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WRACK DEPOSITION ON DIFFERENT BEACH TYPES: SPATIAL AND TEMPORAL VARIATION IN THE PATTERN OF SUBSIDY

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Abstract. The onshore deposition of macroalgal and macrophyte wrack provides a potentially significant marine subsidy to intertidal and supratidal herbivore and decomposer communities. Based on the study of daily input loads to beaches, we estimated summer wrack deposition of up to 140 Mg (dry mass)/km shoreline in Barkley Sound, British Columbia. However, input rates were highly variable depending on beach type, nearshore hydrodynamics, and buoyancy characteristics of the wrack. Cobble beaches retained ~10 times and 30 times more wrack than did gravel and sand beaches, respectively. Cobble and gravel beaches also differed in species composition of new (fresh) wrack input, with *Macrocystis integrifolia* being characteristic for the former and *Nereocystis luetkeana* for the latter, which we attribute to buoyancy characteristics of the floating debris. On sand beaches, *Phyllospadix* spp. and *Enteromorpha* spp. were the dominant wrack species. Species composition of freshly deposited wrack also depended on wave exposure, but predictability based on the species pool within a beach's catchment was restricted. Drift lines of aging wrack differed from freshly deposited wrack in species composition, probably due to wrack decomposition that results in fluxes of nutrients and energy between the adjacent marine and terrestrial habitats. We hold that the characteristics of a given beach, e.g., substratum and wave exposure, and their effects on wrack input, will have important ecological and biogeochemical implications for the marine–terrestrial ecotone.

Key words: British Columbia coastal area; intertidal; kelp; marine–terrestrial ecotone; phytodetritus; seagrass; seaweed; spatial subsidy; subtidal macroalgae; tidal currents; wave exposure; wrack deposition.

Introduction

The notion of "ecosystem" generally implies a system with a high degree of internal control and forcing. No ecosystem, however, is entirely without interaction with, or influence from, adjacent habitats or species assemblages. Allochthonous flow (organic and inorganic material) between aquatic and terrestrial habitats is one such interaction that has a rich tradition of study in stream ecology (e.g., Junk et al. 1989). However, assessment of the magnitude and importance of nutrient fluxes between marine and terrestrial habitats has received scant attention until the last decade or so, being 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). These and related studies have given rise to other, though still limited, investigations of marine–terrestrial nutrient fluxes (e.g., Polis and Hurd 1995 and 1996, Rose and Polis 1998, Kawaguchi and Nakano 2001, Fariña et al. 2003, Roth 2003).

A surprisingly little-studied system at the marine–terrestrial interface in terms of the notion of spatial subsidies (sensu Polis et al. 1997) is the role of beach-cast phytodetritus (hereafter collectively termed "wrack") on supralittoral beach communities. It is well established that vast amounts of dislodged algae and seagrasses are washed into nearshore and shore habitats and with significant ecological consequence (Duggins et al. 1989, Bustamante et al. 1995). Beaches mediate the transfer of materials, energy, and organisms from the pelagic and neritic ocean zones, including surf diatoms, macrophytes of stranded wrack, carrion, and dissolved and particulate organics, all of which are deposited by waves and tides. In many instances, this "spatial subsidy" is particularly important in that both sand and cobble beaches are physically stressful, low-productivity environments (Kachi and Hirose 1983, Houle 1997). For example, it has been shown that drift algae and seagrasses are capable of altering community structure by providing refugia (Holmquist 1997, Norkko et al. 2000), serving as food to numerous intertidal invertebrates (e.g., Chown 1996, Pennings et al. 2000), and releasing nutrients following bacterial decomposition and thereby altering sediment chemistry (Har-

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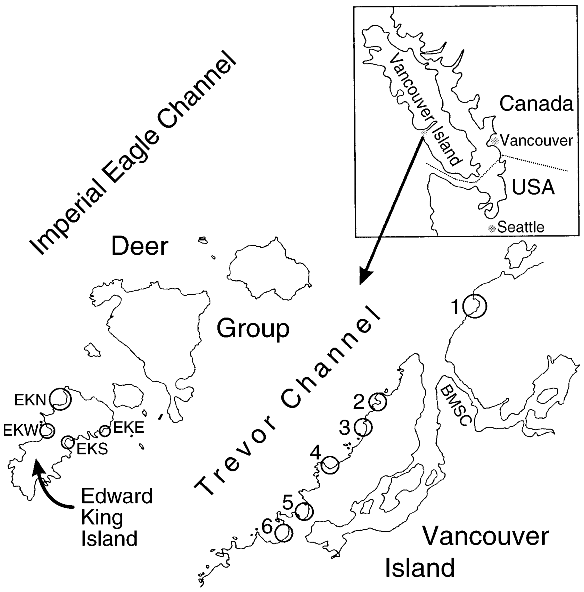

FIG. 1. Study sites in Barkley Sound, British Columbia, Canada (for details, see Table 1).

rison and Mann 1975, Rice and Tenore 1981, Levinton et al. 1984, Pellikaan 1984, Tenore et al. 1984). The complexity of these deposition, macrofaunal utilization, and bacterial decay processes depends on the spatial distribution, amount, and species composition of wrack deposited (Valiela et al. 1997). While Valiela and Rietsma (1995) suggest that deposition of wrack on sand and mud is usually on spatially small scales, comparative studies between larger sediment types have not been done. The details of the agents governing deposition and ultimate fate of wrack require further investigation given the significant ecological and biogeochemical implications.

In a series of studies, we examined the input of marine subsidies to littoral and supralittoral ecosystems via wrack deposition on beaches in Barkley Sound, British Columbia, Canada. The present study tests the hypotheses that the amount and species composition of deposited and trapped wrack depend on (1) the exposure relative to wave action and (2) the substratum of the beach. We predicted differences between beaches that differ in terms of substratum or wave exposure with respect to both amount and species composition of deposited wrack, and hence distinct wrack decomposition rates.

MATERIALS AND METHODS

General approach

The study area was located in Barkley Sound, a large embayment (>550 km^2) on the west coast of Vancouver Island, British Columbia, Canada (Fig. 1). It is divided into three major channels, two of which are part of this study. Imperial Eagle Channel (~100 m deep) lies in the center and is most exposed to the offshore environment; Trevor Channel is narrow and deep (150 m) and is heavily influenced by freshwater outflow from the Sarita River and Alberni Inlet. Along the southeast shore (i.e., the main island) of Trevor Channel, six beaches with similar aspect were selected according to the major substratum of the beach (Fig. 1): two beaches with cobble substratum, two with gravel, and two with sand (Table 1). The beaches were typically lunate shaped with the northeastern side of the beach being the most exposed to the prevailing wind and wave action. The cobble beaches, Dixon Point and West Scott's Bay (48°50′47.0″ N, 125°07′41.7″ W and 48°49′56.8″ N, 125°08′53.3″ W), were characterized by having a surface substratum mainly composed of large cobbles (according to the Wentworth scale) from ~100 to 250 mm. The cobble beaches typically exhibited a mixed gravel and sand matrix beneath the cobbles. The gravel beaches, First Beach and West Breakers Beach, NE (48°49′0.48″ N, 125°09′48.6″ W and 48°49′28.4′ N, 125°09′23.7″ W) were composed of medium-sized gravel (~7–15 mm) with the largest gravel being on top and decreasing in size with depth. The sand beaches, Second Beach and West Breakers Beach, SW (48°48′56.3″ N, 125°10′02.7″ W and 48°49′26.6″ N, 125° 09′27.3″ W) consisted of uniform fine-grained sand (~0.1–0.2 mm). All beaches were flanked by rocky headlands typical of this region.

Four sites on Edward King (EK) Island (bordering Trevor Channel to the northwest) were selected according to their exposure to wave action (Fig. 1, Table 1), one site each being exposed (EKN: 48°50′01.1″ N,

TABLE 1. Selected characteristics of study sites in Barkley Sound (see Fig. 1).

Site	Name	Substratum	Exposure	Aspect
1	Dixon Pont	cobble	moderately exposed	west
2	West Scott's Bay	cobble	moderately exposed	west
3	West Breakers Beach, NE	gravel	moderately exposed	west
4	West Breakers Beach, SW	sand	moderately exposed	northwest
5	First Beach	gravel	moderately exposed	northwest
6	Second Beach	sand	moderately exposed	west
EKS	Edward King Island, South	cobble	sheltered	southeast
EKE	Edward King Island, East	cobble	moderately sheltered	southeast
EKW	Edward King Island, West	cobble	moderately exposed	west
EKN	Edward King Island, North	cobble	exposed	west

125°12′46.2″ W), moderately exposed (EKW: 48°49′44.9″ N, 125°12′57.8″ W), moderately sheltered (EKE: 48°49′45.7″ N, 125°12′18.8″ W), and sheltered (EKS: 48°49′39.9″ N, 125°12′47.0″ W). All these were lunate-shaped cobble beaches with some mixed gravel underneath, the former two facing west, the latter two facing southeast.

Wrack collection on main island beaches

Transects ($n = 3$ each at two beaches of each substratum type) were run perpendicular to the water on the northeast side of the beaches. The transects ran from the highest tide line to the lowest water level experienced during a typical low tide, except on the cobble beaches where the transects stopped at a point equal to the *Fucus* spp. line.

A 2 m wide polyurethane tarp was placed along each transect. All organic matter in the 2 m wide swaths was placed on the tarp and covered. Collections began at slack high tide and followed through to low tide. Material was collected until after it had been deposited on the beach but without contact with wave action for ~10 min. On cobble beaches, cobbles were lifted down to the sand/gravel matrix underneath which all macroscopic organic matter was collected. The gravel beaches were strained by hand to a 30-cm depth, and all wrack within the column was taken. On the sand beaches, wrack was only deposited on, and hence collected from, the surface.

On cobble and gravel beaches all wrack that washed ashore within the first 90 min was collected separately from that which came ashore during the balance of tidal ebb. Total wet mass of the wrack was measured in the field (accurate to within 10 g). The wrack was sorted according to species. In the laboratory a subsample was dried at 60°C for 2 d. From this we established a wet–dry calibration where 500 g of wrack wet mass equals 120 ± 10 g dry mass, indicating an average water content of 76 ± 2%. The five most abundant species that contributed to the total wrack load (according to wet mass) were individually measured. The remaining species were lumped into the category ''other,'' and the total mass was taken. This procedure was repeated for the remainder of the tidal ebb. Collected and weighed wrack was placed far above the highest tidal line to prevent it from being redeposited in the transect during the next tidal cycle.

Owing to $n = 3$ replicates per beach, we used nonparametric statistics to test for differences in wrack amount between beaches with different substratum type and between different ebb stages (Kruskal-Wallis H test). Differences were analyzed with Mann-Whitney U tests following Bonferroni corrections. Species composition of wrack deposited at different beach types and at different ebb stages were compared with χ^2 tests (Jelinski 1991).

Wrack collection on Edward King Island

On Edward King Island, we sampled both fresh drift lines deposited by the last mean high tide and 2-week-old wrack lines that were left behind by the previous spring high tide. Segments of the drift lines with a length of 20 cm ($n = 3$ for each drift line) were cleared of wrack by hand, brought to the laboratory, immediately sorted by species, and oven dried at 60°C for 48 h. Species that contributed <5% to the total mass of a given sample were grouped as ''other.'' Owing to $n = 3$ replicates per beach, we used nonparametric Kruskal-Wallis H tests to detect differences in wrack amounts between beaches of different exposure. Differences were then analyzed with Mann-Whitney U tests following Bonferroni correction. Species composition of wrack deposited at different beach types was compared with χ^2 tests (Jelinski 1991).

RESULTS

Influence of substratum type

The total volume of wrack deposited differed significantly between the cobble, gravel, and sand beaches ($P < 0.001$). We differentiated between the standing load, defined as the total amount of wrack that accumulated ashore, and the input load, the amount of wrack deposited during the most recent tidal cycle. The standing load, by contrast, is composed of wrack deposited during the last tidal cycle as well as all wrack deposited previously in some earlier tidal event, and contains wrack in all stages of decomposition, from freshly deposited to unidentifiable rotting masses. The input load is mostly composed of healthy specimens.

Cobble beaches had the highest loading of wrack among all sample sites for both standing load and input load (Fig. 2) followed by gravel beaches and sand beaches, respectively. However, contrary to our predictions, accumulation over several days was not simply the sum of average daily input (Fig. 3). For example, on one cobble beach we found that deposition over one tidal cycle (maximum 3.9 kg/m shoreline) could even exceed the total accumulation over 6 and 9 d (2.3 and 3.4 kg, respectively). Gravel beaches showed similar patterns where the deposition of wrack during one tidal cycle (maximum 1.1 kg) sometimes exceeded its accumulation over 11 d (0.8 kg). The sand beach, by contrast, showed increased deposition over longer sampling periods, albeit the 6-d accumulation sometimes exceeded the 11-d accumulation (Fig. 3). These results suggest that wrack accumulation cannot be predicted by the pattern of daily deposition; rather, removal by tides and waves and biological degradation appears to account for the discrepancy between standing load and daily input.

Average species composition of both standing wrack load and daily input varied considerably among beach types (Table 2, $P < 0.001$). Species retention for each of cobble, gravel, and sand beaches was similar be-

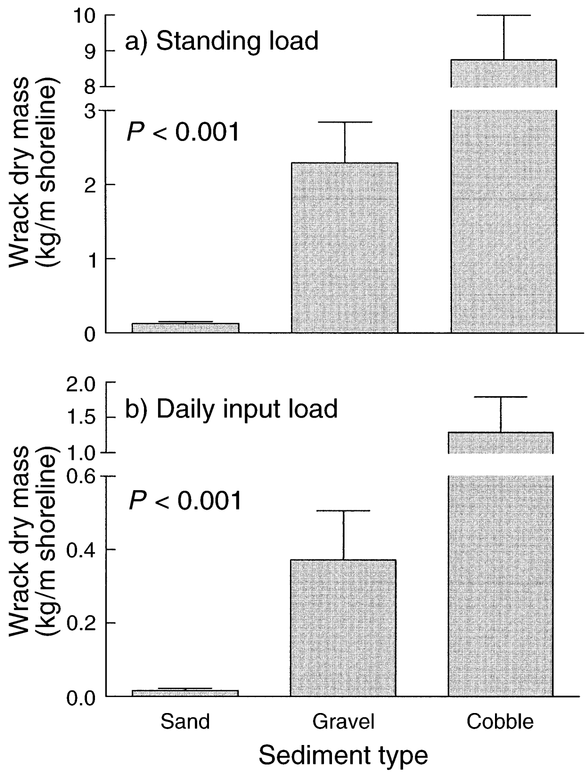

FIG 2. (a) Standing load and (b) daily input load of wrack to beaches with different substratum types in Barkley Sound (see Fig. 1, Table 1) in July–August 2003. Data are median ± median absolute deviation ($n = 3$ each at two beaches of each substratum type); note the log scale. For each substratum type, we sampled two beaches independently; at each of these beaches (six in total), we sampled three transects as described in the *Materials and Methods* section.

tween the similar beach substrata. *Fucus* spp. constituted the main export of biomass to the cobble and gravel beaches (32% and 24%, respectively, Fig. 4). On cobble beaches *Macrocystis integrifolia* comprised 18% of the wrack. Gravel beaches were characterized by significant amounts of *Nereocystis luetkeana* (14%), *Egregia menziesii* (18%), and *Phyllospadix* spp. (18%). The wrack washed ashore on the sand beaches was dominated by *Enteromorpha* spp. (56%), and in general was less speciose (Table 2), with *Phyllospadix* spp. (25%) and a mix of terrestrial debris dominating the beach-tossed wrack.

Influence of ebb stage

Deposition rates differed according to stage of the ebb tide. Both cobble and gravel beaches had the highest deposition of wrack during the first 1.5 h of tidal recession (Fig. 5). The input load was significantly higher, during both the first 90 min and the remaining tidal cycle, on the former (1.1 and 0.3 kg/m shoreline, respectively, $P < 0.05$) than on the latter (0.3 and 0.1 kg, respectively, $P < 0.001$). Input load for the different tidal heights for the sand beaches was not calculated due to the small total mass of wrack deposited.

Species composition of wrack on both cobble and gravel beaches varied during the course of the ebb tide (Fig. 6, $P < 0.001$). *M. integrifolia* was the most abundant species (24% by mass) on the cobble beaches during the first 90 min of wrack deposition, followed by *Fucus* spp. (20%) and *E. menziesii* (20%). Species composition of the remaining ebb tide period was dominated by *Fucus* spp. (37%) and terrestrial debris that included small branches, leaves, pine needles, and cones. The ''other'' category was mostly composed of the blades of larger algae such as *Nereocystis luetkeana* and *M. integrifolia*, accompanied by *Ulva* spp. The gravel beaches also showed different species compositions during the different stages of tidal ebb (Fig. 6, $P < 0.001$). The majority of the first 90 min of input load consisted of *Fucus* spp. (27%), *Phyllospadix* spp. (20%), and *N. luetkeana* and *E. menziesii* (14% each). This contrasted with the balance of the tidal ebb when we found *Ulva* spp. (41%), *N. luetkeana* (19%), and *Phyllospadix* spp. (13%) as the dominant species.

Influence of wave action

On Edward King Island the drift line had an average width of 20–30 cm and a depth up to 15 cm. Beaches varying according to wave exposure differed significantly relative to one another in both input load (Table 3, $P < 0.01$) and species composition of the drift line (Fig. 7, $P < 0.001$). Mass of deposited wrack was maximal on the moderately sheltered and moderately exposed beaches, with lower values on the sheltered and exposed beaches (Table 3). This observation was not simply due to the aspect of the beaches. Had that been the case, we would likely have found similar values for the exposed and the moderately exposed as well as the sheltered and the moderately sheltered beach, facing west and southeast, respectively.

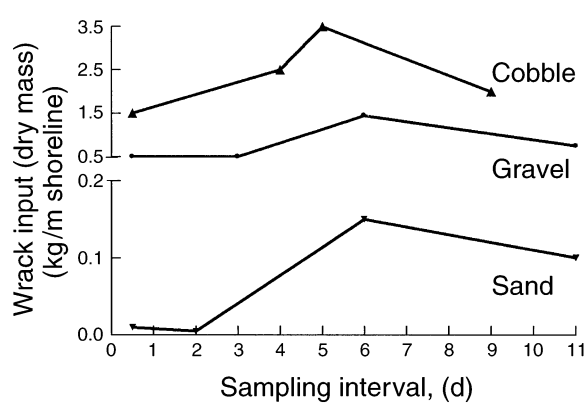

FIG. 3. Changes in standing load over time at beaches with different substratum types in Barkley Sound (see Fig. 1, Table 1) in July–August 2003. Data are median values of two time series each at two beaches per substratum type; note the log scale. For the sake of clarity, variability is not shown.

TABLE 2. Species composition of wrack deposited on beaches with different substratum types in Barkley Sound (see Fig. 1, Table 1) in July–August 2003.

Wrack component	Common name	Sand	Gravel	Cobble
Chlorophyta				
Enteromorpha spp.	green string lettuce	X	X	X
Cladophora spp.	green tuft	X	X	X
Ulva spp.	sea lettuce	X	X	
Phaeophyta				
Costaria costata	five-rib kelp			X
Desmarestia spp.	acid hair		X	
Egregia menziesii	feather boa	X	X	X
Fucus spp.	rock weed	X	X	X
Leathesia difformis	sea cauliflower	X		
Macrocystis integrifolia	giant kelp	X	X	X
Nereocystis luetkeana	bull kelp	X	X	X
Sargassum muticum	Japanese weed			X
Rhodophyta				
Chondracanthus spp.	Turkish towel		X	X
Corallina spp.	coral seaweed			X
Halosaccion glandiforme	dead man's fingers	X	X	X
Mastocarpus spp.	Turkish washcloth			X
Mazzaella splendens	rainbow-leaf			X
Microcladia spp.	sea lace			X
Neorhodomela spp.	black larch		X	
Prionitis spp.	bleach weed		X	X
Anthophyta				
Phyllospadix spp.	surf grass	X	X	X
Zostera marina	eel grass	X	X	X
Terrestrial				
Leaves		X	X	X
Sticks			X	X
Needles and cones		X	X	X

Note: Presence–absence of species and categories was estimated from three sampling dates each of standing load and input load at two beaches of each substratum type.

As for input load, the numbers of wrack species were higher on the moderately sheltered and moderately exposed beaches than on the sheltered or exposed beaches (Table 3, $P < 0.05$). Further, species composition of freshly deposited wrack differed between beaches of varying exposure (Fig. 7; $P < 0.001$). *Alaria* spp. and *Mastocarpus* spp. were exported only to the exposed beach, while *Enteromorpha* spp. and *Leathesia difformis* were deposited only on the sheltered beach. *Ulva* spp., *Porphyra* spp., *Desmarestia* spp., and *Costaria costata* were typical for wrack on the moderately sheltered and moderately exposed beaches. *Egregia menziesii*, *Fucus* spp., and *Phyllospadix* spp. were common on all beaches, the latter two making up the major components in most cases. Overall, the proportion of *Fucus* spp. in freshly deposited wrack increased with increasing beach exposure, with a decreasing relative contribution of *Phyllospadix* spp. (Fig. 7).

DISCUSSION

General remarks

Given the fluid medium of the marine environment, primary production in nearshore stands of macrophytes can be exported to and utilized by other marine and nonmarine systems (Duggins et al. 1989, Bustamante

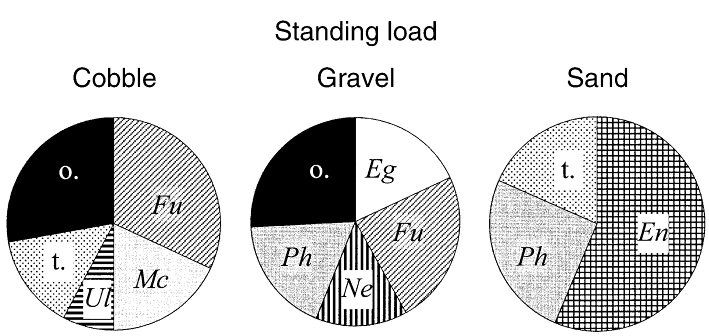

FIG. 4. Species composition of standing load at beaches with different substratum types in Barkley Sound (see Fig. 1, Table 1) in late July 2003. Data are median percentage values of three collections each at two beaches per substratum type. Species abbreviations: *Eg*, *Egregia*; *En*, *Enteromorpha*; *Fu*, *Fucus*; *Mc*, *Macrocystis*; *Ne*, *Nereocystis*; *Ph*, *Phyllospadix*; *Ul*, *Ulva*; t., terrestrial; o., other.

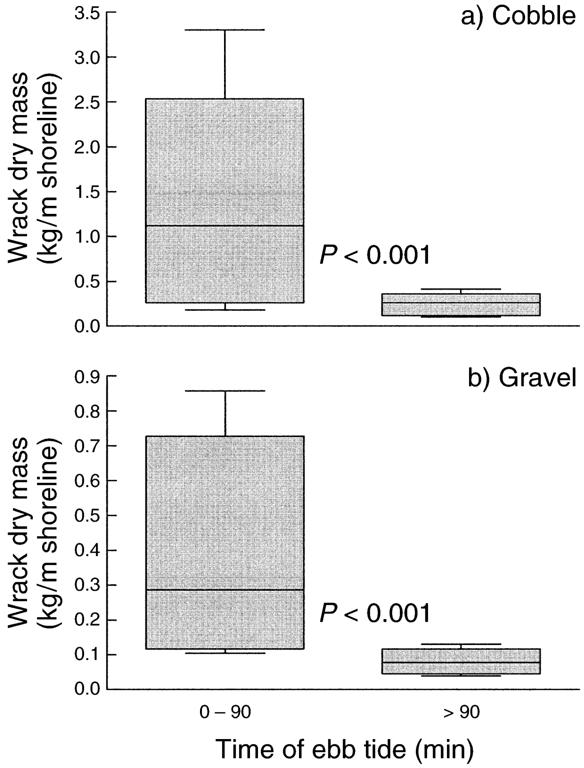

FIG 5. Wrack input during different stages of outgoing ebb to (a) cobble and (b) gravel beaches in Barkley Sound (see Fig. 1, Table 1) in early August 2003. Each box plot represents minimum, 25th percentile, median, 75th percentiles, and maximum of a total of six collections at two beaches.

et al. 1995, Graham et al. 2003). In Barkley Sound we determined deposition rates of up to 140 Mg (dry mass)/km in summer. By comparison, for the Bay of Fundy on the east coast of Canada, Wildish (1988) estimated ~60 $Mg \cdot km^{-1} \cdot yr^{-1}$, and Piriz et al. (2003) calculated ~40–200 $Mg \cdot km^{-1} \cdot yr^{-1}$ for Patagonian coasts. Griffiths et al. (1983) reported similar input loads of 280–520 $Mg \cdot km^{-1} \cdot yr^{-1}$ in South Africa. Significantly lower input rates were estimated by Ochieng and Erftemeijer (1999) (~0.7 $Mg \cdot km^{-1} \cdot yr^{-1}$, with 88% being seagrass and small amounts of *Sargassum* spp. and *Ulva* spp.). Even higher deposition rates of ~360–2900 $Mg \cdot km^{-1} \cdot yr^{-1}$ macroalgae (with >50% contributed by the kelp, *Ecklonia radiata*) and 900–1800 $Mg \cdot km^{-1} \cdot yr^{-1}$ seagrass wrack were documented by Hansen (1984, as cited in Kirkman and Kendrick 1997) for Western Australia. According to Kirkman and Kendrick (1997), about 17% of all marine primary production ends up as wrack on Western Australian beaches.

Importantly, however, these studies did not compare different beach substrata or varying aspects or exposures. We hold that the nature of the tidal cycle interacting with beach types, and their respective differences in wrack input, will have important ecological and biogeochemical implications for the marine–terrestrial ecotone. We describe the main features of these interactions.

Stage of ebb tide

Our observation of the differences in wrack deposition during the course of the outgoing tidal ebb provides strong evidence that both different algal species and alternate structures of similar species are deposited at different stages of ebb. Not only is ~80% of the total input load deposited during the first 90 min of the ebb tide, but the species that are deposited during this tidal stage are different from those that are deposited in the latter parts of the ebb flow. We believe that the differences in species compositions deposited during the different stages of tidal ebb occur because of positively buoyant properties of algal blades or thalli. For example, *Egregia*, which has numerous gas vesicles (pneumatocysts), was among the four most abundant species during the first 90 min of ebb on both cobble and gravel beaches, but contributed significantly less to the wrack load during later stages ($P < 0.001$). Further, on both the cobble and gravel beaches, *Fucus* blades that first washed ashore had buoyant receptacles at the tips of the blades, while the *Fucus* specimens that washed ashore during the rest of the tidal ebb were typically younger, nonreproductive fronds that remain neutrally buoyant in the water column. Similarly, the *Macrocystis* and *Nereocystis* that washed onto the cobble and gravel beaches during the first portion of the ebb tide typically were still attached to their buoyant

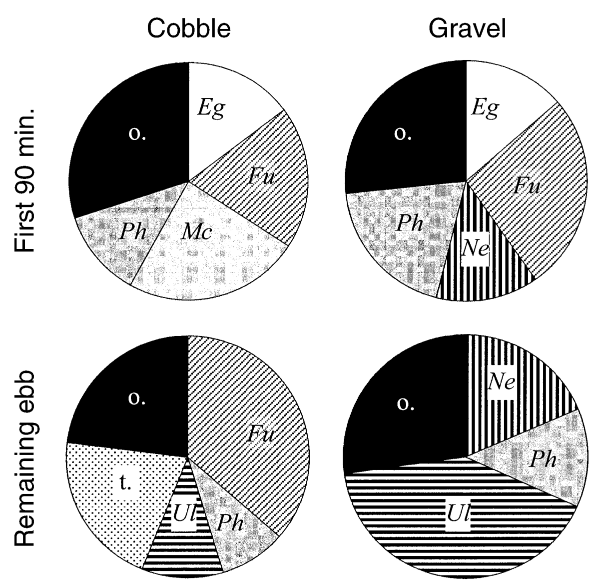

FIG. 6. Species composition of input load to beaches with different substratum types in Barkley Sound (see Fig. 1, Table 1) in July–August 2003 during different stages of outgoing ebb tide. Data are median percentage values of three collections each at two beaches per substratum type. Species abbreviations are as in Fig. 4.

TABLE 3. Species composition, species richness, and dry mass of freshly deposited wrack on beaches at Edward King Island, Barkley Sound (see Fig. 1) in July 2003 differ with respect to aspect and exposure.

Wrack component	Common name	EKS	EKE	EKW	EKN
Chlorophyta					
Enteromorpha spp.	green string lettuce	X			
Codium spp. branched	sea staghorn	X	X		X
Codium spp. cushiony	green spongy cushion				
Ulva spp.	sea lettuce		X	X	
Phaeophyta					
Alaria spp.	winged kelp				X
Costaria costata	five-rib kelp		X		
Desmarestia spp.	acid hair		X		
Egregia menziesii	feather boa	X	X	X	X
Fucus spp.	rock weed	X	X	X	X
Laminaria spp.	tangle		X	X	X
Leathesia difformis	sea cauliflower	X			
Macrocystis integrifolia	giant kelp	X	X	X	X
Nereocystis luetkeana	bull kelp	X	X	X	
Rhodophyta					
Chondracanthus spp.	Turkish towel		X	X	X
Mastocarpus spp.	Turkish washcloth			X	X
Mazzaella spp.	rainbow-leaf		X	X	X
Porphyra spp.	purple laver		X	X	
Anthophyta					
Phyllospadix spp.	surf grass	X	X	X	X
Terrestrial					
Gaultheria shallon	salal	X			
Wood			X		X
Total no. spp.		5 ± 2	11 ± 1	8 ± 1	6 ± 1
Total mass (g/m)		97 ± 57	784 ± 213	659 ± 45	230 ± 154

Notes: Aspect: EKS and EKE, southeast; EKW and EKN, west. Exposure: EKS, sheltered; EKE, moderately sheltered; EKW, moderately exposed; EKN, exposed. Increasing exposure is shown from left to right. Presence–absence of species and categories, total number of species (median ± median absolute deviation), and total mass of freshly deposited wrack (median ± median absolute deviation) were determined based on three sampling dates at each beach.

floats and pneumatocysts that these algae use for flotation. This positive buoyancy aids in deposition during the first portion of the tidal recession. The wrack that washed ashore during the rest of the tidal ebb was composed mainly of neutrally buoyant *Ulva*, *Macrocystis*, and *Nereocystis* blades.

Rates of change in tidal height over time with respect to incoming and outgoing tides are not linear in form. Rather, changes of tidal height over time are small around slack high and low tide and null during slack, but maximal around medium tidal height about three hours after slack, thus following a sine wave (see Fig. 8). Accordingly, forces acting on the substratum through tidal waves are maximal at medium tidal height and minimal during slack (arrows in Fig. 8). This simplified model of tide action suggests slow retraction of the waterline during the first 90 min of outgoing ebb tide. Given a near constant rate of incoming wave action at any given time, the substratum near the high slack tide line thus receives wrack input through wave action over a longer time than does the substratum at medial tidal height (dotted area in Fig. 8). This effect results in increased deposition of wrack over a small area of beach. Thus most waterborne particles will be deposited during this tidal stage. Also, during this time period, deposition of buoyant particles is favored under these conditions. Although this effect is also seen at low slack, the neutral or positively buoyant nature of most particles results in their being carried up the beach during the next flood tide. Overall these observations suggest that the first stage of ebb tide (some 90 min) results in a net deposition of wrack, while the remaining outgoing tide will result in net withdrawal of floating drift or resuspended wrack. This creates a pool of wrack that will be washed back and forth between nearshore waters and beaches (cf. Kirkman and Kendrick 1997, Ochieng and Erftemeijer 1999).

Substratum type

The total volume of wrack deposition among the three types of substratum showed a strong influence of substratum type (categorized as sand, gravel, and cobble), indicating increasing mass of trapped wrack with increasing grain size. These findings are in accord with studies on sand beaches by Valiela and Rietsma (1995), who suggest that deposition of wrack on sand and mud is usually on a small scale. Comparative studies between larger sediment types have not been done to the best of our knowledge. Although the relative proportion of the interstices to the total volume of sediment de-

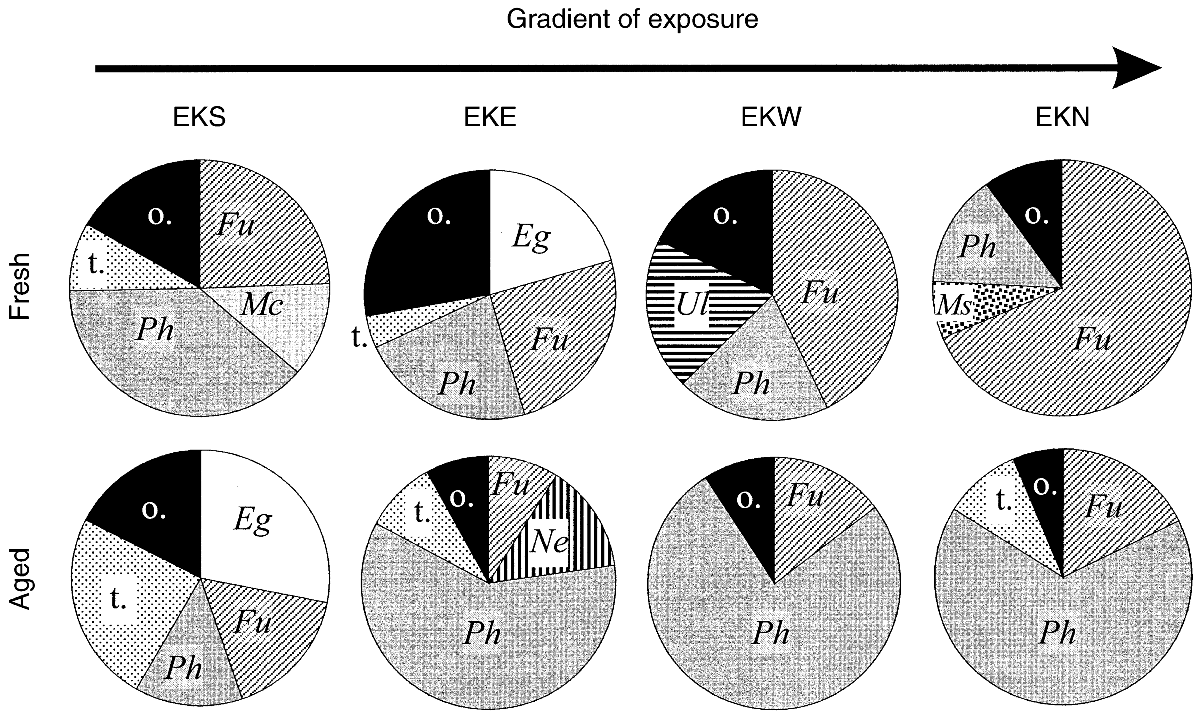

FIG. 7. Species composition of fresh and aged wrack lines at beaches with different wave exposures on Edward King Island (see Fig. 1, Table 1) in July–August 2003. Data are median percentage values of three collections each at fresh and aged wrack lines at each beach. Species abbreviations are as in Fig. 4, with the addition of *Ms*, *Mastocarpus*.

creases with increasing sediment grain size, the absolute size of the pores is obviously the major factor that determines a substratum's characteristics as a wrack trap. Spaces between cobbles are sufficiently voluminous to trap large wrack particles and to retain them despite the surging forces of the outgoing ebb tide. As the wrack becomes physically fragmented, particles move farther down to the cobble matrix and remain in place for microbial degradation even during low tide. In contrast, gravel is sufficiently small to be moved about by wind-waves and tidal currents. Thus a large portion of wrack is partially or wholly buried in the sediment, which, according to our own observations, can be up to 30 cm deep. Sand, however, is too fine grained to allow entrance of wrack and result in burial of wrack under regular wave action. In addition, friction on sand surfaces is weak and thus not capable of retaining wrack particles. Hence overall wrack load is low on sand beaches.

In addition to differences in the overall input load, we found differences in wrack species composition depending on beach type. For example, fresh wrack input on cobble beaches did not contain significant amounts of *Nereocystis* compared to gravel beaches. On gravel beaches, in turn, there was little *Macrocystis* relative to cobble beaches. Both beach types had nearly equal amounts of *Fucus* spp. This is likely due to the favorable habitat for *Fucus* spp. in the lower littoral zone of these beaches as well as the retention characteristics of *Fucus*.

Wave exposure

Comparison of sheltered and exposed beaches revealed a strong influence of wave exposure on the amount and species composition of deposited wrack,

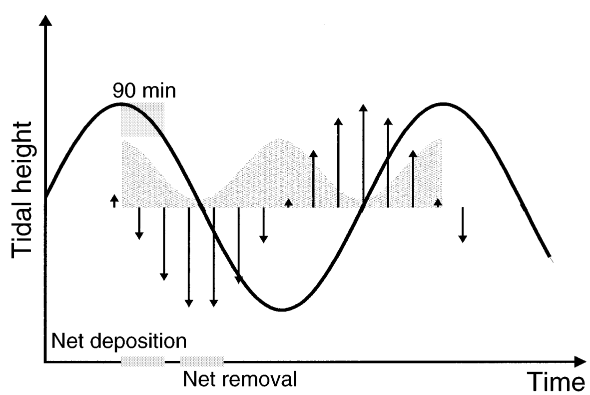

FIG. 8. Idealized tidal height (sine wave), forces of tidal currents (arrows), and time intervals during which waves act upon the same beach area (dotted area). Gray boxes indicate net wrack deposition during the first 90 minutes of outgoing ebb tide, and net wrack removal during the balance of the tidal ebb. (For details see *Stage of ebb tide* in *Discussion* section.)

irrespective of shoreline aspect. Species composition of wrack is clearly a function of the algal community in the catchment of a particular beach, which, in turn, is determined in part by wave exposure. *Egregia menziesii*, for instance, grows best in sheltered locations (Druehl 2000), and was most common in the drift line of the moderately sheltered beach in the present study. Similarly, *Macrocystis integrifolia* is common to the moderately wave-exposed subtidal zone (Druehl 2000), and the sheltered beach studied herein obtained the greatest contribution by this species. However, although both *Fucus* spp. and *Mastocarpus* spp. are more typical of moderately than fully wave-exposed habitats (Druehl 2000), they were most common on the exposed beach in the present study. In contrast *Phyllospadix* spp. are found predominantly in exposed coastline habitats (Druehl 2000), but their relative contribution to wrack input load decreased with increasing beach exposure. Thus other factors than catchment community composition, such as buoyancy of wrack, must also be affecting species composition of the wrack deposited on differently exposed beaches. Kirkman and Kendrick (1997) found that detached macroalgae and seagrass may spend several days drifting freely before deposition ashore, with surface-drifting material being prone to transport by wind and waves but bottom-drifting material being moved by currents. Overall they documented ~4500 Mg (dry mass)/km^2 drifted subtidally near Western Australian shores. Our data on standing loads after different time intervals of wrack deposition suggest that wrack accumulation is an extremely dynamic process (cf. Kirkman and Kendrick 1997, Ochieng and Erftemeijer 1999), with frequent events of resuspension (during high high tides and late outgoing ebb) and redeposition (during low high tides and early outgoing ebb), which might complicate to some extent our estimation of wrack deposition. That is, our calculation of summer wrack deposition based on daily input loads may be an overestimation. On the other hand, wrack deposition during fall and winter by far exceeds input loads during summer in Barkley Sound (M. Orr, *personal observation*), suggesting an underestimation of annual wrack deposition based on summer input rates. Piriz et al. (2003) also found that deposition on Patagonian beaches is highest in the summer (January/February), while Ochieng and Erftemeijer (1999) observed the opposite in Kenya. Long-term studies are needed to clarify this aspect of coastal wrack ecology.

Our findings suggest that moderate exposure results in higher total input load compared to extreme shelter or extreme exposure. Wave exposure directly affects the substratum composition of any particular beach, which, in turn, controls wrack deposition. However, the differently exposed beaches sampled on Edward King Island were all cobble beaches, so that we seem warranted in excluding an effect of substratum type. Ochieng and Erftemeijer (1999) determined highest deposition rates during spring tides; we studied beaches at Edward King Island near neap tide. One might speculate that, due to stronger forces of the moving water body at spring tide, larger amounts of wrack are deposited, but these amounts will be spread over larger beach areas during the first period of outgoing ebb tide. Additional studies, including more beaches of different aspect and substratum type, are needed to confirm our hypothesis and prediction.

The physical processes that govern the deposition of wrack ashore may be further understood by investigating the meteorological and oceanographic patterns within the study area. Weather and sea state are responsible for surface waves and swell, which would increase beach deposition during increased wind speed. Seasonal increases in storm swells have been correlated to increased frond damage and breakage of algal holdfasts (Milligan and DeWreede 2000), and changes in community structure and colonization rates of algal mats during winter and summer seasons are affected by changes in wind-waves and tidal currents (Beukema and De Vlas 1989, Ford et al. 1999). During the course of this study the daily average wind velocity did not exceed 10 km/h (recorded at Cape Beale, <10 km from all study sites), and therefore, we conclude that wind did not have a large influence on this study. Summed daily wind speed (regardless of direction) showed a weak correlation with total wrack deposition. However, local variation in coastline contours and aspect would likely produce highly variable winds for each catchment, and therefore, regional wind patterns may be overwhelmed by local effects. When wind direction was analyzed, daily averages showed little correlation with wrack deposition at different sites. The total regional wind velocity, regardless of direction, may have a greater influence by producing wind-waves, which, in turn, generate shear and stress forces on subtidal algae, causing them to be dislodged. The place of deposition of the resulting drift will then depend on currents, beach morphology, and aspect. However, wave height does not necessarily correlate with wave force (Helmuth and Denny 2003); hence predictions on forces acting on algal canopies or wrack derived from wave exposure may be inaccurate.

Aging of wrack

The discrepancy between the daily input of wrack and the standing load after several days and weeks suggests that many processes act differentially in removing wrack from the beach after deposition, and accumulation of deposited wrack is being countered by numerous abiotic and biotic factors. Thus we observed both overall mass loss of wrack, and changes in its species composition during the course of wrack-line aging.

As for temporal changes in wrack deposition during the course of outgoing ebb tide, the buoyancy of wrack particles may in part mediate these changes in the standing load. The decrease of standing load is partially brought about by removal of freshly deposited wrack with the next tide cycle. Predominantly those deposited particles will be removed by tidal currents that carry buoyant parts facilitating their removal and/or that have been deposited at the lower shore during outgoing ebb tides. In comparing species composition of standing and input load, our results support the latter hypothesis: the standing load was reduced in buoyant wrack but richer in nonbuoyant wrack than the input load. Thus the latter is moved up the shore with the next incoming high tide after its deposition during the late previous ebb tide.

Besides removal of wrack through tidal currents and wave action, the factors contributing to this observation include mechanical breakdown of wrack via drying–rewetting cycles through solar radiation and morning dew (Newell et al. 1996, Vahatalo et al. 1998), flocculation and sedimentation (Harrison 1989, Opsahl and Benner 1993), microbial decomposition of detritus and its fragmentation and mass loss through feeding by detritivores (Newell and Bärlocher 1993, Zimmer et al. 2002, 2004), and feeding preferences of detritivores (Pennings et al. 2000). All these processes will eventually promote the marine–terrestrial transfer of nutrients and energy, since seaweeds, which are considered nutrient sinks in coastal waters, become a nutrient source when they decompose (Hanisak 1993). Energy transfer from coastal to inland systems is brought about by terrestrial consumers that enter the intertidal to feed upon marine food sources. Based on a recent review on ''maritime mammals'' by Carlton and Hodder (2003) and our own unpublished observations during the course of the present study, a complex network of nutritive marine–terrestrial interactions arises that clearly warrants further investigation. Huge amounts of wrack are consumed by coastal amphipods and omnivorous crabs (e.g., Buck et al. 2003, Zimmer et al. 2004; M. Orr, M. Zimmer, D. Jelinski, M. Mews, *personal observation*), which, in turn, serve as food for bears and mink (Carlton and Hodder 2003). Along with wrack-feeding deer (M. Orr, M. Zimmer, D. Jelinski, M. Mews, *personal observation*), they transport marine-derived nutrients into coastal forest systems, providing valuable nutrient sources for terrestrial vegetation.

The role of macrophyte-derived detritus as an input for organic carbon and nitrogen has been extensively examined for subtidal consumers (Stuart et al. 1982, Seiderer and Newell 1985, Mann 1988, Fielding and Davis 1989). However, relatively little attention has been given to food-web dynamics of the rocky intertidal zone (Bustamante and Branch 1996) and the comparison between beaches of different aspects, exposures, and substrata. Our present results clearly indicate differential mass loss of different wrack species, possibly due to both microbial degradation and consumption by supratidal amphipods (M. Mews, M. Zimmer, D. E. Jelinski, *unpublished data*). Seagrasses generally decompose more slowly than macroalgae (e.g., Buchsbaum et al. 1991, Holmer and Olsen 2002, Fourqurean and Schrlau 2003). However, both *Fucus* (Denton and Chapman 1991, Targett et al. 1992, Zimmer et al. 2001) and seagrasses (Agostini et al. 1998, Bianchi et al. 1999) are high in phenolic compounds, which are known to slow down degradation of detritus. Yet according to our data on species composition in aged wrack lines, *Fucus* decomposed much faster than *Phyllospadix*. Further studies are needed to investigate in detail decomposition processes during wrack line aging.

Conclusions

The deposition of wave-tossed macroalgal and macrophyte wrack provides enormous amounts of organic subsidy to the supratidal marine–terrestrial interface in terms of biomass of primary producers that, upon decomposition, serves as a valuable nutrient source. However, the decomposability of wrack is species specific, and both wrack composition and amount depend upon several factors: (1) According to the changing tidal forces acting on wrack deposition and withdrawal, beach-cast wrack is only part of a pool of detached macroalgal and macrophyte material with an extremely dynamic distribution between subtidally floating drift and beach-deposited wrack. Buoyancy characteristics of the floating debris determine its fate. (2) Beach substratum characteristics, grain size, and pore volume control the amount and type of wrack that is trapped between and underneath substratum grains, cobble being more effective in catching wrack than gravel or sand. (3) Wave exposure governs wrack deposition patterns such that beaches of moderate wave exposure obtain highest input loads. Species composition, in part, also depends on wave exposure, but predictions in this regard are complicated by the pool of floating marine debris that is prone to considerable drift; that, in turn, depends on the buoyancy characteristics of the debris. Further, owing to dynamic deposition and removal and decomposition processes, species composition changes over time.

Overall, both the quantity and the quality of the macroalgal and macrophyte marine subsidy to the supratidal load are highly variable, but may, in part, be predictable when sufficient beach characteristics are known. Detailed studies that aim to help us understand this important aspect of marine–terrestrial nutrient and energy fluxes are warranted and planned by our research group.

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