Effects of algal enrichment and salinity on sediment particle reworking activity and associated nutrient generation mediated by the intertidal polychaete *Hediste diversicolor*

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Abstract

The activities of marine benthic invertebrates link to many ecosystem properties and are often used as an alternative to the direct measurement of ecosystem functioning, such as nutrient cycling. However, links between bioturbation metrics and functional classifications of organisms based on bioturbation mode are rarely tested under a range of circumstances and are commonly assumed to be universally applicable. In this study we examine the effects of particle reworking by the polychaete *Hediste diversicolor* on the mediation of nutrient concentrations for a range of salinity and sediment algal enrichment levels. Sediment particle reworking increased in the presence of moderate algal enrichment but was reduced at higher levels of algal enrichment and was not affected by salinity. Nutrient concentrations in the water column, however, responded to the independent effects of salinity and algal enrichment. This study demonstrates that variation in particle reworking and mixing activity of *H. diversicolor* that relate to changes in environmental condition can be sufficient to alter species contributions to ecosystem functioning without altering the mechanistic basis of mediation. Our findings indicate that faunal processes that lead to changes in ecosystem functioning can be differentially expressed in a dynamic environment, and call for more careful consideration in the design and analysis of experiments that attempt to link the functional role of species to ecosystem properties.

Key Words: ecosystem function; bioturbation; functional groups; functional traits; intraspecific variation; *Hediste diversicolor*

Highlights

- Environmental context alters the expression of species functional traits
- Extent and importance of biological mediation are not constant
- Intraspecific variation complicates the universal application of functional traits

1. Introduction

Many ecosystem properties are influenced by the activities of biological communities, which can involve complex relationships between organisms and their environment (Loreau et al., 2001). Classifying organisms into functional groups or by functional traits are popular approaches that aim to describe and quantify how organisms contribute to ecosystem functioning and the functional diversity of communities (Bolam et al., 2014; Bremner et al., 2003; McClanahan, 2014; Muntadas et al., 2015). However, studies which make use of functional classification frameworks in benthic ecosystems rarely account for how species interact with the environment and/or with other species (e.g. Biles et al., 2003; Godbold and Solan, 2009; Langenheder et al., 2010). Yet, there is growing evidence that species interactions (Maire et al., 2010), life histories (Lewis and Galloway, 2008), phenology (Yang and Rudolf, 2010) and environmental conditions (Needham et al., 2011; Nogaro et al., 2007; Ouellette et al., 2004) affect both physiology and behaviour which, in turn, can have disproportionate effects on ecosystem processes and functions (Godbold et al., 2011). However, rather than directly incorporate this intraspecific variation, it is common to assume consistency in species contributions to ecosystem function when applying functional concepts at larger scales (Queirós et al., 2013).

Bioturbation – particle redistribution, burrow ventilation and solute bioirrigation - is widely acknowledged to be an important ecosystem process in determining sediment stability (Meadows et al., 1990; Rhoads and Young, 1970), regulating biogeochemical cycling (nutrient generation: Bertics et al., 2010; Emmerson et al., 2001; Marinelli and Williams, 2003) and linking benthic and pelagic ecosystems (Covich et al., 2004; Mermillod-Blondin et al., 2004). Consequently, bioturbation is often used as proxy of ecosystem function both for classifying species into functional groups (e.g. Pearson, 2001; Solan and Wigham, 2005); and as an indicator of environmental change (Birchenough et al., 2012; Thrush et al., 2006; Widdicombe and Austen, 1998). However, the functional consequences of organisms responding to their environment are not always fixed, particularly when conditions in space or time begin to challenge a species morphological, physiological, and behavioural adaptations to its surroundings (Godbold & Solan 2013). Indeed, some studies have shown that ecosystem function is largely determined by the traits of the dominant species (e.g. Mokany et al., 2008; Vile et al., 2006) and is not context dependent (McLaren and Turkington, 2010), whereas other studies have shown that species change their functional behaviour depending on factors such as climate (Spehn et al., 2002), habitat area (Wardle et al., 2008) or configuration (Godbold et al. 2011), and the presence of other organisms (e.g. invasive species: Peltzer et al., 2009). Whilst it is firmly established that bioturbation can be strongly influenced by the abiotic environment (e.g. flow: Loo et al., 1996, temperature: Ouellette et al., 2004, sediment characteristics and wave exposure: Sanders et al., 2007), links between altered bioturbation levels and changes to ecosystem function are often implied rather than tested directly (François et al., 2002; Mermillod-Blondin et al., 2002). In practice, this means that changes in net bioturbation activity are assumed to lead to corresponding changes in function that can be generalised across species that share similar bioturbation traits and applied across a full spectrum of habitat-specific settings. However, the question of the relative influence of dominant traits and environmental context is particularly important for marine benthic communities (Wohlgemuth et al. 2016; Wohlgemuth et al. 2017) where traits used to classify species into functional groups are seldom directly linked to the ecosystem functions mediated by those species (Murray et al., 2014; Paganelli et al., 2012).

In this study, we examine the influence of changing environmental conditions (salinity and nutrient enrichment) on the bioturbation activities of the polychaete, *Hediste diversicolor*, a dominant and functionally important species in intertidal mud flat ecosystems. Our aims were to determine the effects of changing salinity, a variable to which *H. diversicolor* is known to show tolerance (Fletcher, 1974; Fritzsche and von Oertzen, 1995), and sediment organic enrichment, to which *H. diversicolor* is known to be sensitive (Esselink et al., 1989). Specifically we tested (1) the effects of salinity and algal enrichment, alone and in combination, on sediment particle reworking activity and (2) whether observed changes in sediment particle distribution associated with the activities of *H. diversicolor* relate with changes nutrient concentrations (Δ[NH_4-N], Δ[NO_x-N], Δ[PO_4-P] and Δ[SiO_2-Si]). The consistency or otherwise of species-specific contributions to ecosystem functioning will provide an indication of how robust the assumed link between bioturbation and biogeochemical cycling may be in a changing environment.

2. Methods

2.1. Sediment, fauna and algae collection

Surficial sediment (< 5cm depth, mean particle size ~50 µm; volume percentile range: ~ 4 - 310 µm, Ieno et al. 2006), individuals of *H. diversicolor* and fronds of the green alga *Ulva intestinalis* (Chlorophyceae) were collected from the Ythan Estuary mudflats (57° 20.085’N, 02° 0.206’W) Scotland. Sediment was sieved (500 µm mesh) in a filtered (10 µm) seawater bath (salinity 24, 6 °C) to remove macrofauna. Sieving is preferential to other defaunation techniques, such as anoxia and freezing, as it has the smallest effect on the microbial community (Stocum and Plante, 2006). After a 24 h settlement period (to retain the fine sediment fraction, <63 µm), the supernatant seawater was siphoned off and the sediment was homogenised by stirring. *U. intestinalis* fronds were rinsed in seawater (UV sterilised, 10 µm filter, 6 °C), dried (environmental chamber, 60 °C and 0 % humidity, 2 h) and ground with a mortar and pestle into a powder (following Bulling et al., 2008). *U. intestinalis* is a dominant source of organic input into the Ythan estuary and in summer months can cover approximately 40 % of the intertidal area and reach wet-weight biomasses of 103 kg m^{-2} (Raffaelli, 2000).

2.2. Experimental Setup and design

We investigated the effects of changing levels of salinity, algal enrichment, and their interaction on particle reworking and associated levels of water column nutrients in the presence versus absence of *H. diversicolor*. Transparent Perspex aquaria (internal dimensions, LWH: 12 x 12 x 33 cm, wall thickness 0.5 cm) containing 1.6 L (~10 cm depth) of sediment were randomly allocated to one of three experimental runs (6 days duration; 1 day to allow burrow establishment + 5 days experimental period) maintained in an environmental chamber (VC 4100, Vötsch Industrietechnik, 12 ± 0.1°C) on a 12 h light:dark cycle. Seawater (2 L, UV sterilised, 10 µm filtered, salinity 30) was siphoned off after 24 h, to remove any nutrients released from the sediment during assembly, and replaced with seawater at one of four appropriate salinity treatment levels (2 L, UV sterilised, 10 µm filtered, salinity = 15, 20, 25 or 30). Salinity levels from the area of the estuary where individuals of

H. diversicolor were collected are known to range from near fresh water (salinity, < 5) at low tide to near seawater (salinity, ~33) at high tide (Gillibrand & Balls, 1998). Following Dyson et al. (2007) and others (Bulling et al. 2008, Godbold et al. 2011), powdered *U. intestinalis* was used to enrich the sediment surface layers at four treatment levels (0 g per aquarium; 1 g per aquarium, equivalent to 70 g m^{-2}; 2 g per aquarium, equivalent to 140 g m^{-2}; 3 g per aquarium equivalent to 210 g m^{-2}, all weights given are dry weight). The maximum level allowed a substantial enrichment of the sediment without generating hostile reduced conditions (Raffaelli 2000, Bulling et al. 2008, Godbold et al. 2011 and supported by daily visual observations). Following assembly, individuals of *H. diversicolor* (10 individuals $aquarium^{-1}$ or ~700 individuals m^{-2}; mean ± SD total biomass = 1.906 ± 0.441g $aquarium^{-1}$) were added. Wet weights were recorded and assessed statistically to ensure no significant differences in biomass between aquaria. All aquaria well continuously aerated throughout the experiment and there was no visible evidence (e.g. colour change, Lyle 1983) to suggest the development of an anoxic layer at the sediment-water interface. Our experimental design required a total of 160 aquaria (= 4 salinity x 4 algal enrichment x presence/absence of *H. diversicolor* x 5 replicates) which were randomised across three sequential experimental runs.

Sediment particle reworking was measured non-invasively using a camera system (fluorescent Sediment Profile Imaging; f-SPI, Solan et al., 2004) and fluorescent dyed particles (luminophores, <250μm; coloured craft sand, http://www.brianclegg.co.uk, 20 g per aquarium) housed in a UV illuminated imaging box (32 × 87 × 62 cm with Phillips blacklight, 8 W, Schiffers et al., 2011). The camera (Canon 400D, 10.14 megapixels, effective resolution = 65 × 65 μm per pixel) was set to a shutter speed of 0.25 s, aperture f = 5.6, and equivalent ISO speed 400 and was controlled using third party time-lapse software (GB Timelapse, v.2.0.20.0). Luminophores were evenly distributed (mean ± 1 SD thickness of luminophore layer = 2.26 ± 0.77 mm) across the sediment surface in each aquarium. Images taken at 0 d and 5 d were saved with colour JPEG (Joint Photographic Experts Group) compression. The distribution of luminophore particles within the sediment profile was quantified using a custom written semi-automated macro in the open source Java based software ImageJ (v. 1.44, http://rsbweb.nih.gov/ij/download.html).

Briefly, each image is opened and converted to a red-green-blue (RGB) stack. The user manually traces the sediment water interface using the segmented line tool before adjusting an appropriate threshold level that distinguishes the luminophores (excited under UV light, λ = 375-500 nm) from the sediment. The image was converted to a bitmapped image where the user-defined sediment water interface was flattened so that the sediment water interface aligns with the top pixel row. This allows a binary data matrix for each image to be generated with each cell in the matrix corresponding to a pixel in the image. From these data, and following Murray et al., (2013), the maximum, (Lum_{max}) mean (Lum_{mean}) and median (Lum_{med}) vertical distribution of luminophores were identified after 5 d. The rugosity of the lower extent of the mixed layer (Lum_{rug}) was also calculated as the sum of the Euclidian distances between the deepest luminophores in adjacent pixel columns across the width of the matrix. These descriptors provide an indication of the long-term downward transport of particles (Lum_{max}) and the typical extent of short-term mixing (Lum_{mean}, Lum_{med}), as well as the amount of surficial infaunal activity (Lum_{rug}) to enable time-dependent processes to be distinguished (Solan et al. 2016). Filtered water samples (20 ml, 0.45 µm cellulose acetate membrane filter) were collected and analysed using colorimetric analysis and standard protocols (FIAstar 5000 flow injection analyzer, FOSS Tecator, Höganäs, Sweden). The change (day 5 – day 0) in nutrient concentrations ($\Delta[NH_4\text{-}N]$, $\Delta[NO_x\text{-}N]$, $\Delta[PO_4\text{-}P]$ and $\Delta[SiO_2\text{-}Si]$) over 5 d was determined.

2.3. Statistical Analysis

Individual mixed effects models were developed for each of the response variables (sediment particle reworking: Lum_{max}, Lum_{mean}, Lum_{med}, Lum_{rug}; nutrient concentrations: $\Delta[NH_4\text{-}N]$, $\Delta[NO_x\text{-}N]$, $\Delta[PO_4\text{-}P]$ and $\Delta[SiO_2\text{-}Si]$) with nominal explanatory variables of either salinity and algal enrichment (ecosystem process models) or salinity, algal enrichment and presence/absence of *H.diversicolor* (ecosystem function models). Aquaria without *H. diversicolor* were excluded from analyses of sediment particle reworking as our focus was to compare the relative performance of *H. diversicolor*, rather than to establish present versus absence effects. In all models each explanatory variable was specified as a fixed effect and experimental run was specified as a random effect in order to account for any between run variation. During the initial model building phase of the analysis, where diagnostic residual plots indicated the presence of heteroscedasticity that was not accounted for by the fixed and random effects, variance covariates were included to model the variance structure, thus avoiding the need for data transformation (following Pinheiro and Bates 2000). Significance of the fixed effects were assessed by comparing nested models fitted using maximum likelihood (ML) followed by likelihood ratio tests. Following the inclusion of appropriate variance covariates (using a varIdent variance structure), diagnostic residual plots indicated homoscedacity. Parameters in the final models were estimated using restricted maximum likelihood (REML, following West et al., 2007). REML was used in preference to ML as it accounts for the loss of degrees of freedom in estimating the fixed effects, thus producing unbiased estimates of the covariance parameters (West et al., 2007). Details of the initial and minimum adequate models and residual plots for each response variable are included as supplementary material (Models S1-6, Figures S1-6). All mixed modelling analyses were carried out using the *nlme* package (v3.1-101; Pinheiro et al., 2011) and figures were produced using the *ggplot2* (v1.0.1, Wickham and Chang 2015) package, within the R statistical and programming environment (version 2.15.0, R Development Core Team 2015). We provide all data used in the analyses in the supplementary material (Table S1).

3. Results

3.1. Effects on infaunal mediated particle redistribution

We found no evidence that salinity, algal enrichment or their interaction affected either the maximum (Lum_{max}: $F_{9,62} = 1.047$, $p = 0.414$) or median mixed depth of sediment reworking (Lum_{med}:

$F_{9,62}$ = 1.208, $p = 0.307$) by *H. diversicolor*. However, the mean mixed depth of sediment mixing Lum_{mean}: $F_{3,74}$ = 6.086, $p < 0.001$, Model S1, Table 1, Figure 1a) and surficial reworking activity (Lum_{rug}: $F_{3,74}$ = 4.806, $p = 0.004$, Model S2, Table 1, Figure 1b) were affected by algal enrichment. Specifically, the mean (± 1 SD) Lum_{mean} ranged from 0.931 ± 0.345 cm in aquaria with 3 g algal enrichment to 1.464 ± 0.842 cm in aquaria with 1 g algal enrichment, whilst mean (± 1 SD) Lum_{rug} ranged from 74.111 ± 31.379 cm (mean ± 1 SD) in aquaria with 3 g algal enrichment to 137.348 ± 83.434 cm (mean ± 1 SD) in aquaria with 1 g algal enrichment. For both measures sediment reworking was highest at low levels of algal enrichment, but the difference between no algal enrichment and 1 g of algal enrichment was only significant for surficial activity (Lum_{mean}: coefficient = 0.129, t = 1.261, p = 0.211, Lum_{rug}: coefficient = 47. 784, t = 5.508, $p = 0.014$). Salinity had no effect on sediment particle reworking for any of the measured variables.

3.2. Effects on nutrient concentrations

Nutrient concentrations were affected by algal enrichment, salinity and *H. diversicolor* presence, although effects did not always interact (Table 1). We found that $\Delta[NH_4\text{-}N]$ was dependent on two separate interactions between salinity and *H. diversicolor* presence ($F_{3,135}$ = 3.166, $p = 0.027$; Model S3, Figure 2a) and between algal enrichment and *H. diversicolor* presence ($F_{3,135}$ = 14.366, p = <0.001, Model S3, Figure 2b). *H. diversicolor* presence tended to positively affect $\Delta[NH_4\text{-}N]$, whilst increasing algal enrichment tended to negatively affect $\Delta[NH_4\text{-}N]$ and the effects of salinity did not show a strong pattern (Figure 2a,b). Mean (± 1 SD) $\Delta[NH_4\text{-}N]$ was highest at a salinity of 20, irrespective of whether *H. diversicolor* was present (3.979 ± 0.959 mM) or absent (1.656 ± 0.800 mM), and lowest at a salinity of 30 (0.802 ± 0.530 mM, *H. diversicolor* absent) or 25 (2.567 ± 0.828 mM, *H. diversicolor* present). When *H. diversicolor* was absent, algal enrichment at 3 g aquarium^{-1} affected the mean $\Delta[NH_4\text{-}N]$ relative to no algal enrichment (0 g: mean ± 1 SD = 1.175 ± 0.385 3 g: mean ± 1 SD = 0.849 ± 0.555 mM; coefficient = 0.710, t = 2.860, $p = 0.005$), but not when compared to the other algal enrichment levels (2 g algal enrichment, coefficient = -0.311, t = -1.244, $p = 0.216$; 1 g algal enrichment, coefficient = -0.290, t = -1.170, *p* = 0.244). When *H. diversicolor* was present, Δ[NH_4-N] declined at all levels of algal enrichment relative to aquaria with no algal enrichment (0 g: mean ± 1 SD = 4.011 ± 1.068 mM, 1 g algal enrichment: coefficient = -0.503, t = -2.081, *p* = 0.039; 2 g algal enrichment: coefficient = -0.790, t = -3.281, *p* = 0.001; 3 g algal enrichment: coefficient = -1.561, t = -6.448, *p* = <0.001).

Δ[NO_X-N] was dependent on an interaction between algal enrichment and the presence of *H. diversicolor* ($F_{3,147}$ = 2.953, *p* = 0.035, Model S4, Figures 2c) and an additive effect of salinity ($F_{3,147}$ = 18.985, *p* <0.001, Model S4, Figures 2d). Mean (± SD) Δ[NO_X-N] was highest in aquaria without algal enrichment (0.210 ± 0.117 mM), but this effect was less pronounced when *H. diversicolor were* present (0.158 ± 0.099 mM) relative to when they were absent (0.262 ± 0.112 mM, coefficient = -0.107, t = -2.976, *p* = 0.003). Where the sediment was enriched with algae there was a decrease in Δ[NO_X-N] relative to no enrichment in all aquaria (1 g algal enrichment: coefficient = -0.323, t = -12.580, *p* <0.001; 2 g algal enrichment: coefficient = -0.341, t = -12.998, *p* <0.001; 3 g algal enrichment: coefficient = -0.355, t = -13.564, *p* <0.001). In addition, relative to a salinity of 30 (-0.028 ± 0.151 mM), there was a greater reduction in [NO_X-N] at salinities of 25 (coefficient = 0.036, t = 5.629, *p* <0.001) and 20 (coefficient = 0.019, t = 2.953, *p* = 0.004), but higher at a salinity of 15 (coefficient = 0.043, t = 6.829, *p* <0.001).

For Δ[PO_4-P], we found an interaction between salinity and algal enrichment ($F_{9,141}$ = 9.498, *p* <0.001, Model S5, Figure 3a) but the presence of *H. diversicolor* had no significant effect in comparison to aquaria without macrofauna. In aquaria with no algal enrichment there was no effect of salinity on Δ[PO_4-P]. In our highest salinity treatment (30), mean Δ[PO_4-P] increased when the sediment was enriched with algae (1 g algal enrichment, coefficient = 0.079, t = 5.746, *p* <0.001; 2 g algal enrichment, coefficient = 0.132, t = 19.337, *p* <0.001; 3 g algal enrichment, coefficient = 0.145, t = 14.266, *p* <0.001). This trend was less pronounced at other salinity levels (Figure 3a).

Δ[SiO_2-Si] was dependent on an interaction between the effects of salinity and *H. diversicolor* ($F_{3,147}$ = 19.144, *p* <0.001, Model S6, Figure 4a) and an additive effect of algal enrichment (Figure 4b). At all salinity levels there was a greater Δ[SiO_2-Si] in aquaria containing *H. diversicolor* than in aquaria where *H. diversicolor* was absent, a difference that was most pronounced at a salinity of 30 (mean ± SD; *H. diversicolor* present: 10.821 ± 1.925 mM; *H. diversicolor* absent, 5.369 ± 1.072 mM). The additive effect of algal enrichment was driven by change in Δ[SiO_2-Si] at the highest level of algal enrichment where there was a reduction in Δ[SiO_2-Si] (coefficient = -0.695, t = -2.674, *p* = 0.008; Figure 4b).

4. Discussion

These results demonstrate that changes in environmental conditions can generate context-specific effects on ecosystem functioning that do not necessarily correspond with the controls over ecosystem processes (Godbold et al., 2011). This discrepancy can occur because the way in which functional traits are expressed is not fixed at the species level, but is dependent on individuals' responses to immediate biotic and environmental conditions (Wohlgemuth et al. 2017). Previous syntheses have assumed that species, such as *H. diversicolor*, that show adaptation to highly variable environmental conditions will not exhibit significant changes in their functional contribution (Queirós et al., 2015). Our findings suggest that this view is naïve as it decouples the link between ecosystem process and function by assuming that the expression of a functionally important trait in terms of ecosystem functioning is a linear function of, or is otherwise directly linked to, trait occurrence. For instance, *H. diversicolor* is capable of switching feeding mode in response to environmental conditions (Riisgård and Larsen, 2010; Riisgård, 1994; Scaps, 2002). Such context-dependent changes in behaviour do not necessarily result in a detectable change in particle reworking (Gilbert et al. 1994) but may influence biogeochemical processes at both small (Bulling et al., 2010) and large scales (Godbold et al., 2011). However, whilst macrofaunal activity can dominate the mediation of nutrient cycling, it is important to note that microorganisms do respond to changes in salinity (Kirchman et al. 2005; Pavloudi et al., 2016), and that changes in seawater chemistry and microbial responses are also important determinants of major biogeochemical pathways (nitrogen: Herbert, 1999, Rysgaard et al., 1999; phosphate: Huang and Morris, 2005; Jordan et al., 2008; silicate: Leynaert et al., 2011). Indeed, changes in nutrient concentration across the salinity gradient applied here are consistent with expectations based on sediment nutrient release observations along natural salinity gradients (Boynton and Kemp, 1985; Hopkinson et al., 1999; Mortimer et al., 1999; Seitzinger et al., 1991). Specifically, higher rates of NH_4 occur at mid-salinity values where sediment oxygen demand is likely to be lower, whilst PO_4 tended to be lower when sediments were bioturbated and/or enriched. These changes may reflect alterations to microbial community composition and diversity (e.g. archaea, Xie et al. 2014; bacteria, Zheng et al. 2015) that are sufficient to alter nitrogen processing (Franklin et al. 2017), increasing the relative nitrification contribution coupled to denitrification and anammox pathways at low salinity, or DNRA coupled to anammox pathways at higher salinity (Hines et al. 2015).

Whilst it is tempting to speculate the most likely mechanistic explanation, we were unable to determine whether the effects we observed reflect the physiological responses of *H. diversicolor* to altered salinity levels (Hauton, 2016), a switch in emphasis of functionally important microbial mediated pathways, or microbial/invertebrate responses to other synergistic or antagonistic interactions between salinity and other environmental variables (Smyth & Elliott, 2016). Nonetheless, the significance of *H. diversicolor* can be readily distinguished from geochemical effects as the presence of this species resulted in marked changes in nutrient dynamics relative to when it was absent.

Our study documents a clear effect of algal enrichment on both sediment reworking and nutrient cycling. Levels of organic matter within estuaries fluctuate throughout the year, and can lead to changes in species activity and ecosystem functioning (Bulling et al., 2008; Dyson et al., 2007;

Godbold et al., 2011) that are well established (Pearson and Rosenberg, 1978, but see Grall and Chauvaud, 2002). *H. diversicolor* populations are known to enhance mineralisation and denitrification in estuarine sediments (Hansen and Kristensen, 1998), increasing oxygen consumption even at low organic enrichment levels (Fitch and Crowe, 2011). Following expectation, the present experiment identified a significant algal enrichment effect on particle reworking activity, but algal enrichment effects on nutrient cycling did not match the patterns observed between treatments for particle reworking activity. This lack of congruence partly reflects the interdependencies that exist between organic enrichment and salinity on nitrogen, phosphorus and silicate levels, but also reflects the typically low association between bioturbation metrics that are based on the redistribution of particles and ecosystem functioning (Murray et al., 2014; Solan et al., 2008). The latter has important methodological implications, not least the introduction of more comprehensive functional descriptors (Hale et al., 2014), and highlights a difficulty in incorporating and relating context dependent changes in species behaviour in dynamic environments (Teal et al., 2009). Changes in environmental conditions, for example, can regulate bioturbation rates or intensities, or introduce additional behaviours (e.g. bioirrigation, Ouellette et al., 2004), that disproportionately influence ecosystem functioning over short (Biles et al., 2003) or extended (Godbold et al., 2013) time scales. Equally, however, the mediating role of bioturbation may not always be the most influential driver of biogeochemical cycling as environmental conditions become more prominent (Godbold and Solan, 2009).

Despite the influential role of invertebrate bioturbation on the biogeochemistry of benthic environments (Covich et al., 2004), it is clear that bioturbation quantification alone may be insufficient to understand the dynamics of biogeochemical cycling. Whilst we recognise that there is some evidence to support the use of indices based on benthic community composition data (e.g. BTA, Bremner et al., 2006; BPc, Van Hoey et al., 2013), recent work has emphasised a need to interrogate presumed links between species and specific ecosystem properties (Grall and Chauvaud, 2002; Murray et al., 2014; Wrede et al. 2017). We propose that this should include examination of instances where a change in bioturbation is not observed alongside changes in context and/or seasonal timing. Such findings are rarely examined for functional changes, or reported in the literature (Solan et al., 2016; Wohlgemuth et al. 2017; Wrede et al. 2017). They are however, highly likely to offer valuable insights with respect to intraspecific trait variability within and between populations (Wohlgemuth et al. 2017) whilst offering an opportunity to identify traits that feature more or less prominently across multiple ecosystem functions. A concerted effort is needed to understand which, and when, physiological, behavioural, and morphological traits have a transformative effect on multiple ecosystem properties and to incorporate such information into ecosystem models that simulate the functional consequences of species responses to environmental change.

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Table and Figure Legends

Table 1: Summary of statistical models investigating the effects of *H. diversicolor*, salinity and algal enrichment on changes in nutrient concentrations.

Figure 1: The effects of algal enrichment on sediment particle redistribution by *H. diversicolor*. In (a), mean maximum luminophore depth (Lum_{mean}) and in (b) surficial sediment particle reworking (Lum_{rug}) associated with *H. diversicolor* for each algal enrichment level. Observations greater than 1.75 x inter-quartile range are represented by black dots.

Figure 2: Salinity, algal enrichment and macrofaunal effects on concentrations of NH_4-N and NO_X-N. Changes in water column concentrations of (a,b) NH_4-N and (c,d) NO_x-N in the (a,c) absence and (b,d) presence of *H. diversicolor*. Observations greater than 1.75 x inter-quartile range are represented by black dots.

Figure 3: Salinity and algal enrichment effects on concentrations of PO_4-P in aquaria without macrofauna (a) and aquaria containing individuals of *H. diversicolor* (b). Observations greater than 1.75 x inter-quartile range are represented by black dots. Shading of the boxes represents the

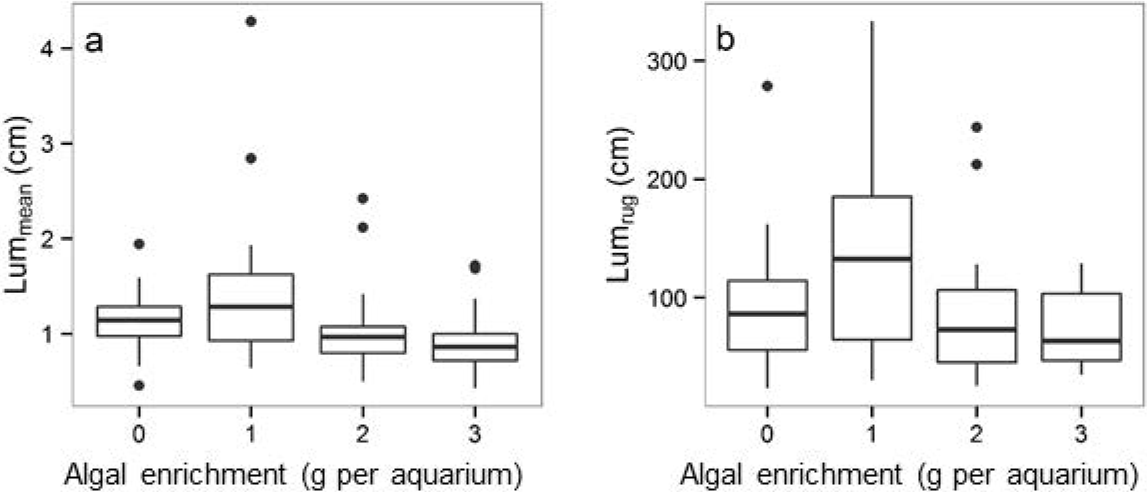
salinity level with white representing the lowest salinity (15) and the darkest grey representing the highest salinity (30).

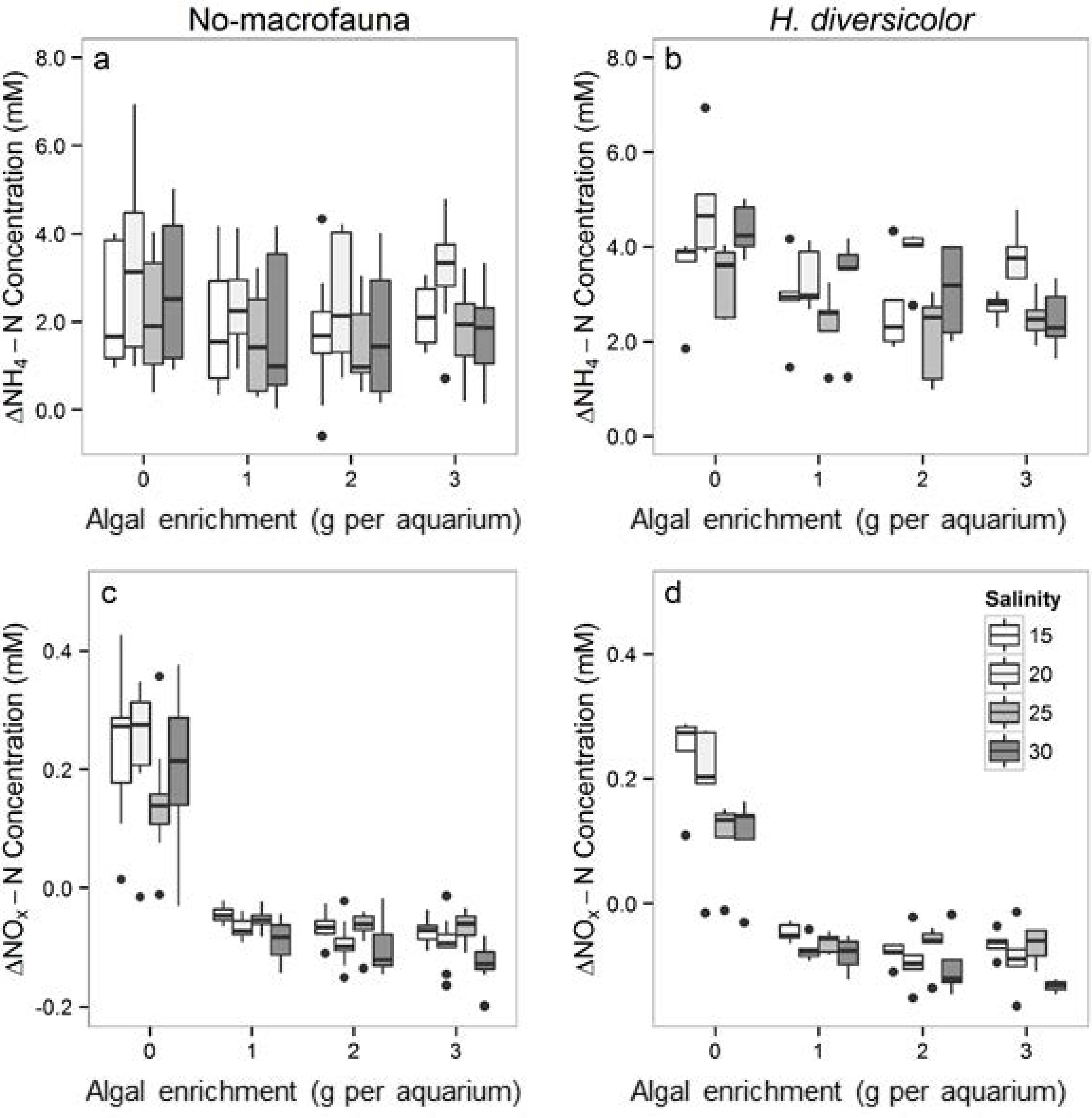
Figure 4: Salinity and algal enrichment effects on concentrations of SiO_2-Si in aquaria without macrofauna (a) and aquaria containing individuals of *H. diversicolor* (b). Observations greater than 1.75 x inter-quartile range are represented by black dots. Shading of the boxes represents the salinity level with white representing the lowest salinity (15) and the darkest grey representing the highest salinity (30).

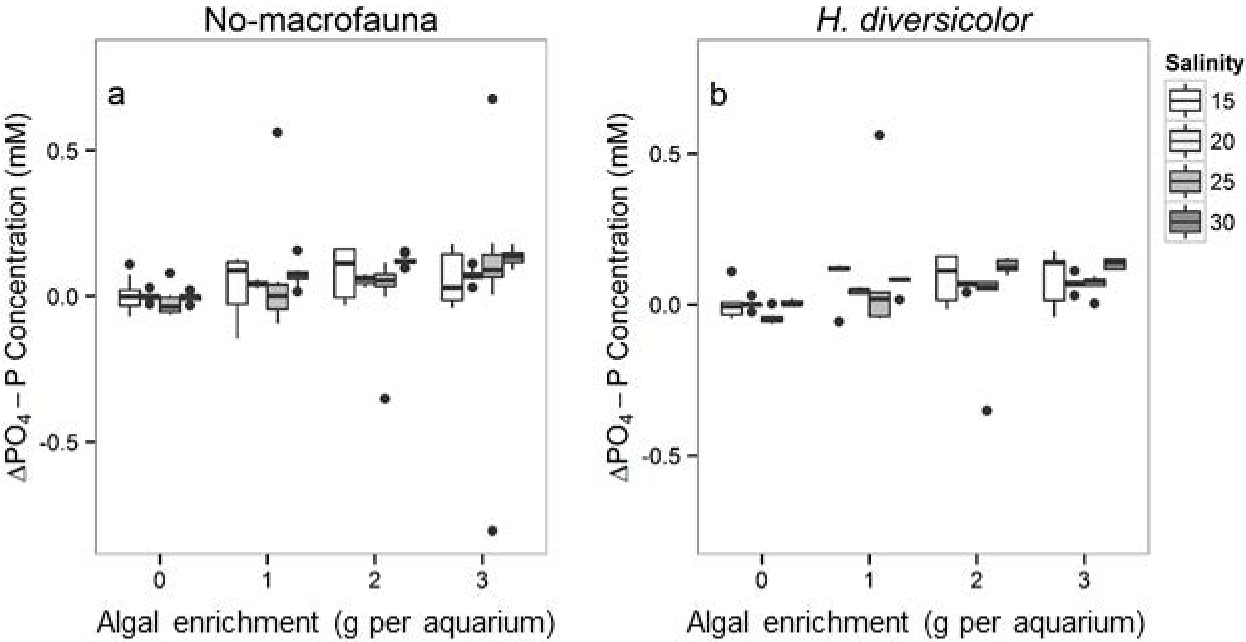
Tables

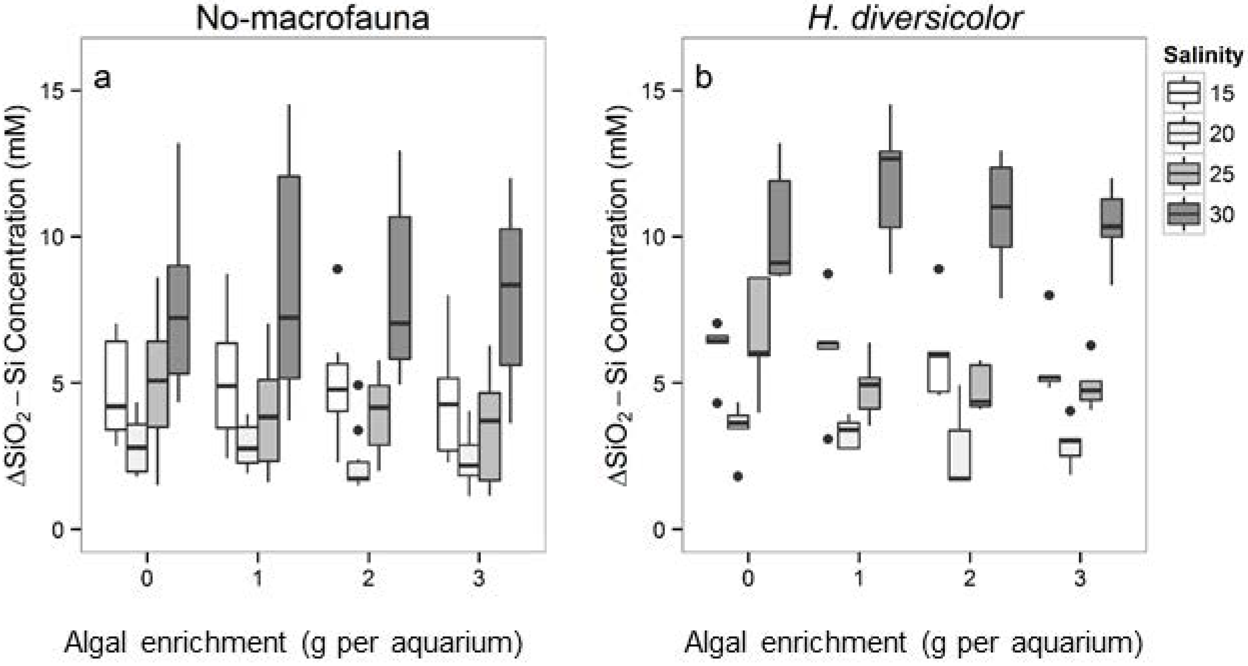
Table 1:

Response variable	Significant terms	Degrees of freedom	Likelihood ratio	*p value*
Lum_{mean}	Algal enrichment	3	12.116	0.007
Lum_{rug}	Algal enrichment	3	13.129	0.004
Δ[NH_4-N]	Salinity × *H. diversicolor*	3	10.824	0.013
	Algal enrichment × *H. diversicolor*	3	39.026	<0.001
Δ[NO_X-N]	Algal enrichment × *H. diversicolor*	3	8.579	0.035
	Salinity	6	55.214	<0.001
Δ[PO_4-P]	Salinity × Algal enrichment	9	42.143	<0.001
	H. diversicolor	1	5.421	0.020
Δ[SiO_2-Si]	Salinity × *H. diversicolor*	3	52.044	<0.001
	Algal enrichment	3	9.608	0.022


a
b
Lum$_{mean}$ (cm)
Lum$_{rug}$ (cm)
4
3
2
1
300
200
100
0
1
2
3
Algal enrichment (g per aquarium)
Algal enrichment (g per aquarium)


No-macrofauna
H. diversicolor
a
b
c
d
ΔNH4 – N Concentration (mM)
ΔNOx – N Concentration (mM)
8.0
6.0
4.0
2.0
0.0
0.4
0.2
0.0
-0.2
0
1
2
3
Algal enrichment (g per aquarium)
Salinity
15
20
25
30


No-macrofauna
H. diversicolor
a
b
ΔPO4 – P Concentration (mM)
0.5
0.0
-0.5
0
1
2
3
Algal enrichment (g per aquarium)
Salinity
15
20
25
30


No-macrofauna
H. diversicolor
a
b
ΔSiO2 – Si Concentration (mM)
0
5
10
15
0
1
2
3
Algal enrichment (g per aquarium)
Salinity
15
20
25
30