Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada

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ABSTRACT: The fate of subtidally drifting macrophytal detritus after its deposition ashore was studied based on short-term mass loss effects and species composition of beach-cast detritus. Different species of macroalgae and seagrass varied in both physical and microbial decay, as well as faunal decomposition rates. Their preferred status as food for detritivorous amphipods also varied. Thus, beach-cast detritus changed in species composition during detritus aging. Estimated turnover rates, based on daily input rates and mass loss rates, ranged from <1 d for *Nereocystis luetkeana*, *Macrocystis integrifolia* and *Ulva* spp. to roughly 30 d for *Fucus* spp. and *Phyllospadix* spp. Thus, the dynamics of nutrient fluxes within the marine–terrestrial ecotone depends not only on the spatial distribution and amount of beach-cast detritus, but also on its species composition.

KEY WORDS: Marine–terrestrial ecotone · Beach-cast wrack · Decomposition · Macroalgae · Seagrass · Talitrid amphipods

INTRODUCTION

Living seaweeds function as nutrient sinks in coastal waters. However, following senescence, storms or other heavy weather, they become detrital material that is often deposited ashore, where it decomposes and ends up as a nutrient source (Hanisak 1993). Thus, marine phytodetritus (henceforth termed 'wrack') can result in large net fluxes of nutrients from the subtidal/intertidal areas to beaches and other nearshore terrestrial systems (Ochieng & Erftemeijer 1999, Piriz et al. 2003, Orr et al. 2005). The role of macrophyte-derived wrack as an input for organic carbon and nitrogen has been extensively examined for subtidal consumers (Seiderer & Newell 1985, Mann 1988, Fielding & Davis 1989). In contrast, relatively little attention has been given to the consequences for food web dynamics of the intertidal zone (Bustamante & Branch 1996). The degree to which this 'spatial subsidy' (sensu Polis et al. 1997) has consequences for intertidal and supralittoral macro- and meiofauna depends on both the quantity and the species composition of beach-cast wrack.

In a previous study, Orr et al. (2005) observed both overall mass loss of wrack and changes in its species composition during the course of wrackline aging. The factors contributing to this observation include mechanical breakdown of wrack as a consequence of repeated drying–rewetting events brought about through solar radiation, morning dew and rain (Newell et al. 1996, Vahatalo et al. 1998), flocculation and sedimentation (Harrison 1989), removal of wrack through tidal currents and wave action (Orr et al. 2005), as well as leaching and microbial decomposition of detritus and its fragmentation through feeding by detritivores (Newell & Bärlocher 1993, Zimmer et al. 2002, 2004). Tidal events render the input of wrack to, and removal from, the wrackline a dynamic process that allows *in situ* decomposition through leaching and microbial and faunal beach dwellers for no more than 1 d in some instances (Orr et al. 2005). Thus, we were interested in short-term (=1 d) mass loss of freshly deposited wrack

patches. The present study aimed to evaluate short-term wrack mass loss in terms of food preferences of detritivores that are found to forage on this allochthonous material. Here, we differentiate between mass loss solely owing to leaching of water-soluble compounds and microbial activity (henceforth decay) and mass loss by decomposition, i.e. by decay plus feeding by detritivorous macroinvertebrates.

We hypothesize that the species composition of aged wracklines (~2 wk) can be explained by (1) differential input and removal of wrack species (Orr et al. 2005), (2) differential decay rates of initially present wrack species, and (3) the activity of supratidal detritivores colonizing beach-cast wrack.

MATERIALS AND METHODS

The main study site was in Barkley Sound, a large embayment (>> 550 km^2) on the west coast of Vancouver Island, British Columbia, Canada (Fig. 1). We chose 4 beaches on Edward King Island with different exposure to wave action but similar sediment characteristics (for details, see Orr et al. 2005) for field studies on *in situ* decomposition, namely: EKS (sheltered):

48° 49′ 39.9″ N, 125° 12′ 47.0″ W, EKE (sheltered): 48° 49′ 45.7″ N, 125° 12′ 18.8″ W, EKW (exposed): 48° 49′ 44.9″ N, 125° 12′ 57.8″ W, EKN (exposed): 48° 50′ 01.1″ N, 125° 12′ 46.2″W. The first two beaches had southeast-facing aspects; the latter two, west-facing. All beaches were lunate-shaped, with cobbles on the surface underlain by a gravel mixture. Field studies were performed in August 2003.

In situ decay of freshly deposited wrack was studied using nylon mesh bags (100 × 100 mm^2) with a mesh size of 350 µm (n = 7 for each beach), which prevented the intrusion of meso- and macroinvertebrate detritivores (mostly amphipods). Detritivore-aided decomposition was studied using nylon bags (150 × 100 mm^2) with a mesh size of 10 mm (n = 7 for each beach). We collected near-shore floating debris of 5 algal species common to subtidal catchments in the area: *Nereocystis luetkeana*, *Macrocystis integrifolia*, *Fucus* spp*., Ulva* spp*. and Phyllospadix* spp. This material, which would serve as drift wrack, was blotted dry in the laboratory, weighed, and placed in mesh bags after re-wetting with seawater. Later that same day, mesh bags with ca. 0.6 g dry weight wrack (this is well within the range of daily wrack input observed by Orr et al. 2005 at the same site) were buried in the most recent, fresh, wet drift line, and collected approximately 24 h later. In the laboratory, wrack remnants were rinsed with deionized water to remove inorganic material, oven-dried (24 h at 60°C) and weighed. Samples (n = 7) of each fresh wrack species were oven-dried (24 h at 60°C) and weighed to obtain a fresh:dry mass ratio of freshly deposited wrack. Differences between dry mass before (calculated) and after the experiment served as measure of wrack mass loss through decay and detritivore activity.

For feeding preference tests with one of the most abundant amphipods, *Megalorchestia pugettensis*, we collected the 5 most common species of algae (*Fucus* spp., *Ulva* spp., *Macrocystis integrifolia*, *Chondracanthus corymbiferus*, and *Phyllospadix* spp.) as well as leaf litter of salal *Gaultheria shallon*, a terrestrial shrub species that accumulates in wracklines higher on the beach platform (cf. Orr et al. 2005). In the laboratory, detritus was thoroughly washed with deionized water, oven-dried at 30°C for 48 h to simulate air-drying in the deposited drift line, and then cut into pieces and weighed to determine the initial dry mass. After re-wetting by
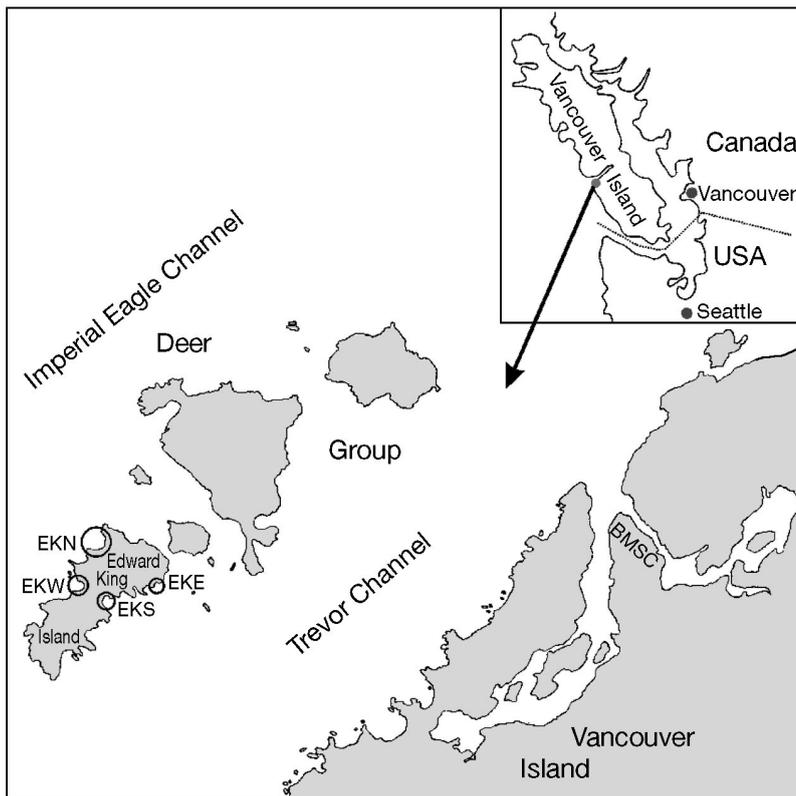

Fig. 1. Study sites on Edward King Island, Barkley Sound, British Columbia, Canada. BMSC: Bamfield Marine Sciences Centre

spraying with seawater, pieces of all different types of detritus were offered simultaneously to 10 amphipods (n = 9) in Petri dishes that had 5 mm of wet sand. After 2 d, the remaining detritus was removed, washed with deionized water, dried and weighed again. Consumption was determined as milligram wrack consumed by 10 amphipods during 2 d. These data were used for statistical analyses through resampling statistics as described in Stovvy et al. (2006), using 9999 iterations for each comparison, followed by pairwise comparisons subjected to Bonferroni corrections. For graphical presentation these data were transformed to percent of total amount consumed.

RESULTS

Our mesh bag decomposition experiment revealed that freshly deposited *Nereocystis luetkeana* decomposed rapidly through decay (350 µm mesh size: no access for meso- and macroinvertebrate decomposers) with mass loss rates of 60 to 90% d^{-1}. Decay of *Macrocystis integrifolia* and *Phyllospadix* spp. ranged from 10 to 40% d^{-1}; *Ulva* spp. and *Fucus* spp. degraded with rates of less than 30 and 15% d^{-1}, respectively (Fig. 2a). Access of meso- and macroinvertebrates (10 mm mesh size) increased mass loss of *N. luetkeana*, *M. integrifolia* and *Ulva* spp. more than 1.2-, 2.8-, and 3.7-fold, respectively (Fig. 2b). Mass loss of *Fucus* spp. was essentially not affected by the presence of detritivores. *N. luetkeana*, *M. integrifolia* and *Ulva* spp. (except for EKS) were removed completely from the mesh bags during the 24 h incubation. Thus, actual mass loss might be expected to be much higher in the field, with the present data showing only the minimum of decay. These patterns were similar among the 4 beaches irrespective of their aspect or exposure.

Feeding preference tests using the amphipod *Megalorchestia pugettensis* revealed feeding rates (Fig. 3) that to some degree corroborated the overall decomposition rates deduced from the comparison of fresh and aged drift lines (Fig. 4). Among 6 available food sources, *Macrocystis integrifolia* and *Fucus* spp. were clearly preferred over *Chondracanthus corymbiferus*, *Ulva* spp., *Phyllospadix* spp. and *Gaultheria shallon* (salal) leaf litter, the latter being little consumed.

DISCUSSION

Our findings clearly indicate differential mass loss of different wrack species due to decay and faunal decomposition processes. This coincides with reported differences in species composition between fresh and aged wracklines (Orr et al. 2005 and present Fig. 4).
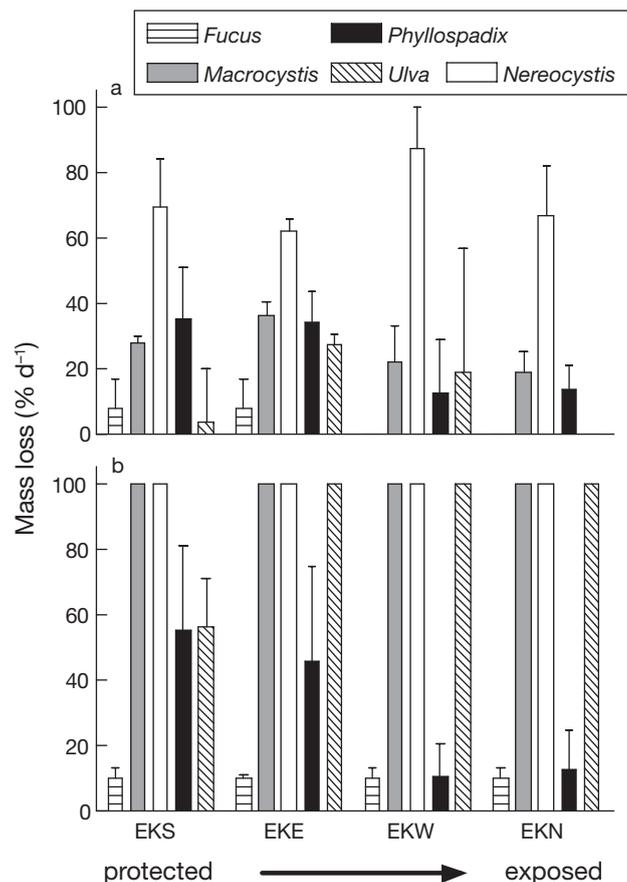

Fig. 2. Mass loss (mean + SD, n = 7 for each beach) of selected wrack species in mesh bags due to (a) decay through leaching and microbial activity, and (b) decomposition (decay plus detritivore feeding; see 'Introduction') at different beaches on Edward King Island (Fig. 1). In (b) *Macrocystis integrifolia*, *Nereocystis luetkeana* and *Ulva* spp. were degraded completely at all beaches (except for *Ulva* spp. at Site EKS)

While *Nereocystis luetkeana* wrack was characterized by rapid mass loss through decay, *Ulva* spp. and *Fucus* spp. lost mass more slowly, with *Macrocystis integrifolia* and *Phyllospadix* spp. exhibiting intermediate decay rates. These differences can be explained in part by variation in the chemical composition of the wrack. *Fucus* spp. is high in phenolic compounds (Targett et al. 1992, Zimmer et al. 2001) that are known to slow down decay of detritus. This might shift the microbial preference to other brown algae with lower phenol content such *Nereocystis luetkeana* and *M. integrifolia* (Pennings et al. 2000). In contrast to *Fucus* spp., wrack of *N. luetkeana* and *M. integrifolia* is extensively covered by mucus soon after deposition ashore. This mucus mainly consists of alginate, the major structural component of brown algae cell walls. Leaching of this component highly promotes mass loss. *Phyllospadix* spp. is also high in phenols (Agostini et
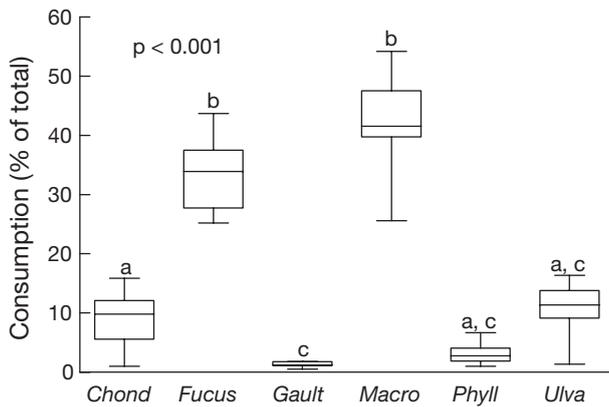
Fig. 3. *Megalorchestia pugettensis.* Feeding preference of amphipod, simultaneously offered selected wrack: *Chondracanthus corymbiferus* (*Chond*), *Fucus* spp. (*Fucus*), *Gaultheria shallon* (*Gault*), *Macrocystis integrifolia* (*Macro*), *Phyllospadix* spp. (*Phyll*), *Ulva* spp. (*Ulva*). Box plots represent median, 25% percentiles, and minimum and maximum (n = 7). Different lower-case letters designate significant differences ($\alpha \le 0.05$)

al. 1998, Bianchi et al. 1999) and in addition does contain lignin and cellulose. Nevertheless decay of *Phyllospadix* spp. was comparable to that of *M. integrifolia*, indicating that factors other than phenolic or lignocellulose contents must be considered here. There are essentially no phenolics in *Ulva* spp., which are also characterized by a low C:N ratio favorable for foraging (Pennings et al. 2000). Notwithstanding these 2 features, *Ulva* spp. did not decompose as fast as *N. luetkeana.* Afzal Rizvi & Shameel (2005) found remarkable amounts of phytotoxins in *U. intestinalis*
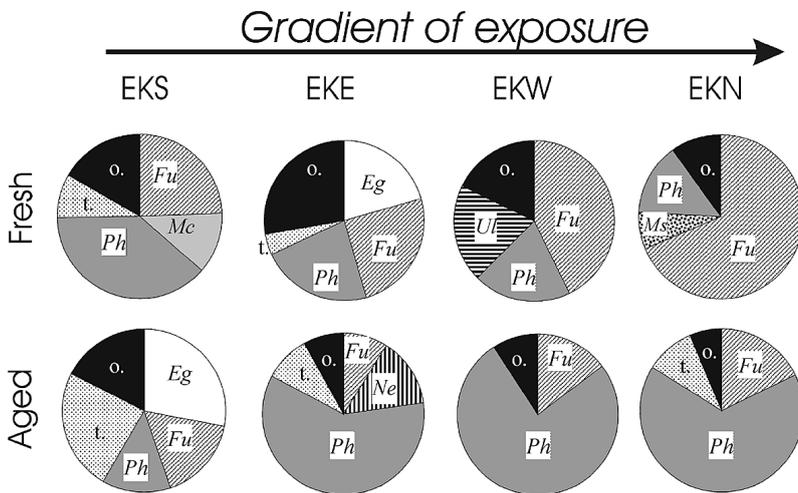

Fig. 4. Species composition of fresh (most recent) and aged (~2 wk) wracklines at beaches with different wave exposures on Edward King Island, July to August 2003. Data are median percent values of 3 collections each at 2 beaches per substratum type. *Eg*: *Egregia menziesii*, *Fu*: *Fucus* spp., *Mc*: *Macrocystis integrifolia*, *Ms*: *Mastocarpus papillatus,* *Ne*: *Nereocystis luetkeana*, *Ph*: *Phyllospadix* spp., *Ul*: *Ulva* spp., t.: terrestrial; o.: other (from Orr et al. 2005)

that might also be active against microbes, inhibiting microbial colonization and decay of algal thalli.

In accordance with the rapid mass losses we observed in the field, *Macrocystis integrifolia* was one of the preferred food sources for *Megalorchestia pugettensis*, a common detritivore feeding upon wrack on beaches in Barkley Sound, but *Fucus* spp. was just as well accepted as *M. integrifolia*. Like *Megalorchestia pugettensis*, *Talitrus saltator*, a common talitrid amphipod at beaches in northern Europe, preferentially feeds on *F. serratus* in Brittany, France (Adin & Riera 2003). Both drift and wrack of *M. integrifolia* exhibit a significantly lower C:N ratio than those of *Fucus* spp., as well as a lower content of phenolic compounds (Pennings et al. 2000, Zimmer et al. 2001). However, *Traskorchestia traskiana*, another common beach hopper on cobble beaches at Barkley Sound, prefers freshly detached *Fucus* spp. (and *Ulva* spp.) over *Nereocystis luetkeana* and *M. integrifolia*; wrack is preferred over drift, and consumption of *M. integrifolia*, *Ulva* spp. and *Fucus* spp. increases by a factor of 6 to 8, while *N. luetkeana* wrack is consumed at only twice the rate as *N. luetkeana* drift (Pennings et al. 2000). Thus, factors other than mucus and phenolics or C:N ratio must be responsible for amphipod feeding preferences. In the case of *T. traskiana*, the content of organic carbon rather than the oft-mentioned nitrogen determines feeding preferences (Pennings et al. 2000). Although the availability of nitrogen is one of the most important limiting factors for detritivores, the quality of the available carbon source, i.e. its digestibility, has been suggested as a main contributing factor (Hobbie 2000). Detritivorous amphipods may use wrack-colonizing microbiota as a source of easily accessible nitrogen, while an important carbon source is obtained from wrack plant material (Wildish 1988). Detailed comparative studies about tensile strength of the plant material, lipid content or secondary compounds other than phenolics, as well as microbial biomass on beach-cast wrack and its significance for beach detritivores are needed.

Jędrzejczak (2002) and Feike (2004) observed insignificant contributions of macrofaunal decomposers to the breakdown of beach-cast seagrass on sandy beaches in Poland and Germany, respectively. In contrast, Griffiths et al. (1983) found that on South African sand beaches half the kelp wrack input is consumed by talitrid amphipods. When meso- and macro-detritivores were permitted access in our wrack decomposi-

tion experiments (10 mm mesh size, Fig. 2b) these 2 contradicting findings were corroborated: detritivores did not contribute to the decay of *Phyllospadix* spp., but did increase mass loss of *Fucus* spp. at those 2 exposed beaches that, according to Orr et al. (2005) (cf. present Fig. 4) accommodate large amounts of this wrack, while the effects of detritivores were insignificant at those 2 sheltered beaches that, according to Orr et al. (2005; cf. present Fig. 4) accommodate only relatively small amounts of *Fucus* spp. (Fig. 2). These findings are, at least in part, in accordance with the feeding preferences of *Megalorchestia pugettensis* ingesting only small amounts of *Phyllospadix* spp. but preferring *Fucus* spp. over most other wrack types. In contrast, the faunal impact on degradation of *Nereocystis luetkeana*, *Macrocystis integrifolia*, and *Ulva* spp. was high, resulting in complete removal of the algal tissue. This means an up to 4-fold acceleration of decomposition processes in mesh bags that provided access for detritivorous invertebrates; taking into account the complete removal of *N. luetkeana*, *M. integrifolia* and *Ulva* spp. from large-meshed bags, we may even assume a much higher increase in wrack mass loss if more material is provided in the field. Considering our experimental design to reflect the average daily input of wrack into the upper intertidal zone (cf. Orr et al. 2005), we hold that all the daily deposited wrack of *N. luetkeana*, *M. integrifolia* and *Ulva* spp. will be removed from the wrackline through the activity of detritivores within 1 d, while no more than 15% of the daily input of *Fucus* spp. wrack is degraded on a daily basis (Orr et al. 2005). We obtained similar values for *Phyllospadix* spp. on exposed beaches, but comparably high mass losses of roughly 50% of the daily input at sheltered sites. Overall, our data explain the persistence of these wrack types in aging wracklines that has been described by Orr et al. (2005; cf. present Fig. 4). By comparison, communities of kelp flies (Diptera: Helcomyzidae) in subantarctic South Georgia consumed 100 to 120 g kelp m^{-2} d^{-1}, reducing the wrack dry mass by 70% in 7 d (Chown 1996). Williams (1984) observed decomposition rates of 50% in a freshly detached chlorophyte, *Caulerpa cupressoides*, after 7 d in the tropical water column, as well as in oxic beach sediments and anoxic seagrass-bed sediments. In an artificial tank connected to a subtropical lagoon in Florida, submerged wrack of the green *U. lactuca* and the red *Gracilaria verrucosa* was reduced by 50% after 5 and 3 wk, respectively, at 25 to 30°C (Hanisak 1993). However, decomposition rates varied greatly over time in Hanisak's (1993) study, being highest after 5 and 3 wk, respectively. Our findings suggest that decomposition of beach-cast wrack proceeds much faster in drift lines on Barkley Sound beaches: considering the potential decomposing activity of invertebrate detritivores, as in Williams' (1984)

and Hanisak's (1993) studies, the entire amount of daily deposited *N. luetkeana*, *M. integrifolia* and *Ulva* spp. will be decomposed within 1 d, i.e. before the next higher of 2 succeeding unequal high tides can remove the wrack from the beach into subtidal wrack pools (cf. Orr et al. 2005). In contrast, based on the daily input estimated by Orr et al. (2005) and an extrapolation of the present results on mass loss to a per meter square basis, wrack of *Fucus* spp. and *Phyllospadix* spp. would last for about 30 d, were it to remain in place for a sufficiently long period. However, this will only be the case for wracklines deposited by spring high tides, since beach-cast material is prone to highly dynamic removal through tidal events (Orr et al. 2005). This observation of rapid decomposition of some (but not all) types of wrack may explain why Orr et al. (2005) did not find significant amounts of *N. luetkeana*, *M. integrifolia* and *Ulva* spp. in most aged wrack deposits on cobble beaches, despite these algae being common in subtidal waters in Barkley Sound (authors' unpubl. obs.), while others, such as *Fucus* spp. and *Phyllospadix* spp., persist in the wrack upon aging (Fig. 4).

We were surprised to find extremely low mass loss rates of *Fucus* spp. through decay at exposed sites where this species (owing to its predominant contribution to living macrophyte biomass) contributes significantly to the total wrack input (Fig. 4). However, in accordance with the feeding preference of *Megalorchestia pugettensis*, detritivore access to the wrack significantly increased mass loss of *Fucus* spp. at these sites, while this was not the case at the sheltered sites with a relatively insignificant contribution of *Fucus* spp. to the wrackline. We suggest that these between-site differences are due to adaptations of the detritivorous beach fauna to the prevailing food source, be it in terms of different species composition or through individual physiological response within the same species. In contrast, mass loss of *Phyllospadix* spp. through decay tended to be higher at those (sheltered) sites where this species (owing to its predominant contribution to subtidal macrophyte biomass) contributes significantly to the total wrack input than at those (exposed) sites with relatively little *Phyllospadix* spp. input to the wrackline (cf. Fig. 4). In accordance with the feeding preferences of *M. pugettensis*, detritivores did not affect mass loss of *Phyllospadix* spp. in the field.

From the present results, we can explain the nature of some transient patterns of beach-cast wrack at Barkley Sound and its underlying mechanisms. Detailed studies on the nutritive ecology of both wrack-dwelling amphipods and microbial decomposers are needed to strengthen our understanding of decomposition patterns of beach-cast wrack, and thus nutrient fluxes within the marine–terrestrial ecotone.

LITERATURE CITED

Adin R, Riera P (2003) Preferential food source utilization among stranded macroalgae by *Talitrus saltator* (Amphipod, Talitridae): a stable isotope study in the northern coast of Brittany (France). Estuar Coast Shelf Sci 56:91–98

Afzal Rizvi M, Shameel M (2005) Pharmaceutical biology of seaweeds from the Karachi Coast of Pakistan. Pharm Biol 43:97–107

Agostini S, Desjobert JM, Pergent G (1998) Distribution of phenolic compounds in the seagrass *Posidonia oceanica.* Phytochemistry 48:611–617

Bianchi TS, Avgyrou M, Chippett HF (1999) Contribution of vascular-plant carbon to surface sediments across the coastal margin of Cyprus (eastern Mediterranean). Org Geochem 30:287–297

Bustamante RH, Branch GM (1996) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. J Exp Mar Biol Ecol 196:1–28

Chown SL (1996) Kelp degradation by *Paractora trichosterna* (Thomson) (Diptera: Helcomyzidae) at sub-Antarctic South Georgia. Polar Biol 16:171–178

Feike M (2004) Die Bedeutung des Strandanwurfes für das Ökosystem Sandstrand. PhD thesis, University of Rostock

Fielding PJ, Davis CL (1989) Carbon and nitrogen resources available to kelp bed filter feeders in an upwelling environment. Mar Ecol Prog Ser 55:181–189

Griffiths CL, Stenton-Dozey JME, Koop K (1983) Kelp wrack and the flow of energy through a sandy beach ecosystem. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. Junk Publications, The Hague, p 547–556

Hanisak MD (1993) Nitrogen release from decomposing seaweeds: species and temperature effects. J Appl Phycol 5: 175–181

Harrison PG (1989) Detrital processing in seagrass systems: a review of factors affecting decay rate, remineralization and detritivory. Aquat Bot 23:263–288

Hobbie SE (2000) Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in a Hawaiian montane forest. Ecosystems 3:484–494

Jędrzejczak MF (2002) Stranded *Zostera marina* L. vs wrack fauna community interactions on a Baltic sandy beach (Hel, Poland): a short-term pilot study. Part I. Driftline effects of fragmented detritivory, leaching and decay rates. Oceanologia 44:273–286

Mann KH (1988) Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnol Oceanogr 33:910–930

Newell SY, Bärlocher F (1993) Removal of fungal and total organic material from decaying cordgrass leaves by shredder snails. J Exp Mar Biol Ecol 171:39–49

Newell SY, Arsuffi TL, Palm LA (1996) Misting and nitrogen fertilization of shoots of a saltmarsh grass: effects upon fungal decay of leaf blades. Oecologia 108:495–502

Ochieng CA, Erftemeijer PLA (1999) Accumulation of seagrass beach cast along the Kenyan coast: a quantitative assessment. Aquat Bot 65:221–238

Orr M, Zimmer M, Jelinski DE, Mews M (2005) Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86:1496–1507

Pennings SC, Carefoot TH, Zimmer M, Danko JP, Ziegler A (2000) Feeding preferences of supralittoral isopods and amphipods. Can J Zool 78:1918–1929

Piriz ML, Eyras MC, Rostagno CM (2003) Changes in biomass and botanical composition of beach-cast seaweeds in a disturbed coastal area from Argentine Patagonia. J Appl Phycol 15:67–74

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. Annu Rev Ecol Syst 28: 289–316

Seiderer LJ, Newell RC (1985) Relative significance of phytoplankton bacteria and plant detritus as carbon and nitrogen resources for the kelp bed filter-feeder *Choromytilus meridionalis.* Mar Ecol Prog Ser 22:127–139

Stovvy KA, Weldrick CK, Mews M, Zimmer M, Jelinski DE (2006) Intertidal course woody debris: a spatial subsidy as shelter or feeding habitat for gastropods? Estuar Coast Shelf Sci 66:197–203

Targett NM, Coen LD, Boettcher AA, Tanner CE (1992) Biogeographic comparisons of marine algal polyphenolics: evidence against a latitudinal trend. Oecologia 89:464–470

Vahatalo A, Sondergaard M, Markager S (1998) Impact of solar radiation on the decomposition of detrital leaves of eelgrass *Zostera marina.* Mar Ecol Prog Ser 170:107–117

Wildish DJ (1988) Ecology and natural history of aquatic Talitroidae. Can J Zool 66:2340–2359

Williams SL (1984) Decomposition of the tropical macroalga *Caulerpa cupressoides* (West) C. Agardh: field and laboratory studies. J Exp Mar Biol Ecol 80:109–124

Zimmer M, Danko JP, Pennings SC, Danford AR, Ziegler A, Uglow RF, Carefoot TH (2001) Hepatopancreatic endosymbionts in coastal isopods (Crustacea: Isopoda), and their contribution to digestion. Mar Biol 138:955–963

Zimmer M, Pennings SC, Buck TL, Carefoot TH (2002) Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. Funct Ecol 16:596–60

Zimmer M, Pennings SC, Buck TL, Carefoot TH (2004) Salt marsh litter and detritivores: a closer look at redundancy. Estuaries 27:753–769