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Determining How Functionally Diverse Intertidal Sediment Species Preserve Mudflat Ecosystem Properties after Abrupt Biodiversity Loss.

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Abstract:

As a result of anthropogenic climate change, extreme climatic events have increased in frequency, severity and longevity. The consequences for community structure after a catastrophic event have been well studied. However, changes in ecosystem functioning that occur after such an event, including ecosystem recovery are still uncertain. Here we simulate a catastrophic event in an intertidal sedimentary habitat. We also simulate four recovery scenarios: 1. No Recovery, 2. Migration Recovery, and recovery by differential opportunistic colonisation by 3. the polychaete worm *Hediste diversicolor* and 4. the mud snail *Peringia ulvae*, two locally dominant infauna species. These are compared to a control scenario not subjected to the event. The simulated extreme event caused a shift in habitat state due to a reduction in mobile macrofauna abundance and an increase in microphytobenthos biomass. Migratory recovery of species and the simulated opportunistic expansion of a single species ameliorated this shift and, for some metrics, functional compensation for the loss of other species and the preservation of certain ecosystem functions was observed. The dominant species identity during post-event habitat recovery can have considerable effects on important ecosystem processes and functions with consequences that may result in functional regime shifts in a habitat and alter coastal stability.

INTRODUCTION

The estuarine and coastal environments are some of the most ecologically diverse in the world with high primary productivity and nutrient turnover (Nixon *et al.*, 1986). In the UK, macrofauna dominated cohesive fine grained shores may act as protection from storm surge events as bio-geomorphological features are a natural coastal protection (Spencer, Brooks, and Möller, 2014) preventing erosion and reducing the risk of flood (Möller *et al.*, 2014). Current and predicted environmental change, such as temperature change, ocean acidification, drought, flood, storm surges, and increased frequency of climatic extreme events in general, will inevitably have an effect on these important habitats (Covich *et al.*, 2004; Worm *et al.*, 2006). With the coastal habitat providing such important economic and ecosystem services it is necessary to be able to accurately predict the effects of increased frequency and strength of events on estuaries and upper intertidal areas at a local scale. These events can have a potential long-term indirect effect on coastal sedimentary environments through epi- and in-faunal community modification leading to changes in species abundance and trait expression (Hale *et al.*, 2017, Sciberras *et al.*, 2017). These changes will affect intertidal sediment properties as a result of environmental and anthropogenic factors such as climate change and sea level rise (Davis and Shaw, 2001; Parmesan *et al.*, 1999; Walther, 2002). A currently understudied variable affecting intertidal sedimentary habitats is the relative effects of macrofaunal species on the erodibility of sediments, which will determine the ability of these environments to perform essential ecosystem functions following external perturbation.

There has been an impetus to quantify the effects of biodiversity loss on mudflat ecological processes and functioning (Clare *et al.*, 2016; Solan *et al.*, 2008). An informative approach has been to use simple model communities in the laboratory to allow the determination of the mechanisms by which intertidal species and communities affect the important ecosystem functions of the mudflat (Raffaelli *et al.*, 2003; Solan *et al.*, 2008). Few studies thus far have used this experimental approach to look at biodiversity effects on ecosystem processes in the field and assess *in situ* properties such as sediment erodibility. Field experiments allow for the influence of real world factors on the experimental treatments, such as temporal and spatial resource heterogeneity and environmental fluctuation, increasing the relevance of the results to the natural world (Fridley, 2001). This study uses mesocosms placed on a representative intertidal sediment site to simulate a catastrophic community event resulting in the removal of the majority of the infaunal macro-community.

With respect to sediment stability, the macrofaunal organisms found on a mudflat can be broadly split into two categories: stabilisers and destabilisers (Black *et al.*, 2002; Widdows and Brinsley, 2002), although some species may fall into both categories over spatial or temporal scales. Stabilising organisms can influence the hydrodynamics in the benthic boundary layer by altering tidal currents and wave action by providing physical protection to the bed or can enhance cohesiveness and increase the critical erosion threshold through mucous (extra-cellular polymeric substancse; EPS) production (Malarkey *et al.*, 2015; Reise, 2002; Tolhurst, Gust, and Paterson, 2002). Destabilising organisms can act by increasing surface roughness, sediment water content, producing faecal pellets, and grazing or removing bio-stabilisers (Paterson and Black, 1999, Black *et al.*, 2002, Widdows and Brinsley, 2002).

In this study we use two common intertidal mudflat species, each with different modes of action and therefore different effects on sediment stability, to examine how changes in species abundance can affect sediment stability. The nereid polychaete ,*Hediste diversicolor* exists in permanent or semi-permanent burrows and exhibits a range of feeding methods including surface deposit feeder, omnivore, scavenger, sub-surface deposit feeder and passive suspension feeder (Fauchald and Jumars, 1979, Barnes, 1994). Burrows may act to stabilise sediment through mucous binding or destabilise if in close proximity. The mudsnail *Peringia ulvae* is a surface and sub-surface deposit feeder (Sauriau, Mouret, and Rince, 1989) feeding on the microphytobenthos (Gall and Blanchard, 1995), small organic particles, and bacteria (Green, 1968). *Peringia ulvae* grazing can increase bed roughness by leaving tracks on the sediment surface and creating small sub-surface burrows (Hale *et al.*, 2014, Hale *et al.*, 2015a). Feeding on microphytobenthos, by both species, can indirectly destabilise sediment through reduction in microphytobenthos and EPS. These two species were chosen as representative species for this experiment as they are abundant locally and on intertidal mudflats in the UK and Europe.

We expect that the presence, abundance and trait expression of an infaunal macrofaunal community has a significant effect on sediment erodibility, with species-specific activities resulting faunal-mediated changes to the stability of the mudflat through active and passive destabilisation activities and microphytobentos grazing. Here we test this hypothesis using a minimally disruptive defaunation method to remove the majority of the mudflat macrofaunal community to allow examination of the effect of a catastrophic loss of the community. Additionally, we simulate species recovery by replacing the fauna with a known biomass of *Hediste diversicolor* or *Peringia ulvae* to determine how potential post-disturbance community recovery through opportunistic expansion of single species abundance due to lack of competition for space can affect sediment properties.

METHODS

To examine the effects of abrupt biodiversity loss and post-loss differential opportunistic colonisation by dominant infauna an experiment was carried out on tidal mudflats (approximately 0.3m below mean high water, 3 x 28 m area) at Breydon Water, Great Yarmouth (Figure 1) between the 13th of April and the 5th of May 2012. Five scenarios (n = 4) were allocated to 20 mesocosms (PVC drainage pipe, 160 mm internal diameter, height 150 mm with six 45 mm diameter circles cut out equal distances around the top of the pipe such that the tip of the circles are 5 mm from the top and covered with 300 µm nylon mesh, Figure 2; Supplementary Figure S1). Following Godbold, Solan, and Killham (2009). Migration through the top of the mesocosms was prevented by a shaped 300 µm nylon mesh 'cap' held with cable ties. Migration from the bottom of the mesocosms was prevented by a sheet of 40 µm thick cellophane. To collect intact sediment cores for the experiment the mesocosms were pushed into the sediment to 100 mm depth, so the bottom of the circles were at the sediment surface, and the entire unit (mesocosm and 100 mm deep intact sediment) taken from the mudflat using the extractors hands to remove the core. Any excess sediment from deeper than 100 mm was removed and returned to the extraction hole. The depth was chosen as we are primarily interested in the interactions occurring at the sediment surface (where sediment erosion occurs) and enclosing sediment to 100 mm will capture the majority of the species of interest that are active at or near the sediment surface (Snelgrove, 1999). For the Control scenario (C) the collected core was returned to the mudflat immediately within the mesocosm, which was then withdrawn. No cryo-defaunaton or any treatment was applied to this mud core it is therefore assumed to contain the natural level of macrofaunal biomass found at the site in April (mean ± SE wet weight macrofaunal biomass = 21.83 ± 9.90 g per m^2, n = 5, dominated by *Hediste diversicolor*, *Peringia ulvae* and *Corophium volutator*; maximum richness 8 species; samples taken using experimental pipe units to 100 mm depth 3 days prior to experiment).

To simulate an abrupt event, cryodefaunation carried out on-site was used to reduce the abundance of sediment infauna (Hale *et al.*, 2015b). Briefly, this method involves retrieving an intact sediment core from the mudflat within the custom mesocosm, submerging it completely in liquid nitrogen to flash freeze the core, and returning it to the mudflat. The cryo-defaunation is not meant to simulate a realistic climatic or cooling event, rather it is a method for species removal analogous to any disruptive event and was chosen as the defaunation method as it is preferable to other disruptive methods of species removal, such as sediment sieving. It allows partial defaunation of sediment species with limited sediment disturbance, reducing experimental effects caused by disruption of other non-target sediment properties (Hale *et al.*, 2015b; Tolhurst *et al.*, 2012). This method therefore allows the measurement of functional changes caused by modification of species abundance and density to be examined without confounding effects caused by disruptive defaunation. Once partially defaunated, these cores were allocated to one of four recovery scenarios.

To examine the effect of natural recovery through potential re-recruitment through migration, cryodefaunated cores were returned to the mudflat without a mesocosm. This scenario is hereafter referred to as the ‘Migration Recovery scenario’ (M). This is the most likely scenario to occur following a natural defaunation event. To examine the effect of no faunal recovery, a scenario where species may not recover due to lack of recruitment or persistence of the defaunating event (e.g. a persistent virus), cryodefaunated cores were returned to the mudflat contained in a mesocosm with the mesh cap and cellophane bottom in place, hereafter referred to as the ‘No Recovery scenario’ (N). Two species recovery scenarios examined the effect of differential opportunistic colonisation and functional compensation by a single species of infauna. Individuals of the dominant species at the experimental site, *Hediste diversicolor* (scenario HD) or *Peringia ulvae* (scenario PU), were added to cryodefaunated mesocosms, simulating the opportunistic recovery of these species to the total original pre-defaunated biomass measured at the field site immediately preceding the experiment. The average individual species biomass was used to calculate the number of individuals needed to replace biomass lost due to cryo-defaunation. For the HD scenario this was 5 *H. diversicolor* individuals and for the PU scenario this was 10 *P. ulvae* individuals. These species recovery scenarios also had a mesh cap and bottom cellophane film to prevent immigration of further individuals and emigration of study species.

After 14 days, sediment stability, microphytobenthos biomass (Honeywill, Paterson, and Hagerthey, 2002) and ‘health’ (maximum quantum yield: photosystem II quatum efficiency and activity; Kromkamp, Barranguet, and Peene, 1998) and sediment particle size distribution were assessed to indicate ecosystem effects of functional changes in the species pool caused by sediment defaunation and species manipulation. This length of time was chosen to allow the post-event communities to resume natural (i.e. no longer disrupted, establishing behaviour, such as burrow re-creation) and allow recovery of meio- and microfauna (Kaiser, Broad, and Hall, 2001). This interval is not long enough to allow the assessment of long-term post-event sediment changes, but allows quantification of stability of the habitat in the short-term following an event when recovering or recovered communities may be most vulnerable to subsequent events. A cohesive strength meter (CSM) was used to obtain the sediment erosion threshold (Nm^{-2}), (Tolhurst *et al.*, 1999; Tolhurst *et al.*, 2000; Vardy *et al.*, 2007), and the suspension index (the gradient of the drop in transmission across the CSM chamber at the point the erosion threshold is passed where a larger value means a faster erosion rate*;* arbitrary units), a semi quantitative measure of the erosion rate (Tolhurst *et al.*, 1999). 1 Nm^{-2} is equal to 1 Pa and 1 $kgm^{-1}s^{-2}$ A pulse amplitude modulated fluorometer (PAM) was used to obtain microphytobenthos minimum fluorescence (F_o; arbitrary units), a proxy for microphytobenthos biomass (Eggert *et al.*, 2006; Honeywill, Paterson, and Hagerthey, 2002; Jesus *et al.*, 2006) and the maximum quantum yield (Y), a proxy for microphytobenthos health (Honeywill, Paterson, and Hagerthey, 2002; Jesus *et al.*, 2006; Kromkamp, Barranguet, and Peene, 1998; Maxwell and Johnson, 2000). To determine sediment particle size distribution at the sediment surface, which can affect sediment erodability (Grabowski, Droppo, and Wharton, 2011) and is altered by fine grain capture by microphytobenthos (Yallop *et al.*, 1994), sediment minicores of depth 1 cm were collected using a 2 cm diameter syringe for particle size analysis (Underwood, Paterson, and Parkes, 1995) and analysed using laser diffraction (Mastersizer 2000, Malvern, Worcestershire, UK, no pre-treatment of samples). Particle size data was processed using a geometric method of moments technique in GRADISTAT (Version 6; Blott and Pye, 2001) to obtain mean particle size (µm), particle D_{10} (µm), the 10 % cumulative percentile value, and mud (grains <63 µm) content (%). These measurements give an indication of how fine or coarse the sediment is, and therefore give additional information on how erodibility is indirectly affected by fauna through changes in grain size distribution. Sampling of replicates over the low tide period was distributed representatively between treatments and location to avoid short-term (hours) temporal (sediment drying, compaction and migration of microphytobenthos and macrofauna related changes to sediment properties over the low tide period; Perkins *et al.*, 2003, Tolhurst and Chapman, 2005) and spatial (shore height; Davidson, Crook, and Barnes, 2004; Paterson *et al.*, 2000)) confounding of the variables being measured and ensure the results observed were as a result of treatments applied and not natural physical factors (see Supplementary Tables 2 and 3).

As this experiment was carried out using *in situ* mesocosms it is potentially affected by a number of experimental artefacts, however the use of mesocosms to prevent colonisation of defaunated sediments and maintain the species dominance biomass was necessary. This method is still suitable to draw robust conclusions as to the effects of macrofauna species on their environment and potential recovery of this and other environments after simulation of defaunation following an extreme climatic event as we can compare the effects of defaunation with and without a mesocosm by examining the difference between the no recovery and migration scenarios without mesocosms and between those treatments that were held within a mesocosm (the no recovery scenario: N, and the faunal recovery scenarios: HD and PU).

To determine the effect of an abrupt species defaunation event and potential recovery by migration from surrounding species pools or opportunistic species expansion we developed regression models in R (Version 2.15.13; R Core Team, 2013) and each treatment was treated as a discrete unique identity (i.e. treatments were not combined and were factors rather than continuous variables; Solan *et al.*, 2008). The data had no outlying values (Cook's distance), but showed heterogeneity of variance, due to the comparison of treatments containing different species biomass due to the different recovery scenarios, so generalised least squares approach was taken (Pinheiro and Bates, 2000; West, Welch, and Galecki, 2006; Zuur, Ieno, and Smith, 2007; Zuur, Ieno, and Elphick, 2009a). These analyses were performed using the mixed modelling and nonlinear mixed effects package (nlme) in R (Pinheiro *et al.*, 2013). Restricted maximum likelihood estimation (REML) with examination of the model Akaike information criteria (AIC) scores and plots of fitted values against the residuals (Zuur *et al.*, 2009b) were used to determine the most appropriate model for each statistical test. Further description of the statistical analyses carried out is provided in Supplementary Information S4 and the model summaries are provided in Supplementary Model Summaries. In summary statements within the manuscript we give the mean ± standard error for measured responses where n = 4 and for generalised least squares statistical tests we provide the likelihood ratio (L-ratio) and the calculated p-value (p). For between treatment comparisons we provide the ratios between the response estimates and their standard errors (t), and the associated p-value under a t approximation (p).

RESULTS

Cryodefaunation of 100 mm deep cores was a successful method for partial defaunation, causing a mean (± standard error; n= 4; c.f. for all mean variables stated hereafter) reduction in the abundance of *Hediste* *diversicolor* from 13.0 ± 4.5 to 6.6 ± 1.6 individuals per experimental pipe unit, *Peringia ulvae* from 11.0 ± 2.8 to 5.8 ± 1.9 individuals per experimental pipe unit, and *Corophium volutator* from 30.8 ± 11.6 to 16.8 ± 3.1 individuals per experimental pipe unit, (comparison of C versus N scenario). Total species abundance per experimental pipe unit was reduced by 47 ± 0.01 %. It should also be noted that due to the necessity of using a mesocosm to enclose the sediments testing the N, HD and PU scenarios to ensure species are excluded or prevented from migrating out of the test area there is the possibility there is a procedural experimental effect affecting the sediments held within a mesocosm. We therefore try to avoid making definitive conclusions based upon significant differences observed between data collected from sediment not held within a mesocosm (C, M) and those held within (N, HD, PU), but we can still comment on the potential trends observed and how they may affect ecosystem services following a natural species defaunation event.

No temporal effect over the tidal cycle was observed for any of the measurements taken (Linear regression; Supplementary Table 2). No effect of shore height was observed on any of the response variables as well (Linear regression and gls; Supplementary Table 3).

In the control scenario cores (C, n = 4, Figure 3a) the erosion threshold at Breydon Water ranged from less than 0.1 to 0.5 Nm^{-2}. The scenarios showed significant differences in their erosion thresholds (Figure 3a; L-ratio = 12.4, d.f. = 4, p = 0.015, Supplementary Model S5) and all defaunated scenarios (M, N, HD, PU) had a larger mean erosion threshold, whether held within a mesocosm or not (0.8 ± 0.4, 1.4 ± 0.3, 0.5 ± 0.1, 0.7 ± 0.2 Nm^{-2} respectively). Comparing those scenarios without mesocosms: the Migration Recovery scenario sediment (M) did not have a significantly larger mean erosion threshold than the C scenario (0.3 ± 0.1 Nm^{-2}; n = 4; t = 1.2, p = 0.2425). For those sediments held within a mesocosm the N scenario had a significantly larger erosion threshold than the HD scenario (t = 2.6, p = 0.0176), but not the PU scenario (L-ratio = 1.7, p = 0.089),

The control and recovery scenarios showed significant differences in the sediment erosion rate (Figure 3b; L-ratio = 14.3, d.f. = 4, p = 0.006, Supplementary Model S6). The mean suspension index of the C scenario sediments was the largest (C; 15.57 ± 1.22), but only a significantly larger erosion rate than those of the No Recovery scenario (N; 6.5 ± 1.8; t = 3.7, p = 0.002) and scenario PU (7.9 ± 1.9; t = 3.0, p = 0.008), both held within a mesocosm. Comparing sediment held within the mesocosms, scenario N had a larger mean erosion rate than that of scenario HD (15.0 ± 0.9; t = 3.7, p = 0.002) and scenario HD had a faster mean erosion rate than scenario PU (t = 3.0, p = 0.009).

Experimental scenario had a significant effect on sediment microphytobenthos minimum fluorescence (F_o; Figure 3c; L-ratio = 22.9, d.f. = 10, p < 0.001, Supplementary Model S7). Scenario C had a mean minimum fluorescence (413.94 ± 29.19), lower than that of all the other defaunated scenarios (M, N, HD, PU), significantly lower than scenarios N (1222 ± 142.4, t = 4.8, p < 0.001), HD (813.9 ± 146.6, t = 2.3, p = 0.033) and PU (1115.6 ± 164.3, t = 3.7, p = 0.002), but not significantly lower than scenario M, the other sediment scenario not held within a mesocosm (627.1 ± 86.0, t = 2.0, p = 0.057). Those scenarios held within a mesocosm were not significantly different from each other. There was no significant effect of the no recovery, migration or two species replacement scenarios on the PAM measured maximum quantum yield (L-ratio = 1.8, d.f. = 10, p = 0.778, Supplementary Model S8, Supplementary Figure S9).

Minicore sediments were classified as either very fine sand or very coarse silt under the GRADISTAT program scale (Blott and Pye, 2001). With respect to sediment particle size distribution, species manipulation only resulted in significant changes in minicore sediment particle D_{10} (μm; Figure 3d; L-ratio =13.5, d.f. = 4, p = 0.009 Supplementary Model S10). Minicore sediment particle size D_{10} (μm) showed little variation, ranging from 7.4 to 11.9 μm across all the treatments. Differences in sediment particle size were confounded by mesocosm presence; scenario M (8.8 ± 0.5 μm) did not significantly differ from scenario C (9.0 ± 0.3 μm; t = -0.2, p = 0.830), however scenario N had a significantly larger mean particle D_{10} than scenario C (t = 3.6, p = 0.002) and scenario M (t = 2.6, p = 0.020). Scenario PU (10.4 ± 0.3 μm) also had a larger mean particle D_{10} than the scenario C (n = 4; t = 2.8, p = 0.013) and scenario M (t = 2.2, p = 0.042). There was no effect of the scenarios on the minicore sediment mean particle size (μm; L-ratio = 7.8, d.f. = 4, p = 0.100, Supplementary Model S11, Supplementary Figure S12) or minicore sediment mud content (%; L-ratio = 6.8, d.f. = 4, p = 0.145, Supplementary Model S13, Supplementary Figure 14).

DISCUSSION

We find that potential loss of macrofaunal species from intertidal sediments *in situ* after a catastrophic defaunation event increases the erosion threshold and decreases the suspension index of the sediment, at least in the short term recovery period. This indicates the development of a substrate that is more resistant to bulk erosion following defaunation. Tidal shear stress can vary considerably (0.7 Nm^{-2} maximum in the Humber, UK, Christie, Dyer, and Turner, 1999; 3.2 Nm^{-2} maximum in the Severn UK, Whitehouse and Mitchener, 1998) but are often very low (<0.7 Nm^{-2}). The no recovery scenario provides a mechanistic insight when compared to the other treatments containing faunal compositions (C, M, HD, PU). The changes observed are ecologically significant as sudden decrease in macrofaunal density without recovery could shift the system from a dynamic resuspendible sediment habitat, where erosion is likely to occur, to a stabilised microphytobenthos and algal dominated sediment, where it is not, or would only occur in more severe events. This indicates that the prevention of macrofaunal recovery keeps grazing pressure low. When macrofauna are allowed to recolonize the sediment (scenario M), grazing keeps the microphytobenthos biomass from increasing to that observed in the no recovery scenario (De Deckere, Tolhurst, and de Brouwer, 2001). Defaunated sediment (scenario N) is rapidly colonised by microalgae in the laboratory (Tolhurst *et al.*, 2008) and in the field (Davis and Lee, 1983) leading to sediment stabilisation through the production of extracellular polymeric substances (EPS) (Paterson, 1989; Paterson, 1997; Stolzenbach, 1989; Tolhurst, Gust, and Paterson, 2002). This indirect effect of macrofaunal species activity on sediment stability has also been observed by Andersen (2001), Austen, Andersen, and Edelvang, (1999), Daborn *et al.*, (1993), and Smith, Hughes, and Cox, (1996). However, this finding is in contrast to Murphy and Tolhurst (2009) who showed that the removal of some fauna *in situ*, predominantly Nereidae, the family to which *H. diversicolor* belongs, did not significantly affect many sediment properties that are related to sediment stability and microphytobenthos biomass (including chlorophyll concentration, sediment grain size, total organic matter, water content, and total carbohydrate concentration). In contrast, removing the microphytobenthos significantly altered the macrofauna structure and many sediment properties (Murphy and Tolhurst, 2009). This difference may be due to the multiple feeding modes exhibited by *H. diversicolor*, which in this case appears to be surface grazing on microphytobenthos in the absence of other (defaunated) prey species, an example of an indirect effect of a potential defaunation event on faunal behaviour and hence sediment properties and ecosystem functioning. The replacement of species biomass with *H. diversicolor,* resulting in sediment with a consequent smaller erosion threshold, larger suspension index and smaller microphytobenthos biomass, compared to the mesocosm held no recovery scenario, indicates that *Hediste* are having an effect on sediment stability through reduction in microphytobenthos grazing. However, *P. ulvae*, whose primary feeding mode is surface grazing, have a similar effect on the erosion threshold, but do not affect the suspension index or microphytobenthos biomass. Therefore a post-event opportunistic expansion of *P. ulvae* would not result in recovery of the sediment habitat properties in the same way as if there was a post-event expansion in *H. diversicolor* biomass.

We also find that after sediment defaunation there was a shift in particle size to a larger grain size in the defaunated cores. The defaunated cores had a larger mean particle size, an increased particle size D_{10}, and a slight decrease in sediment mud content. This indicates there are less small particles present in the sediment samples. This compares to the small but non-significant increase in the amount of mud after defaunation and a significant increase in grain size after removal of microphytobenthos found by Murphy and Tolhurst (2009). However due to the increase in grain size observed for all sediment treatments held within a mesocosm it is possible that this is a procedural effect in our case.

The activity of *H. diversicolor* may be able to compensate for the loss of the majority of the rest of the macrofauna due to its multiple feeding modes and surface bioturbation (De Deckere, Tolhurst, and de Brouwer, 2001; Widdows, Brinsley, and Pope, 2009). *P. ulvae*, whose activity is limited to the surface layers of sediment and does not exhibit multiple feeding modes, is not able to compensate for the loss of the other infaunal species. *P. ulvae* only affects the erosion threshold. This could be through both physical and biological processes as *P. ulvae* grazing increases surface roughness and direct sediment disruption (Blanchard *et al.*, 1997; Orvain, Le Hir, and Sauriau, 2003; Orvain *et al.*, 2004) while causing a reduction in microphytobenthos biomass (Andersen, 2001, Austen, Andersen, and Edelvang, 1999; Orvain *et al.*, 2004; Smith, Hughes, and Cox, 1996). The small mean erosion threshold observed is probably as a result of type 1 erosion, erosion of a loose surface layer (Amos *et al.*, 1992; Tolhurst *et al.*, 2000). The destabilising influence of *P. ulvae* does not extend as deep down into the sediment as it does with the gallery creating *H. diversicolor* (see Hale *et al.*, 2014 for images of the depth of bioturbation by *H. diversicolor* and *H.ulvae*), as *P. ulvae* are not found to burrow extensively if the sediment is too hard (Little and Nix, 1976), which may be the case in the defaunated sediment which has reduced abundance of destabilising macrofauna and is colonised and stabilised by microphytobenthos (Tolhurst *et al.*, 2008, Davis and Lee, 1983).

CONCLUSIONS

With current climate change we expect to see changes in faunal abundance, distribution and species dominance. This study shows that changes in species presence and abundance could have considerable effects on sedimentary ecosystem functions and processes. We show a sudden decrease in macrofaunal density without recovery could lead to a shift from a dynamic resuspendible sediment habitat to a stabilised microphytobenthos dominated sediment. Additionally, differential recovery through simulated opportunistic expansion of a single infaunal species has the potential to lead to functional changes in the sedimentary environment (Clare *et al.*, 2016). For some metrics, functional compensation for the loss of other species and the preservation of certain ecosystem functions was observed, however, recovery is species specific. These potential shifts in the sedimentary habitat will have consequences for the biogeochemistry of the complex sediment-water interface of intertidal sediments. Understanding these potential changes will enable us to better manage these habitats and mitigate the effects of climate change on intertidal mudflats.

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FIGURE CAPTIONS

Figure 1. The location of the experimental area (black dot; N52º 37.030’, E01º 41.390’) at Breydon Water, Great Yarmouth, UK. Ordnance survey map from OS OpenData.

Figure 2. The mesocosm setup. The sediment is enclosed within a PVC drainage pipe, 160 mm internal diameter, height 150 mm with six 45 mm diameter circlular holes covered in 300 µm nylon mesh at equal distances around the top of the pipe. The top is covered with 300 µm nylon mesh held with cable ties and the bottom is bounded by a sheet of 40 µm thick cellophane.

Figure 3. Functional measurements of the control (C) and the Migration Recovery sediment (M), both returned to the mudflat without a mesocosm, and the No Recovery (N), *Hediste diversicolor* replacement (HD) and *Peringia ulvae* replacement (PU) scenarios, all returned to the mudflat held within a mesocosm, of the a) sediment erosion threshold (Nm^{-2}), b) suspension index (arbitrary units), c) microphytobenthos minimum fluorescence (arbitrary units), and d) minicore particle D_{10} (µm). Error bars are standard error (n = 4).