Herbivory on macro-algae affects colonization of beach-cast algal wrack by detritivores but not its decomposition

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Abstract

Spatial subsidies have increasingly been considered significant sources of matter and energy to unproductive ecosystems. However, subsidy quality may both differ between subsidizing sources and vary over time. In our studies, sub-littoral herbivory by snails or isopods on red or brown macro-algae induced changes in algal tissues that affected colonization of beach-cast algal wrack by supra-littoral detritivores (amphipods). However, microbial decay and decomposition through the joint action of detritivores and microbes of algal wrack in the supra-littoral remained unaffected by whether or not red or brown algae had been fed upon by snails or isopods. Thus, herbivory on marine macro-algae affects the cross-system

connection of sub-littoral and supra-littoral food webs transiently, but these effects diminish upon ageing of macro-algal wrack in the supra-littoral zone.

1. Introduction

Spatial subsidies (sensu Polis et al. 1997) cross boundaries between seemingly distinct ecosystems and provide nutrients and energy to the recipient system. In this respect, cross-system subsidies have strong implications for species interactions and food web dynamics. Subsidies of materials and organisms can affect all trophic levels of food webs either directly or indirectly. Many food webs rely on cross-system subsidies of detritus for sources of energy and nutrients (Huxel & McCann 1998). Recently, the marine-terrestrial ecotone around the intertidal area of marine coasts has received increasing attention in this respect (e.g. Polis & Hurd 1995, 1996, Rose & Polis 1998, Kawaguchi & Nakano 2001, Fariña et al. 2003, Roth 2003), having been spawned in large part by the now well-documented salmon-bear-forest interaction (Ben-David et al. 1998, Willson et al. 1998, Cederholm et al. 1999, Naiman et al. 2002). The major contributor to marine subsidies into the supralittoral terrestrial zone is beach-cast macrophyte wrack (Orr et al. 2005, and references therein), which provides food (e.g. Mews et al. 2006) and shelter (e.g. Lewis et al. 2007) to invertebrate inhabitants of sand and cobble beaches.

Considering the input of senescent or dead biomass of primary producers from herbivory-influenced standing stocks into detritus pathways, it is not surprising that herbivory-induced changes in plant tissue chemistry also affect detritivores and detritivore-mediated decomposition processes (e.g. Bardgett et al. 1998, Chapman et al. 2003), since similar plant traits affect herbivores that feed on living plant tissue and detritivores that consume detrital plant material (Cornelissen et al. 1999, Wardle et al. 2002, Cortez et al. 2007). In terrestrial systems, there is increasing evidence for the slowed decomposition of leaf litter derived from herbivore-affected trees through herbivore-induced chemical defences of plants (Schweitzer et al. 2005, Fonte & Schowalter 2005), and for herbivore-specific herbivory effects on decomposition (Kay et al. 2008).

Examples of herbivore-induced defence have also been reported in marine algae (Van Alstyne 1988, Yates & Peckol 1993, Cronin & Hay 1996, Pavia & Toth 2000, Rohde et al. 2004, Rothäusler et al. 2005). Algal responses to herbivory depend on both the herbivore species and the algal species. Both direct feeding by the isopod *Idotea balthica* and feeding on neighbouring plants induced chemical defence in the bladder wrack *Fucus vesiculosus*, whereas the snail *Littorina littorea* only induced defence by direct grazing (Rohde et al. 2004). This species has also

been proven to down-regulate defence in the absence of herbivores (Rohde & Wahl 2008). The brown alga *Lessonia nigrescens* responded to amphipods but not to sea urchins, and another brown alga, *Glossophora kunthii*, showed inducible defence against one species of amphipods (*Parhyalella ruffoi*). The red alga *Grateloupia doryphora* did not respond to herbivory by any of the tested grazers, whereas another red alga, *Chondracanthus chamissoi*, responded to one species of amphipods (*Hyale hirtipalma*) and an isopod (*Isocladus bahamondei*) (Rothäusler et al. 2005). Ceh et al. (2005) observed reduced consumption of *Hypnea pannosa* (red alga), *Sargassum asperifolium* (brown alga) and *Cystoseira myrica* (brown alga) by the amphipod *Cymadusa filosa* following previous herbivory by that same mesograzer. Furthermore, the effects of induced defences on potential herbivores may vary among herbivores (Pavia & Toth 2000, Amsler 2001). The sea urchin *Tetrapygus niger* was not affected by induced defences in *L. nigrescens*, but *H. hirtipalma* was (Rothäusler et al. 2005). However, the debate surrounding the structural basis of chemical defence in marine macrophytes is controversial (for discussion, Jormalainen et al. 2003, Kubanek et al. 2004, Macaya et al. 2005), and essentially nothing is known about how herbivore-induced changes in macrophyte tissue chemistry translate into decomposition processes.

Marine detritus frequently subsidizes the terrestrial fringe of coastal ecotones, as much of the annually produced sub-littoral macro-algal biomass is exported into adjacent littoral and supra-littoral habitats. The deposition of macrophyte wrack, detached thalli and blades of macro-algae and sea-grasses, is of major significance as food and/or habitat for invertebrates of the relatively unproductive supra-littoral zone (e.g. Inglis 1989, Colombini et al. 2000, Orr et al. 2005, Mews et al. 2006, Lewis et al. 2007, Rodil et al. 2008). Species-specific decomposition rates of beach-cast wrack through microbial and detritivore action (Mews et al. 2006) may in part be explained by interspecific differences of algal tissue in defence against herbivory. To this end, detritivores prefer aged wrack to fresh wrack (Pennings et al. 2000), possibly because of the decreasing levels of defensive compounds upon ageing (Cronin & Hay 1996, Pennings et al. 2000, Norderhaug et al. 2003). However, the effects of herbivory on the value of macrophyte wrack as a spatial subsidy have, to the best of our knowledge, not been examined experimentally to date.

Differences among macrophyte wrack with respect to habitat quality (cf. Bonte et al. 2003) or nutritive value at different stages of ageing and decomposition (cf. Pennings et al. 2000, Olabarria et al. 2007) affect the population dynamics and activity of invertebrates in stressful environments (cf. Ford et al. 1999, Rossi & Underwood 2002). In particular, wrack

patches of native vs. invasive algae have recently been described as being colonized, and probably utilized, differently by beach invertebrates (Rodil et al. 2008). Hence, we used common herbivores [the isopod *Idotea balthica* (Pallas) (Isopoda: Valvifera) and the snail *Littorina littorea* (Linnaeus) (Gastropoda: Neotaenioglossa)] that feed upon the common brown alga [*Fucus vesiculosus* L. (Phaeophyta)] and a currently establishing non-native red alga [*Gracilaria vermiculophylla* Papenfuss (Rhodophyta)]. Induced defences have been demonstrated for both *Fucus* (see above; Rohde et al. 2004, Rohde & Wahl 2008) and *Gracilaria* (Nylund et al. 2011, Rempt et al. 2012), being active against, e.g. isopod and snail herbivores. Such generalist herbivores (e.g. *I. balthica* and *L. littorea*) prefer *F. vesiculosus* over *G. vermiculophylla*, but readily feed upon the latter when no alternative food source is available (Weinberger et al. 2008, Nejrup et al. 2012), albeit with low growth rates (Nejrup et al. 2012). However, daily biomass uptake by grazers hardly exceeds 10% of the average daily net growth of *G. vermiculophylla* in natural stands (Weinberger et al. 2008), resulting in lower herbivore pressure than on native macroalgae (Nejrup et al. 2012). Hence, *G. vermiculophylla* accumulates in shallow and sheltered waters from where it can be washed ashore during storm events. The invasive *G. vermiculophylla* differs remarkably from the native *F. vesiculosus* in both chemistry and morphology. Both the chemistry and the morphology of macrophytes have been coined major determinants of colonization and utilization by invertebrates as food and habitat (cf. Rodil et al. 2008).

We hypothesize that changes in algal tissue induced by herbivory in the sub-littoral persist beyond detachment, deposition ashore and ageing of wrack, and affect colonization and decomposition of beach-cast algal tissue in the supra-littoral. We test this hypothesis in laboratory (colonization by detritivorous amphipods) and field (decomposition through microbial and macro-detritivore activity) studies.

2. Material and methods

With a combination of field and laboratory studies, we aimed to disentangle the short- (lab) and long-term (field) effects of sub-littoral herbivory on colonization and decomposition, respectively, of beach-cast macroalgal wrack.

2.1. Algae

Algae were collected in spring in coastal waters along the Kiel Fjord (*Fucus*: 54°27′17″N, 10°11′53″E; *Gracilaria*: 54°21′08″N, 10°08′32″E). Prior to the experiment, they were kept in a climate chamber (11°C;

simulated natural long-day light conditions) in separate systems with a continuous flow-through of filtered seawater from the Kiel Fjord for four weeks. Algae of each species were randomly designated separately to three distinct groups in separate flow-through systems: algae without herbivores to prevent or reduce any induced defence against herbivory (cf. Rohde & Wahl 2008); algae with snails (*Littorina littorea* (L.), Gastropoda) to induce defence against snail herbivory; algae with isopods (*Idotea balthica* (Pallas), Isopoda) to induce defence against isopod herbivory.

2.2. Animals

For studying the colonization of freshly deposited wrack by detritivores, we chose beach fleas (Amphipoda: Talitridae: *Orchestia gammarellus* (Pallas)), frequently considered primary macrofaunal colonizers of fresh beach-cast algal wrack on sand and cobble beaches (Griffiths & Stenton-Dozey 1981, Inglis 1989, Colombini et al. 2000, Pelletier et al. 2011). Beach fleas play a major role as consumers of *Fucus* wrack (Adin & Riera 2003).

Both detritivores (*O. gammarellus*) and herbivores (*L. littorea*, *I. balthica*) were collected in spring in the supra-littoral and sub-littoral, respectively, of a sandy beach of the Kiel Fjord (54°27′17″N, 10°11′53″E). Herbivores were immediately added to flow-through systems that contained the algae to be manipulated (see above). Detritivores were kept in a climate chamber (15°C, low-light long-day conditions) for up to two weeks with their natural food source, mixed algal wrack from the site they had been collected, ad libitum, before they were used for colonization preference tests.

2.3. Experimental design

2.3.1. Colonization

Plastic boxes ($20 \times 12 \times 13$ cm^3; $N = 10$ for each assay) were filled with 2 cm wetted sand that had previously been washed thoroughly and oven-dried (60°C, 48 h). On one (randomly chosen) side of the sand area, we placed a piece of algal tissue (either *Fucus* or *Gracilaria*) that had been in contact with either isopods or snails; on the other side, we placed a similar-sized piece of algal tissue (of the same species) that had not been in contact with herbivores for four weeks. Control boxes, free of algae, enabled any intrinsic spatial preference of beach fleas to be excluded (no preference for any side of the box: $p > 0.6$).

In an approach to test the effects of wrack ageing, which is accompanied by leaching of water-soluble compounds (experimentally simulated by

drying and rewetting), we air-dried half of the algal tissue obtained from the pre-experimental treatment with or without herbivores (see above) to constant weight and re-wetted it in seawater prior to placing it in the preference boxes. To each box ($N = 10$ for each treatment level) we added 20 amphipods, mimicking the natural densities of ca 800 m^{-2} in natural drift lines in the vicinity of Kiel (authors' observation). The amphipods remained inside the box for 24 h (15°C) and were kept in the dark to prevent any visual orientation or disturbance.

After 24 h, a shield was quickly placed along the longitudinal centre of each box to separate the areas of herbivory-treated and control algae and to keep the amphipods in place. Subsequently, the amphipods in each side of the box were counted. Beach fleas find algal wrack through olfactory cues and colonize freshly deposited patches within < 1 h (Pelletier et al. 2011). They use wrack patches both as habitat and feeding ground and remain underneath or in the close vicinity of these patches, where they are most frequently found in the field (cf. Lewis et al. 2007, Pelletier et al. 2011). Adult beach fleas can consume up to 60% of their dry body mass per day (Griffiths et al. 1983), and the composition of beach-cast wrack affects their small-scale distribution on sand and gravel beaches (Crawley & Hyndes 2007, Olabarria et al. 2007). Taking all this together, we hold that wrack patches, once colonized by beach fleas, remain densely inhabited (at least in the upper intertidal where patches are rarely submerged: Pelletier et al. 2011). Minor fluxes of immigration and emigration will result in a steady state of colonization until the ageing and decomposition of a particular wrack patch render it less attractive as a habitat and feeding ground.

To evaluate colonization preferences, we calculated the percentage of amphipods on each side of the box and chose the value that exceeded 50% (i.e. equal distribution in both sides) as the estimator of the preference for one algal source or the other. For testing the statistical significance of preferences, we used absolute amphipod counts. To avoid fallacies in the statistical analyses of the preference tests (cf. Roa 1992, Manly 1993), colonization preferences were analysed through resampling statistics (poptools: http://www.poptools.org) according to Storry et al. (2006). In brief, resampling within data pairs (single preference boxes) was performed as 'Shuffling' (i.e. without replacement). Subsequently, a Monte Carlo Analysis with 9,999 iterations was performed on the numerical difference between the numbers of amphipods on both sides of the box. As evaluation criterion we chose 'resampled values' > 'experimental values'. The number of resampled cases that met this criterion divided by the number of iterations provided the p value.

2.4. Decomposition

The decomposition of wrack ashore requires the joint action of microbial decomposers and detritivores that support each other (cf. Mews et al. 2006). Jędrzejczak (2002) and Feike (2004) did not find any significant contributions of macrofaunal decomposers to the breakdown of beach-cast seagrass on sandy beaches in Poland or Germany respectively. In contrast, Griffiths et al. (1983) found that on South African sandy beaches half the kelp wrack input was consumed by talitrid amphipods. On western Canadian shores, the contribution of the macrofauna to macrophyte wrack decomposition depended on the wrack composition (Mews et al. 2006). These authors observed an up to fourfold acceleration of decomposition by detritivorous invertebrates as compared to microbial decay in animal-free mesh bags. Feeding rates by intertidal macrofauna change significantly once beach-cast wrack starts to age (Pennings et al. 2000).

Hence we studied the medium- (1 week) and long-term (3 weeks) decomposition of beach-cast wrack in situ within the supra-littoral of the same beach where amphipods had been captured for the preference tests ($54°27'17''$N, $10°11'53''$E). Samples ($N = 10$ for each treatment) of freshly detached wrack of *Fucus* or *Gracilaria* (either fed upon by snails or isopods or without contact with herbivores for four weeks; see above) were air-dried at room temperature to constant weight (6 days) – to simulate natural ageing within the drift line – and weighed. Dry algal tissue was placed in a mesh bag (10×10 cm^2). In order to separately quantify the effect of microbes and macro-detritivores (cf. Mews et al. 2006), we used two mesh sizes, 1×1 mm^2 and 4×4 mm^2. Rather than using larger meshes (e.g. Mews et al. 2006), we chose this mesh size to minimize loss of algal fragments but to allow for the immigration of amphipods and other macro-detritivores. Bags, filled with wrack of either herbivore-treated or untreated red or brown algae, were deposited within the existing drift line of mainly *Fucus* wrack that was home to high densities (ca 800 m^{-2}) of amphipods.

After 1 week (medium-term decomposition) and 3 weeks (long-term decomposition), we collected the mesh bags. In the laboratory, algal remains were dried to constant weight and weighed for calculating the difference from the initial dry weight of the same sample. Owing to severe storms during the field incubation, some samples were lost so that the initial replicate number of 10 was reduced to 6–9; in the case of snail-treated *Fucus* none of the samples could be recovered in sufficient quantity after three weeks.

Mass loss differences (separately for 1- and 3-week treatments) were analysed by two-way ANOVA (separately for *Fucus* and *Gracilaria*) to separate the effects of induced anti-herbivore defence and presence (large

mesh size) vs. absence (small mesh size) of macro-detritivores on decomposition rates. For the sake of simplicity, mass loss data are depicted as the percentage of the mass loss we obtained from control (herbivore-free) algal tissue as a result of microbial decay without macro-detritivores (small mesh size).

3. Results

3.1. Colonization

Pre-experimental feeding by isopods on macro-algal tissue did not affect the attractiveness of freshly detached and deposited *Fucus* wrack as a habitat and/or food source for amphipods (Figure 1a), but amphipods significantly more densely (62%) colonized the wrack of *Fucus* that had not been in contact with herbivores than that of snail-treated *Fucus* (Figure 1b; negative effect of snail herbivory: $p = 0.04$). In contrast, the freshly deposited wrack of snail-treated *Gracilaria* was preferentially colonized (64%) by amphipods (Figure 1d; positive effect of snail herbivory:
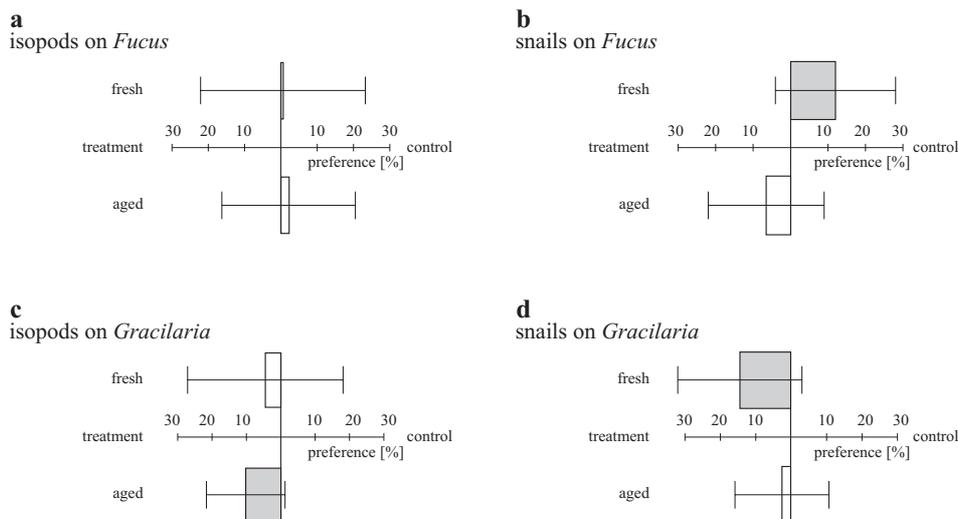
Figure 1. Colonization preference (% of total number) of amphipods (*Orchestia gammarellus*) for wrack of algae that had not been in contact with herbivores for 4 weeks ('control') versus a) wrack of *Fucus vesiculosus* after feeding by isopods (*Idotea balthica*), b) wrack of *Fucus* after feeding by snails (*Littorina littorea*), c) wrack of *Gracilaria vermiculophylla* after feeding by isopods, d) wrack of *Gracilaria* after feeding by snails; grey bars indicate a significant ($\alpha = 0.05$) preference for wrack of herbivore-treated (bar to the left: 'treatment') or untreated (bar to the right: 'control') algae; bars represent mean + SD of 10 replicates

a

b
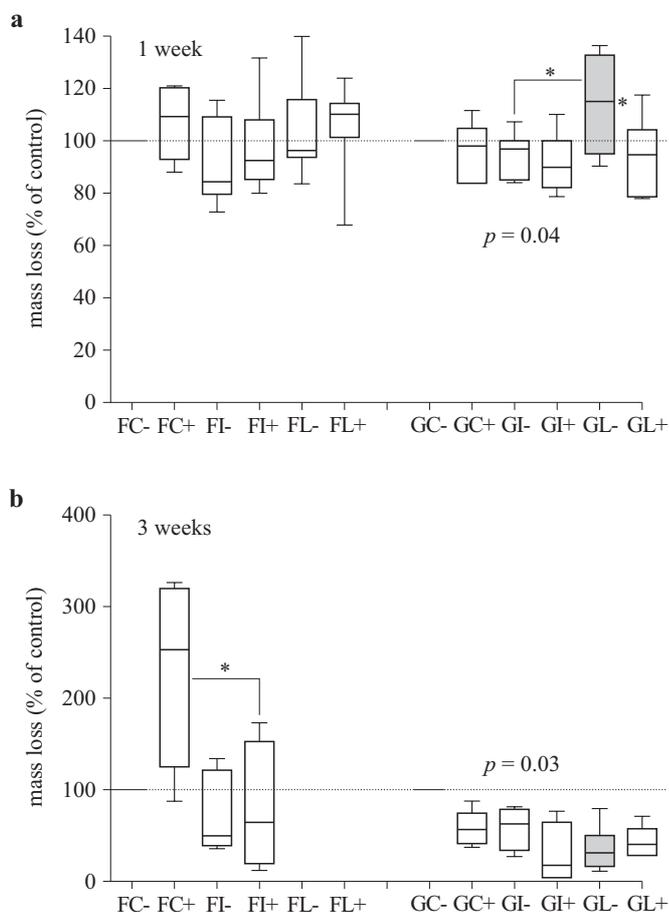
Figure 2. Mass loss of wrack of algae (F – *Fucus vesiculosus*: left, G – *Gracilaria vermiculophylla*: right) that had been in contact with snails (L – *Littorina littorea*) or isopods (I – *Idotea balthica*) or without contact with herbivores (C – control) for four weeks prior to the experiment in in situ-decomposition studies for 1 week (a) and 3 weeks (b). Wrack was either prone to microbial decay (–) or was accessible to macro-detritivores (+); the dotted line (100%) indicates microbial decay rates of wrack of herbivore-free control algae; box plots show minimum and maximum values, and first, second (median) and third quartiles; owing to heavy storms during the incubation, none of the snail-treated *Fucus* samples (FL−/FL+) could be recovered in sufficient quantity from the field. Asterisks indicate statistical differences between treatments ($\alpha = 0.05$); grey boxes designate treatments with mass loss that differs significantly from that of the respective control; *p*-values indicate significance levels of the herbivory effect detected through within-algal species two-way ANOVA

$p = 0.02$). On the other hand, *Gracilaria* wrack was preferentially colonized by amphipods (60%) when algal tissue had been fed upon by isopods only

Table 1. Effects of herbivory and the presence of detritivores on mass loss (two-way ANOVA) of *Fucus* wrack (a) after 1 week and (b) after 3 weeks in situ

(a)

	df	F	p
model	4	435.912	< 0.001
detritivores	1	0.861	0.359
herbivores	1	0.499	0.484
detritivores × herbivores	1	0.017	0.896
error	32		
total	36		

(b)

	df	F	p
model	4	4.967	0.006
detritivores	1	0.599	0.448
herbivores	1	0.001	0.998
detritivores × herbivores	1	0.195	0.663
error	20		
total	24		

after the wrack had been dried and rewetted to simulate ageing and leaching of soluble compounds (Figure 1c; positive effect of isopod herbivory after wrack ageing: $p = 0.02$).

3.2. Decomposition

During three weeks in situ, *Fucus* wrack lost up to 30% of its initial mass, whereas *Gracilaria* wrack was reduced by up to 50%. Compared to the herbivory-free controls, pre-experimental feeding by isopods tended to reduce decomposition rates (both with and without detritivores) during the first week, but insignificantly so (Figure 2a, left), and pre-experimental feeding by snails slightly increased microbial decay rates (small mesh: without detritivores) of *Gracilaria* wrack (Figure 2a, right; effect of snail herbivory on microbial decay: $p = 0.09$). After three weeks, detritivores had increased decomposition rates of control *Fucus* two-fold but insignificantly, and pre-experimental herbivory by isopods decreased decomposition of *Fucus* wrack by detritivores (Figure 2b, left; negative effect of isopod herbivory on detritivores: $p = 0.06$). Pre-experimental herbivory reduced decomposition rates of *Gracilaria* wrack over three weeks, but significantly so (negative effect of snail herbivory on microbial decay: $p = 0.02$) only in the case of snail-treated algae when macro-detritivores did not have access to algal wrack (Figure 2b, right).

Table 2. Effects of herbivory and the presence of detritivores on mass loss (two-way ANOVA) of *Gracilaria* wrack (a) after 1 week and (b) after 3 weeks in situ

(a)

	df	F	p
model	4	353.803	< 0.001
detritivores	1	5.141	0.029
herbivores	1	0.090	0.766
detritivores × herbivores	1	0.575	0.453
error	38		
total	42		

(b)

	df	F	p
model	4	8.654	< 0.001
detritivores	1	1.027	0.318
herbivores	1	1.718	0.199
detritivores × herbivores	1	0.167	0.686
error	32		
total	36		

Overall, however, there was no consistent pattern of effects of the herbivory- or mesh bag-treatment on the decomposition of *Fucus* (Table 1) or *Gracilaria* (Table 2) wrack over 1 or 3 weeks. Thus, induced anti-herbivore defence in macroalgae did not affect the decomposition of beach-cast wrack in situ, irrespective of which herbivore had fed on the algal tissue (not shown). It was only *Gracilaria* wrack decomposition after 1 week that was affected by the presence of macro-detritivores (Table 2a), with on average slightly reduced decomposition when macro-detritivores were present (Figure 2a).

4. Discussion

As early as 1996, Grime et al. demonstrated a causal connection between anti-herbivore defence in terrestrial vascular plants and the decomposition rate of the leaf litter of various plant species, and this pattern was confirmed across bio-geographical and climatic zones by Cornelissen et al. (1999). In this respect, herbivorous and detritivorous consumers of terrestrial vegetation respond to the same plant traits in terms of preference and consumption (e.g. Cornelissen et al. 1999, Wardle et al. 2002, Cortez et al. 2007), and chemical changes in vegetal composition in response to herbivory will also affect detritivores and decomposition rates (e.g. Schweitzer et al. 2005, Fonte & Schowalter 2005).

Our present results suggest that this pattern only partially holds true for the decomposition of marine macro-algal wrack in the terrestrial realm. Whereas initial colonization of freshly deposited wrack patches by beach fleas is affected by herbivore-induced changes in algal tissue, differences between anti-herbivore defended and undefended algal tissue seem to diminish over time and to not affect the decomposition of algal wrack.

4.1. Persistence of herbivore-induced changes in algal tissue

Obviously, herbivore-induced changes in algal chemistry persisted following deposition of algal tissue ashore (since colonization of algal wrack by detritivores was affected by herbivory). However, in contrast to the above findings for terrestrial vegetation, the effects of algal anti-herbivore defence (1) depended on both the algal and herbivore species as far as colonization patterns are concerned, and (2) changed with ageing of algal wrack ashore. In view of the controversial debate regarding which algal compounds are involved in chemical anti-herbivore defence (Pavia et al. 1997, Deal et al. 2003, Jormalainen et al. 2003, Kubanek et al. 2004, Macaya et al. 2005), as well as the lack of chemical analysis within the present study, we can but speculate about the nature of such herbivore-induced changes. High concentrations of phenolic compounds, for instance, correlate with low densities of surface-associated microbes (Van Alstyne et al. 1999), and phenolic compounds are known to impair decomposition processes (Palm & Sanchez 1991, Mafongoya et al. 1998, Northrup et al. 1998).

4.2. Colonization of beach-cast wrack by detritivores

While herbivory by snails reduced the colonization of freshly beach-cast *Fucus* wrack by amphipods, the colonization of fresh *Gracilaria* wrack was promoted following herbivory by snails. Ageing diminished any effect of herbivory by snails, but highlighted the effect of isopod herbivory on *Gracilaria*, with increased attractiveness of isopod-grazed algal tissue to detritivorous amphipods.

Hence, isopods and snails induce different chemical defences in *Fucus*, as has already been shown by Rohde et al. (2004). Further, snail-induced chemical defences differ between *Fucus* and *Gracilaria*, as they hampered colonization of *Fucus* wrack but promoted colonization of *Gracilaria* wrack. Both effects vanished with wrack-ageing, suggesting the involvement of chemical compounds that are prone to microbial or physico-chemical degradation.

Similarly, isopod-induced chemical compounds in *Gracilaria* appear to degrade with wrack-ageing, but their degradation products increase the attractiveness of the wrack to beach fleas. Pennings et al. (2000) found an increased preference of two amphipods and an isopod from the supra-littoral zone for aged wrack of seven different macro-algae. They hypothesized increasing organic and mineral contents with ageing to mediate these preferences. Alternatively, or additionally, reduced levels of defensive compounds may have made aged wrack more palatable than fresh wrack (for brown algae: Cronin & Hay 1996, Pennings et al. 2000, Norderhaug et al. 2003). Given sufficient time, there are successional changes in the wrack fauna (Griffiths & Stenton-Dozey 1981, Inglis 1989, Colombini et al. 2000, Olabarria et al. 2007) that might be explained by changes in wrack chemistry.

Although transient, the effects of sub-littoral herbivory on supra-littoral colonization of macro-algal wrack may affect the marine-terrestrial ecotone. Amphipods in the wrack line provide food to various predators, both marine and terrestrial (Lewis et al. 2007). Differences among wrack patches in terms of attractiveness to supra-littoral detritivores may therefore translate into differences in cross-system nutrient fluxes, when herbivore pressure becomes regionally massive.

4.3. Decomposition of beach-cast wrack

Decomposition rates clearly differed among algal species, but herbivory did not affect decomposition. In contrast to previous findings of the significant acceleration of decomposition by detritivores (e.g. Griffiths et al. 1983, Williams 1984, Chown 1996, Mews et al. 2006), detritivores either had no effect on or reduced the mass loss of algal wrack (*Gracilaria* during the first week of decomposition). Similarly, Jędrzejczak (2002) and Feike (2004) found no significant contributions of macrofaunal decomposers to the breakdown of beach-cast seagrass.

Nevertheless, in pair-wise comparison, detritivores promoted mass loss of *Fucus* wrack after herbivory by isopods in comparison to the herbivore-free control during three weeks, somewhat paralleling the increased attractiveness of isopod-treated *Gracilaria* wrack upon ageing. Microbial decay of *Gracilaria* wrack after herbivory by the isopod was faster than after herbivory by snails during the first week. We hold that this was the result of enhanced microbial activity, possibly due to the snail mucus left on algal surfaces (cf. Zimmer et al. 2004; Mews et al. 2006, Ewers et al. 2012). The same effect would explain the significant preference of amphipods for freshly snail-treated *Gracilaria* wrack. However, detritivores significantly hampered mass loss of *Gracilaria* wrack after herbivory by snails. These

findings appear to stand in contrast with the enhanced colonization of snail-grazed *Gracilaria* wrack, but overall they show that any chemical changes in the algal tissue due to herbivory attenuate rapidly during decomposition ashore (see above; cf. Cronin & Hay 1996, Pennings et al. 2000, Norderhaug et al. 2003). Both *Fucus* (Mews et al. 2006; this study) and *Gracilaria* (Hanisak 1993; this study) decompose slowly enough to persist in the wrack line for long enough to lose any herbivore-induced chemical compound. Deposits of other species of algal wrack, however, decompose completely within just a few days (Mews et al. 2006). In these fast-decomposing species, any herbivore-specific effect on the fate of algal wrack (see above) that had diminished in *Fucus* and *Gracilaria* after one week ashore may affect short-term decomposition processes. Further studies with additional algae and additional herbivores may provide valuable insights into this particular aspect of the marine-terrestrial ecotone.

5. Conclusions

We provide evidence for herbivory resulting in herbivore- and alga-specific changes in algal chemistry that persist until algal tissue is deposited ashore as wrack. Thus, herbivory on macro-algae in the sub-littoral transiently affects the fate of freshly beach-cast algal wrack by detritivorous invertebrates in the supra-littoral. However, provided that macro-algal wrack remains ashore for long enough, any effect of herbivore-induced change in algal chemistry vanishes early during decomposition.

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