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

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5 Rachel Hale^{1,*}, Richard O. Jacques², Trevor J. Tolhurst³

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7 ¹School of Ocean and Earth Science, National Oceanography Centre, Southampton, University of Southampton

8 Waterfront Campus, Southampton, SO14 3ZH, UK

9 *Corresponding author email: r.hale@soton.ac.uk

10

11 ²Department of Chemistry and Pharmacy, University of East Anglia, Norwich Research Park, Norwich, NR4

12 7TJ, UK

13

14 ³Department of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich, NR4 7TJ,

15 UK

16

17 Telephone: (UK) +447761 035 728

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21 Abstract:

22 As a result of anthropogenic climate change, extreme climatic events have increased in frequency,
23 severity and longevity. The consequences for community structure after a catastrophic event have been well
24 studied. However, changes in ecosystem functioning that occur after such an event, including ecosystem
25 recovery are still uncertain. Here we simulate a catastrophic event in an intertidal sedimentary habitat. We also
26 simulate four recovery scenarios: 1. No Recovery, 2. Migration Recovery, and recovery by differential
27 opportunistic colonisation by 3. the polychaete worm *Hediste diversicolor* and 4. the mud snail *Peringia ulvae*,
28 two locally dominant infauna species. These are compared to a control scenario not subjected to the event. The
29 simulated extreme event caused a shift in habitat state due to a reduction in mobile macrofauna abundance and
30 an increase in microphytobenthos biomass. Migratory recovery of species and the simulated opportunistic
31 expansion of a single species ameliorated this shift and, for some metrics, functional compensation for the loss
32 of other species and the preservation of certain ecosystem functions was observed. The dominant species
33 identity during post-event habitat recovery can have considerable effects on important ecosystem processes and
34 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.

65 With respect to sediment stability, the macrofaunal organisms found on a mudflat can be broadly split
66 into two categories: stabilisers and destabilisers (Black *et al.*, 2002; Widdows and Brinsley, 2002), although
67 some species may fall into both categories over spatial or temporal scales. Stabilising organisms can influence
68 the hydrodynamics in the benthic boundary layer by altering tidal currents and wave action by providing
69 physical protection to the bed or can enhance cohesiveness and increase the critical erosion threshold through
70 mucous (extra-cellular polymeric substance; EPS) production (Malarkey *et al.*, 2015; Reise, 2002; Tolhurst,
71 Gust, and Paterson, 2002). Destabilising organisms can act by increasing surface roughness, sediment water
72 content, producing faecal pellets, and grazing or removing bio-stabilisers (Paterson and Black, 1999, Black *et al.*,
73 2002, Widdows and Brinsley, 2002).

74

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

87

88 We expect that the presence, abundance and trait expression of an infaunal macrofaunal community has
89 a significant effect on sediment erodibility, with species-specific activities resulting faunal-mediated changes to
90 the stability of the mudflat through active and passive destabilisation activities and microphytobenthos grazing.
91 Here we test this hypothesis using a minimally disruptive defaunation method to remove the majority of the
92 mudflat macrofaunal community to allow examination of the effect of a catastrophic loss of the community.
93 Additionally, we simulate species recovery by replacing the fauna with a known biomass of *Hediste diversicolor*

94 or *Peringia ulvae* to determine how potential post-disturbance community recovery through opportunistic
95 expansion of single species abundance due to lack of competition for space can affect sediment properties.

96

97

METHODS

98

99 To examine the effects of abrupt biodiversity loss and post-loss differential opportunistic colonisation
100 by dominant infauna an experiment was carried out on tidal mudflats (approximately 0.3m below mean high
101 water, 3 x 28 m area) at Breydon Water, Great Yarmouth (Figure 1) between the 13th of April and the 5th of May
102 2012. Five scenarios (n = 4) were allocated to 20 mesocosms (PVC drainage pipe, 160 mm internal diameter,
103 height 150 mm with six 45 mm diameter circles cut out equal distances around the top of the pipe such that the
104 tip of the circles are 5 mm from the top and covered with 300 µm nylon mesh, Figure 2; Supplementary Figure
105 S1). Following Godbold, Solan, and Killham (2009). Migration through the top of the mesocosms was
106 prevented by a shaped 300 µm nylon mesh 'cap' held with cable ties. Migration from the bottom of the
107 mesocosms was prevented by a sheet of 40 µm thick cellophane. To collect intact sediment cores for the
108 experiment the mesocosms were pushed into the sediment to 100 mm depth, so the bottom of the circles were at
109 the sediment surface, and the entire unit (mesocosm and 100 mm deep intact sediment) taken from the mudflat
110 using the extractors hands to remove the core. Any excess sediment from deeper than 100 mm was removed and
111 returned to the extraction hole. The depth was chosen as we are primarily interested in the interactions occurring
112 at the sediment surface (where sediment erosion occurs) and enclosing sediment to 100 mm will capture the
113 majority of the species of interest that are active at or near the sediment surface (Snelgrove, 1999). For the
114 Control scenario (C) the collected core was returned to the mudflat immediately within the mesocosm, which
115 was then withdrawn. No cryo-defaunation or any treatment was applied to this mud core it is therefore assumed
116 to contain the natural level of macrofaunal biomass found at the site in April (mean ± SE wet weight
117 macrofaunal biomass = 21.83 ± 9.90 g per m², n = 5, dominated by *Hediste diversicolor*, *Peringia ulvae* and
118 *Corophium volutator*; maximum richness 8 species; samples taken using experimental pipe units to 100 mm
119 depth 3 days prior to experiment).

120

121 To simulate an abrupt event, cryodefaunation carried out on-site was used to reduce the abundance of
122 sediment infauna (Hale *et al.*, 2015b). Briefly, this method involves retrieving an intact sediment core from the
123 mudflat within the custom mesocosm, submerging it completely in liquid nitrogen to flash freeze the core, and

124 returning it to the mudflat. The cryo-defaunation is not meant to simulate a realistic climatic or cooling event,
125 rather it is a method for species removal analogous to any disruptive event and was chosen as the defaunation
126 method as it is preferable to other disruptive methods of species removal, such as sediment sieving. It allows
127 partial defaunation of sediment species with limited sediment disturbance, reducing experimental effects caused
128 by disruption of other non-target sediment properties (Hale *et al.*, 2015b; Tolhurst *et al.*, 2012). This method
129 therefore allows the measurement of functional changes caused by modification of species abundance and
130 density to be examined without confounding effects caused by disruptive defaunation. Once partially defaunated,
131 these cores were allocated to one of four recovery scenarios.

132
133 To examine the effect of natural recovery through potential re-recruitment through migration,
134 cryodefaunated cores were returned to the mudflat without a mesocosm. This scenario is hereafter referred to as
135 the 'Migration Recovery scenario' (M). This is the most likely scenario to occur following a natural defaunation
136 event. To examine the effect of no faunal recovery, a scenario where species may not recover due to lack of
137 recruitment or persistence of the defaunating event (e.g. a persistent virus), cryodefaunated cores were returned
138 to the mudflat contained in a mesocosm with the mesh cap and cellophane bottom in place, hereafter referred to
139 as the 'No Recovery scenario' (N). Two species recovery scenarios examined the effect of differential
140 opportunistic colonisation and functional compensation by a single species of infauna. Individuals of the
141 dominant species at the experimental site, *Hediste diversicolor* (scenario HD) or *Peringia ulvae* (scenario PU),
142 were added to cryodefaunated mesocosms, simulating the opportunistic recovery of these species to the total
143 original pre-defaunated biomass measured at the field site immediately preceding the experiment. The average
144 individual species biomass was used to calculate the number of individuals needed to replace biomass lost due
145 to cryo-defaunation. For the HD scenario this was 5 *H. diversicolor* individuals and for the PU scenario this was
146 10 *P. ulvae* individuals. These species recovery scenarios also had a mesh cap and bottom cellophane film to
147 prevent immigration of further individuals and emigration of study species.

148
149 After 14 days, sediment stability, microphytobenthos biomass (Honeywill, Paterson, and Hagerthey,
150 2002) and 'health' (maximum quantum yield: photosystem II quantum efficiency and activity; Kromkamp,
151 Barranguet, and Peene, 1998) and sediment particle size distribution were assessed to indicate ecosystem effects
152 of functional changes in the species pool caused by sediment defaunation and species manipulation. This length
153 of time was chosen to allow the post-event communities to resume natural (i.e. no longer disrupted, establishing

154 behaviour, such as burrow re-creation) and allow recovery of meio- and microfauna (Kaiser, Broad, and Hall,
155 2001). This interval is not long enough to allow the assessment of long-term post-event sediment changes, but
156 allows quantification of stability of the habitat in the short-term following an event when recovering or
157 recovered communities may be most vulnerable to subsequent events. A cohesive strength meter (CSM) was
158 used to obtain the sediment erosion threshold (Nm^{-2}), (Tolhurst *et al.*, 1999; Tolhurst *et al.*, 2000; Vardy *et al.*,
159 2007), and the suspension index (the gradient of the drop in transmission across the CSM chamber at the point
160 the erosion threshold is passed where a larger value means a faster erosion rate; arbitrary units), a semi
161 quantitative measure of the erosion rate (Tolhurst *et al.*, 1999). 1 Nm^{-2} is equal to 1 Pa and $1 \text{ kgm}^{-1}\text{s}^{-2}$. A pulse
162 amplitude modulated fluorometer (PAM) was used to obtain microphytobenthos minimum fluorescence (F_0 ;
163 arbitrary units), a proxy for microphytobenthos biomass (Eggert *et al.*, 2006; Honeywill, Paterson, and
164 Hagerthey, 2002; Jesus *et al.*, 2006) and the maximum quantum yield (Y), a proxy for microphytobenthos health
165 (Honeywill, Paterson, and Hagerthey, 2002; Jesus *et al.*, 2006; Kromkamp, Barranguet, and Peene, 1998;
166 Maxwell and Johnson, 2000). To determine sediment particle size distribution at the sediment surface, which
167 can affect sediment erodability (Grabowski, Droppo, and Wharton, 2011) and is altered by fine grain capture by
168 microphytobenthos (Yallop *et al.*, 1994), sediment minicores of depth 1 cm were collected using a 2 cm
169 diameter syringe for particle size analysis (Underwood, Paterson, and Parkes, 1995) and analysed using laser
170 diffraction (Mastersizer 2000, Malvern, Worcestershire, UK, no pre-treatment of samples). Particle size data
171 was processed using a geometric method of moments technique in GRADISTAT (Version 6; Blott and Pye,
172 2001) to obtain mean particle size (μm), particle D_{10} (μm), the 10 % cumulative percentile value, and mud
173 (grains $<63 \mu\text{m}$) content (%). These measurements give an indication of how fine or coarse the sediment is, and
174 therefore give additional information on how erodibility is indirectly affected by fauna through changes in grain
175 size distribution. Sampling of replicates over the low tide period was distributed representatively between
176 treatments and location to avoid short-term (hours) temporal (sediment drying, compaction and migration of
177 microphytobenthos and macrofauna related changes to sediment properties over the low tide period; Perkins *et*
178 *al.*, 2003, Tolhurst and Chapman, 2005) and spatial (shore height; Davidson, Crook, and Barnes, 2004; Paterson
179 *et al.*, 2000)) confounding of the variables being measured and ensure the results observed were as a result of
180 treatments applied and not natural physical factors (see Supplementary Tables 2 and 3).

181

182 As this experiment was carried out using *in situ* mesocosms it is potentially affected by a number of
183 experimental artefacts, however the use of mesocosms to prevent colonisation of defaunated sediments and

184 maintain the species dominance biomass was necessary. This method is still suitable to draw robust conclusions
185 as to the effects of macrofauna species on their environment and potential recovery of this and other
186 environments after simulation of defaunation following an extreme climatic event as we can compare the effects
187 of defaunation with and without a mesocosm by examining the difference between the no recovery and
188 migration scenarios without mesocosms and between those treatments that were held within a mesocosm (the no
189 recovery scenario: N, and the faunal recovery scenarios: HD and PU).

190

191

192 To determine the effect of an abrupt species defaunation event and potential recovery by migration
193 from surrounding species pools or opportunistic species expansion we developed regression models in R
194 (Version 2.15.13; R Core Team, 2013) and each treatment was treated as a discrete unique identity (i.e.
195 treatments were not combined and were factors rather than continuous variables; Solan *et al.*, 2008). The data
196 had no outlying values (Cook's distance), but showed heterogeneity of variance, due to the comparison of
197 treatments containing different species biomass due to the different recovery scenarios, so generalised least
198 squares approach was taken (Pinheiro and Bates, 2000; West, Welch, and Galecki, 2006; Zuur, Ieno, and Smith,
199 2007; Zuur, Ieno, and Elphick, 2009a). These analyses were performed using the mixed modelling and nonlinear
200 mixed effects package (nlme) in R (Pinheiro *et al.*, 2013). Restricted maximum likelihood estimation (REML)
201 with examination of the model Akaike information criteria (AIC) scores and plots of fitted values against the
202 residuals (Zuur *et al.*, 2009b) were used to determine the most appropriate model for each statistical test. Further
203 description of the statistical analyses carried out is provided in Supplementary Information S4 and the model
204 summaries are provided in Supplementary Model Summaries. In summary statements within the manuscript we
205 give the mean \pm standard error for measured responses where $n = 4$ and for generalised least squares statistical
206 tests we provide the likelihood ratio (L-ratio) and the calculated p-value (p). For between treatment comparisons
207 we provide the ratios between the response estimates and their standard errors (t), and the associated p-value
208 under a t approximation (p).

209

210

RESULTS

211

212 Cryodefaunation of 100 mm deep cores was a successful method for partial defaunation, causing a
213 mean (\pm standard error; $n = 4$; c.f. for all mean variables stated hereafter) reduction in the abundance of *Hediste*

214 *diversicolor* from 13.0 ± 4.5 to 6.6 ± 1.6 individuals per experimental pipe unit, *Peringia ulvae* from 11.0 ± 2.8
215 to 5.8 ± 1.9 individuals per experimental pipe unit, and *Corophium volutator* from 30.8 ± 11.6 to 16.8 ± 3.1
216 individuals per experimental pipe unit, (comparison of C versus N scenario). Total species abundance per
217 experimental pipe unit was reduced by 47 ± 0.01 %. It should also be noted that due to the necessity of using a
218 mesocosm to enclose the sediments testing the N, HD and PU scenarios to ensure species are excluded or
219 prevented from migrating out of the test area there is the possibility there is a procedural experimental effect
220 affecting the sediments held within a mesocosm. We therefore try to avoid making definitive conclusions based
221 upon significant differences observed between data collected from sediment not held within a mesocosm (C, M)
222 and those held within (N, HD, PU), but we can still comment on the potential trends observed and how they may
223 affect ecosystem services following a natural species defaunation event.

224
225 No temporal effect over the tidal cycle was observed for any of the measurements taken (Linear regression;
226 Supplementary Table 2). No effect of shore height was observed on any of the response variables as well
227 (Linear regression and gls; Supplementary Table 3).

228
229 In the control scenario cores (C, $n = 4$, Figure 3a) the erosion threshold at Breydon Water ranged from
230 less than 0.1 to 0.5 Nm^{-2} . The scenarios showed significant differences in their erosion thresholds (Figure 3a; L-
231 ratio = 12.4, d.f. = 4, $p = 0.015$, Supplementary Model S5) and all defaunated scenarios (M, N, HD, PU) had a
232 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
233 Nm^{-2} respectively). Comparing those scenarios without mesocosms: the Migration Recovery scenario sediment
234 (M) did not have a significantly larger mean erosion threshold than the C scenario ($0.3 \pm 0.1 \text{ Nm}^{-2}$; $n = 4$; $t = 1.2$,
235 $p = 0.2425$). For those sediments held within a mesocosm the N scenario had a significantly larger erosion
236 threshold than the HD scenario ($t = 2.6$, $p = 0.0176$), but not the PU scenario (L-ratio = 1.7, $p = 0.089$),

237
238 The control and recovery scenarios showed significant differences in the sediment erosion rate (Figure 3b;
239 L-ratio = 14.3, d.f. = 4, $p = 0.006$, Supplementary Model S6). The mean suspension index of the C scenario
240 sediments was the largest (C; 15.57 ± 1.22), but only a significantly larger erosion rate than those of the No
241 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
242 within a mesocosm. Comparing sediment held within the mesocosms, scenario N had a larger mean erosion rate

243 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
244 scenario PU ($t = 3.0$, $p = 0.009$).

245

246 Experimental scenario had a significant effect on sediment microphytobenthos minimum fluorescence
247 (F_0 ; Figure 3c; L-ratio = 22.9, d.f. = 10, $p < 0.001$, Supplementary Model S7). Scenario C had a mean minimum
248 fluorescence (413.94 ± 29.19), lower than that of all the other defaunated scenarios (M, N, HD, PU),
249 significantly lower than scenarios N (1222 ± 142.4 , $t = 4.8$, $p < 0.001$), HD (813.9 ± 146.6 , $t = 2.3$, $p = 0.033$)
250 and PU (1115.6 ± 164.3 , $t = 3.7$, $p = 0.002$), but not significantly lower than scenario M, the other sediment
251 scenario not held within a mesocosm (627.1 ± 86.0 , $t = 2.0$, $p = 0.057$). Those scenarios held within a mesocosm
252 were not significantly different from each other. There was no significant effect of the no recovery, migration or
253 two species replacement scenarios on the PAM measured maximum quantum yield (L-ratio = 1.8, d.f. = 10, $p =$
254 0.778 , Supplementary Model S8, Supplementary Figure S9).

255

256 Minicore sediments were classified as either very fine sand or very coarse silt under the GRADISTAT
257 program scale (Blott and Pye, 2001). With respect to sediment particle size distribution, species manipulation
258 only resulted in significant changes in minicore sediment particle D_{10} (μm ; Figure 3d; L-ratio = 13.5, d.f. = 4, p
259 = 0.009 Supplementary Model S10). Minicore sediment particle size D_{10} (μm) showed little variation, ranging
260 from 7.4 to 11.9 μm across all the treatments. Differences in sediment particle size were confounded by
261 mesocosm presence; scenario M ($8.8 \pm 0.5 \mu\text{m}$) did not significantly differ from scenario C ($9.0 \pm 0.3 \mu\text{m}$; $t = -$
262 0.2 , $p = 0.830$), however scenario N had a significantly larger mean particle D_{10} than scenario C ($t = 3.6$, $p =$
263 0.002) and scenario M ($t = 2.6$, $p = 0.020$). Scenario PU ($10.4 \pm 0.3 \mu\text{m}$) also had a larger mean particle D_{10} than
264 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
265 scenarios on the minicore sediment mean particle size (μm ; L-ratio = 7.8, d.f. = 4, $p = 0.100$, Supplementary
266 Model S11, Supplementary Figure S12) or minicore sediment mud content (%; L-ratio = 6.8, d.f. = 4, $p = 0.145$,
267 Supplementary Model S13, Supplementary Figure 14).

268

269

DISCUSSION

270

271 We find that potential loss of macrofaunal species from intertidal sediments *in situ* after a catastrophic
272 defaunation event increases the erosion threshold and decreases the suspension index of the sediment, at least in

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

303 would not result in recovery of the sediment habitat properties in the same way as if there was a post-event
304 expansion in *H. diversicolor* biomass.

305

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

313

314 The activity of *H. diversicolor* may be able to compensate for the loss of the majority of the rest of the
315 macrofauna due to its multiple feeding modes and surface bioturbation (De Deckere, Tolhurst, and de Brouwer,
316 2001; Widdows, Brinsley, and Pope, 2009). *P. ulvae*, whose activity is limited to the surface layers of sediment
317 and does not exhibit multiple feeding modes, is not able to compensate for the loss of the other infaunal species.
318 *P. ulvae* only affects the erosion threshold. This could be through both physical and biological processes as *P.*
319 *ulvae* grazing increases surface roughness and direct sediment disruption (Blanchard *et al.*, 1997; Orvain, Le Hir,
320 and Sauriau, 2003; Orvain *et al.*, 2004) while causing a reduction in microphytobenthos biomass (Andersen,
321 2001, Austen, Andersen, and Edelvang, 1999; Orvain *et al.*, 2004; Smith, Hughes, and Cox, 1996). The small
322 mean erosion threshold observed is probably as a result of type 1 erosion, erosion of a loose surface layer (Amos
323 *et al.*, 1992; Tolhurst *et al.*, 2000). The destabilising influence of *P. ulvae* does not extend as deep down into the
324 sediment as it does with the gallery creating *H. diversicolor* (see Hale *et al.*, 2014 for images of the depth of
325 bioturbation by *H. diversicolor* and *H. ulvae*), as *P. ulvae* are not found to burrow extensively if the sediment is
326 too hard (Little and Nix, 1976), which may be the case in the defaunated sediment which has reduced abundance
327 of destabilising macrofauna and is colonised and stabilised by microphytobenthos (Tolhurst *et al.*, 2008, Davis
328 and Lee, 1983).

329

330

CONCLUSIONS

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332 With current climate change we expect to see changes in faunal abundance, distribution and species
333 dominance. This study shows that changes in species presence and abundance could have considerable effects
334 on sedimentary ecosystem functions and processes. We show a sudden decrease in macrofaunal density without
335 recovery could lead to a shift from a dynamic resuspendible sediment habitat to a stabilised microphytobenthos
336 dominated sediment. Additionally, differential recovery through simulated opportunistic expansion of a single
337 infaunal species has the potential to lead to functional changes in the sedimentary environment (Clare *et al.*,
338 2016). For some metrics, functional compensation for the loss of other species and the preservation of certain
339 ecosystem functions was observed, however, recovery is species specific. These potential shifts in the
340 sedimentary habitat will have consequences for the biogeochemistry of the complex sediment-water interface of
341 intertidal sediments. Understanding these potential changes will enable us to better manage these habitats and
342 mitigate the effects of climate change on intertidal mudflats.

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FIGURE CAPTIONS

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596 Figure 1. The location of the experimental area (black dot; N52° 37.030', E01° 41.390') at Breydon Water,
597 Great Yarmouth, UK. Ordnance survey map from OS OpenData.

598

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

603

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

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