RESEARCH ARTICLE

Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources

Mariano Lastra · Henry M. Page · Jenifer E. Dugan · David M. Hubbard · Ivan F. Rodil

Abstract Allochthonous subsidies of organic material can profoundly influence population and community structure; however, the role of consumers in the processing of these inputs is less understood but may be closely linked to community and ecosystem function. Inputs of drift macrophytes subsidize sandy beach communities and food webs in many regions. We estimated feeding rates of dominant sandy beach consumers, the talitrid amphipods (*Megalorchestia corniculata*, in southern California, USA, and *Talitrus saltator*, in southern Galicia, Spain), and their impacts on drift macrophyte subsidies in field and laboratory experiments. Feeding rate varied with macrophyte type and, for *T. saltator*, air temperature. Size-specific feeding rates of talitrid amphipods were greatest on brown macroalgae (*Macrocystis*, *Egregia*, *Saccorhiza* and *Fucus*). Rates for large individuals of both species ranged from ~40 mg wet wt individual^{-1}12 h^{-1} on brown macroalgae to negligible feeding by *M. corniculata* on a vascular plant (surfgrass). Amphipod growth rates were also greatest on *Macrocystis* and lowest on surfgrass, *Phyllospadix*. For a Californian beach with substantial inputs of macrophyte wrack (>70 kg wet wt m^{-1} month^{-1} in summer), we estimated that the population of talitrid amphipods could process an average of 55% of the palatable *Macrocystis* input. Our results indicate that talitrid amphipod populations can have a significant impact on drift macrophyte processing and fate and that the quantity and composition of drift macrophytes could, in turn, limit populations of beach consumers.

M. Lastra (✉) · I. F. Rodil
Departamento de Ecología y Biología Animal,
Universidad de Vigo, 36310 Vigo, Spain
e-mail: mlastra@uvigo.es

H. M. Page · J. E. Dugan · D. M. Hubbard
Marine Science Insitute, University of California,
Santa Barbara, CA 93106, USA

Introduction

Allochthonous inputs of organic matter can strongly influence population and community structure in many ecosystems (e.g., Polis and Hurd 1996; Cross et al. 2006). Such effects are expected to be greatest where a highly productive system interfaces with and exports materials to a relatively less productive system (Barrett et al. 2005). Ecosystems that are subsidized by allochthonous inputs often support a high abundance and diversity of primary and secondary consumers (Polis and Hurd 1996; Bustamante et al. 1995; Anderson and Polis 1999; Dugan et al. 2003), however, the role of subsidized consumers in the processing of these inputs is less understood.

Sandy beach ecosystems form a dynamic interface between marine and terrestrial environments. These systems are generally characterized by low in situ primary productivity (McLachlan and Brown 2006) and beach food webs are subsidized by allochthonous inputs from the coastal ocean (Griffiths et al. 1983; Dugan et al. 2003; reviewed by Colombini and Chelazzi 2003). Beach consumers are supported primarily by these allochthonous inputs, which include macrophyte wrack, consisting of drift macroalgal and vascular plant material, as well as phytoplankton, carrion, and other organic material (Griffiths et al. 1983; McLachlan and Brown 2006). In regions where the production of reef macroalgae, such as kelps, is high (e.g., Kirkman 1984; Dayton 1985; Hobday 2000), inputs of drift macrophytes to beaches can be extensive. For example, annual inputs of kelp wrack exceeding 470 and up to

2,100 kg wet weight m^{-1} of shoreline were estimated for sandy beaches of southern California and the west coast of South Africa, respectively (Hayes 1974; Stenton-Dozey and Griffiths 1983). The species composition and biomass of macrophyte inputs to beaches vary both spatially and temporally (e.g., Stenton-Dozey and Griffiths 1983; Marsden 1991; Dugan et al. 2003; Orr et al. 2005). Following deposition on the beach as wrack, drift macrophytes are subjected to a variety of processes including consumption by beach herbivores, in situ microbial degradation, desiccation, and export by tides and currents (Griffiths et al. 1983; Griffiths and Stenton-Dozey 1981; Inglis 1989; Jędrzejczak 2002; Orr et al. 2005).

Biological processing of macrophyte inputs through consumption by herbivores is a potentially important pathway by which this imported detrital material is cycled through the beach ecosystem (Hayes 1974; Griffiths et al. 1983; Chown 1996). Talitrid amphipods are often the most abundant herbivores on exposed sandy beaches, comprising up to 90% of the abundance (Stenton-Dozey and Griffiths 1983) and achieving high densities (>10,000 individuals m^{-1}) on some beaches (e.g., Jaramillo and McLachlan 1993; Dugan et al. 2003; Lastra et al. 2006). These abundant herbivores are supported by macrophyte wrack and are important trophic intermediates between macrophytes and higher level insect and avian consumers (Griffiths et al. 1983; Dugan et al. 2003).

Although feeding by herbivores may remove appreciable amounts of recently deposited macrophytes from a beach, few data are available that permit general estimates of the importance of this pathway to the fate of macrophyte wrack and reported figures vary widely. For example, estimated consumption of brown macroalgae inputs by beach herbivores has been reported as negligible (<1%, Inglis 1989) or very low (4–9%, Hayes 1974; Koop and Lucas 1983) to substantial (>70%, Griffiths et al. 1983).

The rates of consumption of drift macrophytes by different herbivore species may depend on the macrophyte species and associated physicochemical and morphological characteristics (Wakefield and Murray 1998; Van Alstyne et al. 2001; Pennings et al. 2000). Thus, biomass, composition and palatability of macrophytes arriving on the beach may play an important role in determining the fate of these inputs (Van Alstyne et al. 1999; 2001; Orr et al. 2005). Likewise, the abundance, composition and structure of the consumer community inhabiting a beach could influence the processing and availability of macrophyte wrack. In turn, spatial and temporal variability in wrack composition and biomass may affect composition, abundance and demographic rates of amphipods and other consumers within the beach community (Stenton-Dozey and Griffiths 1983; Dugan et al. 2003).

The overall goal of this study was to investigate factors that potentially influence the processing and consumption rate of macrophyte wrack by talitrid amphipods, including macrophyte species, amphipod size and abundance, and air temperature, and to explore the effect of macrophyte species on the growth performance of these amphipods. Specifically, we (1) estimated the size-specific feeding rates of talitrid amphipods on common drift macrophytes in the field and laboratory in two widely separated geographic regions, (2) explored amphipod food preferences in a field experiment, (3) evaluated the effect of macrophyte species on amphipod growth, and (4) estimated the impact of talitrid amphipods on drift macrophyte processing and fate.

Materials and methods

Study sites

Field sampling and experiments were carried out on sandy beaches in southern California, USA, and the southeast coast of Galicia, Spain (Fig. 1). Talitrid amphipods are important primary consumers of drift macrophyte wrack in both regions. Isla Vista beach, located along protected outer coast in Santa Barbara County, southern California (34°24′33″N, 119°52′9″W) is a narrow bluff-backed, reflective to low intermediate state beach (Dean's Parameter, $\Omega = 0.7$–3.8, Short and Wright 1983) ~3 km in length that experiences mixed semi-diurnal tides. The intertidal width of the beach (bluff base to low swash level) ranges from ~30 to 70 m. Isla Vista beach receives inputs of the kelps, *Macrocystis pyrifera* (giant kelp, hereafter *Macrocystis*) and *Egregia menziesii* (feather boa kelp, hereafter *Egregia*) and the vascular plant, *Phyllospadix torreyi* (surfgrass, hereafter *Phyllospadix*), as well as a variety of other brown,
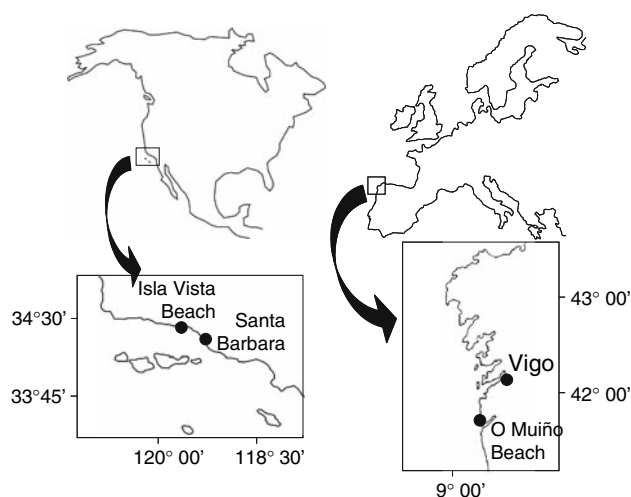
Fig. 1 Location of the study beaches: Isla Vista beach in southern California, USA and O Muiño beach in southwest Galicia, Spain

red and green algal species from rocky reefs and kelp forests located just offshore. This beach supports an abundant, species rich (39 species) community of intertidal macro-invertebrates (Hubbard and Dugan 2003).

O Muiño beach, located in southern Galicia (northwest coast of Spain) (41°52′21″N, 8°52′9″W) is a protected, dune-backed reflective beach ($\Omega = 0.2$) ~700 m in length. The intertidal width of the beach from the edge of the dunes to the low swash is ~100 m. O Muiño beach receives inputs of the brown macroalgae, *Saccorhiza polyschides* (furbelow, hereafter *Saccorhiza*) and *Fucus spiralis* (spiral wrack, hereafter *Fucus*) and the green alga, *Ulva lactuca* (sea lettuce, hereafter *Ulva*), as well as several species of red algae from nearby rocky intertidal and subtidal habitats. Large beds of macroalgae comparable to those offshore of Isla Vista beach above were absent. The number of macro-invertebrate species on the beach (7 species) is typical of reflective beaches in northwest Spain (Incera 2004; Lastra et al. 2006).

Field sampling

Composition and biomass of macrophyte wrack

The species composition and biomass of macrophyte wrack on Isla Vista beach were estimated in August 2003 along 3 transects (30 m in length) extending perpendicular to the water line from the landward intertidal boundary (sea bluff) to the upper swash zone. A table of random numbers was used to set the distances between the transects along a 100 m segment of the beach. All the macrophyte wrack present within a 1 m wide strip of beach centered on each of the transects was collected, separated by species, shaken to remove adhering sand and weighed to the nearest 100 g. Mean biomass values for each macrophyte species were calculated by averaging data from the three transects and expressed in terms of kilograms wet weight of each species per meter of beach shoreline.

The species composition and biomass of macrophyte wrack on O Muiño beach were estimated in October 2003 along 4 transects (26 m in length) extending from 1 m above the upper edge of the highest drift line of wrack to the swash zone. The four transects were located using a random number table along a 50 m segment of beach. Six equally spaced, paired 10 cm diameter cores were taken to a depth of 15 cm along each transect. The cores were sieved (mesh size 1.0 mm) to separate wrack from the sand. All the wrack was placed in labeled plastic bags, transported to the laboratory at the University of Vigo, and frozen. In the laboratory, species composition of macrophytes was determined to the lowest taxonomic level possible. The individual macrophyte taxa were blotted and weighed wet to the nearest 0.1 g. Mean biomass values for each macrophyte

species were calculated by averaging data from the four transects and expressed in terms of grams wet weight of each species per meter of beach shoreline.

Input of macrophyte wrack

To estimate the potential food resources available and allow calculations of macrophyte processing rates by talitrid amphipod populations, we measured the input of drift macrophytes for 30 days on Isla Vista Beach in July–August 2002. This period coincides with a time of year that lacks storm activity and has consistently small waves and minimal beach erosion. Four 25-m wide plots were selected from a 300 m segment of beach using a random number table. These plots were initially cleared of surface and buried wrack by hand on 9 July. Subsequently, all wrack accumulated between the sea bluff and the high swash level was collected by hand, categorized by type, weighed to the nearest 100 g and removed from the plots every 3 days. Wrack was collected following the highest tide for each day of sampling to minimize any effects of tide level on wrack input estimates. Wrack in the active swash zone (below the high swash level) was not removed or estimated. To prevent the redeposition of wrack in the study plots, all wrack removed was transported off the entire 300 m segment of beach. Input for each 3-day period was estimated from the mean biomass of fresh algae for the four plots. These biomass values represented net input for each 3-day period after loss from amphipod feeding. For use in calculating processing by talitrid amphipods, the mean wet biomass of accumulated fresh *Macrocystis* was adjusted to reflect the average proportion of blades in individual plants (64%, D. Reed personal communication) as an estimate of the input of palatable material per meter of beach shoreline.

Density and population structure of talitrid amphipods

To predict the potential impact of talitrid amphipod populations on their food resources, we used data on the density and population structure of *Megalorchestia* collected in 2002 and on *Talitrus* collected during the field feeding experiments in the present study. On Isla Vista beach, the population of *Megalorchestia* was sampled along each of three shore-normal transects extending from the landward intertidal boundary (bluff) to the upper swash zone. A table of random numbers was used to set the distances between the transects along a 25 m segment of beach. Twenty (0.1 m diameter) cores were collected at uniform intervals to a depth of 20 cm along each transect. Sand from each set of ten cores was sieved through a 1.5 mm mesh retaining any animals. For O Muiño beach, the population of *Talitrus* was sampled with the cores used to estimate macrophyte wrack composition and biomass. As above, amphipods were

separated from the sand in each core by sieving (mesh size 1 mm). Samples were placed in ziplock bags, transported to laboratories at the University of California, Santa Barbara or University of Vigo, and frozen. In the laboratory, talitrid amphipods were identified, enumerated, measured (total length to the nearest 1 mm) blotted dry, and weighed to the nearest 0.001 g. Dry weight was determined on subsamples of each species after drying to a constant weight at 60°C. A length-dry weight relationship for each amphipod species was calculated using regression analysis. The size-specific density of *Megalorchestia* and *Talitrus* were expressed per linear meter of beach shoreline (ind m^{-1}).

Field and laboratory experiments

Consumption rate of macrophytes in the field

To estimate the consumption rates of common macrophytes by *Megalorchestia* and *Talitrus*, we conducted field experiments at Isla Vista and O Muiño beaches. Consumption rates were measured by enclosing amphipods in the field in replicate plastic containers of 12 cm diameter and 8 cm depth that were filled with ∼5 cm of moist sand from the respective study beach. Sand was sieved through 1 mm mesh to remove animals and particulates prior to use in experiments. The lids of the containers were perforated with many small (∼1 mm) holes to facilitate air flow. Since consumption rate varies with body size, we used three size classes of amphipods (small, medium, and large) in the feeding experiments. The sizes of animals in the three classes varied between the two species because *Megalorchestia* reaches a larger size (30 mm) than *Talitrus* (20 mm). For *Megalorchestia*, amphipods ranged in total length from 8 to 10 mm, 14 to 17 mm, and 20 to 23 mm, for small, medium, and large size classes, respectively. For *Talitrus*, amphipods ranged in length from 5 to 8 mm, 10 to 12 mm, and 15 to 18 mm, for small, medium, and large size classes, respectively. The two largest size classes of *Megalorchestia* were composed entirely of *M. corniculata*, whereas the smallest size class could also potentially have included a few individuals of a smaller species, *M. benedicti*, since it was difficult to separate this species from *M. corniculata* by eye at that size.

We compared consumption rate of talitrids on three species of macrophytes at each beach. For experiments at Isla Vista beach, the brown macroalgae, *Macrocystis* and *Egregia*, and the vascular plant, *Phyllospadix* were used. These 3 species comprise >90% of total biomass of recently deposited wrack (see "Results"). For O Muiño beach, the brown macroalgae, *Saccorhiza* and *Fucus*, and the green alga, *Ulva*, were used. These three species comprise 50% of the total biomass of recently deposited wrack (see "Results").

To estimate consumption rates, amphipods freshly collected by hand from each beach were added to individual containers as follows: 20 small, 10 medium or 10 large individuals. Once the amphipods had burrowed, a pre-weighed portion of the blade (macroalgae) or several leaves (surfgrass) of single macrophyte species was placed on the sand surface in each experimental container. All macrophyte portions were composed of material that was harvested from the field, blotted to remove excess water and weighed to the nearest 0.001 g prior to addition to the containers. We used harvested material in experiments to simulate recently deposited beach wrack. Although the time from dislodgement of macrophytes in nearby beds to deposition on the beach is unknown, macrophytes deposited on our study beaches typically desiccate during the day, or become buried and less useable to amphipods. Macrophytes were always supplied to each experimental container in excess of anticipated consumption by amphipods (generally 0.8–1.0 g wet wt). To control for a possible weight change of the macrophyte portions independent of feeding by amphipods (e.g., from desiccation, microbial degradation), three controls consisting of containers with sand and pre-weighed portions of each of the macrophyte types, but without amphipods, were also prepared for each experimental trial.

Experimental containers were prepared in the laboratory. Containers were shuffled and picked at random for deployment in the field, where they were spaced ∼1 m apart along the drift line, buried in the sand, but leaving the top few millimeters of each container exposed at each study beach. Both amphipod species are primarily nocturnal, emerging at dusk and burying into the sand at dawn (Craig 1973; Scapini et al. 1992; Nardi et al. 2003). To bracket natural activity patterns, experimental containers were deployed at dusk, left overnight, and collected at dawn (12 h period of deployment). Each amphipod size class × macrophyte species treatment was replicated over three consecutive nights. Field experiments at Isla Vista beach were conducted from 21 to 23 September 2004. Experiments at O Muiño were conducted from 15 to 17 October 2003. Air temperatures during the experiments ranged from 14 to 22°C at Isla Vista beach and from 10 to 15°C at O Muiño beach. At the termination of the experiment, the remaining food was removed, brushed lightly with a small brush to remove adhering sand, blotted to remove excess water, and weighed to the nearest 0.001 g. The total length of each amphipod used in the experiments was measured to the nearest 0.1 mm with vernier calipers.

Consumption rates were calculated per individual (mg consumed ind^{-1} 12 h^{-1}) as: $((T_i \times C_i/C_f) - T_f)/n$ where T_i and T_f are the initial and final blotted wet weights of macrophyte in the treatment, C_i and C_f are the initial and final weights of macrophyte in the controls, and n = number of

individuals in the treatment (e.g., Taylor and Brown 2006). This calculation does not consider interactions over time between weight changes due to feeding and other factors, such as desiccation, and most accurately reflects consumption when weight changes and variability among values in the controls are small (as in this study, generally <5%) (Peterson and Renaud 1989). Consumption rates were expressed per mean individual dry weight using the following length–weight relationships developed from a subset of experimental animals:

(1) *Megalorchestia*: log dry wt (mg) = $3.16 \times$ (log total length, mm) $- 2.41$ ($r^2 = 0.82$, $n = 75$).
(2) *Talitrus*: log dry wt (mg) = $1.99 \times$ (log total length, mm) $- 1.99$ ($r^2 = 0.93$, $n = 66$).

Food preference and population feeding

To investigate the preference of *Megalorchestia* for the three most abundant types of macrophyte wrack and estimate the impact of feeding on their food resources, we deployed whole blades (including pnematocysts) of *Macrocystis*, pieces of rachis with blades of *Egregia*, and leaves of *Phyllospadix* on Isla Vista beach. The experimental wrack portions were blotted to remove excess water, weighed to the nearest 0.01 g, and set out on the driftline overnight on 23 September 2004. Each treatment was prepared in triplicate and nestled into existing wrack on the beach at stations located ~2 m apart along the drift line. Replicate portions of wrack covered with 250-μm mesh that excluded *Megalorchestia*, were used as controls for weight changes independent of amphipod feeding. Just prior to dawn the following morning, the remaining pieces of *Macrocystis, Egregia*, and *Phyllospadix* were retrieved, returned to the laboratory, brushed lightly to remove adhering sand, blotted, and weighed.

Effect of air temperature on consumption rate

The effect of the air temperature on the consumption rate of macrophytes by *Megalorchestia* and *Talitrus* was explored in laboratory experiments using *Macrocystis* and *Saccorhiza*, macroalgal species that were readily consumed in the field experiments. Containers and size classes of amphipods used in the laboratory experiments were the same as those used in the field experiments. Replicate trials were run over three consecutive nights (12 h) in environmental chambers at three temperatures that bracketed the range of temperatures observed during the field experiments at each site (±1°C). Thus, experiments were conducted at 15, 17.5, and 20°C with *Megalorchestia*, and 10, 15, and 20°C with *Talitrus*. Each amphipod size class, temperature treatment combination was replicated three times. Controls containing portions of each macrophyte species, but no amphipods, were included as in the field experiment. Photoperiod in the environmental chambers was similar to that in the field (~12 h of daylight). At the conclusion of the experiment, the total length of each amphipod used in the experiments was measured as above.

Effect of macrophyte type on amphipod growth rate

To examine the effect of macrophyte species on amphipod growth rate, we enclosed ten *Megalorchestia* (8–10 mm in length) in a container (as described above) together with portions of blade of either *Macrocystis* or *Egregia*, or leaves of the surfgrass, *Phyllospadix*. Macrophytes were supplied to each experimental container in excess of anticipated consumption by amphipods in 24 h. Each of the three macrophyte treatments was replicated four times. Containers were deployed randomly (as above) in the upper part of the beach (above the driftline) and left in place for 7 days (20–27 September 2006). During this period, the containers were checked each morning, all uneaten algae or surfgrass was removed, and fresh portions of macrophyte species added in excess of consumption. Total blotted wet weight of the amphipods was measured to the nearest 0.001 g at the beginning and at the end of the experiment. Amphipod growth was calculated as the difference between the initial and final weights for the composited ten animals in each container.

Data analysis

Density and biomass data are expressed per meter of shoreline in the alongshore direction. All the statistical analyses were done using SYSTAT 11.0 (SPSS). We tested for treatment effects (macrophyte species, air temperature) on the consumption rate of macrophytes in the field and laboratory enclosure experiments using analysis of covariance (ANCOVA) with individual weight as the covariate. We tested for differences in the consumption of macrophytes deployed overnight in the field using one-way analysis of variance (ANOVA). If the main effects were significant, we used the Tukey post hoc test to identify significant differences among treatments.

Results

Composition and standing crop of macrophyte wrack

Macrophyte wrack at Isla Vista beach was composed primarily of giant kelp, *Macrocystis* (50% of total) and surfgrass *Phyllospadix* (37%) with lesser amounts of other algae and negligible amounts of terrestrial material (Fig. 2). The total mean biomass of recently deposited wrack at this
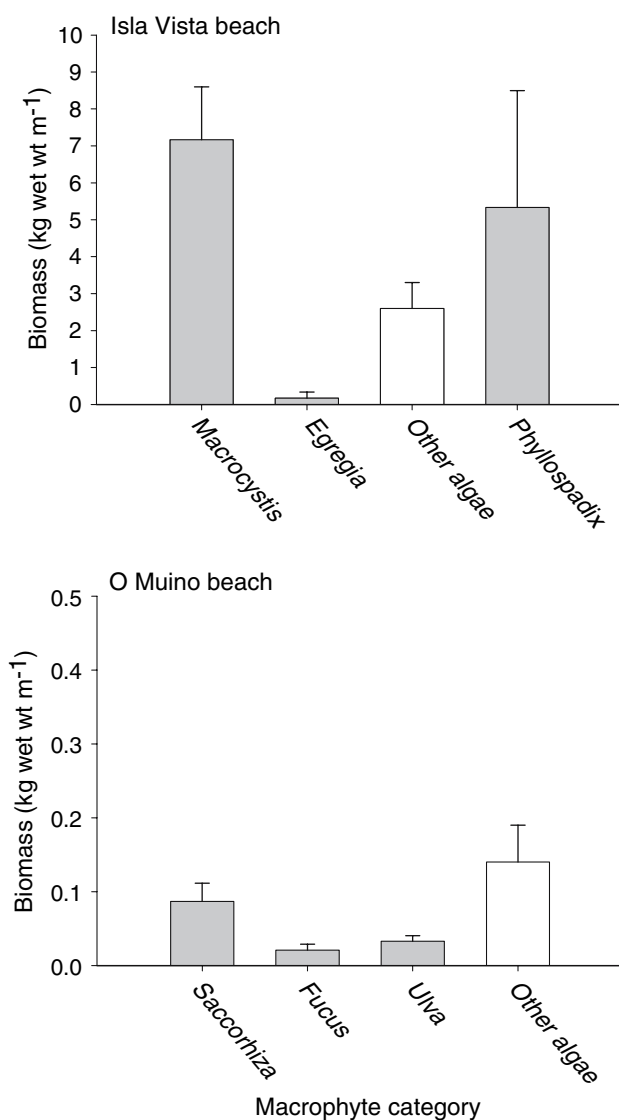
Fig. 2 Composition of the biomass (wet weight) of macrophyte wrack at Isla Vista beach and O Muiño beach

beach was 21.4 kg wet wt m^{-1}. Recently deposited macrophyte wrack at O Muiño beach was composed of a variety of species, including the brown macroalgae *Saccorhiza* (14% of total) and *Fucus* (3%), and the green alga *Ulva* (5%), along with several species of red algae (22%) (Fig. 2). Vascular plant material originating from the nearby Miño River and estuary comprised a high proportion of wrack on the beach (53%). The mean biomass of recently deposited macrophyte wrack on O Muiño beach was 0.61 kg wet wt m^{-1}.

Input of macrophyte wrack

The measured net input of freshly deposited marine macrophytes to Isla Vista Beach during the 30 day study period averaged 5,300 g wet wt m^{-1} 3 days^{-1} (±2,423) and varied

over 4-fold (2,081–9,215 g wet wt m^{-1} 3 days^{-1}) among sampling dates. Net input of fresh wrack was dominated by brown macroalgae but varied considerably among the kelp species at Isla Vista beach. The net input of fresh *Macrocystis* was greatest, averaging 2,715 g wet wt m^{-1} 3 days^{-1} (±1,087) over the 30 days, while that of *Egregia* was more than an order of magnitude lower, averaging 180 g wet wt m^{-1} 3 d^{-1} (±138). The net input of surfgrass, *Phyllospadix*, was also high, averaging 2,006 g wet wt m^{-1} 3 d^{-1} (±1,154).

Consumption rate of macrophytes in the field

For *Megalorchestia*, mean individual consumption rate was significantly correlated with individual body weight in the *Macrocystis* ($P < 0.001$, $r^2 = 0.72$) and *Egregia* ($P < 0.001$, $r^2 = 0.79$) treatments, but not in the *Phyllospadix* ($P > 0.1$, $r^2 = 0.15$) treatment (Fig. 3). The weight of the controls decreased <4% for *Macrocystis*, *Egregia*, and *Phyllospadix*. For *Talitrus*, individual consumption rate was correlated with body weight in all treatments (*Saccorhiza*, $P < 0.001$, $r^2 = 0.82$; *Fucus*, $P < 0.01$, $r^2 = 0.96$; *Ulva*, $P < 0.05$, $r^2 = 0.73$) (Fig. 3). The weight of the controls decreased generally <5% for *Saccorhiza* and *Fucus* and 25% for *Ulva*.

There was a significant effect of macrophyte species on consumption rate for both *Megalorchestia* and *Talitrus* (Fig. 3). For *Megalorchestia*, there was no difference in consumption rate between the *Macrocystis* and *Egregia*
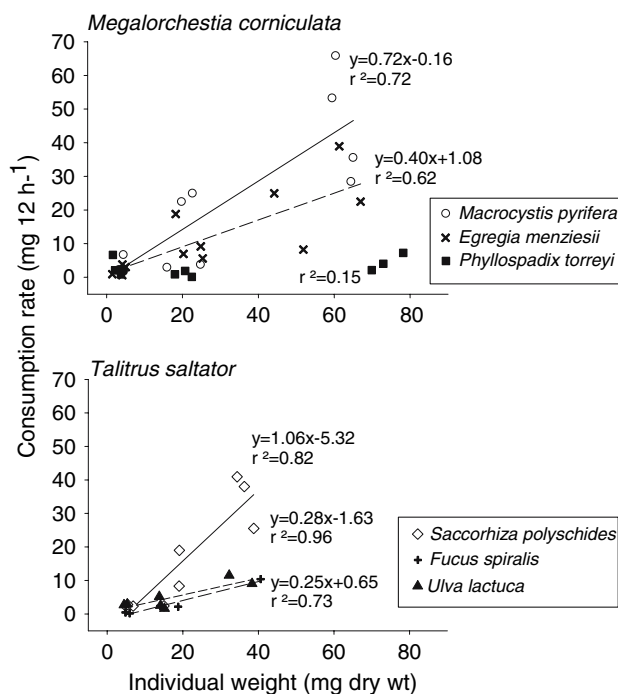
Fig. 3 Consumption rate of macrophytes as a function of amphipod dry weight for *Megalorchestia corniculata* and *Talitrus saltator* in field containers

treatments ($P = 0.086$, test for homogeneity of slopes, $P = 0.091$, ANCOVA); however, amphipods did not consume detectable amounts of *Phyllospadix*. For *Talitrus*, there was a significant difference in consumption rate between the *Saccorhiza* and the *Fucus* and *Ulva* treatments ($P = 0.002$, $F = 9.82$, test for homogeneity of slopes, $P < 0.01$, Tukey post hoc test), but not between *Fucus* and *Ulva* treatments ($P = 0.84$, Tukey post hoc test).

Field preference and population feeding

The consumption of *Macrocystis*, *Egregia*, and *Phyllospadix* deployed on Isla Vista beach overnight by *Megalorchestia* populations differed significantly among treatments ($P < 0.001$, $F = 39.62$, $df = 2, 12$, One-way ANOVA: Fig. 4). *Macrocystis* was readily consumed (87%) ($x = 6.6 \pm 0.5$ g, $x \pm 1$SE); the blade portion of this alga was almost entirely eaten leaving only the thicker pnematocyst intact. Less (53%) of the deployed *Egregia* was consumed (4.0 ± 0.2 g) ($P = 0.012$, Tukey post hoc test); the blade portion of this alga was also preferred, leaving the thicker rachis. Only negligible amounts of *Phyllospadix* (1%) ($x = 0.01$ g) were eaten. The weight of the controls decreased 7, 3, and 2% for *Macrocystis*, *Egregia*, and *Phyllospadix*, respectively. These values are incorporated into the calculation of consumption (see "Materials and methods").

Effect of air temperature on consumption rate

There was no effect of the experimental air temperature on the consumption rate of *Macrocystis* by *Megalorchestia* at
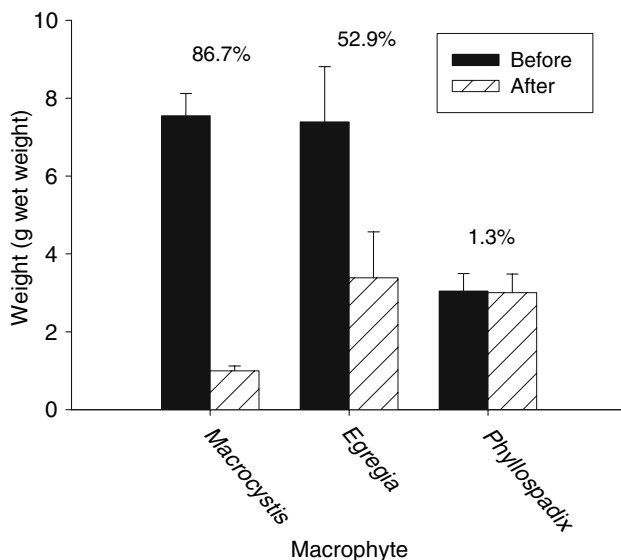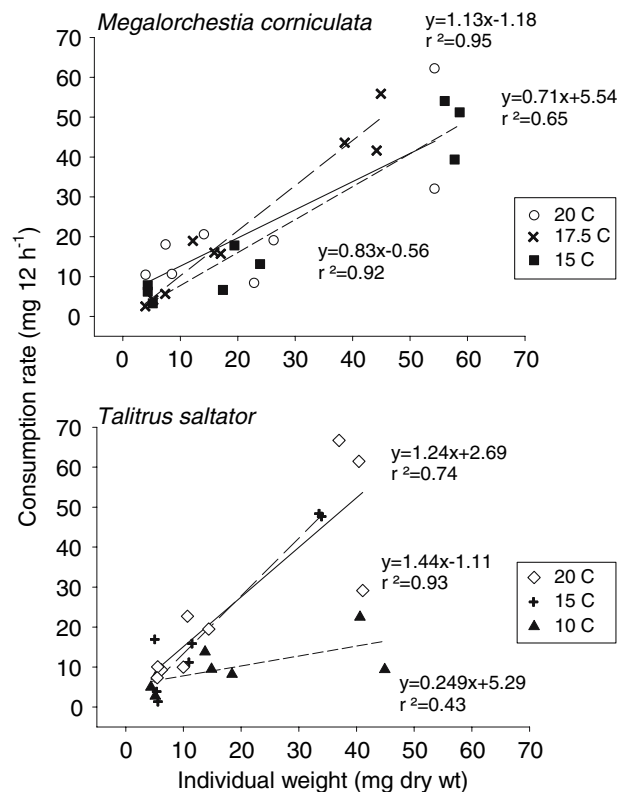
Fig. 4 Consumption of *Macrocystis pyrifera*, *Egregia menziesii*, and *Phyllospadix torreyi* deployed overnight on Isla Vista beach. Percentage change indicated above *bars*. Weight change overnight corrected for change independent of feeding (see text)

the three temperatures tested ($P = 0.30$, ANCOVA: Fig. 5). There was a significant difference in the consumption rate of *Saccorhiza* by *Talitrus*, among temperature treatments ($P = 0.137$, test for homogeneity of slopes, $P = 0.031$, $F = 4.105$, $df = 2, 22$, ANCOVA) with rates lower at 10°C compared with 15 and 20°C ($P < 0.05$, Tukey post hoc test).

For *Megalorchestia* offered *Macrocystis*, there was no difference in the consumption rate–body weight relationship between field and laboratory ($P = 0.37$, test for homogeneity of slopes, $P = 0.125$, ANCOVA). For *Talitrus* offered *Saccorhiza*, however, there was a significant difference in this relationship with consumption rates measured in field lower than to those measured at 15 and 20°C ($P = 0.26$, test for homogeneity of slopes, $P = 0.009$, $F = 3.338$, $df = 1, 22$, ANCOVA), and higher than those observed at 10°C ($P = 0.003$, $F = 13.273$, $df = 1, 13$, test for homogeneity of slopes) in the laboratory.

Effect of macrophyte species on amphipod growth rate

There was a significant effect of macrophyte species on the short-term growth rate of *Megalorchestia* ($P < 0.001$,

Fig. 5 Consumption rate of *Macrocystis pyrifera* and *Saccorhiza polyschides* as a function of amphipod dry weight at different air temperatures for *Megalorchestia corniculata* and *Talitrus saltator* in the laboratory

$F = 28.7$, $df = 2, 9$, One-way ANOVA: Fig. 6). Growth rate differed among all macrophyte treatments ($P < 0.05$, Tukey post hoc test); amphipods grew most rapidly in the *Macrocystis* treatment, with little growth in the *Phyllospadix* treatment. Mortality of amphipods ranged from 10 to 17% and did not differ significantly among treatments ($P > 0.05$, ANOVA).
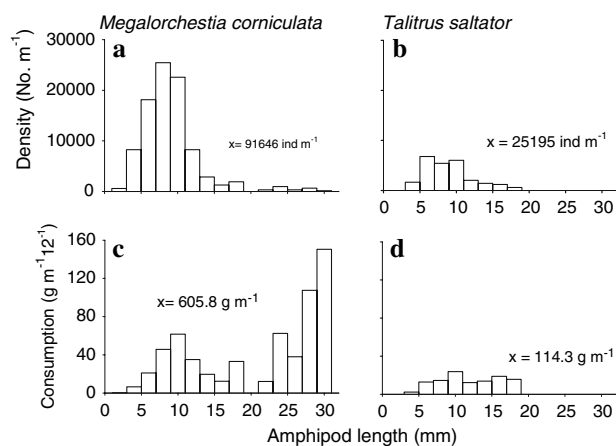
Density and population structure of talitrid amphipods

Densities of talitrid amphipods were three times higher at Isla Vista beach (91,646 ind m^{-1}) compared with O Muiño beach (25,195 ind m^{-1}) (Fig. 7). The population structures of *Megalorchestia corniculata* and *Talitrus saltator* at Isla Vista and O Muiño beaches, respectively, were dominated by small individuals; however, *M. corniculata* reached a much larger size (30 mm) than *T. saltator* (20 mm) (Fig. 7). Other talitrid species (*M. benedicti* and *M. californiana*) were also present at Isla Vista beach, but the densities of these species were much lower than for *M. corniculata*.

Processing of drift macrophytes by talitrid amphipod populations

Although individual feeding rates measured on the most abundant brown macroalgal types, *Saccorhiza* and *Macrocystis*, were relatively similar for *Talitrus* and *Megalorchestia*, respectively (Fig. 3), the estimated daily population consumption of these macrophytes varied over 5-fold between the two study beaches (Fig. 7c, d). Using the size frequency data on *Megalorchestia* at Isla Vista beach (Fig. 7a) and the regression equation for the consumption rate of *Macrocystis* (Fig. 3), we estimated that the population of *Megalorchestia* had the potential to consume
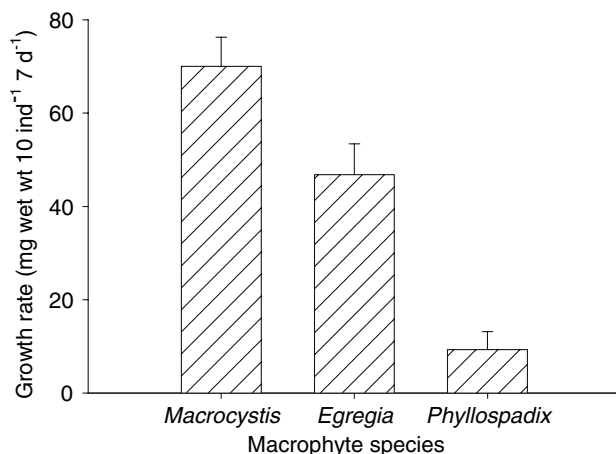
Fig. 6 Comparison of the growth rate of *Megalorchestia corniculata* offered *Macrocystis pyrifera*, *Egregia menziesii*, or *Phyllospadix torreyi* in field containers. $x \pm 1SE$, $n = 4$


Fig. 7 a Density and population structure of **a** *Megalorchestia corniculata* at Isla Vista beach and **b** *Talitrus saltator* at O Muiño beach and potential daily population consumption of **c** *Macrocystis pyrifera* and **d** *Saccorhiza polyschides* by these amphipod species, respectively. Equations for consumption rates of *M. pyrifera* and *S. polyschides* by amphipods in Fig. 3 were used to estimate population consumption

606 g wet wt *Macrocystis* m^{-1} 12 h^{-1} at Isla Vista beach (Fig. 7c). Large individuals of *Meglaorchestia* (>20 mm length), although comprising only ~3% of the population, accounted for ~39% of the *Macrocystis* consumed overnight during the summer (Fig. 7c). In contrast, the potential consumption of *Saccorhiza* by the *Talitrus* population at O Muiño beach, estimated using size frequency data (Fig. 7b) and the regression equation for the consumption rate of *Saccorhiza* (Fig. 3), was much less (114 g m^{-1} 12 h^{-1}) because of the lower density and smaller maximum size of this amphipod species (Fig. 7d).

We estimated the potential importance of talitrid amphipod populations to the processing of recently stranded palatable wrack at Isla Vista beach over a period of 1 month using data on the population consumption rate of *Macrocystis* (Fig. 7c) and the input of *Macrocystis* (Fig. 8). For this calculation, the daily night-time consumption rate of *Macrocystis* by the *Megalorchestia* population of ~90,000 ind m^{-1} on Isla Vista beach was assumed to be constant over 30 days. Estimated net 3-day input of palatable *Macrocystis* (blades only) varied 9-fold, from 436 to 3,931 g m^{-1} averaging 1,738 g m^{-1} ($\pm 1,087$ g m^{-1}) (Fig. 8). When adjusted for the estimated consumption of ~1,800 g wet wt *Macrocystis* m^{-1} 3 days^{-1} (606 g m^{-1} days^{-1}) by the resident talitrid population, the estimated total input of palatable *Macrocystis* to Isla Vista beach ranged from 2,236 to 5,731 g wet wt m^{-1} ($x = 3,538$ g m^{-1} 3 days^{-1}) for the study period (Fig. 8). Our calculations indicate that this population of *Megalorchestia* was capable of consuming from 31 to 81% (average 55%) of the total 3-day input of palatable *Macrocystis* wrack (Fig. 8).
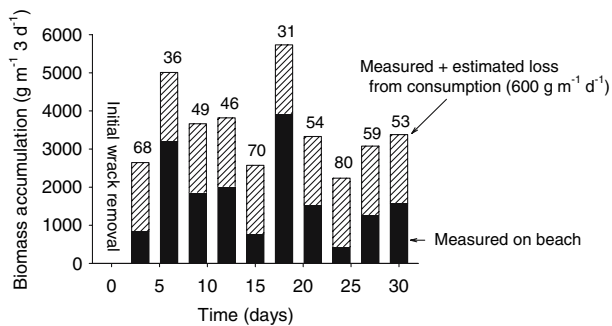
Fig. 8 Mean biomass of *Macrocystis pyrifera* (g wet wt m⁻¹) accumulated in plots cleared of macrophytes at 3-day-intervals at Isla Vista beach in summer 2002 (*black bars*) and estimated losses (derived from Figs. 3, 7) from amphipod feeding (*hatched bars*). *Total height of bars* is the estimated total input of palatable *Macrocystis* for each 3 day period. Estimated percentage lost to herbivory by talitrids is indicated above *bars*

Discussion

Allochthonous inputs of macrophytes subsidized food webs at both of our study beaches and talitrid amphipods comprised the most abundant macrophyte consumers present in these beach communities. These amphipods feed on recently stranded macrophytes and therefore play a potentially important role in the biological processing of macrophyte inputs. However, not all the drift macrophyte species were readily consumed by amphipods. Brown macroalgae, *Macrocystis* (Isla Vista beach) and *Saccorhiza* (O Muiño beach), were consumed rapidly by *Megalorchestia* and *Talitrus*, respectively, whereas the consumption of some other macrophytes (e.g., *Phyllospadix*, Isla Vista beach, *Ulva*, O Muiño beach) was negligible or low. Preferential use of brown macroalgae by *Talitrus* was estimated from stable isotope analyses (Adin and Riera 2003).

Differences in the consumption of macrophytes by talitrid amphipods may be related to one or more plant traits that affect palatability. Two traits commonly suggested to influence food preference and consumption rate are chemical deterrents to herbivory (e.g., phlorotannins in brown algae) and structural toughness (e.g., Steinberg 1988; Denton and Chapman 1991; Wakefield and Murray 1998; Pennings et al. 2000). Few data are available on the presence of chemical deterrents in the macrophyte species used in this study. Concentrations of phlorotannins were low and similar (<2%) in *Macrocystis pyrifera* and *Egregia menziesii* at another site in southern California (Catalina Island, Van Alstyne et al. 1999), which may explain the rapid consumption of these macrophytes by *Megalorchestia* in this study. In contrast, species of *Fucus* are considered unpalatable to many herbivores due to a higher content of phlorotannins than other brown macroalgae (Denton and Chapman 1991).

These compounds may have contributed to the lower consumption rate of *Fucus* by *Talitrus* in comparison to *Saccorhiza*. However, this explanation is not supported in laboratory food preference experiments in which *Fucus* sp. was preferentially consumed over other macroalgal species by the isopod, *Ligia pallasii* and amphipod, *Traskorchestia traskiana*, despite containing higher levels of phenolics than the other algal species tested (Pennings et al. 2000). The influence of chemical deterrents on consumption does not appear to be a satisfactory explanation for the low consumption rate of the sea lettuce, *Ulva*, by *Talitrus*. *Ulva* was a minor biomass component (5%) on O Muiño beach and was poorly consumed by *Talitrus*. Low use of *Ulva* as a food source by this talitrid species was predicted by Adin and Reira (2003). *Ulva* species have been reported to have low phenolic content and structural toughness (Pennings et al. 2000), suggesting that some other factor(s) may have deterred amphipod feeding. The role of plant traits in influencing herbivory is potentially complex and may depend on how these traits (e.g., chemicals, nitrogen content, lipid storage compounds, water content, structural toughness) interact with each other and with feeding history and the digestive capability of consumers (Steinberg and van Altena 1992; Moran and Arrontes 1994; Pennings et al. 2000; Johnston et al. 2005).

In contrast to the palatability of brown macroalgae, consumption of the abundant (37% of wet biomass) surfgrass *Phyllospadix*, by *Megalorchestia* on Isla Vista beach was negligible in all field experiments. This result was most likely related to the structural toughness of this vascular plant (e.g., Valiela and Rietsma 1984; Bärlocher and Newell 1994). Although vascular plant material has been reported to be consumed by talitrid amphipods in salt marsh, sand, and cobble beach habitats, this generally occurs only after aging and microbial degradation of the plant tissue (Lopez et al. 1977; Moore and Francis 1985; Graça et al. 2000; Jędrzejczak 2002). We have not observed feeding on recently deposited surfgrass by *Megalorchestia* in the field. Our observations suggest that deposited surfgrass does not decay to a palatable state on Isla Vista beach, but either desiccates on the sand surface and/or becomes buried where it becomes less available to amphipod and other consumers. As a result, we propose that biological processing of surfgrass by *Megalorchestia* is not an important pathway influencing the fate of this abundant macrophyte on Isla Vista beach.

How generalizable are our estimates of consumption rate of macrophytes by *Megalorchestia* and *Talitrus* to other talitrid amphipod species? Consumption rates on preferred algae (*Macrocystis* and *Saccorhiza*) appeared slightly higher for *Talitrus*, although this pattern was statistically significant only in the laboratory experiments. Consumption rate values for both species fall within the range of

previously reported values; however, comparisons with data on other talitrid amphipods are somewhat problematic because of differences in the methods, environmental conditions, and units used among investigators to measure consumption rates. If we convert our data to the units used in Griffiths et al. (1983) using a water content for *M. pyrifera* and *S. polyschides* of 87.2 and 86.4%, respectively (Lastra, Page, Dugan, unpublished data), *Megalorchestia* and *Talitrus* of 20 mg dry weight consume 9–11% of dry body weight d^{-1} in dry weight of algae. This value is less than the value of ~20% reported in Griffiths et al. (1983) for *Talorchestia capensis* of similar weight feeding on brown algae on a South African beach. However, our consumption rate estimates for a 20 mg dry weight individual *Megalorchestia* or *Talitrus* of 0.09 and 0.11 mg dry algae mg dry wt ind^{-1}, respectively, were higher than values reported for *Orchestia gammarellus* feeding on *Laminaria digitata* (0.011 and 0.059 mg dry weight algae g dry weight individual^{-1}12 h^{-1}) (Moore and Francis 1985).

Consumption rates of macrophytes may be influenced by air temperature as shown for *Talitrus* offered *Saccorhiza* in the laboratory; rates were significantly lower at 10°C, the lowest night-time temperature recorded for O Muiño beach during our experiments, compared with 15 and 20°C (Fig. 5). No effect of air temperatures in the range of 15–20°C was found on the consumption rate of *Macrocystis* by *Megalorchestia*. Nevertheless, our results for *Talitrus* suggest that air temperature could influence the consumption rate of macrophytes and needs to be considered in assessing the potential importance of feeding by talitrid amphipods in the processing of macrophyte inputs.

In addition, as expected, consumption rate was strongly dependent on body size; thus, the size structure and density of the amphipod population can be expected to significantly influence the importance of these consumers to the processing of macrophyte wrack on beaches. The population structures of *Megalorchestia* and *Talitrus* on Isla Vista and O Muiño beach, respectively, were both dominated by small individuals (≤10 mm length), but differed in the higher density and larger maximum size of *Megalorchestia* (Fig. 7). This resulted in large differences (>5-fold) in estimated daily consumption rates of the most abundant brown macroalgal wrack species between these populations. Based on daily rates, we estimated the abundant population of *Megalorchestia* at Isla Vista beach could potentially consume 18 kg wet wt *Macrocystis* m^{-1} month^{-1} with a small number of large individuals accounting for 39% of that consumption, while the potential consumption of *Saccorhiza* by the less abundant population of a smaller species, *Talitrus*, at O Muiño beach was estimated as 3.4 kg wet wt m^{-1} month^{-1}.

Our results suggest that variation in the consumption rate of the different species of drift macrophytes by consumers

can potentially affect the turnover rates and hence the biomass and composition of wrack that accumulates on the beach over time. In this regard, talitrid amphipods can act as "biological filters", removing more palatable macrophyte material and species through consumption, leaving less palatable species and material, such as *Phyllospadix* and the stipes and floats of brown algae to accumulate and degrade through mechanical and microbial pathways. This is supported by our calculations of the potential importance of talitrid amphipod populations to the biological processing of recently stranded palatable wrack for a beach with high wrack input (Fig. 8) which estimated that this amphipod population was capable of consuming an average of 55% of the *Macrocystis* wrack input every 3 days in the summer (Fig. 8). In contrast, this population consumes only negligible amounts of the abundant *Phyllospadix* deposited at rates of >2 kg m^{-1} 3 days^{-1} on this beach and that this wrack type more likely dries and accumulates on the beach relative to the kelps, *Macrocystis* and *Egregia*. The consumption of experimental blades of *Macrocystis* deployed overnight on Isla Vista beach (Fig. 4) supports these calculations indicating that talitrid amphipods can consume a high proportion of recently stranded *Macrocystis* (87%) and *Egregia* blades (53%) but leave *Phyllospadix* blades virtually untouched. Similarly, Griffiths et al. (1983) estimated that talitrid amphipods consumed a large fraction (~50%) of the kelp deposited during the year on a beach with high wrack input in South Africa.

While our results demonstrate that talitrid amphipods play an important role in the biological processing of macrophyte inputs, the interaction between their feeding activities and the supply of drift macrophytes could also influence other components of the sandy beach community. When the supply of palatable macrophytes is low relative to population consumption rates, we propose that amphipod feeding can have a large indirect effect on the sandy beach community through the removal of a potential resource (habitat, food) used by other wrack-dependent species (e.g., isopods, beetles, flies). At high macrophyte input rates, amphipod feeding activities may facilitate wrack processing by other consumers, as well as microbial activity.

In addition, our study suggests that variation in wrack supply and composition has significant consequences for the demographic attributes of talitrid amphipod populations. This conclusion is supported by studies showing the importance of food quality to the individual performance of amphipods (Robertson and Lucas 1983; Kneib et al. 1997; Taylor and Brown 2006; this study) and the positive relationships reported between the availability of wrack and talitrid amphipod abundance or biomass (Stenton Dozey and Griffiths 1983; Dugan et al. 2003; Jaramillo et al. 2006).

Our results support the concept that the dynamics of macrophyte wrack input and fate are closely coupled with

the structure and production of sandy beach communities and food webs. Allochthonous inputs of wrack to beaches subsidize invertebrate consumers, while feeding by consumers, such as the talitrid amphipods studied here, affects the turnover and fate of wrack. These consumers, in turn, are prey resources for higher predators, such as shorebirds (e.g., Griffiths et al. 1983; Hubbard and Dugan 2003), whose abundance can track prey and wrack availability on beaches (Tarr and Tarr 1987; Dugan et al. 2003). Drivers that affect the production and composition of marine macrophytes (e.g., ENSO events, storms, urchin grazing, invasive algae) and the supply of wrack inputs (e.g., beach grooming, sea level change, beach erosion) have significant implications for consumer populations, food webs, higher predators, and wrack processing on sandy beaches. In this regard, our study highlights the potential importance of biological processing of macrophyte inputs by talitrid amphipods and other consumers to the overall ecological functioning of sandy beach communities as well as the capacity of these subsidized communities to rapidly process and transform large amounts of imported material.

References

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

Anderson WB, Polis GA (1999) Marine subsidies of island communities in the Gulf of California: evidence from stable carbon and nitrogen isotopes. Oikos 81:75–80

Bärlocher F, Newell SY (1994) Phenolics and proteins affecting palatability of *Spartina* leaves to the gastropod *Littorina irrorata*. Pubbl Staz Zool Napoli I Mar Ecol 15:65–75

Barrett K, Anderson WB, Wait DA, Grismer LL, Polis GA, Rose MD (2005) Marine subsidies alter the diet and abundance of insular and coastal lizard populations. Oikos 109:145–153

Bustamante RH, Branch GM, Eekhout S (1995) Maintenance of an exceptional intertidal grazer biomass in South Africa:subsidy by intertidal kelps. Ecology 76:2314–2329

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

Colombini I, Chelazzi L (2003) Influence of marine allochthonous input on sandy beach communities. Oceanogr Mar Biol Annu Rev 41:115–159

Craig PC (1973) Behavioral and distribution of the sand-beach amphipod *Orchestoidea corniculata*. Mar Biol 23:101–109

Cross WF, Wallace JB, Rosemond AD, Eggert SL (2006) Whole-system nutrient enrichment increases secondary production in a detritus-based ecosystem. Ecology 87:1556–1565

Dayton PK (1985) Ecology of kelp communities. Annu Rev Ecol Syst 16:215–245

Denton A., Chapman ARO (1991) Feeding preferences of gammarid amphipods among four species of *Fucus*. Mar Biol 109:503–506

Dugan JE, Hubbard DM, McCrary MD, Pierson MO (2003) The response of macrofauna communities and shorebirds to macrophyte wrack subsides on exposed sandy beaches of southern California. Estuar Coast Shelf Sci 58S:25–40 doi:10.1016/S0272-7714(03)0045-3

Graça MA, Newell SY, Kneib RT (2000) Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt-marsh invertebrates. Mar Biol 136:281–289

Griffiths CL, Stenton-Dozey JME (1981) The fauna and rate of degradation of stranded kelp. Estuar Coast Shelf Sci 12:645–653

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

Hayes WB (1974) Sand beach energetics: importance of the isopod *Tylos punctatus*. Ecology 55:838–847

Hobday AJ (2000) Abundance and dispersal of drifting kelp, *Macrocystis pyrifera* rafts in the Southern California Bight. Mar Ecol Prog Ser 195:101–116

Hubbard DM, JE Dugan (2003) Shorebird use of an exposed sandy beach in southern California. Estuar Coast Shelf Sci 58S:169–182

Incera M (2004) Influencia de los factores ambientales sobre la macrofauna y la composición bioquímica del sedimento en intermareales arenosos. PhD Dissertation, University of Vigo, Spain. 299 pp

Inglis G (1989) The colonization and degradation of stranded *Macrocystis pyrifera* (L.) by the macrofauna of a New Zealand sandy beach. J Exp Mar Biol Ecol 125:203–217

Jaramillo E, McLachlan A (1993) Community and population responses of the macroinfauna to physical factors over a range of exposed sandy beaches in south-central Chile. Estuar Coast Shelf Sci 37:615–624

Jaramillo E, De la Huz C, Duarte E, Contreras H (2006) Algal wrack deposits and infaunal arthropods on sandy beaches of the Chilean coast. Rev Chil Hist Nat 79:337–351

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 II. Driftline effects of succession changes and colonisation by beach fauna. Oceanologia 44:367–387

Johnston M, Johnston D, Richardson A (2005) Digestive capabilities reflect the major food sources in three species of talitrid amphipods. Comp Biochem Physiol Biochem Mol Biol 140:251–257

Kirkman H (1984) Standing stock and production of *Ecklonia radiata* (C. Ag.) J. Agardh. J Exp Mar Biol Ecol 76:119–130

Kneib RT, Newell SY, Hermeno ET (1997) Survival, growth and reproduction of the salt marsh amphipod *Uhlorchestia spartinophila* reared on natural diets of senescent and dead *Spartina alterniflora* leaves. Mar Biol 128:423–431

Koop K, Lucas MI (1983) Carbon flow and nutrient regeneration from the decomposition of macrophyte debris in a sandy beach microcosm. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. W. Junk, The Hague, pp 249–262

Lastra M, De la Huz R, Sánchez Mata AG, Rodil IF, Aerts K, Beloso S, López J (2006) Ecology of exposed sandy beaches in northern Spain: environmental factors controlling macrofauna communities. J Sea Res 55:128–140

Lopez GR, Levinton JS, Slobodkin LB (1977) The effect of grazing by the detritivore *Orchestia grillus* on *Spartina* litter and its associated microbial community. Oecologia 30:111–127

Marsden ID (1991) Kelp-sandhopper interactions on a sand beach in New Zealand. I. Drift composition and distribution. J Exp Mar Biol Ecol 152:61–74

McLachlan A, Brown AC (2006) The ecology of sandy shores. 2nd edn, Academic Press, Amsterdam, 392 pp

Moore PG, Francis CH (1985) Some observations on food and feeding of the supralittoral beach hopper *Orchestia gammarellus* (Pallas) (Crustacea: Amphipoda). Ophelia 24:183–197

Moran JAG, Arrontes J (1994) Factors affecting food preference in a widespread intertidal isopod. J Exp Mar Biol Ecol 182:111–121

Nardi M, Morgan E, Scapini F (2003) Seasonal variation in the free running period in two *Talitrus saltator* populations from Italian beaches differing in morphodynamics and human disturbance. Estuar Coast Shelf Sci 58s:199–206

Orr M, Zimmer R, 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

Peterson CH, Renaud PE (1989) Analysis of feeding preference experiments. Oecologia 80:82–86

Polis GA, Hurd SD (1996) Linking marine terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am Nat 147:396–423

Robertson AI, Lucas JS (1983) Food choice, feeding rates and turnover of macrophyte biomass by a surf-zone inhabiting amphipod. J Exp Mar Biol Ecol 72:99–124

Scapini F, Chelazzi L, Colombini I, Fallaci M (1992) Surface activity, zonation and migrations of *Talitrus saltator* on a Mediterranean beach. Mar Biol 112:145–157

Short AD, Wright LD (1983) Physical variability of sandy beaches. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. W. Junk, The Hague, pp 133–144

Steinberg PD (1988) Effects of quantitative and qualitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. J Exp Mar Biol Ecol 120:221–237

Steinberg PD, van Altena I (1992) Tolerance of marine invertebrate herbivores to brown algal phlorotannins in temperate Australasia. Ecol Monogr 62(2):189–222

Stenton-Dozey JM, Griffiths CL (1983) The fauna associated with kelp stranded on a sandy beach. In: McLachlan A, Erasmus T (eds) Sandy beaches as ecosystems. W. Junk, The Hague, pp 557–568

Tarr JG, Tarr PW (1987) Seasonal abundance and the distribution of coastal birds on the northern Skeleton Coast, South West Africa/Namibia. Madoqua 15:63–72

Taylor RB, Brown PJ (2006) Herbivory in gammarid amphipod *Aora typica*: relationships between consumption rates, performance and abundance across ten seaweed species. Mar Biol 149(3):455–463

Valiela I, Rietsma CS (1984) Nitrogen, phenolic acids and other feeding cues for salt marsh detritivores. Oecologia 63:350–356

Van Alstyne KL, McCarthy JJ III, Hustead CL, Kearns LJ (1999) Phlorotannin allocation among tissues of northeastern Pacific kelps and rockweeds. J Phycol 35:483–492

Van Alstyne KL, Whitman SL, Ehlig JM (2001) Differences in herbivore preferences, phlorotannin production and nutritional quality between juvenile and adult tissues from marine brown algae. Mar Biol 139:201–210

Wakefield RL, Murray SN (1998) Factors influencing food choice by the seaweed-eating marine snail *Norrisia norrisi* (Trochidae). Mar Biol 130:631–642