ORIGINAL ARTICLE

Effects of experimental small-scale cockle (*Cerastoderma edule* L.) fishing on ecosystem function

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Abstract

The cockle *Cerastoderma edule* L. occurs at commercially exploited densities within both species-poor and species-rich assemblages, dominating the faunal biomass and potentially acting as a key contributor to a number of ecological functions. The questions considered were: Is the delivery of ecological functions affected by the removal of *C. edule*? Does the biodiversity of the affected assemblage affect the extent to which it is altered? To explore these questions, adult cockles were removed from experimental plots at two shores in the North-West of England: a species-poor shore at Warton Sands, Morecambe Bay, and a more diverse shore at Thurstaston, Dee estuary. Impacts on the functioning of the systems were determined during a 4-month study in summer 2007 by direct measurements of benthic primary production, organic matter content and sediment granulometry, and by indirect analyses using Biological Traits Analysis. Removal of adult cockles led to significant changes in faunal assemblage composition and in the distribution of biological traits, with increased biodiversity and an increased prevalence of traits relating to opportunistic taxa observed following the removal of *C. edule*. These changes occurred at both study sites and hence were independent of the initial biodiversity of the assemblages. Sediment granulometry was significantly affected; however, surface chlorophyll and organic matter were not affected. This implies a minimal impact on these functions and a high degree of functional redundancy within the macrofauna. The implications of these findings and future areas of research are discussed.

Problem

There is an increasing drive to consider ecosystem dynamics in terms of ecological functions, the maintaining of these functions being seen as a key factor in sustaining the goods and services provided by ecosystems (*e.g.* E.C. 2007). Ecosystem functions, as defined by Naeem *et al.* (2002), are the 'activities, processes or properties of ecosystems that are influenced by their biota'. In littoral systems, these functions include the cycling of organic carbon and nutrients, food provisioning, biological productivity and energy transfer through the system (Christensen *et al.* 1996).

There has been much debate as to the role that species diversity plays for the functioning of ecosystems (*e.g.* Kaiser 2000) and a number of hypotheses have been developed to explain the effects of species on ecosystem function (Huston 1997; Loreau & Hector 2001). Species do not evolve in order to provide ecological functions. Instead, the delivery of functions is a consequence of the methods that taxa have developed to survive and reproduce, with different taxa developing different approaches to, for example resource capture and reproduction. The 'rivet hypothesis' (Ehrlich & Ehrlich 1991) suggests that each species in an assemblage plays a unique and specialized role, providing a range of functions unique to that

species and that the extinction of a species will result in reduced ecosystem function. Therefore, within highly diverse assemblages, an increased number of species provide a greater range of ecological functions.

Species-rich assemblages may also be more resilient to species extinction than less diverse assemblages, providing a greater insurance against the loss of taxa. This concept is an integral part of the 'redundancy hypothesis' (Walker 1992; Naeem 1998) in that many species in the assemblage are able to deliver each ecological function and the localized extinction of one species is compensated for by other taxa carrying out the same functional roles. The identity of taxa removed, however, is likely to be of importance, with individual taxa making different contributions to each ecological function. Some taxa make a key contribution to one function, whereas other taxa have very little influence upon it. This combination of the rivet and redundancy hypotheses is the basis of the 'keystone hypothesis' (Lavorel & Garnier 2002; Hooper *et al.* 2005). For example, dense aggregations of the filter-feeding mussel *Mytilus edulis* L. have an influence on both the regeneration of nutrients and the primary productivity within coastal systems (Prins & Smaal 1994). *Mytilus edulis* is an efficient filter feeder, removing large amounts of phytoplankton. Dense aggregations also influence near-bed hydrodynamics, causing increased levels of biodeposition and mineralization of biodeposited particles, and resulting in increased levels of nutrient regeneration within mussel beds (Prins & Smaal 1994). *Mytilus* aggregates also provide refugia for other fauna, increasing biodiversity and thus influencing energy flow through the system (Ragnarsson & Raffaelli 1999).

The cockle *Cerastoderma edule* L. is common in intertidal assemblages on all British coasts and has been the target of a commercial fishery for over a century (Dare *et al.* 2004). *Cerastoderma edule* are a major prey item for birds (Drinnan 1957) and demersal fish (Pihl 1985) foraging on intertidal flats and are active filter-feeders, consuming planktonic flora and fauna and re-suspended microphytobenthos (Kamermans 1993, 1994; Sauriau & Kang 2000). At certain times of the year a large proportion of the diet of *C. edule* can be the planktonic juvenile stages of benthic organisms, including *C. edule* itself (Flach 1996). Bivalves eject undigested particulate material as mucous-coated pseudofaeces, which can alter the resuspension characteristics of the benthic boundary layer and add to the organic matter content of surface sediments, acting as a nutrient source for primary producers and a food source for surface deposit-feeding fauna (Hempel 1957; Swanberg 1991; Giles & Pilditch 2006). *Cerastoderma edule* therefore has the potential to impact upon the structuring of intertidal assemblages and be of critical importance in the delivery of ecological functions

in these systems, either directly (*e.g.* impacting on energy flow through the removal of settling juveniles) or indirectly (*e.g.* providing a food source to detritivores via the biodeposition of pseudofaeces). Dense beds of *C. edule* occur in situations where the faunal assemblage is species-diverse and productive, but also where very few taxa are present (*e.g.* Ivell 1981; Attrill 1998). This raises the possibility that these systems deliver quite different ranges and quantities of ecological functions, or that the role of *C. edule* varies in response to the nature of the assemblage. The removal of *C. edule* by a fishery would, presumably, alter the dynamics and ecological functioning of these systems, with the possibility that the response of the more diverse assemblages would differ from that of species-poor assemblages.

The large size of the organism and the availability of harvesting techniques provide an opportunity for the manipulation of cockle diversity within both species-rich and species-poor assemblages. This allows *in situ* field investigations to be carried out: investigating the impact of an experimentally reduced population of a potentially key species on ecological functioning. To date, manipulative experimental investigations of the impacts of altered assemblage composition on ecological functioning have principally been limited to laboratory-based microcosm studies (*e.g.* Michaud *et al.* 2006; Norling *et al.* 2007). Although such studies confer a high degree of control, allowing specific ecological questions to be approached, by their nature such designs remove a large number of unknown variables that would be present within natural systems. Microcosm experiments generally include only a limited number of taxa and hence only a limited representation of the complexity inherent within 'real' systems (Duffy *et al.* 2001; Bulling *et al.* 2008; Olsgard *et al.* 2008). The outcomes of such studies therefore, are generally less able to be applied to natural assemblages and ecosystems. Although *in situ* approaches introduce a greater number of unmeasured variables into experimental systems (and hence limit the degree to which the causality behind any responses can be assigned), they allow inference to a greater extent as to what the response of a 'natural' assemblage may be.

Traditional methods of assessing ecosystem functioning are based upon the direct or proxy measurements of a limited number of ecological functions, such as chlorophyll concentration, sediment organic matter content and sediment granulometry (Thrush *et al.* 2006; Sundbäck *et al.* 2007). However, this approach alone is somewhat limited in that it provides an incomplete view of the functioning of the system as a whole. That is, the responses of one function to a particular effect may be negligible and the observation of a limited number of functions may mean that more subtle changes to ecologi-

cal functioning, *i.e.* those difficult to predict *a priori*, are missed. Biological Traits Analysis (BTA) is a complimentary approach to these 'direct' methods. BTA was developed primarily for lotic systems (Charvet *et al.* 1998) but it has been increasingly applied to marine systems (Frid *et al.* 2000; Bremner *et al.* 2003; Tillin *et al.* 2006; Kenchington *et al.* 2007).

The delivery of ecological functions is, by definition, a consequence of the life history, ecological and physiological strategies that taxa within a system have evolved. Different strategies employed by species affect different ecological functions. For example, the living habit employed by a taxon (*e.g.* being a surface dweller, tube-dweller, active burrower, *etc.*) has an influence on the depth of sediment into which oxygen-rich water can penetrate, thus influencing the regeneration of nutrients and the circulation of toxins within the benthos (Aller 1983; Ziebis *et al.* 1996). Mapping the occurrence of these functionally important traits within a system may therefore be used as a proxy for the analysis of ecological functions. Species may have a number of traits in common; hence BTA allows a comparison between systems where the finite biogeographic ranges of species make the interpretation of taxa-based approaches difficult (Charvet *et al.* 2000). Changes to the prevalence of biological traits within a system can provide an insight as to how the ecological functioning of the assemblage has been affected by an external stressor.

The aim of the current study was to test the redundancy and rivet hypotheses *in situ* within two contrasting estuarine intertidal assemblages. The following questions were asked: Is the delivery of ecological functions affected by the removal of a potentially keystone species? Does the biodiversity of the affected assemblage affect the extent to which it is disturbed? To facilitate this, *C. edule* was experimentally removed from the benthos and ecological functioning assessed through measurements of surface chlorophyll as a proxy for microphytobenthic primary production, organic matter within the sediment as a proxy for benthic community metabolism, and sediment granulometry as a measure of changes to the physical habitat. BTA was carried out on faunal assemblages to assess changes to the functional structure of the faunal communities.

Material and Methods

Site description and experimental design

Experimental manipulations were carried out on two tidal flats in North-West England, UK. Thurstaston (53°20′N, 3°9′W) is located within the Dee estuary and Warton Sands (54°6′N, 2°49′W) within Morecambe Bay. Both are sandy shores, with mean silt contents (<63 μm) of

10.1 ± 1.3% and 15.9 ± 1.9% for Thurstaston and Warton Sands, respectively. The faunal biomass at both sites is dominated by *Cerastoderma edule*, the Baltic tellin *Macoma balthica* (L.), the mud snail *Hydrobia ulvae* (Pennant) and the spionid polychaete *Pygospio elegans* (Claparède). Biomass at Thurstaston is also dominated by the bivalves *Scrobicularia plana* (da Costa) and *Mya arenaria* (L.) and the polychaete *Hediste diversicolor* (OF Müller). A large proportion of the biomass at Warton Sands consists of the predatory polychaete *Nephtys hombergii* (Savigny). Thurstaston contains a more diverse macrofaunal assemblage (*c.* 30 species) than Warton Sands (*c.* 18 species; C. Cesar unpublished observations). Both sites have in the past been commercially fished cockle beds; however, at the time of the experiment, both had been closed to fishing for ∼2 years.

At each shore, four replicate 2 × 2 m plots were established for each of three treatments:
(1) Fished – surface sediment was hand-raked to a depth of ∼10 cm and passed through a 6-mm-square mesh. All *C. edule* retained on the mesh were removed and all other organisms were returned to the plot.
(2) Procedural control – surface sediment was raked as above and all organisms returned to the plot.
(3) Undisturbed control.

The 12 plots on each shore were arranged in a randomized block design, with plot locations marked by a 30-cm plastic peg at each corner of the plot. To minimize interactions between plots, each was located at least 5 m from other plots.

The experiment was initiated in June 2007 and plots were sampled every 4 weeks until September 2007. To minimize the risk of creating artifacts from the repeated sampling of plots, each plot was split into four sub-plots (each representing an area of 1 m^2). At each sampling event, samples were removed from random locations within the central 50 × 50 cm (to avoid edge effects) of only one randomly selected sub-plot; each sub-plot was sampled once only during the course of the experiment.

Every 4 weeks, four surface chlorophyll *a* samples were taken using plastic cores (internal diameter 20 mm) pushed into the sediment to a depth of 15 mm. Samples were wrapped in foil and stored in a cool box until return to the laboratory. Prior to analysis, chlorophyll *a* samples were stored at −80 °C. Sediment granulometry and organic matter content were ascertained from the removal of one sediment sample from each plot (PVC core, internal diameter 30 × 100 mm). On the first and final sampling occasions, four sediment core samples were taken to investigate the faunal assemblage composition at each plot (PVC core, internal diameter 110 × 200 mm depth). These samples were washed over a 500-μm sieve and the residue fixed in 4% formaldehyde.

Infaunal assessment

Macrofauna were identified to the lowest taxonomic level practical and biomass ascertained by wet weight (±0.0001 g). Biomass was chosen as the faunal 'abundance metric' in this investigation as biomass is likely to better represent the distribution of resources within the system than species abundance measures (*e.g.* Chiarucci *et al.* 1999). A high abundance of very small organisms are not likely to partition as great a proportion of ecosystem resources (particularly organic carbon) as fewer, much larger taxa occupying a greater biovolume than their low abundance alone would suggest. This is particularly important when we wish to assay the ecological roles being played by taxa, rather than biodiversity *per se* and this approach is supported by other literature (*e.g.* Wilson 1991; Chiarucci *et al.* 1999; McGill *et al.* 2007). Comparisons of macrofaunal communities were carried out using permutational analysis of variance (PERMANOVA, Anderson 2001) based on Bray–Curtis dissimilarities and probability values calculated from 4999 permutations (see Manly 1997) using the FORTRAN program PERMANOVA (Anderson 2005). When assemblages significantly differed between factors (Shore, Treatment and Time) ($\alpha < 0.05$), *a posteriori* pairwise comparisons were carried out using PERMANOVA and the significantly different factors investigated using the SIMPER procedure in the PRIMER v.6.1.6 software package (Clarke & Warwick 1994; Clarke & Gorley 2006), to identify the contribution of individual taxa to differences between factors.

Biological traits analysis

To investigate the distribution of biological traits within the species assemblages, taxa were scored against 14 biological traits to reflect the life history, morphological and ecological strategies of taxa and to provide a proxy analysis of a number of ecological functions. Each trait was divided into a number of modalities (sub-categories) (Table 1) and a fuzzy coding approach used to score the affinity of each taxon against all of the modalities within each trait (Chevenet *et al.* 1994). Trait information was obtained from a range of sources; where possible, information came from published peer-reviewed literature. Alternatively, information was taken from grey literature or from expert opinion on the taxa. Where trait information for a taxon could not be obtained (in only 3% of cases), 0 scores were used for each modality and hence did not influence the analysis (Chevenet *et al.* 1994). Fuzzy scores were standardized prior to analysis so that within each trait, the modality scores for each taxa summed to one.

Table 1. Biological traits and modalities used in the fuzzy coding of taxa for biological traits analysis (BTA) to describe functional diversity (adapted from Bremner *et al.* 2006; Frid *et al.* 2008). Codes refer to Fig. 2.

trait	modality	code
adult mobility/dispersal potential (distance per year)	none	D0
	<10 m^2	D1
	10–100 m^2	D2
	>100 m^2	D3
age at sexual maturity (years)	0.08–0.5	M1
	0.5–1	M2
	1–2	M3
	>2	M4
fecundity (eggs released per reproductive event)	10 s	F1
	100 s	F2
	1000 s+	F3
food type	Phytobenthos	Ph
	Benthic Invertebrates	Bi
	Carrion	Cr
	Benthic POM	Bp
	Plankton	Pl
	Pelagic POM	Pp
living habit	Tube	Tu
	Burrow	Bu
	Epizoic	Ep
	Free	Fr
living location	Pelagic	Pe
	Surface	Su
	Interface	In
	Shallow (0–20 cm)	Sh
	Deep (>20 cm)	Dp
longevity (years)	<0.5	L1
	0.5–1	L2
	1–2	L3
	2–5	L4
	>5	L5
maximum size (mm)	0–50	S1
	50–100	S2
	100+	S3
movement method	None	Nm
	Swim	Sm
	Crawl	Cw
	Burrow	Br
propagule dispersal	None	N
	Planktonic (0.04 years)	P1
	Plank (0.04–0.08 years)	P2
	Plank (0.08–0.5 years)	P3
	Benthic crawl	Bc
	Raft	Rf
reproductive frequency	Continuous	Co
	1 event per year	Y1
	2+ per year	Y2
	Less than annual	Yx
reproductive method	Asexual	Ax
	Sexual (spawn)	Ss
	Sexual (ovigerous)	So
	Sexual (direct)	Sd

Table 1. Continued

trait	modality	code
resource capture	Deposit	De
	Suspension: active	Sa
	Suspension: passive	Sp
	Opportunist/Scavenger	Sc
	Grazer	Gr
	Predator	Pr
tissue components	Calcareous	Ca
	Fleshy	Fl

To investigate differences in the distribution of biological traits between assemblages, the taxa-trait table was weighted by multiplying the trait scores for each taxon by the biomass of the taxon for each sample. The scores for each modality within each trait were summed. This resulted in a table containing the total biomass of organisms within an assemblage that displayed each trait. The resulting biomass-weighted trait-by-station table was ordinated using fuzzy correspondence analysis (FCA) (Chevenet *et al.* 1994). The ordinate scores for FCA axes one and two were analysed using Kruskal–Wallis analysis against the factors Shore, Treatment and Time. BTA was carried out using the ade4 (version 1.4–5) package for R (version 2.6.2, CRAN 1999; Dray & Dufour 2007).

Sediment properties and chlorophyll *a* concentration

Changes to sediment granulometry were ascertained from the 30×100 mm sediment cores which were dried in a cool (60 °C) oven and weighed (± 0.01 g). Sediments were soaked overnight in sodium hexametaphosphate solution and washed over a 63-μm sieve. After drying at 80 °C, retained sand (>63 μm) was reweighed and percentage silt contents (*i.e.* <63 μm) were inferred by subtraction.

Changes to the organic matter content of the sediments were assayed by loss on ignition (LOI). Samples of *c.* 10 g of dried sediment were ground with a pestle and mortar to even consistency and weighed (± 0.0001 g) before and after ignition at 500 °C for 5 h.

Surface chlorophyll *a* concentrations were taken as an index of microphytobenthic biomass (MacIntyre *et al.* 1996). Surface sediment samples were agitated for 15 min in 90% acetone solution and centrifuged for 15 min at 1200 *g*. Chlorophyll *a* concentration in the supernatant was determined by spectrophotometry, following Lorenzen (1967) and expressed as mass of chlorophyll *a* per unit mass of dry sediment (μg Chl*a* g^{-1}).

Statistical analyses were carried out for each of the sediment properties using linear mixed models (LMM) with the first order auto-regressive (AR1) covariance structure fitted according to the criteria of Wang & Goonewardene (2004), with Time as a repeated variable and experimental Treatment (*i.e.* 'Hand-raked' and 'Hand-raked & cockles removed') and Shore as fixed factors. LMM were selected as the assumption of sphericity, as required in general linear models (GLM), is unlikely to be satisfied (Rowell & Walters 1976). Additionally, unlike GLM, LMM is equally efficient for both balanced and unbalanced designs and hence allows for a degree of missing data and for the fact that due to tidal variations, sampling times were not exactly 4 weeks apart (Wang & Goonewardene 2004; Spilke *et al.* 2005). Percentile data (loss on ignition and silt content) were √-transformed prior to analysis; for clarity however, untransformed values were used in presented figures. LMM analyses were carried out in SPSS v15 (SPSS, Inc.).

Results

Infaunal assemblages

Analyses revealed significant differences in *Cerastoderma edule* biomass between the factors Treatment (LMM, F = 9.79, P = 0.001) and Time (F = 7.13, P = 0.013), but no significant differences within the interactions between factors. Plots subjected to the treatment Fishing had a mean *C. edule* biomass of 89.15 ± 52.41 g·m^{-2}; assemblages within Procedural Controls contained 448.91 ± 245.54 g·m^{-2} *C. edule* and Undisturbed Controls contained 484.09 ± 176.78 g·m^{-2}. Therefore the Fishing treatment did result in a significantly reduced biomass of *C. edule* within experimental plots. *Cerastoderma edule* biomass was also found to increase under the factor Time ($T_1 = 268.08 \pm 124.13$ g·m^{-2}, $T_2 = 413.35 \pm 181.92$ g·m^{-2}), presumably due to the immigration and/or growth of the organisms over the summer period (Flach 1996).

Total macrofaunal biomass was greater at Thurstaston than at Warton Sands (mean total macrofaunal biomass for Thurstaston = 768.7 ± 429.0 g·m^{-2}, for Warton Sands = 353.1 ± 283.6 g·m^{-2}, Mann–Whitney U = 779, P < 0.001). A total of 35 taxa were identified over both assemblages, with 33 at Thurstaston and 19 at Warton Sands (see supplementary Tables S1 and S2 in appendices). Thurstaston showed greater macrofaunal diversity than Warton Sands (Shannon–Weiner mean H'$_{Thurstaston}$ = 1.30 ± 0.37; H'$_{Warton\ Sands}$ = 0.97 ± 0.23, Mann–Whitney U = 742, P = 0.002). Significant differences in faunal assemblage compositions were identified between the two shores (Table 2 and MDS plot, Fig. S1, in supplementary appendices). Faunal biomass within both assemblages was dominated by *C. edule*, contributing $45.3 \pm 28.34\%$ of total faunal biomass at Thurstaston and $52.9 \pm 28.6\%$ at Warton Sands. Other major contributors to faunal biomass at both assemblages were the bivalve *Macoma*

Table 2. PERMANOVA and pairwise *a posteriori* comparisons between faunal biomass compositions within two assemblages (TH = Thurstaston and WS = Warton Sands) under different experimental treatments (F = Fished, P = Procedural Control and C = Undisturbed Control) at two different times (1 = June 2007 and 2 = October 2007). Significant (P < 0.05) differences in the PERMANOVA are shown in bold. For the pairwise *a posteriori* comparisons, only significant results (P < 0.05) are shown. For example, TH, 1: F ≠ P means that there was a significant difference in assemblages at Thurstaston at Time 1 between the Fished and Procedural control plots.

source of variation	df	MS	F	P(perm)	*a posteriori* comparisons
shore	1	16,940.02	18.60	**<0.01**	TH ≠ WS
treatment(Shore)	4	2621.31	2.88	**<0.01**	TH: F ≠ C, P ≠ C; WS: F ≠ C
time	1	549.68	0.60	0.644	
shore × time	1	618.02	0.68	0.586	
treatment(shore) × time	4	2861.33	3.14	**<0.01**	TH, 1: F ≠ P, F ≠ C;
					TH, 2: F ≠ P, P ≠ C
error	36	910.58			

balthica (contributing 20.7 ± 13.1% at Thurstaston and 20.7 ± 15.2% at Warton Sands) and the gastropod *Hydrobia ulvae* (contributing 7.3 ± 9.2% at Thurstaston and 12.8 ± 21.8% at Warton Sands). Most of the difference between the two shores was derived from differences in the biomass of the bivalve species *C. edule*, *M. balthica* and *Scrobicularia plana*, the polychaete *Hediste diversicolor* and the gastropod *H. ulvae* (Table 3). With the exception of *H. ulvae*, which showed a greater biomass at Warton Sands, these taxa were either absent at Warton Sands or present at much reduced biomass.

Total macrofaunal biomass (including biomass of *C. edule*) present within assemblages was significantly reduced following the removal of *C. edule* (LMM, F = 16.27, P < 0.001). There was also a significant increase of biomass with sampling time, with samples taken in October housing a greater biomass than those in June (LMM, F = 7.25, P = 0.010). However, when the biomass data for *C. edule* were excluded from the analysis, although total biomass at Thurstaston was still greater (LMM, F = 84.97, P < 0.001), no significant changes under the experimental treatments were detected and hence non-*C. edule* assemblage biomass was not significantly changed by the treatments. The removal of *C. edule* had a significant effect on biodiversity both with (Shannon–Wiener Index, LMM, F = 11.94, P = 0.002) and without (Shannon–Wiener Index, LMM, F = 4.56, P < 0.05) the *C. edule* data being included in the analyses. Fished plots showed increased biodiversity compared with both Procedural and Undisturbed Controls.

PERMANOVA revealed no significant changes over Time and no Shore × Time interaction within faunal assemblage compositions within either assemblage (Table 2). However, significant differences were observed with regard to Treatment and within the Treatment × Time interaction (Table 2). *A posteriori* pairwise analyses were carried out on the significant outcomes of the PERMANOVA. At Thurstaston, differences in faunal biomass compositions were observed between the Undisturbed Control plots and both the experimentally Fished and the Procedural Controls. SIMPER analyses (Table 3) revealed that much of the differences was due to a reduced biomass of the bivalves *C. edule*, *M. balthica*, and *S. plana* in Fished plots and increased biomass of *H. ulvae* in Undisturbed Control plots. Procedural Control plots showed an increased biomass of the *M. balthica* and

Table 3. Output of the SIMPER analyses displaying the taxa responsible for 90% of the difference between experimental treatments (F = Fished, P = Procedural Control, C = Undisturbed Control) within two assemblages (TH = Thurstaston and WS = Warton Sands) both in terms of overall differences and over two sampling occasions. Only differences revealed as significant by *a posteriori* pairwise comparisons are displayed. Values represent the percentage contribution made to the differences by each taxon. Superscript *a* indicates that the former of the pairwise comparisons has the greater biomass, *b* indicates that the latter comparison has greatest biomass, *e.g.* Thurstaston has a greater biomass of *Hediste diversicolor* than Warton Sands does.

		Thurstaston						Warton Sands
		overall		June 2007		October 2007		overall
species	TH *versus* WS	F *versus* C	P *versus* C	F *versus* P	F *versus* C	F *versus* P	P *versus* C	F *versus* C
Hediste diversicolor	4.86[a]						2.95[b]	
Hydrobia ulvae	4.02[b]	4.14[a]	3.76[b]	4.83[b]	6.27[a]		3.27[b]	
Cerastoderma edule	54.40[a]	64.74[b]	65.77[b]	68.15[b]	57.98[b]	73.95[b]	61.68[a]	83.60[b]
Macoma balthica	15.03[a]	11.21[b]	10.81[a]	17.26[a]	18.59[a]	7.60[b]	7.47[a]	8.79[b]
Scrobicularia plana	14.36[a]	10.17[b]	10.78[b]		9.70[b]	10.21[b]	15.64[a]	

reduced biomass of *C. edule*, *S. plana* and *H. ulvae* compared with Undisturbed Control plots.

At Thurstaston, Treatments were also significantly different between the two sampling times. In June 2007, Fished plots were different from both Procedural and Undisturbed Control plots (Table 2). Fished plots had a reduced biomass of *C. edule* and increased biomass of *M. balthica* compared to both controls. Plots subjected to Fishing had a reduced biomass of *H. ulvae* compared with Procedural Controls, but a greater biomass than Undisturbed Control plots. In October 2007, Procedural Controls were significantly different from both Fished and Undisturbed Control plots, with most of the difference attributable to increased biomass of *C. edule, S. plana* and *M. balthica* within Procedural Controls compared to the other two treatments (Table 3). Procedural Control plots were found to have a decreased biomass of *H. ulvae* and *H. diversicolor* in relation to the Undisturbed Control plots.

At Warton Sands, the only significant difference in taxon biomass was between Fished and Undisturbed Control plots; most of the difference between the Treatments was due to decreased *C. edule* and *M. balthica* biomass within Fished plots (Table 3). This effect was irrespective of the factor Time.
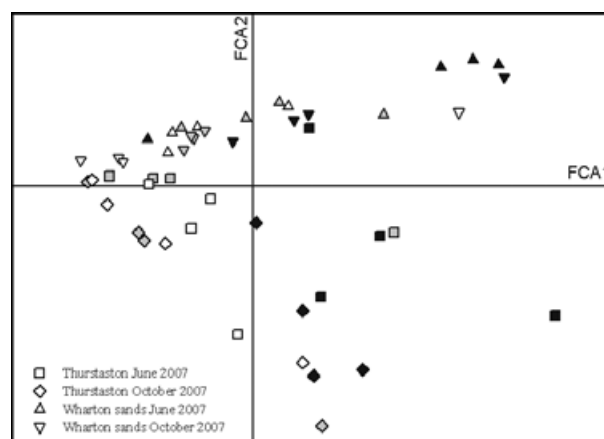
Biological traits analysis

The first two axes of the FCA explained over 78% of variance, with 45% across fuzzy correspondence axis 1 (FCA1) and 34% of variance across axis 2 (FCA2) (Table 4). Much of the variance on FCA1 was represented within traits relating to faunal dispersal (propagule dispersal and adult mobility/dispersal potential), longevity and feeding-related traits (Resource capture and Food type) (Table 4). Ordination scores were compared for FCA1 and revealed a significant separation of samples under the factor Treatment (Kruskal–Wallis, H = 16.82,

$P < 0.001$), with Fished plots tending towards a positive value and the Procedural and Undisturbed Control treatments tending towards negative values on FCA1 (Fig. 1). No significant differences were detected on FCA1 under the factors Shore or Time. Fished samples tended towards a reduction in non-motile fauna, with an increased proportion of highly motile fauna (adult mobility >100 m^2). Fished plots had an increased prevalence of relatively short-lived fauna (0.5–1 and 1–2 year modalities) and a reduced biomass of long-lived organisms (2–5 years). Scavengers were more prominent within Fished plots and these plots had reduced prevalence of active suspension feeders relative to the controls (Fig. 2). The removal of *C. edule* therefore explained much of the variability within the data (factor = Treatment within FCA1) and much of this variability was explained by traits relating to the dispersive abilities, longevities and feeding methods of fauna.

Much of the variance within FCA2 was explained by the living location and maximum size of taxa, the dispersive potential of adult organisms and the food resources exploited (Table 4). No separation of samples on FCA2 was found relating to the factors of Treatment or Time. Significant separation of samples was observed along FCA2 under the factor Shore (Kruskal–Wallis H = 32.62 $P < 0.001$), with samples taken at Warton Sands tending towards positive values and at Thurstaston tending towards negative values on FCA2 (Fig. 1). Assemblages at Warton Sands tended towards a prevalence of smaller (0–50 mm), more motile (>100 m^2·year^{-1}) taxa, dwelling at the sediment-water interface and assemblages at Thurstaston tended towards larger (50–100 mm), deeper-dwelling (>20 cm) and less-motile (<10 m^2·year^{-1}) fauna (Fig. 2).

Table 4. Relative inertia and correlation ratios of biological traits on the first two axes of the fuzzy correspondence analysis. Correlation ratios represent the proportion of variance explained by the different traits across each axis.

	axis 1	axis 2
relative inertia (%)	44.92	33.57
correlation ratio (%)		
propagule dispersal	17.07	6.05
adult dispersal	13.55	13.97
longevity	13.15	4.45
resource capture	12.75	2.18
food type	8.14	12.35
location	5.82	20.42
Max. size	2.56	18.04

Fig. 1. Ordination of the first two axes of the FCA for the two experimental assemblages. FCA1 explained ~45% of variance in the data and FCA2 explained ~34%. Sample treatment is indicated by symbol shading: solid black = Fished, grey = Procedural Control and clear = Undisturbed Control.
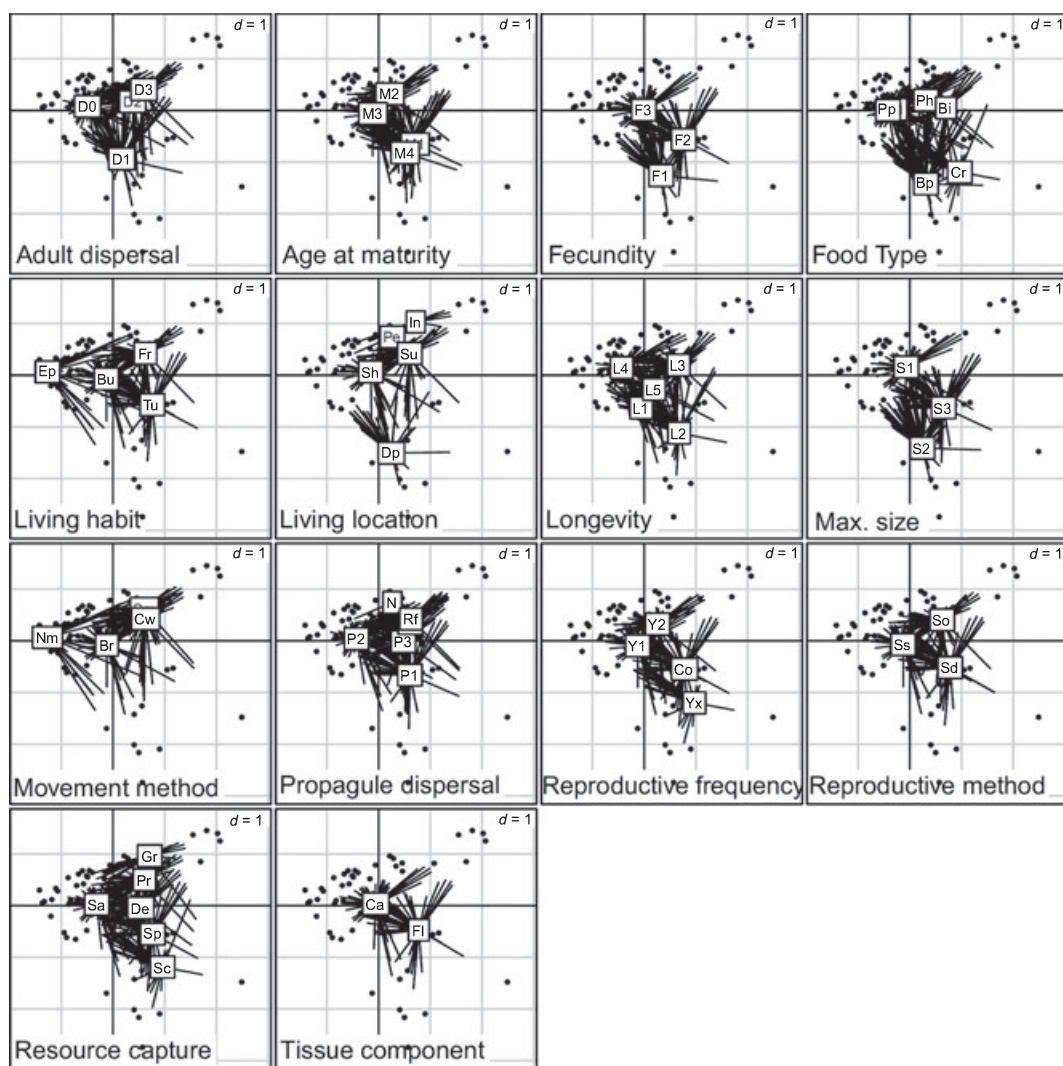
Fig. 2. Ordination of biomass-weighted biological trait categories from the first two axes of the FCA, allowing interpretation of the traits responsible for the differences between assemblages. Points represent the FCA coordinates for each experimental plot (as in Fig. 1) and label locations represent the centroid for each trait modality and lines link the plots to the modalities. Modality labels refer to Table 1.

When *C. edule* were excluded from the BTA, no significant changes to the distribution of biological traits was observed on either FCA1 or FCA2 (Kruskal–Wallis H = 0.53, P = 0.766 and H = 1.21, P = 0.547, respectively). This suggests that the differences in the prevalence of traits following the removal of large *C. edule* are directly caused by *C. edule*, rather than by a shift in the underlying community structure. Differences were observed on FCA1 between the two Shores (H = 33.57 P < 0.001) and there were significant differences between the two sampling Times on both Shores (Thurstaston: H = 10.08, P = 0.001; Warton Sands: H = 5.60, P = 0.018), with increased prevalence of deep-dwelling, relatively non-motile and larger trait characteristics between the June and October sampling occasions. No

significant differences were observed on FCA2 for any of the factors.

Sediment properties and chlorophyll *a* concentration

Sediment properties differed between the two study sites, with significantly higher concentrations of chlorophyll *a* and organic matter content at Thurstaston (Table 5, Fig. 3). Sediment granulometry (indicated by silt content (63 µm)) at Warton Sands was less coarse than that at Thurstaston and changed over time at both shores (Table 5, Fig. 3). No significant differences in chlorophyll *a* concentration or loss on ignition were observed with regards to experimental treatment. However, sediment granulometry did show significant change; sediments in

Table 5. Summary of the linear mixed model analyses for the sediment parameters quantified to investigate ecological functions. Significant values ($\alpha = 0.05$) indicated in bold.

source	df	chlorophyll *a*		LOI		silt content	
		F	P	F	P	F	P
shore	1	**127.42**	**< 0.001**	**15.47**	**< 0.001**	**52.21**	**< 0.001**
raked	1	0.18	0.673	0.04	0.841	0.16	0.690
cockles removed	1	0.30	0.589	1.75	0.198	**5.39**	**0.026**
time	4	1.01	0.379	1.21	0.315	1.94	0.111
shore × raked	1	0.24	0.630	0.05	0.834	0.72	0.403
shore × cockles removed	1	0.03	0.858	0.66	0.425	0.19	0.666
shore × time	4	0.42	0.797	1.78	0.145	**2.86**	**0.028**
raked × time	4	0.27	0.894	0.39	0.818	1.00	0.414
cockles removed × time	4	0.16	0.960	2.11	0.091	0.86	0.491
shore × raked × time	4	0.19	0.944	0.15	0.963	0.92	0.459
shore × cockles removed × time	4	0.05	0.994	1.15	0.342	2.43	0.054

Fished plots contained higher silt contents ($3.99 \pm 0.06\%$) than non-fished plots did ($3.70 \pm 0.10\%$).

To investigate the power of the experiment to detect significant changes, iterative analyses were carried out on the chlorophyll and organic matter data. Under the current design, a change in surface chlorophyll values of ~16% and a change in the organic matter content data of ~2.5% would be necessary to give statistically significant changes.

Discussion

This study has shown that the removal of *Cerastoderma edule* led to a marked increase in faunal diversity within manipulated plots, irrespective of the pre-impact diversity at the site. This suggests that other taxa are prevented from establishing themselves by the presence of *C. edule* even within species-poor assemblages. Following the removal of large *C. edule*, other taxa established within the system, either exploiting the resources liberated by the loss of *C. edule* or in response to the physical disturbance of the habitat. Such changes have been reported in a range of systems (*e.g.* Tuck *et al.* 1998; Sparks-McConkey & Watling 2001; de Juan *et al.* 2007).

The observed changes to macrofaunal communities were reflected in changes to the distribution of biological traits within the assemblages; however, this change was due to the removal of large *C. edule* themselves, rather than to changes in the distribution of underlying traits following removal. Removal of *C. edule* resulted in an increased prevalence of motile, short-lived taxa, with increased occurrences of scavengers, coupled with a relative reduction in non-mobile, longer-lived suspension-feeding fauna. This adds support to the potential of *C. edule* as key contributors to ecological functioning, in that their removal significantly altered the distribution and prevalence of functionally important biological traits. This occurred within both study assemblages and is consistent with other studies investigating the impacts of disturbance on benthic communities. At a smaller scale, Norkko & Bonsdorff (1996) for example found increased abundances of opportunistic taxa beneath experimentally placed algal mats. Larger-scale analyses of North Sea benthos also found a trend towards increased numbers of motile predators and scavengers with high levels of fishing disturbance (Bremner *et al.* 2003; Tillin *et al.* 2006).

Following the observed changes to the macrofaunal communities and distribution of biological traits within the two assemblages, it could be expected that changes to the delivery of the ecological functions would be evident. However, this was not the case with respect to the functions quantified here. *Cerastoderma edule* is an active suspension feeder and a significant portion of its diet can be re-suspended microphytobenthos (Sauriau & Kang 2000; Page & Lastra 2003). Removal of *C. edule*, a principal contributor to macrofaunal biomass, would therefore reduce grazing pressure and result in an increased biomass of primary producers. This was not observed in the current study, with chlorophyll *a* concentration (as a proxy for primary producer biomass) showing no significant relationship to experimental treatment on either study shore.

Organic matter content within the sediment was also studied as a proxy for the overall community metabolism within the assemblages (van Duyl *et al.* 1992). A shift towards a more motile fauna, for example, can influence the rate at which organic matter is incorporated into the sediment, influencing the resources available to the microbial community; this has subsequent impacts onto the provision of oxygen and the mineralization of organic materials within the sediment (Gilbert *et al.* 1995; Fenchel 1996). Assemblages with shorter life histories and more
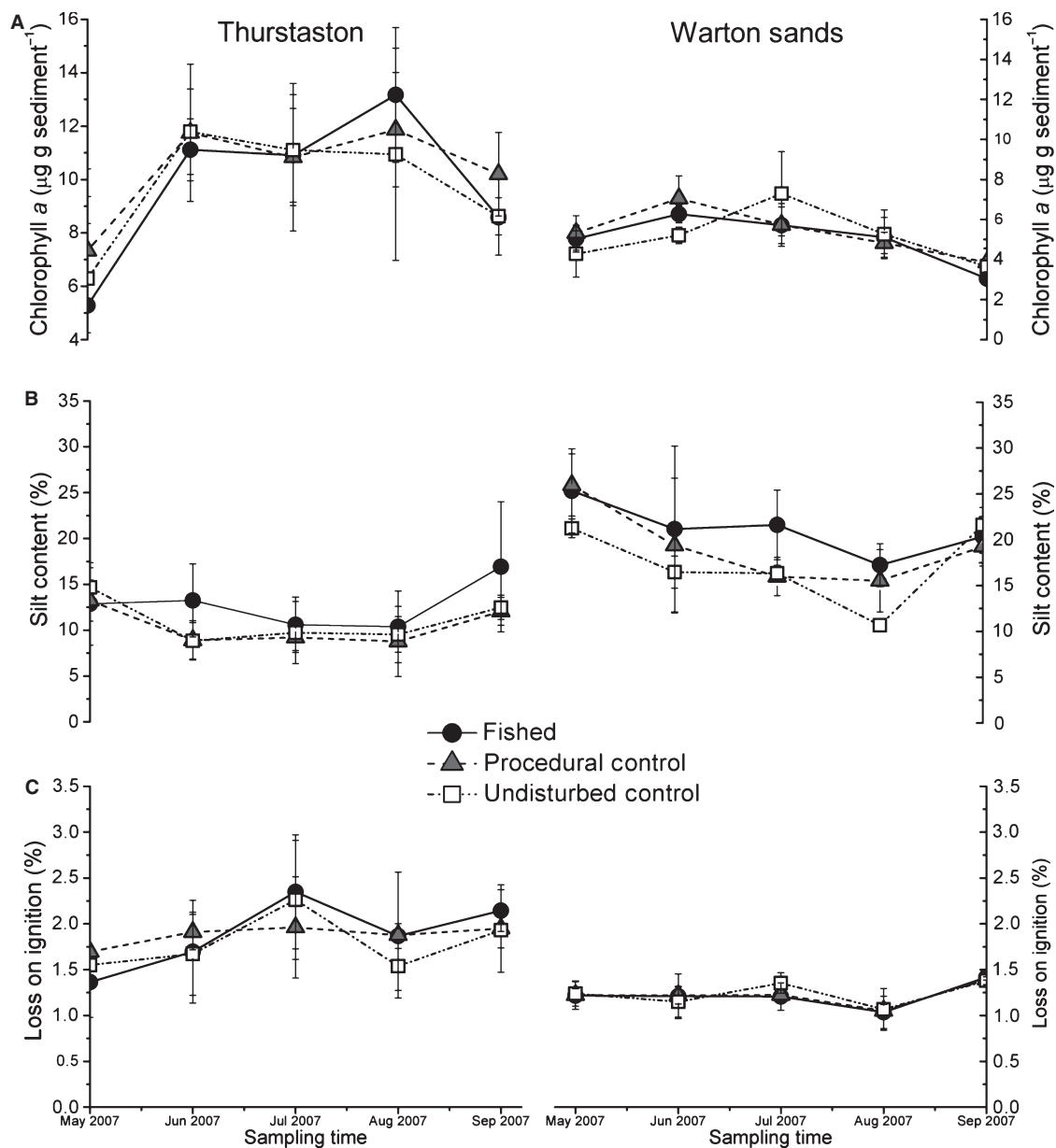
Fig. 3. Mean values (±SD) of the sediment parameters over 4 months following the experimental removal of *Cerastoderma edule* at two locations: (a) chlorophyll *a* concentration (μg·g per dry sediment), (b) silt content (% <63 μm) and (c) organic matter (as % loss on ignition).

opportunistic resource-gathering methods would also influence the trophic relationships throughout the assemblages and hence also the overall metabolism within the system. Therefore, the removal of *C. edule* was expected to result in a change in the availability of organic matter within the benthos. Again, no significant relationship with experimental treatment was observed at either study site.

The third ecological indicator considered was the granulometry of sediments within the assemblages. This is important to the functioning of systems, impacting upon sediment porosity and hence the depth of the redox layer

(Huettel & Rusch 2000) with implications for the settlement of larvae into the benthos (Pinedo *et al.* 2000; Duchêne 2004). *Cerastoderma edule* have been shown to loosen and destabilize sediments (Flach 1996), leaving finer grained particles more prone to resuspension, resulting in a coarsening of sediment granulometry (Ciutat *et al.* 2006, 2007). The findings of the current study concur with this: the removal of large *C. edule* resulted in a higher silt content within plots.

Within the current study, the removal of large *C. edule* had no significant impact on the measured ecological

functions relating to the biological productivity (as indexed by organic matter content and primary producer biomass) within the benthos. These responses, or lack of them, were common to both study shores and hence were independent of the initial biodiversity of the assemblages. Following the removal of large *C. edule*, both the species-rich assemblage at Thurstaston and the species-poor assemblage at Warton Sands showed a shift towards assemblages dominated by traits common to opportunist taxa. It appears, therefore, that ecological functions were conserved following the removal of large *C. edule*, regardless of the underlying macrofaunal diversity present at the sites. A number of possible explanations may account for this. First, the statistical power of the current study may be insufficient to detect subtle changes to the measured functions. Iterative power analyses revealed that, with the natural variability observed in this study, chlorophyll and organic matter contents would have to alter by ∼16% and 2.5%, respectively, to detect a significant change. Such changes are not unfeasible. Swanberg (1991), for example, observed that the presence of *C. edule* resulted in a change in microphytobenthic biomass in the region of 90%. Therefore, it appears that surface chlorophyll and organic matter content did not change significantly under the experimental treatments. Two alternative explanations may also account for this observation: (i) the removal of large *C. edule* and the subsequent changes to the macrofaunal communities (and therefore the distribution of biological traits) within the study systems have no effect on the investigated functions, or (ii) other processes are buffering or masking the response of the systems to the removal of *C. edule* and the subsequent shift in assemblage and trait structure.

Previous, largely laboratory-based, experimental investigations have shown that *C. edule* can influence ecological functions, for example enhancing primary productivity (Swanberg 1991); *C. edule* has also been shown to significantly alter near-bed hydrodynamics and sediment stability (Ciutat *et al.* 2007). Additionally, shifts in the distribution of biological traits within an assemblage have been shown to affect the delivery of ecological functions, for example changes to the prevalence of different methods of bioturbation affect the regeneration of nutrients and penetration of oxygen within sediments (Mermillod-Blondin *et al.* 2005; Waldbusser & Marinelli 2006; Gilbert *et al.* 2007). It is therefore likely that the removal of *C. edule* and the subsequent shift in biological traits would have some effect on the functions under investigation unless other factors were simultaneously changing and compensating for it.

The findings of the current study imply that the ecological functions measured are largely unaffected by significant reductions in the biomass of a potentially key contributor to ecological function. This is contrary to a number of other studies that have identified substantial changes to ecological functions following the removal of large taxa. Kanaya *et al.* (2005), for example, found that deposit-feeding bivalves had significant impacts on primary producer biomass, and Volkenborn (2005) found that the exclusion of the lugworm *Arenicola marina* from intertidal plots had significant effects on a number of ecosystem functions. Conversely, however, Bolam *et al.* (2002) found no effects of macrofaunal biomass or species richness on ecological functioning within a Scottish intertidal mudflat.

In the present study, BTA revealed significant changes to the prevalence of a number of traits within the macrofauna following the removal of large *C. edule*. However, there were no significant changes in the distribution of traits likely to impact upon the composition of the microbial community which primarily drives benthic primary production and microbial metabolism (Azam *et al.* 1993; Paerl 1997; Azam 1998). Additionally, Franklin & Mills (2006) showed that microbial communities display a high degree of functional redundancy, and even considerable changes to the microbial community composition are not reflected by changes to ecological functioning. Therefore, even if changes to the macrofaunal community did alter the microbial community, the substantial functional redundancy within these communities means that the measured functions were unlikely to be affected.

The conservation of functions observed in this investigation is likely, to some degree, to be related to the scale of the study. Subtle and/or small-scale changes in ecological processes are likely to be masked by the substantial natural variability over small scales and larger-scale processes occurring within the habitat (Kendrick *et al.* 1996). A larger-scale study would be more likely to reveal observable impacts (*e.g.* Watling *et al.* 2001; Falcão *et al.* 2003). However, as the aim of the current study was to assay the impacts of small-scale cockle hand-raking on ecological functioning, the spatial and temporal scales used reflected those used within the commercial fishery.

A limitation of the fuzzy-coding approach in BTA requires further consideration. This technique can only provide an indication, based on published and expert information, as to how a taxon may behave. It cannot provide any indicator of how an organism actually does act in a given situation. *Hediste diversicolor*, for example, is able to utilize a number of feeding strategies, depending upon resource availability (Fauchald & Jumars 1979) and *Pygospio elegans* can adopt a wide range of reproductive strategies (Gudmundsson 1985; Anger *et al.* 1986). Additionally, BTA does not account for ontogenetic differences within taxa. In this investigation, large *C. edule* were removed from assemblages and

the remaining *C. edule* were scored identically to large *C. edule* for the purposes of BTA. However, it is likely that younger (*i.e.* smaller) individuals behave differently and display a different range of functional traits than adult individuals, for example displaying different feeding preferences (Sauriau & Kang 2000). It is impossible to ascertain which strategy or strategies an organism is utilizing at any time and whether a change in conditions causes an organism to change its strategy, as the fuzzy coding technique includes all the strategies that can potentially be used by a species. It is necessary to address whether conspecifics under different disturbance regimes adopt the same behavioural/life-history strategies as this would potentially affect how the assemblage is delivering ecological functions. Studies involving BTA should therefore aim to incorporate some inference of the behavioural responses of taxa within affected assemblages.

The conservation of the measured functions does not necessarily mean that fished systems will continue to deliver other ecological functions. The availability of food resources within the system for example, is a key aspect of ecological functioning (Frid *et al.* 2008). As well as being the target of a fishery, *C. edule* are an important food source to demersal fish and shorebird species and are a major contributor to macrofaunal biomass. Large-scale removal of *C. edule* will therefore affect the food availability within and, by definition, the functioning of affected systems. Over longer timescales, this will potentially impact upon the regeneration and sustainability of *C. edule* stocks (Piersma *et al.* 2001; Kraan *et al.* 2007) and directly affect taxa relying on *C. edule* for food (Beukema & Dekker 2006). Therefore, the implications of small-scale, non-ubiquitous cockle harvesting depend upon the aspect of the system under concern. In terms of microbial and small-scale processes, there appears to be little impact; however, the removal of large *C. edule* from the system does impact upon the total macrofaunal biomass within the system and the potential availability of food resources available within the system.

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References

Aller R.C. (1983) The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. *Journal of Marine Research*, **41**, 299–322.

Anderson M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.

Anderson M.J. (2005) *PERMANOVA: A FORTRAN Computer Program for Permutational Multivariate Analysis of Va.riance*. Department of Statistics, University of Auckland, Auckland: 24.

Anger K., Anger V., Hagmeier E. (1986) Laboratory studies on larval growth of *Polydora ligni*, *Polydora ciliata*, and *Pygospio elegans* (Polychaeta, Spionidae). *Helgoland Marine Research*, **40**, 377–395.

Attrill M.J. (1998) *A Rehabilitated Estuarine Ecosystem: The Environment and Ecology of the Thames Estuary*. Kluwer Academic, London: 254 pp.

Azam F. (1998) Microbial control of oceanic carbon flux: the plot thickens. *Science*, **280**, 694–696.

Azam F., Smith D.C., Steward C.F., Hagstrom A. (1993) Bacteria–organic matter coupling and its significance for ocean carbon cycling. *Microbial Ecology*, **28**, 167–179.

Beukema J.J., Dekker R. (2006) Annual cockle *Cerastoderma edule* in the Wadden Sea usually fails to sustain both wintering birds and a commercial fishery. *Marine Ecology Progress Series*, **309**, 189–204.

Bolam S.G., Fernandes T.F., Huxham M. (2002) Diversity, biomass, and ecosystem processes in the marine benthos. *Ecological Monographs*, **72**, 599–615.

Bremner J., Frid C.L.J., Rogers S.I. (2003) Assessing marine ecosystem health: the long-term effects of fishing on functional biodiversity in North Sea benthos. *Aquatic Ecosystem Health and Management*, **6**, 131–137.

Bremner J.D., Paramor O.A.L., Frid C.L.J. (2006) *Developing a Methodology for Incorporating Ecological Structure and Functioning into Designation of Special Areas of Conservation (SAC) in the 0-12 Nautical Mile Zone*. English Nature, Peterborough: 158 pp.

Bulling M.T., Solan M., Dyson K.E., Hernandez-Milian G., Luque P., Pierce G.J., Raffaelli D., Paterson D.M., White P.C.L. (2008) Species effects on ecosystem processes are modified by faunal responses to habitat composition. *Oecologia*, **158**, 511–520.

Charvet S., Kosmala A., Statzner B. (1998) Biomonitoring through biological traits of benthic macroinvertebrates: perspectives for a general tool in stream management. *Archiv fur Hydrobiologie*, **142**, 415–432.

Charvet S., Statzner B., Usseglio-Polatera P., Dumont B. (2000) Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology*, **43**, 277–296.

Chevenet F., Doledec S., Chessel D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater biology*, **31**, 295–309.

Chiarucci A., Wilson J.B., Anderson B.J., De Dominicis V. (1999) Cover versus biomass as an estimate for abundance: does it make a difference to the conclusions? *Journal of Vegetation Science*, **10**, 35–42.

Christensen N.L., Bartuska A.M., Brown J.H., Carpenter S., D'Antonio C., Francis R., Franklin J.F., MacMahon J.A., Noss R.F., Parsons D.J., Peterson C.H., Turner M.G., Woodmansee R.G. (1996) The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecological Applications*, **6**, 665–691.

Ciutat A., Widdows J., Readman J.W. (2006) Influence of cockle *Cerastoderma edule* bioturbation and tidal-current cycles on resuspension of sediment and polycyclic aromatic hydrocarbons. *Marine Ecology Progress Series*, **328**, 51–64.

Ciutat A., Widdows J., Pope N.D. (2007) Effect of *Cerastoderma edule* density on near-bed hydrodynamics and stability of cohesive muddy sediments. *Journal of Experimental Marine Biology and Ecology*, **346**, 114–126.

Clarke K.R., Gorley R.N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.

Clarke K.R., Warwick R.M. (1994) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. CEFAS, Lowestoft: 144 pp.

CRAN (1999) The Comprehensive R Network. http://cran.r–project.org.

Dare P.J., Bell M.C., Walker P., Bannister R.C.A. (2004) *Historical and Current Status of Cockle and Mussel Stocks in the Wash*. CEFAS, Lowestoft: 85 pp.

Dray S., Dufour A.-B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.

Drinnan R.E. (1957) The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible cockle (*Cardium edule*). *Journal of Animal Ecology*, **26**, 441–469.

Duchêne J.-C. (2004) Early recognition of sediment during settlement of *Eupolymnia nebulosa* (Polychaeta: Terebellidae) larvae. *Marine Biology*, **145**, 79–85.

Duffy J.E., MacDonald K.S., Rhode J.M., Parker J.D. (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology*, **82**, 2417–2434.

van Duyl F.C., Kop A.J., Kok A., Sandee A.J.J. (1992) The impact of organic matter and macrozoobenthos on bacterial and oxygen variables in marine sediment boxcosms. *Netherlands Journal of Sea Research*, **29**, 343–355.

E.C. (2007) *Protection and Conservation of the Marine Environment: Framework for Community Action*. Marine Strategy Directive, Strasbourg: 42.

Ehrlich P.R., Ehrlich A. (1991) *Extinction: The Causes and Consequences of the Disappearance of Species*. Random House, New York.

Falcão M., Gaspar M.B., Santos M.N., Caetano M., Vale C. (2003) Short-term environmental impact of clam dredging in coastal waters (south of Portugal): chemical disturbance and subsequent recovery of seabed. *Marine Environmental Research*, **56**, 649–664.

Fauchald K., Jumars P.A. (1979) Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: an annual review*, **17**, 193–284.

Fenchel T. (1996) Worm burrows and oxic microniches in marine sediments. 2. Distribution patterns of ciliated protozoa. *Marine Biology*, **127**, 297–301.

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

Franklin R.B., Mills A.L. (2006) Structural and functional responses of a sewage microbial community to dilution-induced reductions in diversity. *Microbial Ecology*, **52**, 280–288.

Frid C., Rogers S., Nicholson M., Ellis J., Freeman S. (2000) *Using Biological Characteristics to Develop New Indices of Ecosystem Health*. ICES CM 2000/Mini: 02: ICES, Copenhagen: 23 pp.

Frid C.L.J., Paramor O.A.L., Brockington S., Bremner J. (2008) Incorporating ecological functioning into the designation and management of marine protected areas. *Hydrobiologia*, **606**, 69–79.

Gilbert F., Bonin P., Stora G. (1995) Effect of bioturbation on denitrification in a marine sediment from the West Mediterranean littoral. *Hydrobiologia*, **304**, 49–58.

Gilbert F., Hulth S., Grossi V., Poggiale J.-C., Desrosiers G., Rosenberg R., Gérino M., François-Carcaillet F., Michaud E., Stora G. (2007) Sediment reworking by marine benthic species from the Gullmar Fjord (Western Sweden): importance of faunal biovolume. *Journal of Experimental Marine Biology and Ecology*, **348**, 133–144.

Giles H., Pilditch C.A. (2006) Effects of mussel (*Perna canaliculus*) biodeposit decomposition on benthic respiration and nutrient fluxes. *Marine Biology*, **150**, 261–271.

Gudmundsson H. (1985) Life history patterns of polychaete species of the family Spionidae. *Journal of the Marine Biological Association of the United Kingdom*, **65**, 93–111.

Hempel C. (1957) Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden (Polychaeta sedentaria) der deutschen Küsten. *Helgoland Marine Research*, **6**, 100–135.

Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H., Lodge D.M., Loreau M., Naeem S., Schmid B., Setälä H., Symstad A.J., Vandermeer J., Wardle D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Huettel M., Rusch A. (2000) Transport and degradation of phytoplankton in permeable sediment. *Limnology and Oceanography*, **45**, 534–549.

Huston M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–460.

Ivell R. (1981) A quantitative study of a *Cerastoderma–Nephtys* community in the Limfjord, Denmark, with special reference to production of *Cerastoderma edule*. *Journal of Molluscan Studies*, **47**, 147–170.

de Juan S., Thrush S.F., Demestre M. (2007) Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Marine Ecology Progress Series*, **334**, 117–129.

Kaiser J. (2000) Rift over biodiversity divides ecologists. *Science*, **289**, 1282–1283.

Kamermans P. (1993) Food limitation in cockles (*Cerastoderma edule* (L.)): influences of location on tidal flat and of nearby presence of mussel beds. *Netherlands Journal of Sea Research*, **31**, 71–81.

Kamermans P. (1994) Similarity in food source and timing of feeding in deposit- and suspension-feeding bivalves. *Marine Ecology Progress Series*, **104**, 63–75.

Kanaya G., Nobata E., Toya T., Kikuchi E. (2005) Effects of different feeding habits of three bivalve species on sediment characteristics and benthic diatom abundance. *Marine Ecology Progress Series*, **299**, 67–78.

Kenchington E.L., Kenchington T.J., Henry L.-A., Fuller S., Gonzalez P. (2007) Multi-decadal changes in the megabenthos of the Bay of Fundy: the effects of fishing. *Journal of Sea Research*, **58**, 220–240.

Kendrick G.A., Jacoby C.A., Heinemann D. (1996) Benthic microalgae: comparisons of chlorophyll a in mesocosms and field sites. *Hydrobiologia*, **326-327**, 283–289.

Kraan C., Piersma T., Dekinga A., Koolhaas A., van der Meer J. (2007) Dredging for edible cockles (*Cerastoderma edule*) on intertidal flats: short-term consequences of fisher patch-choice decisions for target and non-target benthic fauna. *ICES Journal of Marine Science*, **64**, 1735–1742.

Lavorel S., Garnier E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Loreau M., Hector A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, **42**, 72–76.

Lorenzen C.J. (1967) Determination of chlorophyll and pheo-pigments: spectrophotometric equations. *Limnology and Oceanography*, **12**, 343–346.

MacIntyre H.L., Geider R.J., Miller D.C. (1996) Microphytobenthos: the ecological role of the 'Secret Garden' of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. *Estuaries and Coasts*, **19**, 186–201.

Manly B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London: 399 pp.

McGill B.J., Etienne R.S., Gray J.S., Alonso D., Anderson M.J., Benecha H.K., Dornelas M., Enquist B.J., Green J.L., He F., Hurlbert A.H., Magurran A.E., Marquet P.A., Maurer B.A., Ostling A., Soykan C.U., Ugland K.I., White E.P. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, **10**, 995–1015.

Mermillod-Blondin F., François-Carcaillet F., Rosenberg R. (2005) Biodiversity of benthic invertebrates and organic matter processing in shallow marine sediments: an experi-mental study. *Journal of Experimental Marine Biology and Ecology*, **315**, 187.

Michaud E., Desrosiers G., Mermillod-Blondin F., Sundby B., Stora G. (2006) The functional group approach to bioturbation: II. The effects of the Macoma balthica community on fluxes of nutrients and dissolved organic carbon across the sediment-water interface. *Journal of Experimental Marine Biology and Ecology*, **337**, 178–189.

Naeem S. (1998) Species redundancy and ecosystem reliability. *Conservation Biology*, **12**, 39–45.

Naeem S., Loreau M., Inchausti P. (2002) Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. In: Loreau M., Naeem S., Inchausti P. (Eds), *Biodiversity and Ecosystem Functioning. Synthesis and Perspectives*. Oxford University Press, New York: 3–11.

Norkko A., Bonsdorff E. (1996) Rapid zoobenthic community responses to accumulations of drifting algae. *Marine Ecology Progress Series*, **131**, 143–157.

Norling K., Rosenberg R., Hulth S., Grémare A., Bonsdorff E. (2007) Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series*, **332**, 11–23.

Olsgard F., Schaanning M.T., Widdicombe S., Kendall M.A., Austen M.C. (2008) Effects of bottom trawling on ecosystem functioning. *Journal of Experimental Marine Biology and Ecology*, **366**, 123–133.

Paerl H.W. (1997) Primary productivity and producers. In: Hurst C.J., Hudson G.R., McIrney M.J., Stetzenbach L.D., Walter M.V. (Eds), *Manual of Environmental Microbiology*. American Society of Microbiology Press, Washington, DC: 252–262.

Page H.M., Lastra M. (2003) Diet of intertidal bivalves in the Ría de Arosa (NW Spain): evidence from stable C and N isotope analysis. *Marine Biology*, **143**, 519–532.

Piersma T., Koolhaas A., Dekinga A., Beukema J.J., Dekker R., Essink K. (2001) Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *The Journal of Applied Ecology*, **38**, 976–990.

Pihl L. (1985) Food selection and consumption of mobile epibenthic fauna in shallow marine areas. *Marine Ecology Progress Series*, **22**, 169–179.

Pinedo S., Sardá R., Rey C., Bhaud M. (2000) Effect of sediment particle size on recruitment of *Owenia fusiformis* in the Bay of Blanes (NW Mediterranean Sea): an experimental approach to explain field distribution. *Marine Ecology Progress Series*, **203**, 205–213.

Prins T.C., Smaal A.C. (1994) The role of the blue mussel *Mytilus edulis* in the cycling of nutrients in the Oosterschelde estuary (The Netherlands). *Hydrobiologia*, **282–283**, 413–429.

Ragnarsson S.A., Raffaelli D. (1999) Effects of the mussel *Mytilus edulis* L. on the invertebrate fauna of sediments. *Journal of Experimental Marine Biology and Ecology*, **241**, 31–43.

Rowell J.G., Walters D.E. (1976) Analysing data with repeated observations on each experimental unit. *Journal of Agricultural Science, Cambridge*, **87**, 423–432.

Sauriau P.G., Kang C.K. (2000) Stable isotope evidence of benthic microalgae-based growth and secondary production in the suspension feeder *Cerastoderma edule* (Mollusca, Bivalvia) in the Marennes-Oléron Bay. *Hydrobiologia*, **440**, 317–329.

Sparks-McConkey P.J., Watling L. (2001) Effects on the ecological integrity of a soft-bottom habitat from a trawling disturbance. *Hydrobiologia*, **456**, 73–85.

Spilke J., Piepho H.P., Hu X. (2005) Analysis of unbalanced data by mixed linear models using the MIXED procedure of the SAS system. *Journal of Agronomy and Crop Science*, **191**, 47–54.

Sundbäck K., Petersen D.G., Dahllöf I., Larson F. (2007) Combined nutrient–toxicant effects on a shallow-water marine sediment system: sensitivity and resilience of ecosystem functions. *Marine Ecology Progress Series*, **330**, 13–30.

Swanberg I.L. (1991) The influence of the filter-feeding bivalve *Cerastoderma edule* L. on microphytobenthos: a laboratory study. *Journal of Experimental Marine Biology and Ecology*, **151**, 93–111.

Thrush S.F., Hewitt J.E., Gibbs M., Lundquist C., Norkko A. (2006) Functional role of large organisms in intertidal communities: community effects and ecosystem function. *Ecosystems*, **9**, 1029–1040.

Tillin H.M., Hiddink J.G., Jennings S., Kaiser M.J. (2006) Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, **318**, 31–45.

Tuck I.D., Hall S.J., Robertson M.R., Armstrong E., Basford D.J. (1998) Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Marine Ecology Progress Series*, **162**, 227–242.

Volkenborn N. (2005) Ecosystem engineering in intertidal sand by the lugworm *Arenicola marina*. Ph. D. thesis, University of Bremen.

Waldbusser G.G., Marinelli R.L. (2006) Macrofaunal modification of porewater advection: role of species function, species interaction and kinetics. *Marine Ecology Progress Series*, **311**, 217–231.

Walker B.H. (1992) Biodiversity and ecological redundancy. *Conservation Biology*, **6**, 18–23.

Wang Z., Goonewardene L.A. (2004) The use of MIXED models in the analysis of animal experiments with repeated measures data. *Canadian Journal of Animal Science*, **84**, 1–11.

Watling L., Findlay R.H., Mayer L.M., Schick D.F. (2001) Impact of a scallop drag on the sediment chemistry, microbiota, and faunal assemblages of a shallow subtidal marine benthic community. *Journal of Sea Research*, **46**, 309–324.

Wilson J.B. (1991) Methods for fitting dominance/diversity curves. *Journal of Vegetation Science*, **2**, 35–46.

Ziebis W., Huettel M., Forster S. (1996) Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. *Marine Ecology Progress Series*, **140**, 227–237.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Three-dimensional multidimensional scaling ordination of biomass-weighted community assemblages at two experimental assemblages. Sample treatment is indicated by symbol shading: solid black = Fished, grey = Procedural Control and white = Undisturbed Control. Stress = 0.06.

Table S1. Mean abundance (abund, number m^{-2}) and biomass (biom, $g \cdot m^{-1}$) of taxa observed at Thurstaston in experimentally Fished and Procedural Control and Control plots on two dates.

Table S2. Mean abundance (abund, number m^{-2}) and biomass (biom, $g \cdot m^{-1}$) of taxa observed at Warton Sands in experimentally Fished and Procedural Control and Control plots on two dates.

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