



Context dependency of relationships between biodiversity and ecosystem functioning is different for multiple ecosystem functions

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Increasing concern over the loss of biodiversity has led to attempts to quantify relationships between biodiversity and ecosystem functioning. While manipulative investigations have accumulated substantial evidence to support the notion that decreasing biodiversity can be detrimental to the functioning of ecosystems, recent investigations have identified the potential importance of physical processes in moderating biodiversity – ecosystem function relationships at larger geographical scales. In this study, the relationship between the genus richness of benthic macro-invertebrates and five measures of ecosystem functioning (macrofaunal biomass, depth of the apparent redox discontinuity, fluxes of ammonium and NO_x and the abundance of nematodes) was determined over a large scale wave-induced bed shear stress gradient on the seabed of the northern Irish Sea. Ecosystem functioning was significantly correlated to genus richness for four out of five ecosystem functions. However, wave stress moderated the genus richness – ecosystem functioning relationship for only one of the ecosystem functions; genus richness had a positive effect on the depth of the apparent redox discontinuity in the sediment at high wave stress but not a low wave stress. These results indicate that the effects of biodiversity on some ecosystem functions may be sufficiently strong to generate patterns in ecosystems where other factors are also affecting ecosystem processes, but that the biodiversity–ecosystem function relationship for can be dependent on environmental conditions for specific ecosystem functions.

Increasing concern over current rates of biodiversity loss have highlighted the need to evaluate the consequences of species extirpation on the functioning of key ecosystem processes such as nutrient cycling and primary productivity (Hooper et al. 2005). There is, however, uncertainty as to how results obtained in ecological experiments in general and biodiversity – ecosystem functioning experiments in particular scale up to landscape and regional levels (Carpenter 1996, Schindler 1998, Loreau et al. 2002). A number of recent studies have shown that the relationship between biodiversity and ecosystem functioning can be context dependent in natural ecosystems (Mermillod-Blondin and Rosenberg 2006, Tylianakis et al. 2008). For example, processes such as physical disturbance and flow have been identified as potentially important moderators of biodiversity–ecosystem function relationships in aquatic ecosystems (Cardinale and Palmer 2002, Biles et al. 2003, Cardinale et al. 2005). Cardinale et al. (2005) showed that increasing periphyton species richness increased primary production in streams characterised by unpredictable flow regimes, but not in streams with predictable flow regimes. This has important implications for the management of ecosystems, as species that seem redundant under natural conditions may be important for ecosystem functioning when ecosystems are disturbed. Several mechanisms have

been proposed to explain the relationship between biodiversity and ecosystem functioning. The most important of these are resource partitioning, positive interactions between species and sampling effects (Hooper et al. 2005). Positive interactions have been forwarded as a potential mechanisms underpinning BEF effects in deep-sea benthos (Danovaro et al. 2008), whilst resource partitioning has been shown to be important in a model shallow water marine habitat (Griffin et al. 2008).

Marine soft-sediments are the largest ecosystem on earth, and the oceans account for approximately two thirds of global ecosystem services (Snelgrove et al. 1997). Most important among these are nutrient recycling and secondary production. The biodiversity of invertebrate communities in coastal ecosystems is affected by anthropogenic disturbances, such as bottom trawling, dredging, aggregate extraction and pollution. In this study, the relationship between a measure of the biodiversity of benthic macro-invertebrates and several measures of ecosystem functioning in soft sediments was determined over a natural gradient of wave bed shear stresses in the Irish Sea, as a measure of disturbance. Wind shear at the sea surface leads to the generation of waves, and in relatively shallow water or for large wavelengths, these waves translate into wave-induced bed shear stress. High shear stresses can cause sediment

movement at the seabed and high wave stresses can disturb and cause the death of the benthic invertebrates that live in and on the seabed (Hall 1994, Norkko et al. 2002, Barnes and Conlan 2007). In addition to this, waves affect the sedimentary environment by causing pore-water advection (Vopel et al. 2007).

Benthic invertebrates modify the sedimentary environment by mixing the sediment through their feeding, movements and burrowing actions (bioturbation) and by pumping oxygenated water through the sediment (bioirrigation, Mermillod-Blondin and Rosenberg 2006). These activities affect sediment biogeochemistry by increasing the penetration of oxygen into the sediment and hence stimulating aerobic microbial breakdown of organic matter and nutrient regeneration to the overlying water column. For example, large burrowing invertebrates, such as the sea urchin *Echinocardium cordatum* and mud shrimps such as *Upogebia* sp. and *Calocaris* sp. can have particularly large impacts on sediment stability and biogeochemistry (Lohrer et al. 2004, Widdicombe et al. 2004, Waldbusser and Marinelli 2006). Macrofauna can also increase niche availability and heterogeneity for their meiofaunal co-habitants by ameliorating more stressful anoxic conditions and moving sediments through bioturbation. Indeed a number of investigations have demonstrated that the presence or absence of macrofaunal organisms such as bivalve molluscs, sea urchins and polychaete worms can affect the community structure and vertical distribution of nematode worms (Austen et al. 1998, Schratzberger and Warwick 1998, Pinto et al. 2006). Thus bioturbation is intimately linked to a variety of biogeochemical processes (Rhoads 1974) and biodiversity loss in soft sedimentary ecosystems may affect multiple ecosystem functions.

The relationship between bioturbation and the state of, and processes in ecosystems such as oxygen penetration and nutrient regeneration has been well documented (Biles et al. 2002, Solan et al. 2004a or b??). For simplicity, the state of and processes in ecosystems will be named ecosystem functions here. However, few investigations have attempted to quantify such relationships at large scales where physical processes such as sediment disturbance by wave action are spatially variable. Some manipulative investigations have demonstrated that the influence of bioturbation on nutrient regeneration and oxygen consumption is greater in diffusion dominated (low disturbance, fine sediments and low rates of sediment pore water exchange) than in advection dominated (high disturbance, coarse sediments and consequently high rates of sediment pore water exchange) systems (reviewed by Mermillod-Blondin and Rosenberg 2006). Such observations support the hypothesis that bioturbating organisms act as 'direct vectors' of water flow in diffusion dominated systems while they only 'modulate' flow in advective systems (Boulton et al. 2002, Volkenborn et al. 2007). It may therefore be hypothesised that natural disturbance regimes such as wave bed shear stress will moderate the relationship between biodiversity and ecosystem function in soft sedimentary habitats by increasing diffusion of dissolved oxygen from the sediment-overlying seawater into the pore water and oxygenation of the sediment pore water by sediment resuspension. This in turn is likely to affect other ecosystem processes such as nutrient regeneration.

The objectives of the current investigation were firstly to establish whether the diversity of benthic macro-invertebrates has a positive effect on five different measures of ecosystem functioning in the soft sediment communities of the northern Irish Sea: macrofaunal biomass, the depth of the apparent redox discontinuity (aRPD), ammonium flux, nitrite + nitrate flux (NO_x from now onwards), and meiofauna (the abundance of nematodes). Macrofaunal biomass and nematode abundance are not direct measures of processes but measures of the state of the ecosystem. These indicators of ecosystem functioning represent key variables of coastal ecosystems and can be seen as proxies for the transfer of energy between trophic levels, thus indicating the heterotrophic production of the ecosystem, and nutrient regeneration processes, which reflect the ability of ecosystems to sustain their functions over time (Tumbiolo and Downing 1994, Danovaro et al. 2008). aRPD can be interpreted as a proxy for bioturbation and the fluxes of oxygen in the sediment. Secondly we attempted to determine whether variation in wave bed shear stress moderated the relationship between biodiversity and our ecosystem function measures (i.e. the biodiversity-ecosystem function relationship is context dependent).

Methods

General overview

The relationship between biodiversity and ecosystem function was characterised by relating macrofauna taxa richness to several measures of ecosystem functioning at stations in the northern Irish Sea. Stations were allocated across modelled gradients of wave disturbance characterised by wave induced bed shear stress, in order to assess the effect of disturbance on the relationship between genus richness and ecosystem functioning. Wave induced bed shear stress is a measure representative of the amount of sediment movement at the sediment-water interface.

In this study we used wave bed shear stress rather than the tidally induced bed shear stress as a measure of disturbance. Although tidal shear stress also has an effect on the sediment dynamics, it is regular and periodical nature means that it might more appropriately be considered a chronic stress which structures invertebrate communities across large temporal scales, as opposed to a disturbance which alters the community structure from its' previously equilibrated state (Hall 1994). We sampled the benthic community at a total of 26 stations (Fig. 1), and estimated up to six measures of ecosystem functioning at each of these. We then related biodiversity to ecosystem functioning and examined how this relationship was modified by the physical disturbance regime. We used genus richness (GR) as a measure of biodiversity because reliable identification to species level required much more time than reliable identification to genus. As this was an observational study, our results could have been biased by confounding factors (mud content, depth and tidal shear stress) if they correlated to wave stress and genus richness. This possibility was examined by carrying out the analysis after removing the effect of these confounding factors.

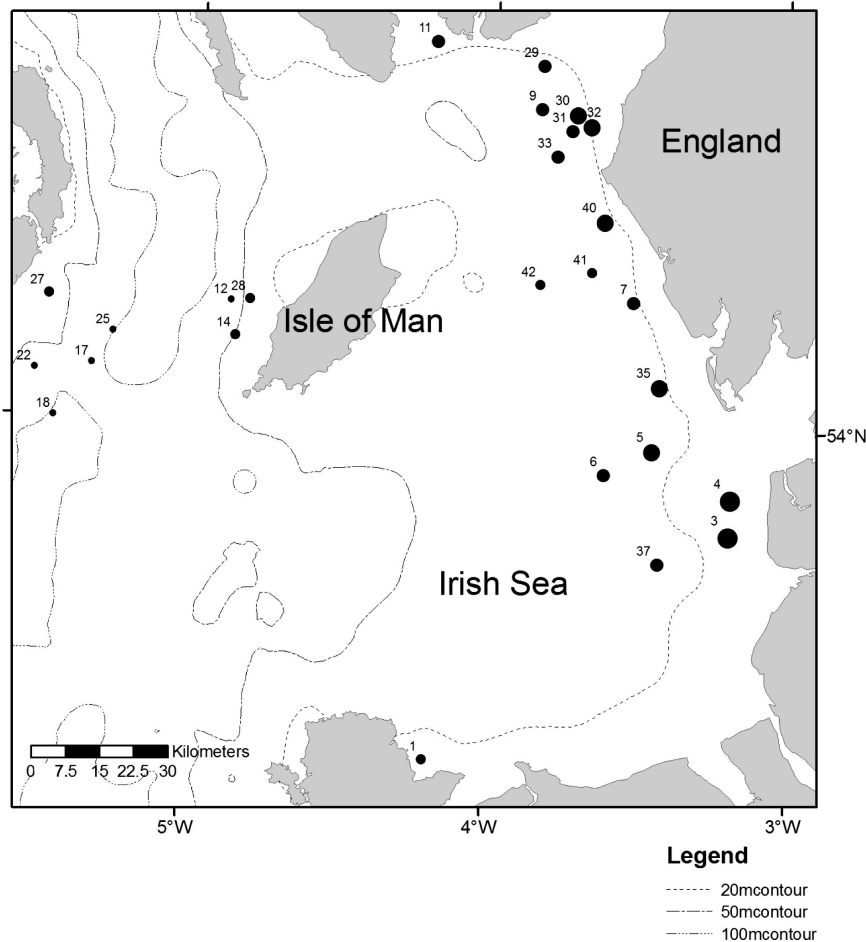


Figure 1. Sampling stations in the Irish Sea. Bubble sizes are proportional to relative wave bed shear stress.

Station selection

We sampled 26 stations in the Irish Sea between 23 and 30 June 2007 using R.V. Prince Madog. One hundred sampling stations were placed at random locations within the northern Irish Sea where the sediment consisted of mud, sandy mud, muddy sand or slightly gravelly muddy sand according to British Geological Survey sediment maps. From these stations, 25 stations were selected randomly at low and high wave stresses to ensure a balanced design. From these 50 stations, 26 could be sampled during the cruise. Strong correlations exist between community structure and sediment type for marine communities, but generally these correlations are indirect as both community structure and sediment type are affected by the hydrodynamic regime (Snelgrove and Butman 1994). Coarser sediments do however have a higher porosity, thereby allowing larger fluxes of pore water and associated solutes. A negative relationship between water depth and wave stress exist as in deeper water the impact of waves on the seabed is reduced. Wave impacts on the seabed also partially control the sediment type, along with tidal currents and the geology of an area. Not all ecosystem function measures could be estimated at all stations because of limitations of the sampling gear; the sediment profile imaging camera (SPI) could not be used at water depths over 40 m because of an equipment fault, and neither the SPI camera nor the box

core always took valid samples in the coarser sediments. At four stations only two ecosystem functioning measures were estimated, at four stations three measures were estimated, at one station four ecosystem functions were measured, at 12 stations five ecosystem function measures were estimated, and at five stations all six ecosystem function measures were estimated (Supplementary material Appendix 1, Table 1).

Oceanographic modelling

Maximum wave-induced bed shear stress was calculated using the spectral wave model SWAN in steady-state mode (Booij et al. 1999). A discrete range of wind speeds and directions was applied initially to a coarse outer nested region of the northwestern European continental shelf. This produced boundary conditions of the action density spectrum that allowed running an independent inner nested region of the Irish Sea (Neill et al. 2008). The range of wind speeds and directions was subsequently applied to this inner nested region to produce a series of lookup tables of wave-induced bed shear stress for each model cell of the Irish Sea at a resolution 1.85 km. Hourly wind data from Valley meteorological station were used in conjunction with the SWAN-generated lookup tables to calculate the maximum wave-induced bed shear stress for each location in the northern Irish Sea during 2003. Wave stress ranged from

0.03 to 2.06 N m⁻² at the selected sampling stations. A wave stress of >0.25 N m⁻² is sufficient to initiate motion of the 125 µm diameter sediments that were typical for this area (Soulsby 1997). Tidal-induced bed stress was calculated to examine correlations between this parameter, biodiversity, ecosystem functioning and other environmental parameters, using the 3D POLCOMS model (Holt and James 2001). Using the same inner nested model grid as that used by the wave model, the maximum tidal-induced bed shear stress during 2003 was calculated throughout the Irish Sea by forcing the lateral boundaries with 15 astronomical tidal constituents, including the dominant M₂ and S₂ (Neill et al. 2007). Maximum bed stress is tightly correlated with the frequency at which wave stress exceeds 0.25 N m⁻² and 0.50 N m⁻² (R² = 0.76 and 0.66, respectively).

Sampling benthic invertebrates and measuring ecosystem functioning

The apparent depth of the oxygenated layers of the seabed was estimated as the apparent redox discontinuity (aRPD) from sediment profile images (Rhoads and Germano 1982, Solan et al. 2004). The term apparent is used in describing this parameter because no actual measurement was made of the redox potential (Diaz and Trefry 2006). The aRPD is a measure of the redox state of the sediment, resulting from bioturbation and abiotic diffusion, and can be estimated from the vertical colour change in the sediment profile, delimited at the lower boundary as the interface between the oxidized (high reflectance) and reduced (low reflectance) sediment. Images were captured during at least five replicate SPI deployments at each station, but insufficient penetration of the camera and water turbidity resulted in only two replicate images in which the sediment-water interface could be reliably identified at some stations.

Two 0.1 m² day grabs were taken at each station to estimate the abundance of nematodes and the genus richness and biomass of macrobenthic invertebrates. Using a syringe corer (1.58 cm², 6 cm deep) five cores were taken at random points within each grab and pooled to integrate spatial variation of meiofaunal distribution on a cm scale and preserved in 4% buffered formalin solution pending laboratory analyses. Meiofauna were extracted from the

samples using the method described by Somerfield and Warwick (1996). Nematodes were the dominant meiofaunal taxon (80–95%) in the samples. Macrofauna was subsequently extracted from the remaining day grab sample using a 1 mm sieve prior to preservation in 4% buffered formalin. Macrofauna was subsequently extracted from the remaining day grab sample using a 1 mm sieve. All preserved animals from the replicate grabs were sorted and identified to genus or the next lowest practicable level in the laboratory, and wet mass was determined after blotting. The number of grabs per station was limited and therefore not all locally present genera will have been present in our samples. As such, GR in this study was a measure of genus density rather than of genus richness per se. Because the same number of replicate grabs was considered for each station, this will not have biased our estimates of biodiversity.

Nutrient fluxes were measured from intact cores that were incubated on the ship for 24 h. Calculations using the estimated oxygen utilization of benthic invertebrates based on their biomass (Vopel et al. 2003) and expected diffusion of oxygen across the air–water interface, indicate that it is unlikely that the oxygen concentration would have fallen below 60% saturation during this period. At each station, two Jonasson Olauson box core samples (0.085 m²) were taken. A PVC core with a diameter of 16 cm and height of 21 cm was inserted into this core to a depth of 15 cm and extracted intact after the overlying water had been drained. Three cm of local sea surface water was then carefully poured into the core to cover the sediment surface, and the core was left to settle for three h. Following this period, duplicate water samples were collected from cores using a 20 ml syringe and transferred to sample pots by ejecting the water through a Whatman GD/X filter of 0.45 µm pore size fitted to the end of the syringe in order to remove suspended particulate matter. The cores were then left to incubate for 24 h and a second sample was taken after this period. The sediment-overlying seawater in the cores was stagnant. Macrofauna was subsequently extracted from the core and treated as the day grab samples described above. Water samples were frozen at –20°C until analysis. Ammonium (NH₄⁺) concentrations were estimated with fluorometry following calibration of a fluorescence spectrophotometer using a series of known ammonium concentrations.

Table 1. The biomass (g WW m⁻²) of the ten most abundant genera in terms of biomass in high and low wave stress stations. *Italic values are abundances that were not in the top ten for that group of stations.*

Class	Genus	Functional group (Solan et al. 2004)	High wave stress biomass (g WW m ⁻²)	Low wave stress biomass (g WW m ⁻²)
Echinoidea	<i>Echinocardium</i>	Slow moving biodiffuser	256.2	59.9
Stelleroidea	<i>Amphiura</i>	Slow moving biodiffuser	134.5	95.9
Bivalvia	<i>Acanthocardia</i>	Sessile biodiffuser	28.3	11.1
Phoronida	<i>Phoronis</i>	Surficial modifier in tube	14.7	6.9
Polychaeta	<i>Pectinaria</i>	Upward or downward conveyer in tube	13.7	1.5
Polychaeta	<i>Nephtys</i>	Slow moving biodiffuser	11.4	8.5
Eumalacostraca	<i>Upogebia</i>	Regenerator that moves freely through burrow system	8.3	2.3
Bivalvia	<i>Dosinia</i>	Sessile biodiffuser	5.9	0.6
Bivalvia	<i>Chamelea</i>	Sessile biodiffuser	5.5	0.1
Bivalvia	<i>Abra</i>	Sessile surficial modifier	5.5	3.9
Polychaeta	<i>Aphrodita</i>	Slow moving biodiffuser	2.7	7.2
Gastropoda	<i>Turritella</i>	Slow moving biodiffuser	0.0	141.0
Eumalacostraca	<i>Calocaris</i>	Regenerator that moves freely through burrow system	0.0	8.5
Gastropoda	<i>Aporrhais</i>	Limited moving surficial modifier	0.0	4.4

Calibration and benthic samples were measured in the fluorometer at an excitation wavelength of 360 nm and an emission wavelength of 420 nm. Nitrate and nitrite (NO_x) were determined with standard colourimetric methodology (Grasshoff et al. 1983) as adapted for flow injection analysis (Hales et al. 2004). Fluxes were calculated as the change in concentration over the 24 h period (a positive flux is defined as a flux out of the sediment). Because the macrofauna relevant to the nutrient data were quantified from our nutrient mesocosms while those that were related to the aRPD and nematode data were quantified from day grab samples, we used two separate measures of macrofaunal biomass and GR for each of these respective sampling strategies. These measures are however still comparable as they were sampled from the same stations.

Statistical analysis

We aimed to examine how ecosystem functioning was affected by macrobenthic genus richness, wave stress and the interaction between these factors. If physical disturbance moderates the relationship between biodiversity and ecosystem functioning, a significant interaction between disturbance and biodiversity can be expected. Genus richness was used as a continuous variable. Wave induced bed shear stress was modelled as a continuous variable and converted into a two-level factor (low and high wave stress, with a cut-off at the median) for the analysis, because the interaction between wave stress and genus richness is much easier to present and interpret when using wave stress as a categorical variable. The number of replicate stations sampled was not considered high enough to allow a powerful analysis using more than two levels for wave stress.

To examine if results were robust to biases by confounding factors (mud content, depth and maximum tidal shear stress), we carried out the same analyses after having corrected for the impact of confounding factors. Because the three potentially confounding factors were strongly correlated, we performed a PCA on these and used principal component 1 (PC1) as a generalized environmental parameter. PC1 explained 75% of the variation of the three environmental parameters. The analyses were then performed using the residuals of the linear regression of ecosystem functioning against PC1.

Results

A total of 163 genera of benthic macro-invertebrates were recorded at the 26 stations. The most abundant genera in terms of biomass at the high wave stress stations were the sea urchin *Echinocardium*, the brittle star *Amphiura* and the bivalve *Acanthocardia*. The most abundant genera in terms of biomass at the low wave stress stations were the gastropod *Turritella*, the brittle star *Amphiura* and the sea urchin *Echinocardium* (Table 1). The list of ten most abundant genera (in terms of biomass) for the low and high wave stress stations had six genera in common.

Most measures of ecosystem functioning were significantly correlated with one or more of the environmental or biotic variables (Table 2). The negative correlation between

Table 2. Correlation matrix of ecosystem functions and environmental parameters. Correlation coefficients indicated with a * are significant at the p = 0.05 level. Italic values are given for the comparisons that are not directly relevant, as nutrient fluxes were measured in cores, with separate biomass measures.

	Genus richness cores	Wave shear stress	Tidal shear stress	Sediment mud content	Depth	Biomass Day grab	aRPD	log Nematode abundance	Biomass core	log NO _x flux	Log NH ₄ ⁺ flux
Genus richness grabs	0.77*	0.38	0.5*	-0.74*	-0.66*	0.8*	0.38	0.44	0.6*	-0.54*	0.43
Genus richness cores		0.63*	0.61*	-0.61*	-0.67*	0.77*	0.15	0.79*	0.7*	-0.42	0.51*
Wave shear stress			0.49*	-0.55*	-0.75*	0.42*	0.32	0.59*	0.58*	-0.54*	0.38
Tidal shear stress				-0.54*	-0.59*	0.48*	-0.26	0.73*	0.79*	-0.61*	0.67*
Sediment mud content					0.77*	-0.66*	0.02	-0.72*	-0.59*	0.62*	-0.49*
Depth						-0.77*	0.41	-0.87*	-0.60*	0.61*	-0.58*
Biomass day grab							-0.31	0.65*	0.73*	-0.59*	0.56*
aRPD								-0.69	-0.53	0.61*	-0.68*
log nematode abundance									0.76*	-0.78*	0.86*
Biomass core										-0.74*	0.79*
log NO _x flux											-0.79*

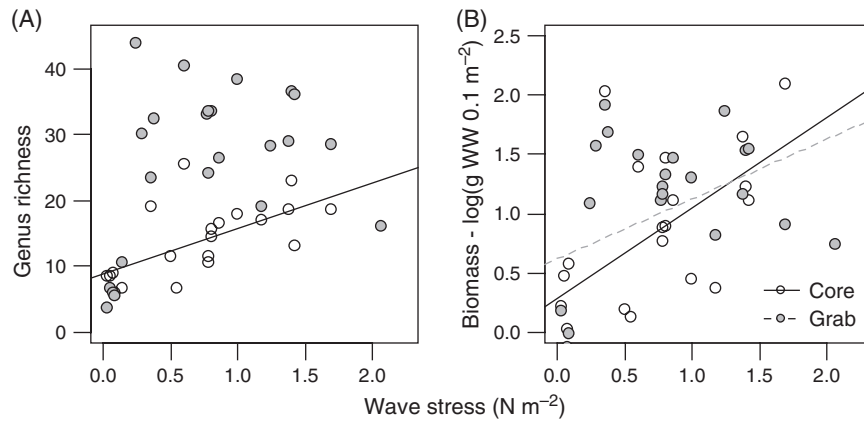


Figure 2. The relationship between wave stress and community measures describing the macrobenthic invertebrates. (A) Genus richness. (B) Biomass. Regression lines were fitted for significant correlations (Table 2). The two different colours of data points represent genus richness and biomass as estimated using the box core and the day grab.

water depth and wave stress was expected as in deeper water the impact of waves on the seabed is reduced. Both genus richness and macrobenthic biomass correlated positively with wave stress, but a wide variation around this relationship was present (Figure 2). The variation around this relationship (varying levels of biodiversity at a given level of wave stress) was vital for examining the effect of the interaction between wave stress and genus richness on ecosystem functioning.

Both biomass measures and the NH_4^+ flux displayed a positive linear relationship with GR, but were not affected by the disturbance regime. There was a positive linear effect of GR on aRPD at low levels of wave stress, while this effect was not evident at high wave stress levels (significant interaction between GR and wave stress, Figure 3, Table 3). This interaction appeared to be caused by a shallower aRPD at low GR in the low stress stations relative to the high stress stations. No significant effect of GR or wave stress on NO_x flux was detected. The abundance of nematodes increased with the genus richness of macrofauna and was higher at high wave stresses (Fig. 3, Table 3).

The analysis using the residuals of the different measures of ecosystem functioning after correcting for the effect of depth, sediment mud content and tidal shear stress showed qualitatively similar results for the biomass from the grabs, aRPD and the NO_x flux. The effect of GR and wave stress were not significant for biomass from the cores, nematode abundance and NH_4^+ flux after correction for the impact of these environmental variables (Supplementary material Appendix 1, Fig. 1, Table 2).

Discussion

This study used an observational approach, where we used existing gradients in natural disturbance regimes and biodiversity at the scale of the northern Irish Sea. We recognize the limitations of inferring causality of the effect of biodiversity from statistical correlations in observational studies. Although the observational approach employed in our study does not allow for the unambiguous assignment of causation to biodiversity or the disturbance regime, it does allow for the examination of the connection between

richness and ecosystem processes on larger spatial scales. An obvious alternative explanation for the observed correlations between GR and ecosystem functioning is that wave stress, or another environmental factor, drives both GR and ecosystem functioning and therefore causes a correlation between these two variables. However, for four out of six ecosystem functions, wave stress was not a factor that explained a significant fraction of the variance in ecosystem functioning, and this suggests that ecosystem functioning was not a direct result of the disturbance regime. For three of these ecosystem functions, the observed effects were not sensitive to confounding by depth, sediment mud content and tidal shear stress, but results were potentially confounded by these environmental variables for the three other ecosystem functions.

We conclude that ecosystem functioning relates to biodiversity for a variety of, but not all, ecosystem functions at large scales in soft sediments. The relationship between ecosystem functioning and biodiversity showed a positive correlation for five ecosystem functions and showed no relationship for one ecosystem function. It is likely then, that positive biodiversity–ecosystem functioning relationships observed in small scale experiments are applicable at large spatial scales and that the effects of biodiversity on ecosystem functioning may be sufficiently strong to generate patterns in ecosystems where other factors are also affecting ecosystem processes for some ecosystem functions, but not others. In a similar observational study, Danovaro et al. (2008) found that in the deep-sea, ecosystem functioning also correlated with the biodiversity, in that case of nematodes, over even larger spatial scales.

The relationship between biodiversity and ecosystem functioning was modified by the disturbance regime for only one of the ecosystem functions considered, aRPD. These results therefore only partly support the hypothesis that the strength of the biodiversity–ecosystem functioning relationship will depend on the disturbance regime of an ecosystem (Cardinale and Palmer 2002, Cardinale et al. 2005). The results do not therefore allow a conclusion on the effect of disturbance on large scale biodiversity–ecosystem functioning relationships that is applicable across different ecosystem functions. However, the observed interaction between wave stress and genus richness that

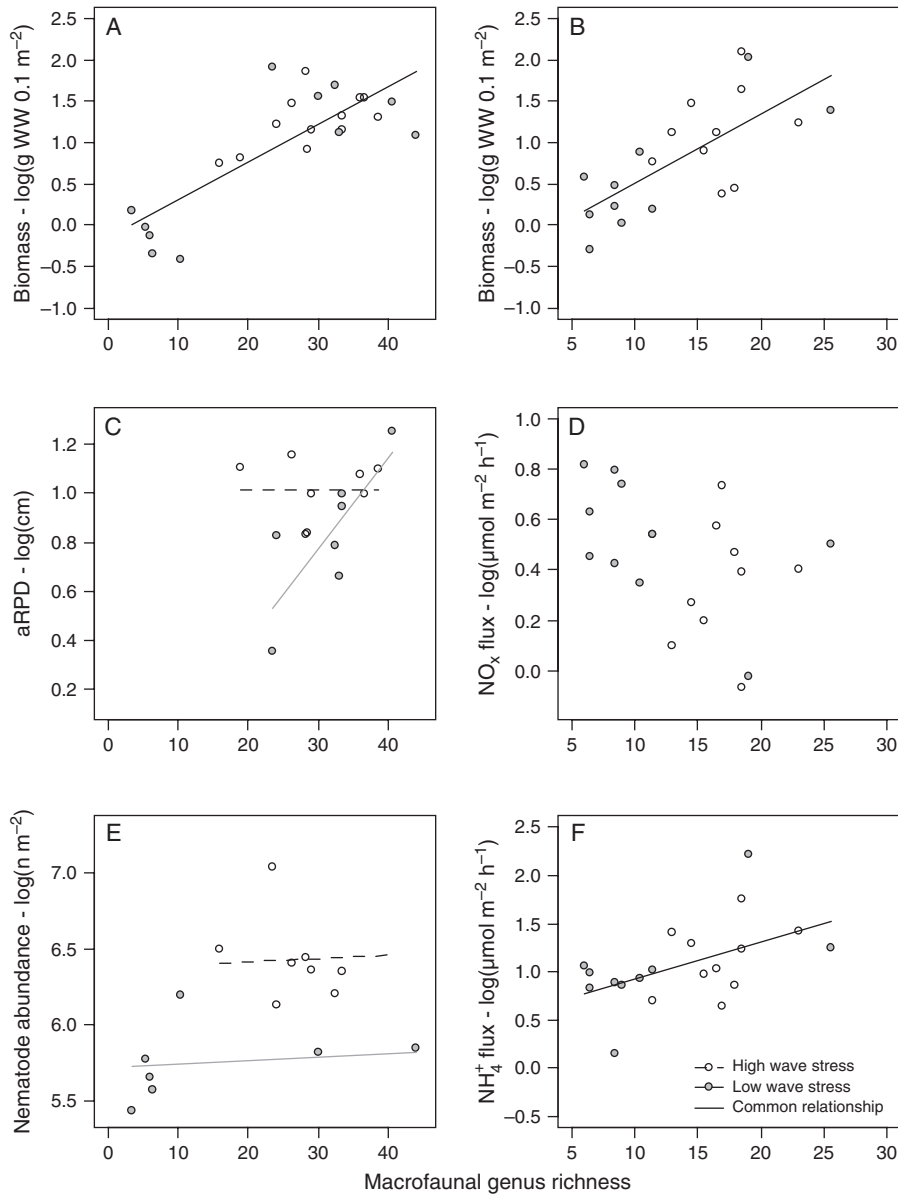


Figure 3. The relationship between GR and ecosystem function for six ecosystem functions. When the effect of wave stress on ecosystem function was significant, separate regression lines were drawn. Open circles are high wave stress locations, closed circles are low wave stress locations.

was observed in the current investigation for aRPD does lend support to the advection/diffusion hypothesis (Boulton et al. 2002, Mermillod-Blondin and Rosenberg 2006) suggesting that biodiversity becomes less important in the maintenance of oxygenated sediments as physical disturbance increases. Placing the results of this investigation alongside similar studies in the wider literature (Cardinale et al. 2005), it is apparent that the role of biodiversity in the maintenance of ecosystem functioning may not only be context dependent across disturbance regimes, but that the nature of this dependency is in turn dependent on the ecosystem under consideration. GR had no effect on ecosystem functioning for the other ecosystem functions or an effect on ecosystem functioning that was not modified by the disturbance regime. The stress amelioration hypothesis was therefore not supported by the majority of

the results in this study. A closer examination of the biochemistry and ecology of sediment ecosystems may provide explanations for this. Macrofauna can interact directly with nematodes through predation, indirectly through competition for resources and by modifying the environmental conditions in the sediment (e.g. oxygen penetration and detritus fluxes or the spatial heterogeneity of such patterns, Austen et al. 1998, 2003). The observed positive relationship between nematode abundance and GR suggests that macrofauna has a positive effect on nematode abundance by modifying their environment. NO_x flux was not significantly affected by GR, while the NH_4^+ flux was significantly positively related to GR, but this relationship was not moderated by wave stress. NH_4^+ is formed during the anaerobic degradation of organic material by bacteria. In addition to this, NH_4^+ is also an excretion product of

Table 3. ANOVA for the six examined ecosystem functions.

Ecosystem function	R ²	Res. DF	GR		Stress		GR * Stress	
			F	P	F	p	F	p
Biomass grab	0.671	19	36.92	<0.001	0.93	0.35	0.91	0.35
Biomass core	0.52	16	16.37	<0.001	0.25	0.62	0.69	0.42
log aRPD	0.59	11	3.87	0.075	5.69	0.04	6.60	0.026
log nematode abundance	0.70	11	7.11	0.021	17.43	0.002	1.41	0.26
log NO _x flux	0.22	16	3.63	0.075	0.39	0.54	0.61	0.45
log NH ₄ ⁺ flux	0.28	16	5.76	0.029	0.42	0.52	0.03	0.87

heterotrophic organisms that is the result of the breakdown of proteins. Typical weight specific excretion rates of NH₄⁺ are in the range of 0–45 µg g⁻¹ WW d⁻¹ (Viitasalo-Frösén et al. 2009). The maximum weight specific NH₄⁺ flux that was observed in this study was 5.17 µg g⁻¹ WW d⁻¹. The higher NH₄⁺ flux is therefore likely to be a direct result of the higher biomass of macrofauna at higher GR (Gardner et al. 1993). As GR had a positive effect on the aRPD at low wave stress, a decrease in NH₄⁺ derived from anaerobic bacteria was expected, rather than the observed increase. This again suggests that NH₄⁺ was produced directly by the macrofauna.

Real ecosystems perform many ecosystem functions and previous studies have shown that it is likely that many more species are necessary to perform multiple functions compared to single functions in isolation (Hector and Bagchi 2007, Gamfeldt et al. 2008). Using the current dataset it is not possible to assess the multifunctional relationship with biodiversity, as this requires measures of the ecosystem functioning contribution of individual species. However, Table 2 indicates that the correlation between the different ecosystem functions is quite weak in some instances and strongly negative in some others. This implies that also in the Irish Sea many different taxa will be necessary to optimally perform all ecosystem functions. All different ecosystem functions that were examined are likely to be inter-related to some extent as they were all assumed to be related to biodiversity and wave stress, and nutrient fluxes are affected by the redox state of the sediment. The non-independence of the different ecosystem functions could lead to a potential overestimate of the number of significant relationships (a type I error inflation) and therefore our results have to be interpreted with care, especially as many results are not highly significant (0.05 > p > 0.01).

These results indicate that the effects of biodiversity on some ecosystem functions are sufficiently strong to generate patterns in marine soft sediment ecosystems where physical factors are also affecting ecosystem processes, but that the biodiversity–ecosystem functioning relationship can be dependent on environmental conditions for specific ecosystem functions. Wave stress can moderate the biodiversity–ecosystem functioning relationship, but was unimportant in moderating the relationship for most ecosystem functions. What has become clear from this study is that different ecosystem functions relate to biodiversity in different ways, although the most common pattern was a positive relationship. The interaction between wave stress and GR that was observed for one of the ecosystem functions, aRPD, has some important implications for the management of natural resources. The

observed interaction suggests that the number of taxa that is required to perform some ecosystem functions depends on the disturbance regime of an ecosystem. This implies that where currently biodiversity is not important for regulating ecosystem functioning and therefore biodiversity loss will not affect ecosystem functioning, biodiversity loss may affect ecosystem functioning when the disturbance regime of that ecosystem changes. More simply, if high biodiversity may seem superfluous for ecosystem functioning under the perceived conditions at a given point in time, changes in the disturbance regime may increase the importance of biodiversity for a given ecosystem function.

These results suggest that research that includes more realistic conditions, such as ecosystems with varying levels of disturbance, will be critical towards further understanding biodiversity–ecosystem functioning relationships. Only the combination of observational, experimental and theoretical work will lead to an understanding of the real world importance of biodiversity for ecosystem functioning.

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