2015-09

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

Franzitta, G

<http://hdl.handle.net/10026.1/4722>

10.1016/j.marenvres.2015.07.012

MARINE ENVIRONMENTAL RESEARCH

Elsevier BV

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

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

Giulio Franzitta^{a*}, Mick E. Hanley^b, Laura Airoidi^c, Cecilia Baggini^b, David T. Bilton^b, Simon D. Rundle^b, Richard C. Thompson^b

^aDepartment of Earth and Marine Sciences, University of Palermo, Via Archirafi 22, 90123 Palermo, Italy.

^bMarine Biology and Ecology Research Centre, Plymouth University, PL4 8AA Plymouth, Devon, United Kingdom.

^cDepartment of Biological, Geological and Environmental Sciences, University of Bologna, Via S.Alberto 163, 48123 Ravenna, Italy.

*Corresponding author: giuliofranz@gmail.com

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 of 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 estuarine transition zones. Understanding the vulnerability of estuaries to changes in local abiotic conditions is important given the need to better integrate coastal processes into a wider management framework at a time when coastlines are increasingly threatened by human activities.

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

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

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 (Mendelsohn 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 km², Erme = 43 km²); mean river flow discharge (Yealm = 1.7 m³/s, Erme = 1.9 m³/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 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, $\pm$ standard deviation), at the three habitats in each river (from freshwater to low salinity and high salinity) were: 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 ($\pm$ 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

weight (60°C for 72 hours).

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

Data analyses

Weight loss for each litter species was calculated as percentage according to the following equation: $\%L = (W_0 - W_t) / W_0 \times 100$, where W_0 is the original dry weight of the 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, including 3 orthogonal 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 ($41.3 \% \pm 0.03$) to Lo ($28.4 \% \pm 0.04$) and Hi ($19.2 \% \pm 0.02$) habitats (Fig. 2a). In contrast, the biomass loss of *Fucus* litter was lower in Fw ($80.5 \% \pm 0.02$) with respect to Lo ($95.4 \% \pm 0.01$) and Hi ($95.2 \% \pm 0.01$) 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 % $\pm$ 0.03 in Fw to 50.2 % $\pm$ 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 $\pm$ 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, $p(\text{MC}) = 0.0166$). 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

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	*	*	*

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

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		
<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

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 tendency for high quality leaf material to experience
 faster consumption 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

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

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

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

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

Acknowledgments

We thank Chris McCullough, Elena Righetti, Jana Rajnohova, Sabrina Heiser, Alex
Fraser, Ann Torr, Richard Ticehurst and Roger Haslam for technical support and two
anonymous referees for comments on an earlier version of this MS. This research was
supported by the THESEUS project (EU FP/7, contract number 244104; Innovative
technologies for safer European coasts in a changing climate) and by a Marco Polo
grant of Bologna University to G.F. We are most grateful to Rodney Bastard and
Anthony Mildmay-White for access to the Yealm and Erme respectively.

References

- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK
- Anderson, M.J., Robinson, J., 2003. Generalized discriminant analysis based on distances. *Australia and New Zealand Journal of Statistics* 45, 301-318.
- Bärlocher, F., 2005. Leaf mass loss estimated by litter bag technique. In 'Methods to Study Litter Decomposition: A Practical Guide' (Eds M. A. S. Graça, F. Bärlocher and M. O. Gessner.) pp. 115-120. (Springer: Dordrecht, Netherlands).
- Bierschenk, A.M., Savage, C., Townsend, C.R., Matthaei, C.D., 2012. Intensity of land use in the catchment influences ecosystem functioning along a freshwater-marine continuum. *Ecosystems* 15, 637-651.
- Bouma, T.J., van Belzen, J., Balke, T., Zhu, Z., Airolidi, L., Blight, A.J., Davies, A.J., Galvan, C., Hawkins, S.J., Hoggart, S.P.G., Lara, J.L., Losada, I.J., Maza, M., Ondiviela, B., Skov, M.W., Strain, E.M., Thompson, R.C., Yang, S., Zanuttigh, B., Zhang, L., Herman, P.M.J., 2014. Identifying knowledge gaps hampering application of intertidal habitats in coastal protection: Opportunities & steps to take. *Coastal Engineering* 87, 147-157.
- Castela, J., Ferreira, V., Graça, M.A.S., 2008. Evaluation of stream ecological integrity using litter decomposition and benthic invertebrates. *Environmental Pollution* 153, 440-449.
- Chauvet, E., 1997. Leaf litter decomposition in large rivers: the case of the River Garonne. *Limnetica* 13, 65-70.
- Clarke, K.R., Warwick, R.M., 2001. 'Change in marine communities: an approach to 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 litter 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 detritivore-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.

400 IPCC, 2007. 'The physical science basis contribution of working group I the fourth
 401 assessment report of the Intergovernmental Panel on Climate Change'.
 402 (Cambridge University Press: Cambridge, UK.)
 403 Intergovernmental Panel on Climate Change (IPCC), 2012. Summary for policymakers,
 404 in Managing the Risks of Extreme Events and Disasters to Advance Climate
 405 Change Adaptation, edited by C. Field et al., pp. 1–19, Cambridge Univ. Press,
 406 Cambridge, UK.
 407 Jewell, M.D., Shipley, B., Paquette, A., Messier, C., Reich, P.B. 2015. A traits-based
 408 test of the home-field advantage in mixed-species tree litter decomposition.
 409 Annals of Botany 116: doi:10.1093/aob/mcv105
 410 Kirwan, M.L., Langley, G.A., Guntenspergen, G.R., Megonigal, J.P., 2013. The impact
 411 of sea-level rise on organic matter decay rates in Chesapeake Bay brackish tidal
 412 marches. Biogeosciences 10, 1869-1876.
 413 Lettice, S., Jansen, M.A.K., Chapman, D.V., 2011. Differential decomposition patterns
 414 of marine and terrestrial biomass in a coastal lagoon. Geo-Eco-Marina 17, 51-
 415 58.
 416 Lopes, M.L., Martins, P., Rodrigues, A.M., Quintino, V., 2013. Macroinvertebrates
 417 communities associated with the decomposition of *Phragmites australis* and
 418 *Fucus vesiculosus* in transitional systems. Journal of Sea Research 83, 72-82.
 419 Lopes, M.L., Martins, P., Ricardo, F., Rodrigues, A.M., Quintino, V., 2011. *In situ*
 420 experimental decomposition studies in estuaries: A comparison of *Phragmites*
 421 *australis* and *Fucus vesiculosus*. Estuarine, Coastal and Shelf Science 92, 573-
 422 580.

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., Hernández, O., Comín, 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.

469 Venice System, 1959. Final resolution of the symposium on the classification of
 470 brackish waters. Archives of Oceanography and Limnology 11(suppl.), 243-248.
 471 Wong, J.X.W., Van Colen, C., Airoidi, L., 2015. Nutrient levels modify saltmarsh
 472 responses to increased inundation in different soil types. Marine Environmental
 473 Research 104, 37–46.
 474 Zanuttigh, B., 2011. Coastal flood protection: What perspective in a changing climate?
 475 The THESEUS approach. Environmental Science & Policy 14, 845-863.
 476 Zappa, G., Shaffrey, L.C., Hodges, K.I., Sansom, P.G., Stephenson, D.B., 2013. A
 477 Multimodel Assessment of Future Projections of North Atlantic and European
 478 Extratropical Cyclones in the CMIP5 Climate Models. Journal of Climate 26,
 479 5846-5862.
 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	*		*