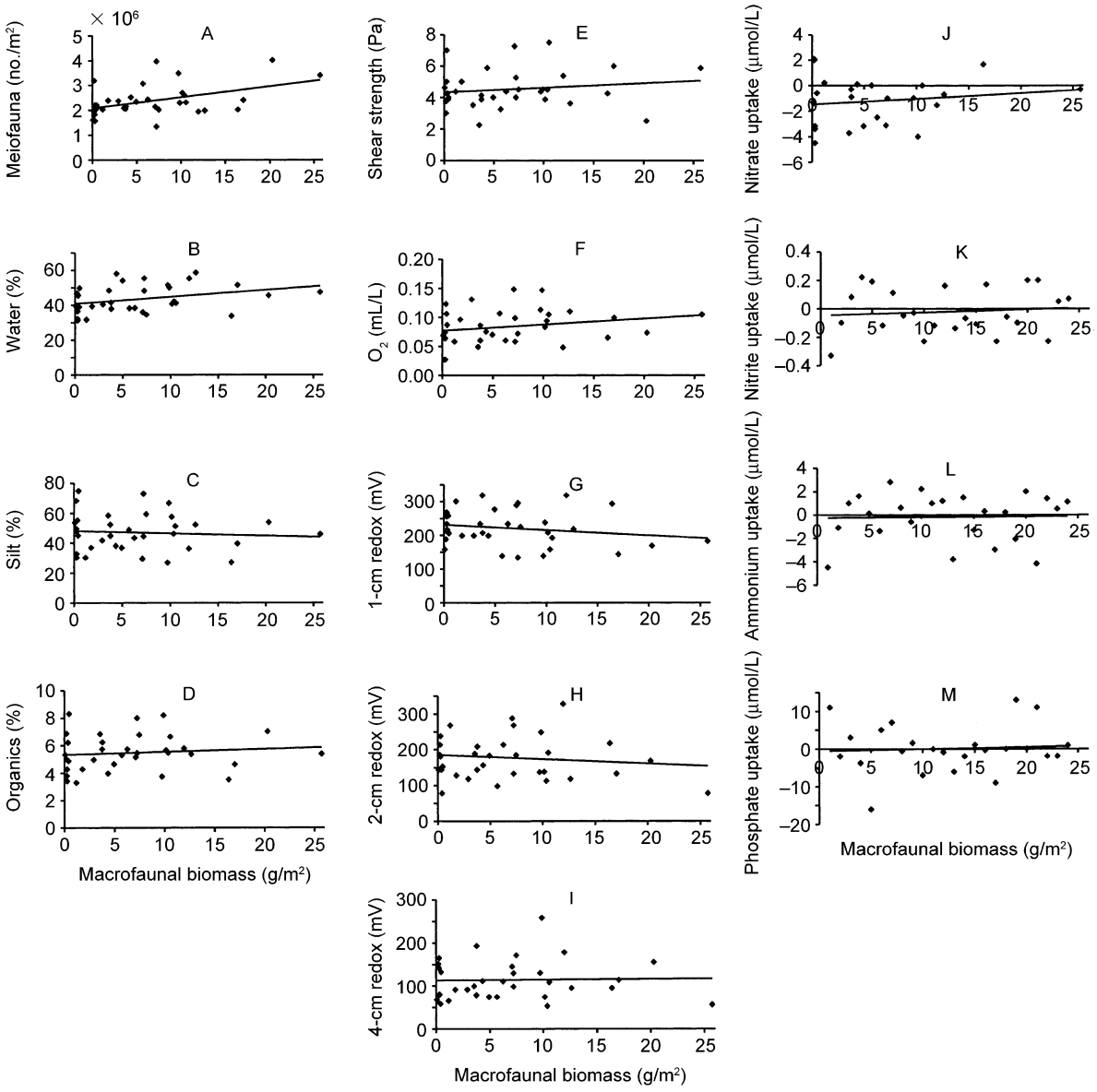

FIG. 9. Scatterplots showing relationships of ecosystem processes with macrofaunal biomass. Lines of best fit have been superimposed. Corresponding r^2 values are as follows: (A) 0.2, (B) 0.1, (C) 0.01, (D) 0.01, (E) 0.02, (F) 0.05, (G) 0.04, (H) 0.02, (I) 0, (J) 0.02, (K) 0, (L) 0, (M) 0.01.

structure has long been recognized in marine ecology (Paine 1966), and there are now also many examples of individual species exerting large functional effects. For example, within soft-bottom habitats, Widdicombe and Austen (1998) found that the subsurface disturbance activity of the heart urchin *Brissopsis lyrifera* significantly affected sediment chemistry, increasing oxygenation and phosphate precipitation and decreasing denitrification. Flach (1996) showed that at moderate densities the cockle *Cerastoderma edule* disturbed the sediment surface by its ''shaking'' and ''plowing'' behavior, significantly reducing the densities of many macrofaunal species and decreasing sediment stability. The disproportionate effect of certain species on ecosystem structure or function has led some of these species to be termed ''critical'' or ''keystone'' species. The demonstration of the presence of such species in marine soft-bottom habitats supports the idiosyncratic species hypothesis where removal of certain species results in a large but unpredictable change in ecosystem processes (Lawton 1994). However, at present there is little knowledge about key species in the marine benthos (Snelgrove et al. 1997), and no general rules that would allow us to predict their presence or identities.

The only candidate for ''critical'' species in the pres-

ent study is *Nephtys hombergii*, which exerted a disproportionately large influence on respiration rates. However, there was no evidence that this species affected any of the other ecosystem processes, and it is possible that critical species are simply absent from the Blackness system. In particular, our treatments lacked large bioturbatory species such as urchins and deep-burrowing polychaetes. These species are known to exert effects on ecosystem function by facilitating oxygenation of deep sediments (Rhoads 1974). Even where critical species are present, they may not play critical roles (Fairweather and Underwood 1991), and this is particularly likely in physically stressed environments such as Blackness, where there is no evidence of strong competitive interactions amongst macrofauna (Huxham et al. 2000). Clearly, studies investigating the relationship between species richness and ecosystem processes in the soft-bottom benthos would benefit greatly from a better knowledge of the identity and role of key species within this habitat (Snelgrove et al. 1997).

3) *Scale effects and functional redundancy*.—Most ecological phenomena operate over specific spatial and temporal scales (Legendre et al. 1997), and aspects of scale have major consequences in ecological investigations (Wiens et al. 1986). Manipulation experiments using controls and replicates are necessarily conducted at limited spatial and temporal scales (Thrush et al. 1997*a*), and consequently, unless we are aware of the constraints imposed by the scale of our experiment, we risk the danger of drawing incorrect generalizations. The present experiment was ultimately spatially constrained by cage size, and temporally constrained by the onset of autumn storms uprooting cages. We must, therefore, be cautious when scaling up the results from this study to conclusions relevant on a more important, landscape scale (Thrush et al. 1997*b*, *c*). Spatial scale effects were minimized as much as possible in this study as the total number of species found even within the low diversity treatments formed a relatively large proportion of the total species pool of macrofauna found at Blackness. Hence, by working at a low diversity site, we were able to manipulate a large proportion of the species present despite operating at a relatively small experimental scale.

One has more confidence in the conclusions generated from small-scale experiments when, in general, they support larger scale observations. Elmgren (1984) investigated carbon flow within the different regions of the species-poor Baltic Sea and compared it to existing data for the relatively species-rich North Sea. He concluded that a low diversity ecosystem may be functionally similar to a higher diversity one: only the loss of a major functional group (rather than of species) resulted in drastic alterations in ecosystem processes (e.g., within the Bothnian Bay where benthic filter-feeders were virtually absent). The conclusions obtained from this large-scale study concur with those in the present study in suggesting that certain ecosystem processes may be insensitive to changes in species richness. The impacts of losing a functional group, which resulted in significant effects on ecosystem performance in Elmgren's study, cannot be assessed in this study since all functional groups were present in all diversity treatments (Table 3). Further support for the importance of functional groups, rather than species per se, comes from the small-scale mesocosm studies of Emmerson and Raffaelli (2000). Manipulations of functional diversity produced significant changes in ecosystem function, whilst the effect of species richness in their study was equivocal.

Previous studies that have investigated the relationship between biodiversity and ecosystem function (e.g., Tilman and Downing 1994, Tilman et al. 1996, Nilsson et al. 1999, Stocker et al. 1999) have often overlooked scaling issues, and the results of experiments carried out on relatively small spatial scales have been extended to generalizations at the landscape or larger scales. While the question of how to scale up from small-scale manipulative experiments to conclusions relevant at larger spatial and temporal scales remains largely unanswered (Thrush et al. 1997*a*), more caution must be employed in these generalizations. Naeem et al. (1995) cautioned extrapolating their mesocosm results to the global scale. Hector et al. (1999) explicitly compared small-scale (within site) and large-scale (between site) patterns. Their work suggests that the results from a single site may not always conform to larger scale patterns. Proposed solutions to this problem include undertaking deliberately large-scale experiments, combining manipulative experiments with larger scale surveys, and cycling from experimental results to larger scale conclusions (Schneider et al. 1997). More studies in marine soft-bottom habitats are needed to examine whether the results reported here are general for the marine benthos, and for other ecosystem functions than those studied here. Only then will it be possible to cautiously predict larger scale effects.

4) *Importance of meiofauna*.—In the present study, macrofaunal communities of different species richness were established by allowing colonization of defaunated sediments through exclosure cages. However, the meiofauna are orders of magnitude times more abundant (Warwick et al. 1975, Baird and Milne 1981) than the macrofauna in intertidal mudflats, and there is evidence to suggest that they are more important with respect to some ecosystem processes (Fenchel 1969, Gerlach 1971). The ratio of production to biomass (P/B ratio) is ~10 for meiofauna and only ~2.5 for macrofauna (Platt and Warwick 1980, Raffaelli and Hawkins 1996); thus, meiofauna have the potential to cycle nutrients faster and respond more quickly to environmental changes than macrofauna. Because of their size, experimental manipulation of meiofauna in the field is difficult, and in the present study, meiofaunal abun-

dance was similar between diversity and biomass treatments (2.0–2.5 million per m^2), and meiofaunal diversity (below a gross taxonomical level) was unknown. This could suggest that intertidal mudflats are bottom-up systems, with ecosystem processes being predominantly driven by the meiofauna. If so, changes in macrofaunal species richness in these systems will not impair ecosystem performance, and attempts to measure ecosystem function/diversity relationships in this habitat will be very difficult because they will involve manipulating meiofaunal diversity.

In conclusion, the present study is the first field manipulation to explicitly test the relationship between species richness and biomass and ecosystem performance in the marine benthic environment. Although the results support the null hypotheses, they are consistent with other work that suggests that functional diversity, rather than species richness, may be important in maintaining ecosystem processes. The high natural variability of most of the ecosystem processes in our study, and the potential importance of scaling issues, imply that field tests of the relationship between species richness and ecosystem performance in the benthos may be very difficult. To overcome these challenges, a combination of studies will be needed, which exploit the relative precision of small-scale mesocosm work and the real-world relevance of larger scale manipulations and comparisons.

Acknowledgments

We are grateful to Julian Augley, Francois Edwards, Mike Richards, and Ildiko Roberts for their help in the field. Michael Huston and two anonymous referees made helpful comments on an earlier version. This work was supported by the Natural Environment Research Council, grant no. GR9/3898.

Literature Cited

Aarssen, L. W. 1997. High productivity in grassland ecosystems: affected by species diversity or productive species? Oikos **80**(1):183–184.

Aller, R. C. 1982. The effects of macrobenthos on chemical properties of marine sediment and overlying water. Pages 53–102 *in* P. L. McCall and M. J. S. Tevesz, editors. Animal-sediment relations. Plenum, New York, New York, USA.

Aller, R. C. 1988. Benthic fauna and biogeochemical processes in marine sediments: the role of burrow structures. Pages 301–338 *in* T. H. Blackburn and J. Sorensen, editors. Nitrogen cycling in coastal marine environments. John Wiley and Sons, New York, New York, USA.

Alongi, D. M., A. Sasekumar, F. Tirendi, and P. Dixon. 1998. The influence of stand age on benthic decomposition and recycling of organic matter in managed mangrove forests of Malaysia. Journal of Experimental Marine Biology and Ecology **225**(2):197–218.

Andre, M., F. Brechlgnac, and P. Thibault. 1994. Biodiversity in model ecosystems. Nature **371**:565.

Arndt, C., and D. Schiedek. 1997. *Nephtys hombergii*, a free-living predator in marine sediments: energy production under environmental stress. Marine Biology **129**:643–650.

Baird, D., and H. Milne. 1981. Energy flow in the Ythan Estuary, Aberdeenshire, Scotland. Estuarine, Coastal and Shelf Science **13**:455–472.

Beukema, J. J. 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. Netherlands Journal of Sea Research **10**(2): 236–261.

Costanza, R., et al. 1997. The value of the world's ecosystem services and natural capital. Nature **387**:253–260.

Daro, M. H., and P. Polk. 1973. The autecology of *Polydora ciliata* along the Belgian coast. Netherlands Journal of Sea Research **6**(1–2):130–140.

Ehrlich, P. R., and E. O. Wilson. 1991. Biodiversity studies: science and policy. Science **25**:758–762.

Elmgren, R. 1984. Trophic dynamics in the enclosed, brackish Baltic Sea. Rapports et Proces-verbeaux des Reunions. Conseil International pour l'Exploration de la Mer **183**: 152–169.

Elmgren, R., and C. Hill. 1997. Ecosystem function at low biodiversity—the Baltic example. Pages 319–336 *in* R. F. G. Ormond, J. D. Gage, and M. V. Angel, editors. Marine biodiversity. Patterns and processes. Cambridge University Press, Cambridge, UK.

Emmerson, M. C., and D. G. Raffaelli. 2000. Detecting the effects of diversity on measures of ecosystem function: experimental design, null models and empirical observations. Oikos **91**:191–203.

Fairweather, P. G., and A. G. Underwood. 1991. Experimental removals of a rocky intertidal predator: variations within two habitats in the effects on prey. Journal of Experimental Marine Biology and Ecology **154**:29–75.

Fauchald, K., and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology Annual Review **17**:193–284.

Fenchel, T. 1969. The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, and its chemical and physical factors and the microfauna communities with special reference to the ciliated Protozoa. Ophelia **6**:1–182.

Fernandes, T., M. Huxham, and S. Piper. 1999. Predator caging experiments: a test of the importance of scale. Journal of Experimental Marine Biology and Ecology **241**:137–154.

Flach, E. C. 1996. The influence of the cockle, *Cerastoderma edule*, on the macrobenthic community of the tidal flats in the Wadden Sea. Marine Ecology **17**(1–3):87–98.

Fourqurean, J. W., T. O. Moore, B. Fry, and J. T. Hollibaugh. 1997. Spatial and temporal variation in C:N:P ratios, delta N-15 and delta C-13 of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. Marine Ecology Progress Series **157**:147–157.

Gattuso, J. P., M. Frankignoulle, and R. Wollast. 1998. Carbon and carbonate metabolism in coastal aquatic ecosystems. Annual Review of Ecological Systems **29**:405–434.

Gerlach, S. A. 1971. On the importance of marine meiofauna for benthos communities. Oecologia **6**:176–190.

Givnish, T. J. 1994. Does diversity beget stability? Nature **371**:113–114.

Grime, J. P. 1997. Biodiversity and ecosystem function: the debate deepens. Science **277**:1260–1261.

Gunther, C. P. 1992. Dispersal of intertidal invertebrates: a strategy to react to disturbances of different scales? Netherlands Journal of Sea Research **30**:45–56.

Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. Science **286**:1123–1127.

Hodgson, J. G., K. Thompson, P. J. Wilson, and A. Bogaard. 1998. Does biodiversity determine ecosystem function? The Ecotron experiment. Functional Ecology **12**:843–856.

Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science **277**:1302–1305.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**: 187–211.

Huston, M. A. 1997. Hidden treatments in ecological ex-

periments: re-evaluating the ecosystem function of biodiversity. Oecologia **110**:449–460.
Huttel, M. 1990. Influence of the lugworm *Arenicola marina* on porewater nutrient profiles of sandflat sediments. Marine Ecology Progress Series **62**:241–248.
Huxham, M., I. Roberts, and J. Bremner. 2000. A field test of the intermediate disturbance hypothesis in the soft-bottom intertidal. International Review of Hydrobiology **8**: 379–394.
Irlandi, E. A. 1994. Large-scale and small-scale effects of habitat structure on rates of predation—how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. Oecologia **98**:176–183.
Irlandi, E. A., W. G. Ambrose, and B. A. Orlando. 1995. Landscape ecology and the marine environment—how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. Oikos **72**:307–313.
Kristensen, E. 1984. Effect of natural concentrations on nutrient exchange between a polychaete burrow in estuarine sediment and the overlying water. Journal of Experimental Marine Biology and Ecology **75**:171–190.
Kristensen, E. 1988. Benthic fauna and biogeochemical processes in marine sediments: microbial activities and fluxes. Pages 275–299 *in* T. H. Blackburn and J. Sorensen, editors. Nitrogen cycling in coastal marine environments. John Wiley and Sons, New York, New York, USA.
Kristensen, E., and T. H. Blackburn. 1987. The fate of organic carbon and nitrogen in experimental marine sediment systems: influence of bioturbation and anoxia. Journal of Marine Research **45**:231–257.
Kristensen, E., M. H. Jensen, G. T. Banta, K. Hansen, M. Holmer, and G. M. King. 1998. Transformation and transport of inorganic nitrogen in sediments of a southeast Asian mangrove. Aquatic Microbial Ecology **15**(2):165–175.
Lawton, J. H. 1994. What do species do in ecosystems? Oikos **71**:367–374.
Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, and R. B. Whitlatch. 1997. Spatial structure of bivalves in a sandflat: scales and regenerating processes. Journal of Experimental Marine Biology and Ecology **216**:99–128.
McLusky, D. S., F. E. Anderson, and S. Wolfe-Murphy. 1983. Distribution and population recovery of *Arenicola marina* and other benthic fauna after bait digging. Marine Ecology Progress Series **11**:173–179.
Minitab. 1998. MINITAB 12. Minitab, State College, Pennsylvania, USA.
Morgan, T. S. 1997. The formation and dynamics of *Pygospio elegans* tube-beds in the Somme Bay, France. Dissertaion. University of Southampton, Southampton, UK.
Naeem, S., K. Hakansson, J. H. Lawton, M. J. Crawley, and L. J. Thompson. 1996. Biodiversity and plant productivity in a model assemblage of plant species. Oikos **76**:259–264.
Naeem, S., J. T. Lindsey, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature **368**:734–738.
Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1995. Biodiversity in model ecosystems. Nature **371**:565.
Nilsson, M.-C., D. A. Wardle, and A. Dahlberg. 1999. Effect of plant litter species composition and diversity on the boreal forest plant-soil system. Oikos **86**:16–26.
Nixon, S. W. 1982. Remineralization and nutrient cycling in coastal marine ecosystems. Pages 111–138 *in* B. J. Nielson and L. E. Cronin, editors. Estuaries and nutrients. Humana, Williamsburg, Virginia, USA.
Noji, I. M., and T. T. Noji. 1991. Tube lawns of spionid polychaetes and their significance for recolonization of disturbed benthic substrates. Meeresforschung **33**:235–246.
Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–75.
Pearson, T. H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Review **16**:229–311.
Pearson, T. H., and S. O. Stanley. 1979. Comparative measurement of the redox potential of marine sediments as a rapid means of assessing the effect of organic pollution. Marine Biology **53**:371–379.
Platt, H. M., and R. M. Warwick. 1980. The significance of free-living nematodes to the littoral ecosystem. Pages 729–759 *in* H. Price, D. Irvine, and W. Farnham, editors. The shore environment. Blackwell Scientific Publications, Oxford, UK.
Raffaelli, D., and S. Hawkins. 1996. Intertidal ecology. Chapman and Hall, London, UK.
Rhoads, D. C. 1974. Organism-sediment relations on the muddy sea floor. Oceanography and Marine Biology Annual Review **12**:263–300.
Rhoads, D. C., and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research **28**(2): 150–178.
Richards, M. G., M. Huxham, and A. Bryant. 1999. Predation: a causal mechanism for variability in intertidal bivalve populations. Journal of Experimental Marine Biology and Ecology **241**:159–177.
SAS Institute. 1997. SAS/STAT software: changes in enhancements through release 6.12. SAS Institute, Cary, North Carolina, USA.
Schneider, D. C., R. Walters, S. F. Thrush, and P. Dayton. 1997. Scale-up of ecological experiments: density variation in the mobile bivalve *Macomona liliana*. Journal of Experimental Marine Biology and Ecology **216**:129–152.
Smith, C. R., and S. J. Brumsickle. 1989. The effects of patch size and substrate isolation on colonization modes and rates in an intertidal sediment. Limnology and Oceanography **34**(7):1263–1277.
Snelgrove, P. V. R. 1998. The biodiversity of macrofaunal organisms in marine sediments. Biodiversity and Conservation **7**:1123–1132.
Snelgrove, P. V. R. 1999. Getting to the bottom of marine biodiversity: sedimentary habitats. Bioscience **49**(2):129–138.
Snelgrove, P. V. R., T. H. Blackburn, P. A. Hutchings, D. M. Alongi, J. F. Grassle, H. Hummel, G. King, I. Koike, P. J. D. Lambshead, N. B. Ramsing, and V. Soliweiss. 1997. The importance of marine sediment biodiversity in ecosystem processes. Ambio **26**(8):578–583.
Stocker, R., C. Korner, B. Schmid, P. A. Niklaus, and P. W. Leadley. 1999. A field study of the effects of elevated CO_2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. Global Change Biology **5**:95–105.
Strickland, J. D. H., and T. R. Parsons. 1972. A practical handbook of seawater analysis. Second edition. Fisheries Research Board of Canada, Ottawa, Canada.
Symstad, A. J., D. Tilman, J. Willson, and M. H. Knops. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. Oikos **81**: 389–387.
Thrush, S. F., et al. 1997*a*. The sandflat habitat: scaling from experiments to conclusions. Journal of Experimental Marine Biology and Ecology **216**:1–9.
Thrush, S. F., et al. 1997*b*. Matching the outcome of small-scale density manipulation experiments with larger scale patterns: an example of bivalve adult/juvenile interactions. Journal of Experimental Marine Biology and Ecology **216**: 153–169.

Thrush, S. F., et al. 1997*c*. Scaling-up from experiments to complex ecological systems: where to next? Journal of Experimental Marine Biology and Ecology **216**:243–254.

Thrush, S. F., R. D. Pridmore, J. E. Hewitt, and V. J. Cummings. 1992. Adult infauna as facilitators of colonisation on intertidal sandflats. Journal of Experimental Marine Biology and Ecology **159**:253–265.

Tilman, D., and J. D. Downing. 1994. Biodiversity and stability in grasslands. Nature **367**:363–365.

Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science **277**:1300–1302.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718–720.

Wardle, D. A. 1999. Is ''sampling effect'' a problem for experiments investigating biodiversity—ecosystem function relationships? Oikos **87**(2):403–407.

Warwick, R. M., I. R. Joint, and P. J. Radford. 1975. Secondary production of the benthos in an estuarine mud-flat. Pages 429–450 *in* R. L. Jeffries and A. J. Davy, editors. Ecological processes in coastal environments. Blackwell Scientific Publications, Oxford, UK.

Widdicombe, S., and M. C. Austen. 1998. Experimental evidence for the role of *Brissopsis lyrifera* (Forbes, 1841) as a critical species in the maintenance of benthic diversity and the modification of sediment chemistry. Journal of Experimental Marine Biology and Ecology **228**:241–255.

Wiens, J. A., J. F. Addicott, T. Case, and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. Pages 145–153 *in* J. Diamond and T. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Wilsey, B. J., and C. Potvin. 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology **81**:887–892.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice Hall, Upper Saddle River, New Jersey, USA.