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

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Abstract

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

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

Introduction

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

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

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

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

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

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

Materials and methods

Study sites

The experiment was undertaken in the estuaries of the rivers Yealm (50°18.6'N, 04°4.2'W) and Erme (50°18.3'N, 03°57.0'W), in South Devon, UK (Fig. 1). Both rivers rise on Dartmoor flowing south for 16 and 20 km respectively before discharging into Wembury and Bigbury bays. The estuaries of both rivers are characterized by similar physical features: extension (about 6 km); catchment area (Yealm = 55 km^2, Erme = 43 km^2); mean river flow discharge (Yealm = 1.7 m^3/s, Erme = 1.9 m^3/s); large tidal range

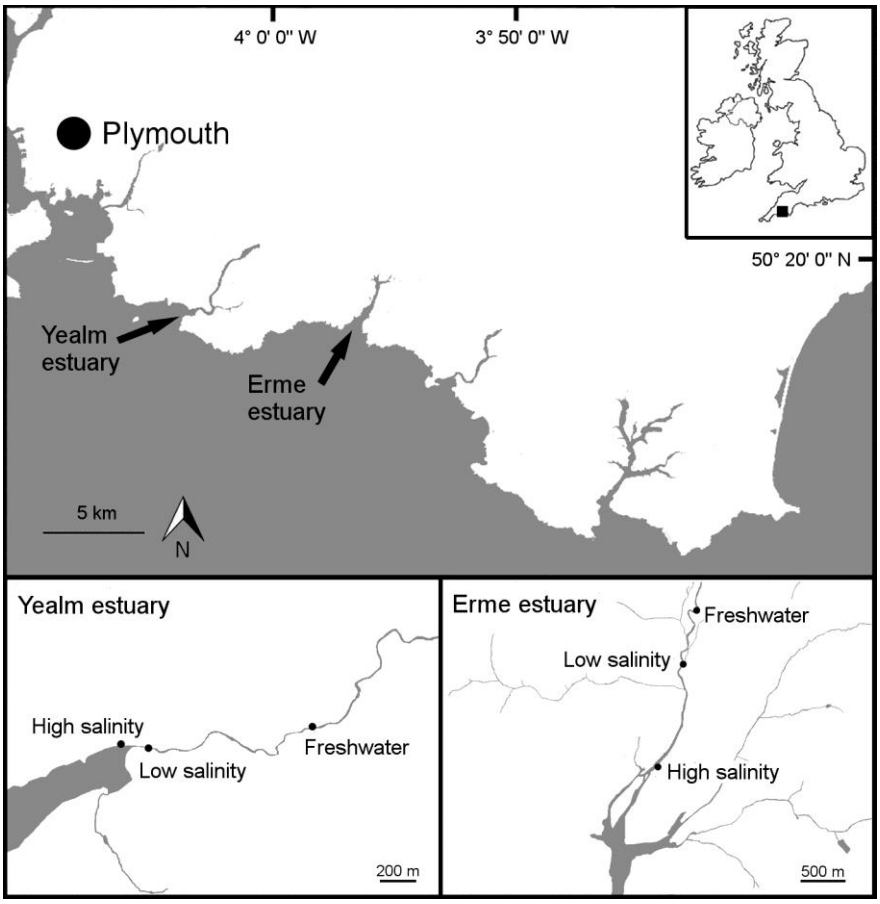

Fig. 1. Study site locations. Large map shows the position of the Yealm and erme estuaries in south Devon. Smaller maps show the locations of with Freshwater, Low salinity and High salinity habitats in each estuary: Yealm and Erme.

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

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

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

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

Experimental procedure

The decomposition experiment was run using 3 species particularly abundant in the three study habitats: these were (respectively) the tree *Quercus robur* L. (Fagaceae); the grass *Spartina anglica* C. E. Hubb. (Poaceae), and the fucoid alga *Fucus vesiculosus* L. (Fucaceae). Naturally dehisced leaves or laminae from the three species were collected in May 2010 from woods adjacent to the freshwater sites (*Quercus*), salt marshes near the low salinity sites (*Spartina*), and the inter-tidal in the area of high salinity sites (*Fucus*) within the catchment of both rivers. The leaf material for the experiment was 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: $\%L=(W_0-W_t)/W_0\times100$, 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).

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

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

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

(Anderson and Robinson, 2003).

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

Results

Detritus breakdown

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

Biomass loss for *Spartina* litter ranged from 61.8 % ± 0.03 in Fw to 50.2 % ± 0.03 in Hi, without significant differences between habitats (Table 1; Fig. 2a). However, we found different trends in breakdown rate of *Spartina* between estuaries. In effect, the biomass loss of *Spartina* reach very different value among the low salinity habitats of the two estuaries. In the Yealm the biomass loss among habitats was the higher in Lo, whereas in the comparison among habitat in the Erme the biomass loss was the lower on Lo (Fig. 3).

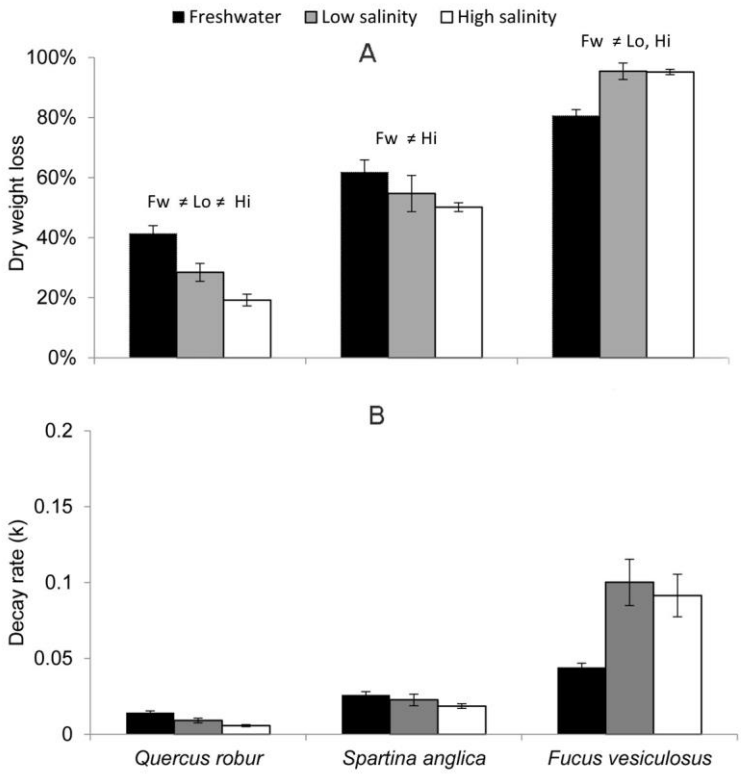

Fig. 2. Leaf litter breakdown of the three detritus types at Freshwater (Fw), Low salinity (Lo) and High salinity (Hi) habitats, indicated by: A) dry weight mass loss with superscript significant differences among habitats for each detritus type; B) decay rates. Data are averages ± 1 S.E.(n=4).

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

*De x Ha. Prior to ANOVA, the data were arcsine transformed in order to meet assumption of homogeneity 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	**	*Quercus vs Spartina*	***	***	***
Es x De x Ha	4	0.011	2.094	ns	*Quercus vs Fucus*	***	***	***
Residuals	54	5			*Spartina vs Fucus*	***	***	***

Macro-faunal distribution

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

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

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

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

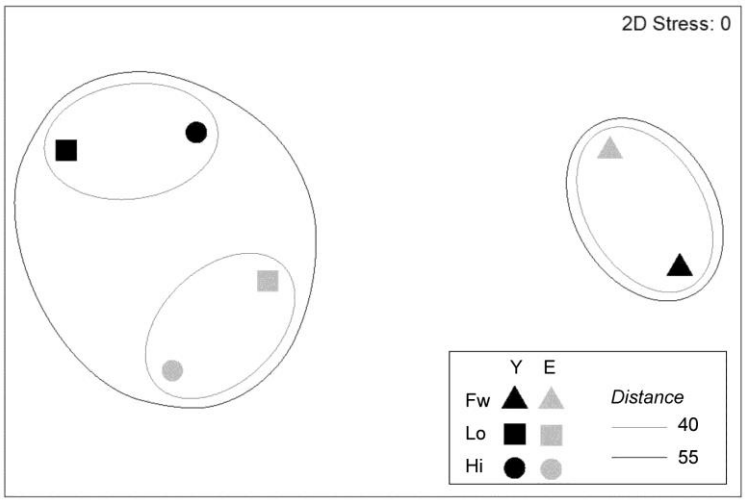

Fig. 3. NMDS ordinations of centroids for estuaries (Yealm versus Erme) and habitats (Fw = Freshwater, Lo = Low salinity, Hi = High salinity; Estuaries: Y = Yealm, E = Erme). Lines show groupings derived using cluster analysis.

*Table 2. PERMANOVA (35 variables, log-transformed data) showing changes in macrofaunal assemblages in relation to Estuary (Yealm vs Erme, random factor), Detritus type (*Quercus, Spartina *and* Fucus*, fixed factor) and Habitat (Freshwater = Fw, Low salinity water = Lo and High salinity water = Hi, fixed factor) with pairwise comparisons for the term De x Ha for pairs of levels of factor 'Ha' at each estuary. Significance (Sign.): * = p < 0.05; ** = p < 0.01, ***= p < 0.001, ns = not significant.*

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	*	*	*

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

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

Taxa	Mean abundance		Diss/SD	Contribution to diss (%)
Average diss = 56.54	Yealm	Erme		
Gammarus zaddachi	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
Carcinus sp.	0	0.93	0.91	8.51
Jaera sp.	0.12	0.99	0.84	8.15
Carcinus sp. (J)	0	0.86	0.84	7.3
Oligochaeta	0.99	0.4	0.5	3.63
Average diss = 85.85	Fw	Lo		
Gammarus zaddachi	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
Ephemerellidae (J)	1.94	0	2.05	6.84
Lepidostomatidae (J)	1.96	0.07	2.02	6.84
Gammarus pulex	1.75	0	1.94	6.12
Elmidae (J)	1.61	0.03	1.84	5.7
Average diss = 81.34	Fw	Hi		
Gammarus zaddachi	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
Ephemerellidae (J)	1.94	0	2.11	7.05
Gammarus pulex	1.75	0	1.94	6.34
Elmidae (J)	1.61	0	1.93	5.91
Carcinus sp.	0	1.03	0.8	4.04
Asellus sp.	1.06	0	0.86	3.91
Average diss = 45.23	Lo	Hi		
Chironomidae (J)	1.57	2.74	1.22	27.77
Gammarus zaddachi	3.91	3.52	1.19	23.89
Hydrobiidae	1.31	0.4	0.81	9.79
Jaera sp.	1.03	0.63	0.88	8.85

Discussion

In this study, we found that each detritus type decomposed at the highest rate in salinity conditions typical of its native habitat, and that major differences among associated detritivore assemblages were apparent according to habitat. So-called ‘home field

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

In a recent bioassay, Bierschenk et al. (2012), reported more rapid breakdown rate of cotton materials in freshwater than mid-estuary, or near-marine habitats, noting that the decomposition response to variation in salinity depends on the type of material. Our results corroborate and extend these observations in that we demonstrate 'home-field advantage' for detritus decomposition along estuarine gradients. *Quercus* litter decomposed much more rapidly in 'freshwater' than in 'high salinity' habitats while *Fucus* litter displayed the opposite trend. Lopes et al. (2011) reported a similar pattern of decomposition for *F. vesiculosus*, although the relatively rapid breakdown of *Fucus* litter in all environments is unsurprising given its low lignin and cellulose content and relatively high N-content compared to vascular plants (Tenore and Hanson, 1980). Indeed there may be a general tendancy for high quality leaf material to experience faster consuption by invertebrates (Fernandes et al., 2015). The more fibrous leaves of *Quercus* spp. naturally have relatively slow decomposition rates (Petersen and Cummins, 1974) compared with saltmarsh plants or marine macro-algae.

While there is a surprising paucity of literature detailing the breakdown of saltmarsh 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 downsteam with freshwater pulses). Our results indicte that
336 these shifts could greatly impact litter decomposition along the estauarine 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

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

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353 **References**

354 Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA for PRIMER: Guide
355 to Software and Statistical Methods. PRIMER-E, Plymouth, UK
356 Anderson, M.J., Robinson, J., 2003. Generalized discriminant analysis based on
357 distances. Australia and New Zealand Journal of Statistics 45, 301-318.
358 Bärlocher, F., 2005. Leaf mass loss estimated by litter bag technique. In ´Methods to
359 Study Litter Decomposition: A Practical Guide´ (Eds M. A. S. Graça, F.
360 Bärlocher and M. O. Gessner.) pp. 115-120. (Springer: Dordrecht, Netherlands).
361 Bierschenk, A.M., Savage, C., Townsend, C.R., Matthaei, C.D., 2012. Intensity of land
362 use in the catchment influences ecosystem functioning along a freshwater-
363 marine continuum. Ecosystems 15, 637-651.Bouma, T.J., van Belzen, J., Balke,
364 T., Zhu, Z., Airoldi, L., Blight, A.J., Davies, A.J., Galvan, C., Hawkins, S.J.,
365 Hoggart, S.P.G., Lara, J.L., Losada, I.J., Maza, M., Ondiviela, B., Skov, M.W.,
366 Strain, E.M., Thompson, R.C., Yang, S., Zanuttigh, B., Zhang, L., Herman,
367 P.M.J., 2014. Identifying knowledge gaps hampering application of intertidal
368 habitats in coastal protection: Opportunities & steps to take. Coastal Engineering
369 87, 147–157.
370 Castela, J., Ferreira, V., Graça, M.A.S., 2008. Evaluation of stream ecological integrity
371 using litter decomposition and benthic invertebrates. Environmental Pollution
372 153, 440-449.
373 Chauvet, E., 1997. Leaf litter decomposition in large rivers: the case of the River
374 Garonne. Limnetica 13, 65-70.
375 Clarke, K.R., Warwick, R.M., 2001. ´Change in marine communities: an approach to
376 statistical analysis and interpretation´, 2nd Edn. (PRIMER-E: Plymouth, UK.)

377 Cummins, K. W. and Klug, M. J. (1979). Feeding ecology of stream invertebrates.
378 *Annual Review of Ecology and Systematics* **10**, 147-172.
379 Cummins, K.W., Wiltzbach, M.A., Gates, D.M., Perry, J.B., Taliaferro, W.B., 1989.
380 Shredders and riparian vegetation: leaf letter that falls into streams influences
381 communities of stream invertebrates. BioScience 39, 24-31.
382 Esteves, L.S., 2014. Managed realignment: a viable long-term coastal management
383 strategy? SpringerBriefs in Environmental Science. New York: Springer.
384 Fernandes, I., Duarte, S., Cássio, F., Pascoal, C., 2015. Plant litter diversity affects
385 invertebrate shredder activity and the quality of fine particulate organic matter in
386 streams. Marine and Freshwater Research 66, doi.org/10.1071/MF14089.
387 Friberg, N., Jacobsen, D., 1994. Feeding plasticity of 2 detrivore-shredders. Freshwater
388 Biology 32, 133-142.
389 Graça, M.A.S., 2001. The role of invertebrates on leaf litter decomposition in streams –
390 a review. International Review of Hydrobiology 86, 383-393.
391 Hanley, M.E., Hoggart, S.P.G., Simmonds, D.J., Bichot, A., Colangelo, M.A., Bozzeda,
392 F., Heurtefeux, H., Ondiviela, B., Ostrowski, R., Recio, M., Trude, R.,
393 Zawadzka-Kahlau, E., Thompson, R.C., 2014. Shifting sands? Coastal protection
394 by sand banks, beaches and dunes. Coastal Engineering 87, 136-146.
395 Hoggart, S.P.G., Hanley, M.E., Parker, D.J., Simmonds, D.J., Franklin, E.L.,White A.C.,
396 Bilton, D.T., Rundle, S.D., Penning-Rowsell, E.C., Trifonova, E., Vergiev, S.,
397 Filipova-Marinova, M., Kotsev, I., Thompson, R.C., 2014. The consequences of
398 doing nothing: The effects of seawater flooding on coastal zones. Coastal
399 Engineering 87, 169-182.

IPCC, 2007. ´The physical science basis contribution of working group I the fourth assessment report of the Intergovernmental Panel on Climate Change´. (Cambridge University Press: Cambridge, UK.)

Intergovernmental Panel on Climate Change (IPCC), 2012. Summary for policymakers, in Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation, edited by C. Field et al., pp. 1–19, Cambridge Univ. Press, Cambridge, UK.

Jewell, M.D., Shipley, B., Paquette, A., Messier, C., Reich, P.B. 2015. A traits-based test of the home-field advantage in mixed-species tree litter decomposition. Annals of Botany 116: doi:10.1093/aob/mcv105

Kirwan, M.L., Langley, G.A., Guntenspergen, G.R., Megonigal, J.P., 2013. The impact of sea-level rise on organic matter decay rates in Chesapeake Bay brackish tidal marches. Biogeosciences 10, 1869-1876.

Lettice, S., Jansen, M.A.K., Chapman, D.V., 2011. Differential decomposition patterns of marine and terrestrial biomass in a coastal lagoon. Geo-Eco-Marina 17, 51-58.

Lopes, M.L., Martins, P., Rodrigues, A.M., Quintino, V., 2013. Macroinvertebrates communities associated with the decomposition of *Phragmites australis* and *Fucus vesiculosus* in transitional systems. Journal of Sea Research 83, 72-82.

Lopes, M.L., Martins, P., Ricardoa, F., Rodrigues, A.M., Quintino, V., 2011. *In situ* experimental decomposition studies in estuaries: A comparison of *Phragmites australis* and *Fucus vesiculosus*. Estuarine, Coastal and Shelf Science 92, 573-580.

423 Marinucci, A.C., 1982. Trophic importance of *Spartina alterniflora* production and
424 decomposition to the marsh-estuarine ecosystem. Biological Conservation 22,
425 35-58.
426 Martins, P., Lopes, M.L., Rodrigues, A.M., Gomes, N.C., Quintino, V., 2012. Bacterial
427 communities associated with the decomposition of *Fucus vesiculosus* in
428 transitional waters. Estuarine, Coastal and Shelf Science 110, 116-124.
429 McLusky, D.S., Elliott, M., 2004. The Estuarine Ecosystem. Ecology, Threats and
430 Management, 3rd Edn. (Oxford University Press: Oxford, UK.).
431 Mendelssohn, I.A., Sorrell, B.K., Brix , H., Schierup, H-H., Lorenzen, B., Maltby, E.,
432 1999. Controls on soil cellulose decomposition along a salinity gradient in a
433 *Phragmites australis* wetland in Denmark. Aquatic Botany 64, 381-398.
434 Menéndez, M., Martinez, M., Hernàndez, O., Comìn, F. A., 2001. Comparison of leaf
435 decomposition in two Mediterranean rivers: a large eutrophic river and an
436 oligotrophic stream (S Catalonia, NE Spain). International Review for
437 Hydrobiology 86, 475-486.
438 Milcu, A., Manning, P., 2011. All size classes of soil fauna and litter quality control the
439 acceleration of litter decay in its home environment. Oikos 120, 1366-1370.
440 Nicholls, R.J., 2004. Coastal flooding and wetland loss in the 21st century: changes
441 under the SRES scenarios. Global Environmental Change 14, 69-86.
442 Petersen, R.C., Cummins, K.W., 1974. Leaf processing in a woodland stream.
443 Freshwater Biology 4, 343-368.
444 Pontee N.I,, Parsons, A., 2010. A review of coastal risk management in the UK.
445 Maritime Engineering 163, 31-42.

446 Pontee N.I,, Parsons, A., 2012. Adaptation as part of sustainable shoreline management
447 in England and Wales. Maritime Engineering 165, 113-130.
448 Quintino, V., Sangiorgio, F., Ricardo, F., Mamede, R., Pires, A., Freitas, R., Rodrigues,
449 A.M., Basset, A., 2009. *In situ* experimental study of reed leaf decomposition
450 along a full salinity gradient. Estuarine, Coastal and Shelf Science 85, 497-506.
451 Roache, M.C., Bailey, P.C., Boon, P.I., 2006. Effects of salinity on the decay of the
452 freshwater macrophyte, Triglochin procerum. Aquatic Botany 84, 45-52.
453 Sangiorgio, F., Basset, A., Pinna, M., Sabetta, L., Abbiati, M., Ponti, M., Minocci, M.,
454 Orfanidis, S., Arvanitidis, C., Nicolaidou, A., Moncheva, S., Trayanova, A.,
455 Georgescu, L., Dragan, S., Beqiraj, S., Koutsoubas, D., Evagelopoulos, A., 2008.
456 Environmental factors affecting *Phragmites australis* litter decomposition in
457 Mediterranean and Black Sea transitional waters. Aquatic Conservation: Marine
458 and Freshwater Ecosystems 18, 16-26.
459 Sheehan, E.V., Coleman, R.A., Thompson, R.C., Attrill, M.J., 2010. Crab-tiling reduces
460 the diversity of estuarine infauna. Marine Ecology Progress Series 411, 137-148.
461 Tate, A.S., Battaglia, L.L., 2013. Community disassembly and reassembly following
462 experimental storm surge and wrack application. Journal of Vegetation Science
463 24, 46-57.
464 Telesh, I.V., Khlebovich, V.V., 2010. Principal processes within the estuarine salinity
465 gradient: A review. Marine Pollution Bulletin 61, 149-155.
466 Tenore, K.R., Hanson, R.B., 1980. Availability of detritus of different types and ages to
467 a polychaete macroconsumer *Capitella capitata*. Limnology and Oceanography
468 25, 553-558.

Venice System, 1959. Final resolution of the symposium on the classification of brackish waters. Archives of Oceanography and Limnology 11(suppl.), 243-248.

Wong, J.X.W., Van Colen, C., Airoldi, L., 2015. Nutrient levels modify saltmarsh responses to increased inundation in different soil types. Marine Environmental Research 104, 37–46.

Zanuttigh, B., 2011. Coastal flood protection: What perspective in a changing climate? The THESEUS approach. Environmental Science & Policy 14, 845-863.

Zappa, G., Shaffrey, L.C., Hodges, K.I., Sansom, P.G., Stephenson, D.B., 2013. A Multimodel Assessment of Future Projections of North Atlantic and European Extratropical Cyclones in the CMIP5 Climate Models. Journal of Climate 26, 5846-5862.

Appendix

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

Taxa	Fw	Lo	Hi
Ancylidae	*		
Arachnidae	*	*	
Asellus sp.	*	*	
Brachycentridae (J)	*		
Carcinus sp.		*	*
Carcinus sp. (J)		*	*
Chironomidae (J)	*	*	*
Corophium sp.			*
Dytiscidae (J)	*		
Elmidae	*	*	
Elmidae (J)	*	*	
Ephemerellidae (J)	*		
Gammarus pulex	*		
Gammarus zaddachi		*	*
Goeridae (J)	*	*	
Gyrinidae (J)	*		
Hydraenidae (J)	*		
Hydrobiidae	*	*	*
Jaera 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)	*		
Sphaeroma sp.		*	*
Tineidae	*		*

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