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Home advantage? Decomposition across the freshwater-estuarine transition zone varies with litter origin and local salinity

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1 **Abstract**

2 Expected increases in the frequency and intensity of storm surges and river flooding
3 may affect greatly the relative salinity of estuarine environments over coming decades.
4 In this experiment we used detritus from three contrasting environments (marine -
5 *Fucus vesiculosus*; estuarine *Spartina anglica*; terrestrial *Quercus robur*) to test the
6 prediction that the decomposition of the different types of litter would be highest in
7 the environment with which they are associated. Patterns of decomposition broadly
8 fitted our prediction: *Quercus* detritus decomposed more rapidly in freshwater
9 compared with saline conditions while *Fucus* showed the opposite trend; *Spartina*
10 showed an intermediate response. Variation in macro-invertebrate assemblages was
11 detected along the salinity gradient but with different patterns between estuaries,
12 suggesting that breakdown rates may be linked in part to local invertebrate assemblages.
13 Nonetheless, our results suggest that perturbation of salinity gradients through climate
14 change could affect the process of litter decomposition and thus impact upon nutrient
15 cycling in estuarine transition zones. Understanding the vulnerability of estuaries to
16 changes in local abiotic conditions is important given the need to better integrate coastal
17 processes into a wider management framework at a time when coastlines are
18 increasingly threatened by human activities.

19

20 *Keywords:* decomposition; flooding; global change; invertebrate assemblage; litter bags.

21

22

23 **Introduction**

24 Coastal ecosystems, including estuaries and salt marshes, face threats from various
25 environmental stressors associated with global climate change (Nicholls, 2004; IPCC,
26 2012; Zappa et al., 2013, Wong et al., 2015). Increased sea level and more intense and
27 frequent storm surge events are likely to cause extensive shoreline erosion as well as
28 saltwater intrusion into coastal rivers (Bear et al., 1999; IPCC, 2012). However, coastal
29 protection is unlikely to be efficiently achieved simply by ‘hard armouring’ (Zanuttigh,
30 2011; Pontee and Parsons, 2010, 2012; Esteves, 2014). The innovative approaches for a
31 sustainable coastal flood management incorporate natural processes and include the
32 inundation of some coastal areas (Zanuttigh, 2011; Esteves, 2014; Hanley et al., 2014;
33 Hoggart et al., 2014). Adopting integrated coastal defence approaches such as ‘managed
34 retreat’ and ‘no active intervention’, however, requires an understanding of the
35 ecological impact of floodings or other changes in flow regimes on recipient ecosystems
36 and their functions (Pontee and Parsons, 2010; Bouma et al., 2014; Hoggart et al.,
37 2014).

38 Decomposition is a fundamental process in the functioning of the estuarine ecosystem
39 (McLusky and Elliott, 2004), facilitating the recycling of nutrients and chemical
40 elements, and thereby sustaining important food chains and primary production
41 (Cummins et al., 1989; Graça, 2001; Quintino et al., 2009). The decomposition of
42 organic material in aquatic ecosystems proceeds in three sequential stages: leaching,
43 conditioning, and then fragmentation (Petersen and Cummins, 1974). Shortly after
44 falling into the water, leaf-litter rapidly loses mass due to the leaching of soluble organic
45 and inorganic constituents. This stage is followed by microbial colonization, causing
46 numerous modifications to leaf condition and enhancing acceptability and colonization

47 by macro-invertebrate detritivores responsible for the leaf fragmentation. The rate of
48 this process depends on the physico-chemical characteristics of the leaf material, the
49 local composition of both microbial and macrofaunal communities, and the abiotic
50 environmental conditions of the environment (e.g. salinity, nutrients, water temperature,
51 oxygen concentration, pH) (see Lopes et al., 2011 and references therein).

52 In estuaries, where salinity represents the main ecological factor defining habitat
53 boundaries (Telesh and Khlebovich, 2010), the abiotic conditions gradually change
54 along a gradient from marine to freshwater. Any significant changes in the intensity and
55 frequency of seawater inflows into estuaries and rainfalls into rivers of the kind
56 expected through climate change, are likely to modify the overall local abiotic
57 conditions, with possible alteration of the decomposition process (Mendelsohn et al.,
58 1999). Detritus from marine sources could be moved further inland and upstream
59 through catchments (see Tate and Battaglia, 2013 for an example), whilst estuarine and
60 marine systems might be expected to receive increased quantities of terrestrial leaf litter.
61 The consequence of such perturbation could be that detritus processing is due with local
62 mismatch between the salinity regime. Such mismatch would lead to direct effects on
63 breakdown rates, or indirectly affect decomposition via changes in the associated
64 detritivore assemblage, or a combination of both. To date, only few studies have
65 explicitly examined how changes in local salinity and macrofauna affects detritus
66 breakdown although those that do (Lettice et al., 2011; Lopes et al., 2011; Bierschenk et
67 al., 2012) report that decomposition rates varied according to salinity gradients and that
68 detritus originating from without the local system decomposed more slowly. Moreover,
69 the composition of the associated detritivore community changed along the salinity
70 gradient (but see Lopes et al., 2013). These results suggest that detritus decomposes

71 more effectively in the environmental conditions of its native habitat. Nevertheless,
72 there has been no comparison of the decomposition of terrestrial, saltmarsh, and marine
73 litters across the range of salinities found in a typical estuary.

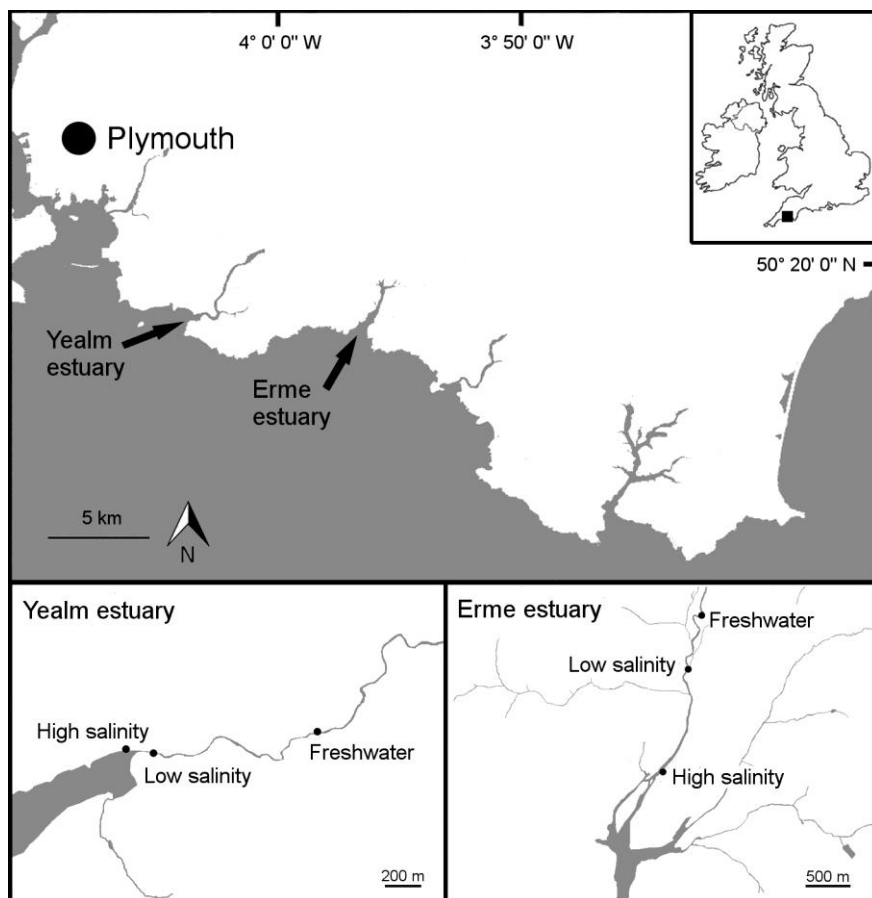
74 Here we report the results of a field experiment to investigate the breakdown rates of
75 terrestrial, saltmarsh, and marine derived detritus (respectively *Quercus robur*, *Spartina*
76 *anglica* and *Fucus vesiculosus*) across the salinity gradient in two neighbouring
77 estuaries in southern England. We also surveyed the composition of invertebrate
78 assemblages associated with the detritus in each habitat. In so doing, we provide the
79 first insights into the potential vulnerability of estuarine systems to shifts in local
80 conditions expected from climate-related changes in freshwater flooding and seawater
81 inundation events.

82

83 **Materials and methods**

84 *Study sites*

85 The experiment was undertaken in the estuaries of the rivers Yealm (50°18.6'N,
86 04°4.2'W) and Erme (50°18.3'N, 03°57.0'W), in South Devon, UK (Fig. 1). Both rivers
87 rise on Dartmoor flowing south for 16 and 20 km respectively before discharging into
88 Wembury and Bigbury bays. The estuaries of both rivers are characterized by similar
89 physical features: extension (about 6 km); catchment area (Yealm = 55 km², Erme = 43
90 km²); mean river flow discharge (Yealm = 1.7 m³/s, Erme = 1.9 m³/s); large tidal range



91 *Fig. 1. Study site locations. Large map shows the position of the Yealm and Erme estuaries in south*
 92 *Devon. Smaller maps show the locations of with Freshwater, Low salinity and High salinity habitats in*
 93 *each estuary: Yealm and Erme.*

94 (4.7 m) and a full salinity range from marine to freshwater (Sheehan et al., 2010). In
 95 both rivers, saltwater ingress into the freshwater zone is strongly limited by the presence
 96 of weirs.

97 At each estuary, three habitats were selected along the salinity gradient, according to the
 98 Venice System (1959) for the Classification of Estuarine Waters: 'freshwater' (limnetic);
 99 'low salinity' water (mesohaline); 'high salinity' water (polyhaline). In the Yealm the
 100 three habitats were located along 800 m stretch of estuary, whilst in the Erme the
 101 passage from freshwater to high salinity occurred over a 2 km distance. The two
 102 'freshwater' habitats (Fw) were located at 600 m and 300 m upstream of a weir in the

103 Yealm and Erme respectively (above the normal tidal limit – NTL), and were
104 characterized by wooded banksides dominated by broad-leaved trees. The two 'low
105 salinity' habitats (Lo) were located in areas equidistant between the NTL weirs and the
106 open coast, in sites where euryhaline species such as *Ulva* spp. indicated a brackish
107 regime. The riparian vegetation in these habitats were characterised by species typical
108 of upper saltmarsh vegetation. The two 'high salinity' habitats (Hi) were located in areas
109 dominated by marine macro-algae, and banksides featuring scattered trees and open
110 terrestrial vegetation.

111 Salinity was recorded continuously by loggers submerged and anchored to the river bed
112 for 4 weeks, from end of May to June 2010 (i.e. during the decomposition experiment).
113 The mean salinity values (expressed as Practical Salinity Unit, \pm standard deviation), at
114 the three habitats in each river (from freshwater to low salinity and high salinity) were:
115 0.0 (\pm 0.0), 17.6 (\pm 2.2), 23.0 (\pm 1.8), in the Yealm; and 0.0 (\pm 0.0), 12.4 (\pm 3.0), 20.1 (\pm
116 3.1) in the Erme.

117 ***Experimental procedure***

118 The decomposition experiment was run using 3 species particularly abundant in the
119 three study habitats: these were (respectively) the tree *Quercus robur* L. (Fagaceae); the
120 grass *Spartina anglica* C. E. Hubb. (Poaceae), and the fucoid alga *Fucus vesiculosus* L.
121 (Fucaceae). Naturally dehisced leaves or laminae from the three species were collected
122 in May 2010 from woods adjacent to the freshwater sites (*Quercus*), salt marshes near
123 the low salinity sites (*Spartina*), and the inter-tidal in the area of high salinity sites
124 (*Fucus*) within the catchment of both rivers. The leaf material for the experiment was
125 randomly selected from the collection sites and subsequently oven-dried to constant

126 weight (60°C for 72 hours).

127 Since detritus from the three sources had different dry densities, we prepared litter bags
128 with different weights but similar volumes in order to offer comparable surfaces for
129 detritivore colonization. The litter bags (nylon cloth, 100 x 100 mm, 5 mm mesh size;
130 Bärlocher 2005) were half filled with dried detritus, (corresponding to 5 g of *Quercus*, 8
131 g of *Spartina* and 12 g of *Fucus*). In the case of *Spartina* the leaves were cut into 8 cm
132 long fragments (excluding the basal and apical parts). The 5 mm mesh size was chosen
133 to allow colonization by macroinvertebrates yet at the same time reduce the potential for
134 detritus loss due to fragmented litter falling out of the bags (Quintino et al., 2009). Four
135 replicate bags for each species were deployed at each of the three habitats (Fw, Lo, Hi)
136 at each of the two estuaries (Yealm, Erme). The bags were attached to ropes anchored to
137 the river bed by bags of pebbles and steel pegs hammered into the sediment, to prevent
138 occasional emersion in low tides and limit abrasion. We exposed the detritus for 38 days
139 (late May to late June 2010), based on decomposition rates estimated from previous
140 studies (Sangiorgio et al., 2008; Quintino et al., 2009). After this time, the litter bags
141 were retrieved and preserved in plastic bags containing 70% alcohol. The detritus was
142 washed to remove sediment, dried in an oven at 60°C for 72 hours and reweighed.
143 Macro-invertebrates were separated from the sediment with a 500 µm mesh size,
144 identified at the lowest possible taxonomic level and counted.

145 ***Data analyses***

146 Weight loss for each litter species was calculated as percentage according to the
147 following equation: $\%L = (W_0 - W_t) / W_0 \times 100$, where W_0 is the original dry weight of the
148 litter and W_t was the dry weight remaining after 38 days (Petersen and Cummins, 1974).

149 Furthermore, in order to compare the decomposition rates for *Quercus*, *Fucus* and
150 *Spartina* with those described in other studies, weight loss was also calculated
151 according to the decay exponential function $k = -(1/t) \times \ln(W_t/W_0)$ (Petersen and
152 Cummins, 1974).

153 Differences in relative weight loss between litter species, habitats, and estuaries were
154 tested via a three-way ANOVA, including 3 orthogonal factors “Estuary“ (Es, two levels:
155 Y – Yealm, E – Erme, random), “Detritus” (De, three levels: *Quercus*, *Spartina* and
156 *Fucus*, fixed) and “Habitat” (Ha, three levels: Fw - Freshwater, Lo - Low salinity, Hi -
157 High salinity, fixed). There were four replicates for each factor combination. ANOVA
158 was carried out using SPSS v.18 package. Prior to ANOVA, the data were examined for
159 normality and homogeneity of variance using Levene’s test, and Arcsine (%)
160 transformed to meet the required assumptions of homogeneity of variance. Tukey’s
161 HSD test was used to perform pairwise comparison for significant differences.

162 Differences in the multivariate structure of macrofaunal, detritivore assemblages as a
163 function of different detritus types, habitat, and estuary location were assessed via a
164 three-way PERMANOVA using the same logic described above. The analysis was
165 performed with PERMANOVA + add on package for the PRIMER v6 software (Clarke
166 and Warwick, 2001; Anderson et al., 2008). Data were log transformed to preserve
167 information on relative abundance of each species, while reducing differences in scales
168 among variables (Clarke and Warwick, 2001), and used to build a matrix of Bray-Curtis
169 similarity coefficients. For the analysis, 9999 unrestricted random permutations of
170 residuals were used to generate p-values. For some terms in the analysis, there were not
171 enough permutable units to get a reliable permutation test, so a p-value was obtained
172 using a Monte Carlo random sample from the asymptotic permutation distribution

173 (Anderson and Robinson, 2003).

174 A non-metric multidimensional scaling (NMDS) ordination, calculated on the same
175 Bray-Curtis similarity matrix, was used to visualize multivariate patterns of distribution
176 of the macrofaunal assemblages (Clarke and Warwick 2001). Given the large number of
177 replicates ($n = 72$), we plotted centroids for the combined factor Estuary-Habitat. The
178 similarity percentage routine (SIMPER) was used to highlight which taxa provided the
179 largest contribution to dissimilarities between categories (Clarke and Warwick, 2001).

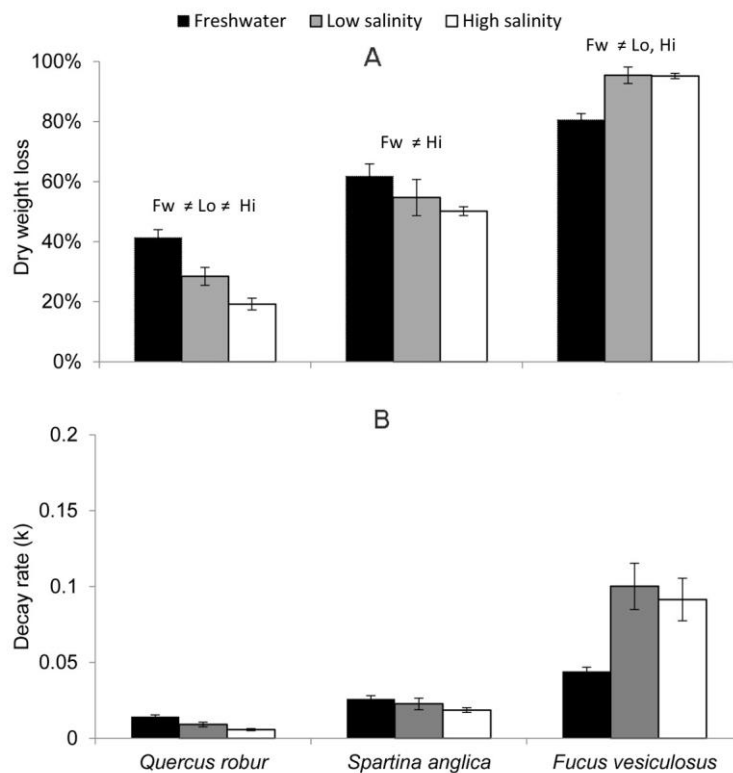
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181 **Results**

182 *Detritus breakdown*

183 All litter bags were successfully recovered. Biomass loss through the 38 days of
184 exposure varied considerably according to detritus type and position along the estuarine
185 salinity gradient. Overall, *Quercus* litter breakdown was slowest, with weight loss never
186 exceeding 42 %, whereas *Fucus* litter decomposed fastest, up to 95 % weight loss over
187 the 38 days exposure (Fig. 2a). Detritus from terrestrial vegetation and marine furoid
188 macroalgae showed the opposite trend in breakdown rate along the salinity gradient
189 (Figs 2a; 2b). Significant differences were detected between habitats for both *Quercus*
190 and *Fucus* (Table 1). Biomass loss of *Quercus* litter declined from Fw ($41.3 \% \pm 0.03$)
191 to Lo ($28.4 \% \pm 0.04$) and Hi ($19.2 \% \pm 0.02$) habitats (Fig. 2a). In contrast, the biomass
192 loss of *Fucus* litter was lower in Fw ($80.5 \% \pm 0.02$) with respect to Lo ($95.4 \% \pm 0.01$)
193 and Hi ($95.2 \% \pm 0.01$) habitats (Fig. 2a). The trend in breakdown rate of *Quercus* vs
194 *Fucus* along the gradient was consistent between estuaries (Fig. 3).

195 Biomass loss for *Spartina* litter ranged from 61.8 % \pm 0.03 in Fw to 50.2 % \pm 0.03 in
 196 Hi, without significant differences between habitats (Table 1; Fig. 2a). However, we
 197 found different trends in breakdown rate of *Spartina* between estuaries. In effect, the
 198 biomass loss of *Spartina* reach very different value among the low salinity habitats of
 199 the two estuaries. In the Yealm the biomass loss among habitats was the higher in Lo,
 200 whereas in the comparison among habitat in the Erme the biomass loss was the lower on



201 Lo (Fig. 3).

202 Fig. 2. Leaf litter breakdown of the three detritus types at Freshwater (Fw), Low salinity (Lo) and High
 203 salinity (Hi) habitats, indicated by: A) dry weight mass loss with superscript significant differences
 204 among habitats for each detritus type; B) decay rates. Data are averages \pm 1 S.E.(n=4).

205

206 Table 1. ANOVA showing changes in dry weight loss (%) in relation to Estuary (Yealm vs Erme, random
 207 factor), Detritus type (Quercus, Spartina and Fucus, fixed factor) and Habitat (Fw = Freshwater, Lo =
 208 Low salinity water, Hi = High salinity water, fixed factor) with pairwise comparisons for the interaction

209 *De x Ha*. Prior to ANOVA, the data were arcsine transformed in order to meet assumption of homogeneity
 210 of variance. Significance (Sign.): * = $p < 0.05$; ** = $p < 0.01$, *** = $p < 0.001$, ns = not significant.

Source	df	MS	F	Sign.	Pairwise comparisons	Quercus	Spartina	Fucus
Es	1	0.174	0.789	ns	Fw vs Lo	*	ns	***
De	2	4.717	63.721	*	Fw vs Hi	***	**	***
Ha	2	0.026	0.164	ns	Lo vs Hi	*	ns	ns
Es x De	2	0.074	6.788	ns				
Es x Ha	2	0.157	14.384	*		Fw	Lo	Hi
De x Ha	4	0.226	20.738	**	<i>Quercus vs Spartina</i>	***	***	***
Es x De x Ha	4	0.011	2.094	ns	<i>Quercus vs Fucus</i>	***	***	***
Residuals	54	5			<i>Spartina vs Fucus</i>	***	***	***

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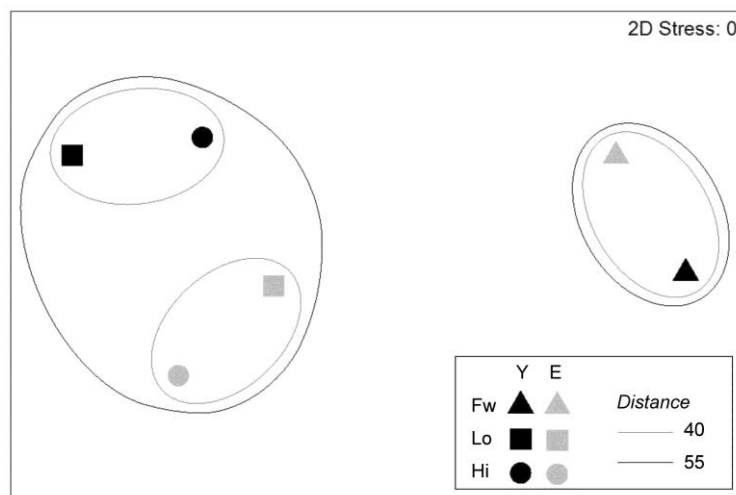
214 ***Macro-faunal distribution***

215 The macrofaunal assemblages comprised 35 taxa, among which the most abundant were
 216 *Gammarus zaddachi* (Amphipoda) and chironomid larvae (Diptera) at 50.4% and
 217 28.6% of the total abundance respectively. *G. zaddachi* dominated Lo and Hi habitats,
 218 whereas chironomids were abundant in Fw. The third most abundant group were
 219 hydrobiid gastropods (7.3%). Other common taxa included the juvenile crustaceans
 220 *Carcinus* sp. (Decapoda) and *Jaera* sp. (Isopoda) and the juvenile insects belonging to
 221 the families Leuctridae (Plecoptera), Ephemerellidae (Ephemeroptera) and
 222 Lepidostomatidae (Trichoptera).

223 Mean taxon richness of macrofauna was higher in Fw (11.2 ± 1.4) compared to Lo (3.9
 224 ± 1.4) and Hi (4.0 ± 0.9). This pattern was largely driven by the diversity of families of
 225 insects in Fw and the dominance of *Gammarus zaddachi* in Lo and Hi. There were also
 226 differences in the numbers of individuals and in dominance patterns between the two
 227 estuaries: in the Yealm we recorded 11,791 individuals, most of which were *Gammarus*
 228 *zaddachi* (63.1 %) and Chironomidae (21.2 %); whereas in the Erme we collected only

229 4,358 individuals but with higher and lower representation of Chironomidae (48.8 %)
 230 and *Gammarus zaddachi* (16.1 %) respectively.

231 Multivariate analyses revealed little variation in the macro-invertebrate assemblages
 232 among detritus species within habitats. The NMDS plot shows variation in assemblages
 233 between habitats along the salinity gradient. While Fw habitats of the two estuaries were
 234 clustered together, Lo and Hi were clustered together within rather than across habitats
 235 (Fig. 3). The PERMANOVA test failed to detect any significant differences between
 236 detritus species in the same habitat site, but did show that invertebrate assemblages
 237 differed between habitats for each detritus species (De x Ha, $p(\text{MC}) = 0.0166$). However
 238 the pattern was not consistent between the two estuaries (Table 2). The *post-hoc*
 239 PERMANOVA test, performed for each estuary separately, confirmed that that
 240 invertebrate assemblages populating each detritus type differed among habitats (Table
 241 2).



242 Fig. 3. NMDS ordinations of centroids for estuaries (Yealm versus Erme) and habitats (Fw = Freshwater,
 243 Lo = Low salinity, Hi = High salinity; Estuaries: Y = Yealm, E = Erme). Lines show groupings derived
 244 using cluster analysis.

245

246 Table 2. PERMANOVA (35 variables, log-transformed data) showing changes in macrofaunal
 247 assemblages in relation to Estuary (Yealm vs Erme, random factor), Detritus type (Quercus, Spartina and
 248 Fucus, fixed factor) and Habitat (Freshwater = Fw, Low salinity water = Lo and High salinity water =
 249 Hi, fixed factor) with pairwise comparisons for the term De x Ha for pairs of levels of factor 'Ha' at each

Source	df	MS	Pseudo-F	Sign.	Pairwise comparisons	Quercus	Spartina	Fucus
Es	1	17652	37.001	***	Yealm			
De	2	3237.9	2.088	ns	Fw vs Lo	***	***	***
Ha	2	40553	3.8265	ns	Fw vs Hi	***	***	***
Es x De	2	1550.7	3.2505	***	Lo vs Hi	**	**	**
Es x Ha	2	10598	22.215	***	Erme			
De x Ha	4	1573.1	2.8695	*	Fw vs Lo	***	**	**
Es x De x Ha	4	584.2	1.1491	ns	Fw vs Hi	***	**	***
Residuals	54	477.07			Lo vs Hi	*	*	*

250 estuary. Significance (Sign.): * = $p < 0.05$; ** = $p < 0.01$, *** = $p < 0.001$, ns = not significant.

251

252

253 SIMPER analysis (Table 3) showed that the Fw habitats of the two estuaries were
 254 characterized by a greater representation of Chironomidae compared to both Lo and Hi
 255 habitats and by the almost exclusive occurrence of *Gammarus pulex* and Leuctridae,
 256 Lepidostomatidae, Ephemerellidae, and Elmidae larvae. Conversely, Lo and Hi habitats
 257 were dominated by *Gammarus zaddachi*, a species particularly abundant in the Yealm
 258 estuary.

259

260 Table 3. SIMPER showing the species most contributing to the Dissimilarities (Diss) detected in
 261 macrofaunal assemblages between different estuaries (Yealm, Erme) and habitats (Fw = Freshwater; Lo
 262 = Low salinity; Hi = High salinity). J = Juvenile.

Taxa	Mean abundance		Diss/SD	Contribution to diss (%)
	Yealm	Erme		
Average diss = 56.54				
<i>Gammarus zaddachi</i>	3.22	1.74	0.8	17.96
Hydrobiidae	1.25	1.56	1.25	13.1
Chironomidae (J)	2.99	3.14	1.1	11.97
<i>Carcinus</i> sp.	0	0.93	0.91	8.51
<i>Jaera</i> sp.	0.12	0.99	0.84	8.15
<i>Carcinus</i> sp. (J)	0	0.86	0.84	7.3
Oligochaeta	0.99	0.4	0.5	3.63
Average diss = 85.85				
	Fw	Lo		
<i>Gammarus zaddachi</i>	0	3.91	2.04	14.2
Chironomidae (J)	4.9	1.57	1.86	12.57
Hydrobiidae	205	1.31	1.62	9.92
Leuctridae (J)	2.3	0	1.57	8.18
Ephemereididae (J)	1.94	0	2.05	6.84
Lepidostomatidae (J)	1.96	0.07	2.02	6.84
<i>Gammarus pulex</i>	1.75	0	1.94	6.12
Elmidae (J)	1.61	0.03	1.84	5.7
Average diss = 81.34				
	Fw	Hi		
<i>Gammarus zaddachi</i>	0	3.52	2.04	13
Hydrobiidae	2.5	0.4	1.43	8.75
Chironomidae (J)	4.9	2.74	1.73	8.49
Leuctridae (J)	2.3	0	1.62	8.31
Lepidostomatidae (J)	1.96	0	2.15	7.34
Ephemereididae (J)	1.94	0	2.11	7.05
<i>Gammarus pulex</i>	1.75	0	1.94	6.34
Elmidae (J)	1.61	0	1.93	5.91
<i>Carcinus</i> sp.	0	1.03	0.8	4.04
<i>Asellus</i> sp.	1.06	0	0.86	3.91
Average diss = 45.23				
	Lo	Hi		
Chironomidae (J)	1.57	2.74	1.22	27.77
<i>Gammarus zaddachi</i>	3.91	3.52	1.19	23.89
Hydrobiidae	1.31	0.4	0.81	9.79
<i>Jaera</i> sp.	1.03	0.63	0.88	8.85

263

264

265 Discussion

266 In this study, we found that each detritus type decomposed at the highest rate in salinity

267 conditions typical of its native habitat, and that major differences among associated

268 detritivore assemblages were apparent according to habitat. So-called 'home field

269 advantage' is well understood for the decomposition process in terrestrial habitats
270 (Milcu and Manning, 2011; Jewell et al., 2015), but less well described for aquatic
271 systems. Given the likely susceptibility of estuarine transitions to rapid and acute shifts
272 in environmental conditions with storm surges and freshwater flooding events, our
273 results show that concomitant variation in detritus distribution and salinity regimes
274 could alter greatly the normal processes of detritus decomposition. Such changes are
275 manifest as a consequence of direct shifts in local abiotic conditions, and the indirect
276 effects of changes in local detritivore assemblages.

277 In a recent bioassay, Bierschenk et al. (2012), reported more rapid breakdown rate of
278 cotton materials in freshwater than mid-estuary, or near-marine habitats, noting that the
279 decomposition response to variation in salinity depends on the type of material. Our
280 results corroborate and extend these observations in that we demonstrate 'home-field
281 advantage' for detritus decomposition along estuarine gradients. *Quercus* litter
282 decomposed much more rapidly in 'freshwater' than in 'high salinity' habitats while
283 *Fucus* litter displayed the opposite trend. Lopes et al. (2011) reported a similar pattern
284 of decomposition for *F. vesiculosus*, although the relatively rapid breakdown of *Fucus*
285 litter in all environments is unsurprising given its low lignin and cellulose content and
286 relatively high N-content compared to vascular plants (Tenore and Hanson, 1980).

287 Indeed there may be a general tendency for high quality leaf material to experience
288 faster consumption by invertebrates (Fernandes et al., 2015). The more fibrous leaves of
289 *Quercus* spp. naturally have relatively slow decomposition rates (Petersen and
290 Cummins, 1974) compared with saltmarsh plants or marine macro-algae.

291 While there is a surprising paucity of literature detailing the breakdown of saltmarsh
292 halophytes and marine macro-algae in temperate freshwater ecosystems, the few studies

293 that have examined the issue report similar (Castela et al., 2008), or slower (Lopez et
294 al., 2001), decomposition rates to those recorded here for *Spartina*. *Spartina* litter is
295 high in recalcitrant lignins, but despite this *Spartina* spp. have a broad range of
296 decomposition rates, influenced by position in the marsh and hydrological regime
297 (Marinucci, 1982; Kirwan et al., 2013). As with *Quercus* and *Fucus*, it seems that
298 *Spartina* may be degraded faster in areas it naturally occupies (i.e. 'low salinity' habitat),
299 but interestingly this was only observed in the Yealm estuary. The observed difference
300 in *Spartina* decomposition between estuaries might be related to local variations in flow
301 regimes, which can influence decompositional process via mechanical breakdown,
302 microbial colonization and oxygen concentration (Menéndez et al., 2001). The 'low
303 salinity' habitat of the Yealm was characterized by fast running water and a rocky bed,
304 but the corresponding habitat in the Erme had slower flow and fine-grained sediments
305 (Franzitta personal observation). In the latter, lower oxygen concentration may have
306 limited decomposer activity (Chauvet, 1997).

307 Although we cannot rule out the possibility that observed species-specific variation in
308 litter decomposition between habitats was linked to microbial diversity, abundance, and
309 activity (Roache et al., 2006; Martins et al., 2012), we did note (estuary-specific)
310 variation in macro-invertebrate assemblages along the salinity gradient. Nonetheless for
311 both estuaries the structure and composition of the detritivore community populating the
312 'low salinity' and 'high salinity' sites were consistent, a consequence of the over-riding
313 dominance of the amphipod, *Gammarus zaddachi*. *Gammarus* is a highly opportunistic
314 feeder (considered a facultative shredder by Cummins and Klug, 1979), but given the
315 choice between different food items exhibits a certain degree of selectivity (Friberg and
316 Jacobsen, 1994). In both saline habitats, the differences in breakdown rate between the

317 marine-derived *Fucus* litter and *Quercus* could suggest that the absence of a more
318 functionally diverse invertebrate assemblage (that includes shredders, scrapers,
319 collectors and herbivores) slowed the decomposition of recalcitrant terrestrial detritus
320 compared to freshwater habitats. Indeed the presence of shredders, principally from the
321 stonefly family Leuctridae and the caddisfly families Leptoceridae, Limnephilidae and
322 Sericostomatidae, in freshwater, and their ability to hydrolyze and assimilate the
323 refractory molecules of lignin, cellulose and hemicellulose (Cummins et al., 1989) is
324 likely responsible for the faster breakdown of the sclerophyll leaves of *Quercus robur*.
325 However, the role played by macroinvertebrates in the decomposition process remains
326 uncertain. Similar to our study, Lopes et al. (2013) report few differences in invertebrate
327 assemblages associated with *Fucus vesiculosus* and *Phragmites australis* along an
328 estuarine gradient, and concluded that macroinvertebrates do not influence leaf litter
329 decomposition.

330 Our's is the first study to report how one key aspect of ecosystem functioning along
331 estuarine transitions might respond to expected changes in the frequency and severity of
332 freshwater flooding and seawater inundation events. Storms surges are likely to both
333 carry large amounts of marine derived detritus further inland and/or alter the salinity of
334 freshwater habitats, while increased river discharge may have the opposite effect (more
335 terrestrial material carried downstream with freshwater pulses). Our results indicate that
336 these shifts could greatly impact litter decomposition along the estuarine transition,
337 partly because of shifts in water salinity, but also because in-situ detritivore
338 communities are ill equipped to cope with 'alien' litter. More generally therefore, we
339 suggest that acute changes in conditions as a result of phenomena associated with
340 anthropogenic climate change may influence the structure and function of estuarine

341 ecosystems and with it their likely resilience to further environmental perturbation and
342 role in coastal protection.

343

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352

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480

481 Appendix

482 Table A.1. List of the taxa detected at the Freshwater (Fw), Low salinity (Lo) and High
483 salinity (Hi) habitat (*: presence; blank: absence).|

Taxa	Fw	Lo	Hi
Ancylidae	*		
Arachnidae	*	*	
<i>Asellus</i> sp.	*	*	
Brachycentridae (J)	*		
<i>Carcinus</i> sp.		*	*
<i>Carcinus</i> sp. (J)		*	*
Chironomidae (J)	*	*	*
<i>Corophium</i> sp.			*
Dytiscidae (J)	*		
Elmidae	*	*	
Elmidae (J)	*	*	
Ephemerellidae (J)	*		
<i>Gammarus pulex</i>	*		
<i>Gammarus zaddachi</i>		*	*
Goeridae (J)	*	*	
Gyrinidae (J)	*		
Hydraenidae (J)	*		
Hydrobiidae	*	*	*
<i>Jaera</i> sp.		*	*
Lepidostomatidae (J)	*	*	
Leptoceridae (J)	*		*
Leptophlebiidae (J)	*		
Leuctridae (J)	*		
Limnephilidae (J)	*		
Nemouridae (J)	*		
Nereidae		*	*
Neritidae	*		
Oligochaeta	*	*	*
Philopotamidae (J)	*		
Platyhelminthes	*		
Polycentropodidae (J)	*		
Rhyacophilidae (J)	*		
Sericostomatidae (J)	*		
<i>Sphaeroma</i> sp.		*	*
Tineidae	*		*