



Benthic disturbance affects intertidal food web dynamics: implications for investigations of ecosystem functioning

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ABSTRACT: Analysis of biological traits within assemblages is increasingly used as a proxy for ecological functioning. However, taxa often show plasticity in the expression of traits and can potentially change trait expression depending on local conditions. While many forms of disturbance will lead to changes in the species composition of the assemblage, small-scale disturbances can trigger alterations in the behaviour of taxa and hence the ecological roles they are delivering. Such changes would not be detected by biological traits analysis (BTA) alone. BTA therefore has the potential to misinform as to the contribution of assemblages to ecological processes. To assess the potential for taxa to change their expression of traits, the feeding modes of 8 taxa from 2 intertidal assemblages in north-west England, UK, were investigated using stable isotope analyses following experimental sediment disturbance and removal of cockles *Cerastoderma edule*. Two of the 8 taxa exhibited significant changes to their isotopic composition within disturbed plots. Short-term plastic changes to food web dynamics following changes in environmental conditions have implications for the suitability of BTA as a tool for investigating ecosystem function. Although BTA provides much insight into the ecological roles of taxa within systems and can be extremely effective at identifying changes associated with different assemblage compositions, it is conceivable that changes to ecological functioning may be undetected by BTA alone, and hence there is the need for this approach to be supported by experimental observation.

KEY WORDS: Trait plasticity · Ecosystem function · Anthropogenic impact · Biological traits analysis · BTA

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INTRODUCTION

Investigations into the role of biodiversity in supporting the functioning of ecosystems have traditionally been based largely on taxonomic approaches, investigating how species richness, evenness and other indices influence the delivery of ecological functions such as primary production and nutrient regeneration (Jonsson & Malmqvist 2000, Zak et al. 2003). Increasingly, these investigations are being supplemented by studies focused on the ecological

roles played by individual taxa; considering, for example, the influence of ecology, behaviour and physiology on ecological processes (e.g. Bremner et al. 2006, Baird et al. 2008). Such studies typically map the occurrences of biological traits or phenotypes within assemblages, grouping taxa by the strategies they have evolved in order to feed, reproduce, move etc. Different strategies affect ecological processes to different extents; for example, bioturbation modes have differing impacts on nutrient cycling within the benthos (Mermillod-Blondin et al. 2005). If the taxa

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within assemblages differ, then the biological traits supplied by the assemblages may also differ. Formal biological traits analysis (BTA) generally assumes that taxa belong to rigid functional groups, offering no potential for organisms to change the traits they are expressing. A fuzzy coding approach allows taxa to express more than one trait category (Chevenet et al. 1994), though this approach still only provides a probabilistic description of the potential range of traits that an organism may be expressing. That is, it is impossible to define the actual, or realised, range of traits being expressed under any given set of environmental or experimental conditions.

Within naturally variable habitats, such as the temperate estuarine intertidal, such uncertainty potentially limits descriptions of ecological function. In these habitats, factors such as salinity, temperature, food availability and the risk of predation often show substantial temporal fluctuations (e.g. Froneman 2001). As such, taxa often show some degree of plasticity in their expression of biological traits, for example, adopting differing reproductive (Gudmundsson 1985, Wilson 1985, Anger et al. 1986), or feeding (Rönn et al. 1988, Esselink & Zwarts 1989) strategies depending on localised conditions.

With the potential for variability in the expression of traits by taxa, it is difficult to discern the traits being expressed by a taxon at any given time and, therefore, the ecological roles being played. Consider, for example, a disturbance event that causes the individuals within an assemblage to alter their expression of some functionally important trait, but does not result in a change in the species composition of the assemblage. The ecological functioning of the system is altered; however, taxonomic based analyses and BTA would suggest that system functioning is unaltered. This has implications for the applicability of functional group and BTA, in that a change in how taxa are expressing ecologically important traits can mean that these approaches provide a misleading indication of the ecological roles that taxa within an assemblage are delivering.

We assessed the extent to which taxa within a benthic assemblage alter the traits they are expressing following disturbance. One trait that has the potential to show a high degree of plasticity is the 'feeding mode' adopted by organisms. Many taxa adopt different feeding preferences depending upon local conditions (Fauchald & Jumars 1979 and references therein). A substantial body of literature describes the feeding modes of marine benthos, and the degree to which taxa express different feeding strategies is known to have the potential to change under chang-

ing environmental conditions. The polychaete *Hediste diversicolor* O.F. Müller, for example, exhibits preferences for suspension or deposit feeding, as well as acting as an active predator, depending upon the availability of food resources (Rönn et al. 1988, Esselink & Zwarts 1989). The feeding methods of taxa are of substantial ecological interest, with trophic relationships playing a fundamental role in the transfer of energy and organic carbon within ecosystems (e.g. Frid et al. 2008).

To assess the potential for changes in the feeding behaviour of taxa and food web dynamics within temperate intertidal assemblages, stable isotope signatures were analysed in taxa taken from experimental plots that had been subjected to physical disturbance and experimental fishing. Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were investigated as proxies of different food resources and trophic level, respectively. These manipulations were part of an investigation into the effect of a fishery for the cockle *Cerastoderma edule* on a number of ecological functions, including biodiversity, functional diversity and primary producer biomass (Cesar & Frid 2009).

MATERIALS AND METHODS

Site description and faunal sampling

Experimental manipulations were carried out at 2 shores in north-west England, at Thurston within the Dee Estuary and Warton Sands within Morecambe Bay (Fig. 1). Macrofaunal assemblages at Thurston housed a greater species richness than those at Warton Sands (Cesar & Frid 2009). Field manipulations and faunal sampling were carried out between June and September 2007. At each shore, 3 experimental treatments were applied to 4 replicate 2×2 m plots arranged in a randomised block design:

(1) Cockles removed (fished): plots were hand-raked once (sediments disturbed to ~10 cm depth) using methods analogous to those used by commercial cockle *Cerastoderma edule* fishers. Raked sediments were passed through a 20 mm wide square mesh and retained cockles removed. All other fauna were returned to the plots.

(2) Procedural control (raked): as in fished treatment, but all organisms (including *C. edule*) were returned to the sediment.

(3) Control: undisturbed plots.

Four months following the initial manipulations, faunal assemblages within the experimental plots

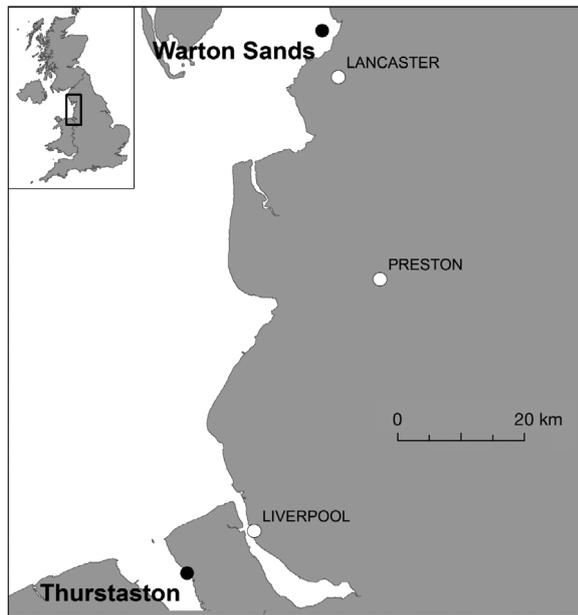


Fig. 1. Experimental systems in north-west England

were sampled and macrofauna fixed with 4% formaldehyde solution and stored in 70% ethanol solution. Those taxa present within at least 3 of the 4 replicate plots of each treatment were selected for stable isotope analysis. At Thurstaston, the bivalves *Cerastoderma edule* L., *Macoma balthica* (L.) and *Mya arenaria* (L.) and the annelids *Tubificoides benedii* (Udekem), *Eteone longa* (Fabricius) and *Hediste diversicolor* were analysed. *C. edule* and *M. balthica* from Warton Sands were analysed as well as the polychaetes *Pygospio elegans* (Claparède) and *Nephtys hombergii* (Savigny). These taxa display a range of feeding modes, have a wide range of potential diets (Table 1) and are likely to be important contributors to ecosystem functioning, representing 79.3% of macrofaunal biomass at Thurstaston and

93.8% of macrofaunal biomass at Warton Sands (Cesar & Frid 2009, C. P. Cesar unpubl. data).

Sample preparation and stable isotope analysis

Adults display different isotopic ratios than juveniles (Lorrain et al. 2002); therefore, analysed individuals of each species were of similar size. Preparation of tissue differed by species. Whole organisms of *Tubificoides benedii*, *Eteone longa* and *Pygospio elegans* were analysed, while the chitinous jaws were removed from *Hediste diversicolor* and *Nephtys hombergii*. The bivalves *Cerastoderma edule*, *Macoma balthica* and *Mya arenaria* were removed from their shells and muscular foot and gut tissue removed under a stereo microscope. Chitinous polychaete jaws and bivalve muscle tissue typically have longer turnover rates and hence take longer to assimilate changes to dietary isotope content than do more metabolically active viscera (Lorrain et al. 2002). Given the relatively short time period of the experimental manipulation (4 mo), these tissues were excluded from this study. Samples were rinsed in deionised water and dried at 60°C for 48 h. Dried samples were thoroughly homogenised to a powder using a mortar and pestle.

Dried powdered aliquots (ca. 1.25 mg) were packed into 8 × 5 mm tin capsules. Ratios of stable carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were ascertained using the elemental analyser of a continuous flow isotope ratio mass spectrometer (PDZ Europa 20/20, UC Davis Stable Isotope Facility). All isotope data were expressed in standard δ notation (measured as ‰), comparing the ratio of the heavy:light isotope to standard reference materials, Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen.

Table 1. Taxa selected for stable isotope analysis to determine the impacts of benthic disturbance on the realised feeding niche in benthic assemblages. The taxa chosen show a number of feeding modes with the potential to exploit a range of food resources

Taxon	Feeding mode	Primary food resource	Source
<i>Cerastoderma edule</i>	Suspension/ re-suspended benthos	Plankton, particulate matter, microphytobenthos	Kamermans (1993), (1994), Sauriau & Kang (2000)
<i>Macoma balthica</i>	Deposit/suspension	Plankton, microphytobenthos	de Goeij & Luttikhuisen (1998)
<i>Mya arenaria</i>	Suspension	Plankton	Nichols (1985)
<i>Tubificoides benedii</i>	Deposit	Particulate matter	Powell et al. (1983), Giere et al. (1984)
<i>Eteone longa</i>	Predator	Invertebrates	Fauchald & Jumars (1979), Michaelis & Vennemann (2005)
<i>Hediste diversicolor</i>	Opportunistic	Plankton, particulate matter, invertebrates	Rönn et al. (1988), Esselink & Zwarts (1989), Vedel (1998)
<i>Pygospio elegans</i>	Deposit/suspension	Plankton, particulate matter	Fauchald & Jumars (1979)
<i>Nephtys hombergii</i>	Predator	Invertebrates	Fauchald & Jumars (1979)

Fixing and preserving faunal samples in formalin and ethanol, respectively, may potentially affect the interpretation of the data, having some, though generally limited, effect on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Sarakinos et al. 2002). The principle aim of this investigation, however, was not to investigate food-web dynamics per se but to investigate whether disturbances have the potential to change feeding behaviour within a faunal assemblage. As all faunal tissue samples spent an equal amount of time in preservative fluids and the tissues of conspecifics were treated in the same manner, comparisons between treatments are valid.

Statistical analyses

For the 2 taxa present at both Thurstaston and Warton Sands (*Cerastoderma edule* and *Macoma balthica*), isotope ratios were compared with an ANOVA, with Experimental Treatment, Species and Shore as factors. The remaining 6 taxa were present only on a single shore (*Tubificoides benedii*, *Eteone longa*, *Hediste diversicolor* and *Mya arenaria* at Thurstaston and *Nephtys hombergii* and *Pygospio elegans* at Warton Sands) and were assessed using the factors Treatment and Species. Where significant differences were observed ($\alpha = 0.05$), post-hoc pairwise comparisons were made between factors using the Bonferroni pair-wise procedure.

RESULTS

Species differed in the ratios of both carbon ($F_{1,24} = 115.19$, $p < 0.001$ and $F_{5,36} = 68.73$, $p < 0.001$ for species found on both or single shores, respectively) and nitrogen ($F_{1,24} = 249.46$, $p < 0.001$ and $F_{5,36} = 217.26$, $p < 0.001$ for species found on both or single shores, respectively) within their tissues. This suggests that taxa were utilising a range of food sources (differing in their $\delta^{13}\text{C}$ values) and occupying multiple trophic levels (differing in their $\delta^{15}\text{N}$ values), with predatory taxa, i.e. *Eteone longa* and *Nephtys hombergii*, showing higher $\delta^{15}\text{N}$ values than primary consumers, in particular *Pygospio elegans*, *Macoma balthica* and *Mya arenaria* (Fig. 2).

The polychaete *Nephtys hombergii* showed significant differences in $\delta^{13}\text{C}$ values among treatments. Within raked plots, mean $\delta^{13}\text{C}$ values for *N. hombergii* were lower than those within control and fished plots ($F_{10,36} = 3.18$, $p = 0.005$) with a mean difference of 1.75‰ (Fig. 2). The cockle *Cerastoderma edule* had significantly lower $\delta^{13}\text{C}$ values in raked and fished plots compared to control plots; however, this was only apparent at Warton Sands ($F_{2,24} = 4.07$, $p = 0.03$), with a mean difference of 1.5‰ (Fig. 2).

Significant differences in $\delta^{15}\text{N}$ values were also observed. $\delta^{15}\text{N}$ values within the tissues of *Nephtys hombergii* were significantly lower within raked and fished plots compared to controls (mean differences of 2.15‰, $F_{10,36} = 6.57$, $p < 0.001$). $\delta^{15}\text{N}$ values for *Cerastoderma edule* were significantly higher in control plots than fished plots (mean difference of 0.8‰) ($F_{2,24} = 4.31$, $p = 0.025$).

Of the 8 species investigated, 2 showed significant differences in isotope ratios following experimental disturbance. Differences were observed in both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Cerastoderma edule* and *Nephtys hombergii*. Caution is, however, warranted concerning δ values $< 1\text{‰}$ (O'Leary et al. 1992), and so the observed differences in $\delta^{15}\text{N}$ values for *C. edule* (0.8‰) will not be considered further.

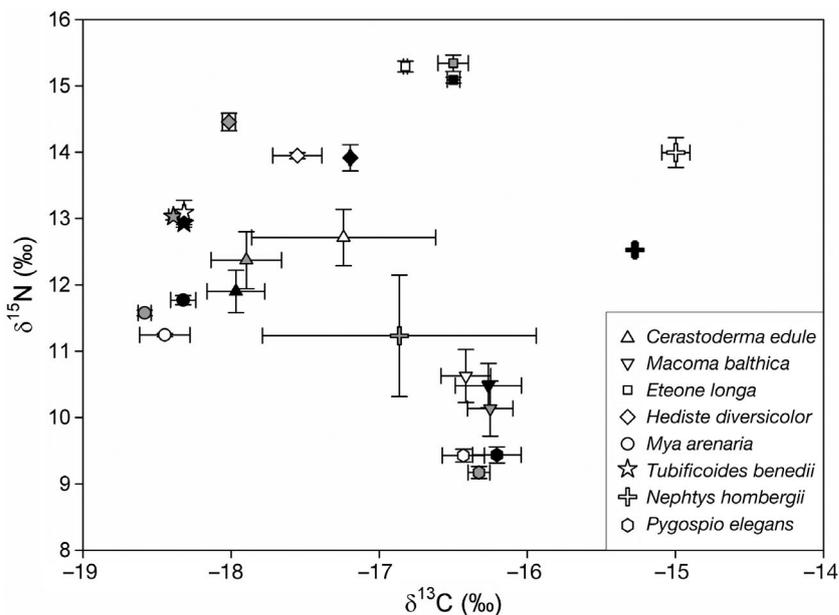


Fig. 2. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (\pm SE) for macrofaunal taxa investigated within assemblages at Thurstaston and Warton Sands, England, subjected to the experimental removal of *Cerastoderma edule* (black symbols), procedural controls (grey symbols) or undisturbed controls (white symbols)

DISCUSSION

This study shows that analyses based on functional groups or biological traits can potentially give a misleading representation of the ecological roles carried out by taxa within an assemblage. This has implications for the application of these measures in the assessment of ecosystem functioning. Within our experimental plots, 4 mo after physical disturbance, significant differences in the proportions of carbon and nitrogen stable isotopes between treatments suggested differences in the diet of those taxa that accounted for around 60% of the living biomass. The data does not allow us to ascertain the specific drivers behind the observed differences. It is possible, for example, that the differences were a result of changes in the feeding behaviour of the macrofauna. Alternatively, the differences may be a product of alterations in the food sources available to taxa, for example, changing the isotopic signature of materials present within the benthos as a result of mixing of aerobic and anaerobic sediments. Regardless of the driver of the observed differences, the results reveal differences in ecosystem functioning between treatments that would not be captured by BTA alone.

The data does, however, indicate differences in the role in the food web of individuals of the same taxa in different treatments over the 4 mo study period and allows inferences to be made regarding the food sources consumed in the various treatments.

Significant reductions in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the predatory polychaete *Nephtys hombergii* were evident within disturbed sediments. $\delta^{15}\text{N}$ values for *N. hombergii* were lower within experimentally raked and fished plots than in controls. This was consistent with increased consumption of food resources from a lower trophic level in disturbed plots. Trophic interactions within natural assemblages are, however, complex. The high degree of connectivity between taxa within food webs means that it is insufficient to assign taxa to rigid and discreet trophic levels (Polis & Strong 1996); instead, $\delta^{15}\text{N}$ values often lie along a continuum with only limited clustering of values into discrete trophic levels (e.g. Garcia et al. 2006). The data suggests, therefore, that *N. hombergii* within experimentally raked and fished plots were consuming a greater proportion of primary consumers (for example, algivorous molluscs and polychaetes) than those within control plots. *Nephtys* spp. feed on a range of prey, including primary consumers and carnivores (Fauchald & Jumars 1979), and hence such a difference in feeding preferences is not unfounded. $\delta^{13}\text{C}$ values were consistent with a shift in

the feeding behaviour of *N. hombergii*, indicating that *N. hombergii* were feeding closer to the base of the food chain within raked plots. This was not, however, recorded in experimentally fished plots. Future research should test the generality of this finding and explicitly identify the different food sources utilised under different environmental conditions.

Intertidal habitats generally display a degree of functional redundancy, with removal of some fauna having little impact on ecological processes (e.g. Murphy & Tolhurst 2009). Physical impacts on ecological function have substantial impacts on benthic ecosystems (e.g. Thrush & Dayton 2002). The suspension and surface deposit feeding cockle *Cerastoderma edule* showed significant differences in $\delta^{13}\text{C}$ values. This suggests that the food sources being consumed and assimilated differed between experimental treatments. Cockles feed on phytoplankton and microphytobenthos (MPB) (Sauriau & Kang 2000). A meta-analysis by Doi et al. (2010) showed that MPB have higher mean $\delta^{13}\text{C}$ values than phytoplankton. Significantly lower $\delta^{13}\text{C}$ values in experimentally disturbed plots suggest that *C. edule* within these plots had diets containing a higher proportion of phytoplankton than those in control plots. This is likely to be related to the physical disturbance of surface sediments in disturbed plots resulting in a reduction in the MPB community. Benthic algal communities tend to re-establish over a timescale of days to weeks (Tolhurst et al. 2008), and hence disturbance would necessitate a short-term shift in *C. edule* feeding towards a diet dominated by phytoplankton.

The current study shows that even relatively small-scale anthropogenic impacts can propagate into alterations in the flow of energy and material in intertidal estuarine assemblages. Anthropogenic impacts on feeding behaviour are also reported within microbial assemblages (e.g. Garstecki & Wickham 2001), subtidal systems (e.g. Ramsay et al. 1996), lake (Vander Zanden et al. 1999) and meadow habitats (Hawlena et al. 2011).

In the present study, 2 taxa, representing 61 and 71% of macrofaunal biomass within Thurston and Warton Sands, respectively (Cesar & Frid 2009, C. P. Cesar unpubl. data), showed significant changes in stable isotope ratios following experimental disturbance. As they represent a substantial proportion of the organic carbon within the study systems, they are likely to have an important influence on many ecosystem processes. The observed changes may affect the validity of the inferences that can be made using BTA to assess ecosystem function. That is, following physical disturbance, isotope ratios suggested that

Cerastoderma edule went from feeding largely from the benthos to a diet consisting of more material from the pelagos. Therefore, following disturbance, there was subsequent increase in benthic-pelagic coupling (albeit over the short term) and this has implications for the transfer and processing of energy and nutrients between the pelagos and the benthos (Loo & Rosenberg 1996). BTA would reveal no change in trait prevalence and hence no implications for benthic-pelagic coupling or other ecological processes.

Studies on the impacts of disturbance within estuarine and intertidal habitats often reveal no or minimal impacts of disturbance on biodiversity, and from this, it is concluded that ecological processes are also unaffected (e.g. Bolam et al. 2002, Cesar & Frid 2009, Jones et al. 2011). The current study has shown that taxa living within dynamic and changeable environments are able to respond to changes by altering their behaviour and their expression of functionally important biological traits. It is, therefore, potentially problematic to conclude that no significant change in species composition will also indicate no change in function. This has implications for the use of biological traits in the analysis of ecological function.

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