

Role of supratidal invertebrates in the decomposition of beach-cast green algae *Ulva* sp.

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ABSTRACT: We examined the effects of supratidal invertebrates on the decomposition of the green alga *Ulva* sp. in Paracas Bay, southern Peru. The species identification of *Ulva* sp. was problematic; thus, we decided to refer to the broadbladed *Ulva* occurring in Paracas Bay by the generic name. We used stable isotopes of carbon and nitrogen to evaluate the flow of energy and nutrients from the decomposing algae to the community of supratidal consumers. We found that supratidal invertebrates had little effect on the decomposition rate of beach-cast macroalgae. Algae lost 46.5% of their initial weight within 18 d from initial stranding ashore. The most abundant arthropods in samples of 100 g wet *Ulva* sp. packs were the springtail *Paraxenylla peruensis* (1165.9 ind. pack⁻¹), a sphaerocerid fly (23.6 adults pack⁻¹) and at least 3 species of mites (82.9 ind. pack⁻¹). In terms of biomass, the main consumers were the talitrid amphipod *Transorchestia chiliensis* (42.8 mg pack⁻¹), *P. peruensis* (2.8 mg pack⁻¹) and mites (1.3 mg pack⁻¹). Carbon isotopic values suggested that *Ulva* sp. was the most important source of energy to arthropod consumers, whereas nitrogen isotopic values indicated that mites and centipedes occupy high trophic positions in the supratidal food web. Paracas Bay abuts a hyper-arid desert wherein vegetation is extremely scarce and patchy. Supratidal invertebrates feeding upon decomposing *Ulva* sp., despite having little direct effect on the rate of *Ulva* sp. decomposition, establish a critical link between the marine and terrestrial ecosystems because they make marine-derived energy and nutrients available to desert consumers.

KEY WORDS: Marine macrophyte · Breakdown · Invertebrate shredders · Carbon and nitrogen stable isotopes · Allochthonous input · Peru · Coastal desert

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INTRODUCTION

Decomposition is a key ecosystem process because it converts nutrients from organic to inorganic forms and makes these nutrients available to primary producers and consumers (Chapin et al. 2002). Decomposing mats of beach-cast macroalgae are important sources of carbon and nutrients for subtidal and intertidal organisms (Bedford & Moore 1984, Bolam et al. 2000). However, few studies have examined the importance of decomposing macroalgae as sources of energy and nutrients for supratidal communities, except for sandy beach ecosystems (Griffiths et al. 1983, Koop & Lucas 1983). The recent focus on terrestrial habitats linked to marine productivity through the movement of nutrients, prey and predators led to numerous investigations, some of which emphasized the importance of

beach-cast macrophytes as a source of allochthonous material for terrestrial producers and consumers (e.g. Bustamante & Branch 1996).

The ecological role of invertebrate shredders has proved difficult to evaluate in the field, with some studies claiming that grazers remove up to 60 to 80% of organic algal input (Griffiths & Stenton-Dozey 1981) and other studies reporting no significant effects of macrofauna on the decomposition rate of beach-cast seaweeds (Inglis 1989, Jedrzejczak 2002). During decomposition, several abiotic and biotic processes cause a decrease in detrital mass and the release of nutrients and CO₂ from decaying organic matter. It is often assumed that invertebrates are directly involved in the decomposition of organic matter; however, little is known about the feeding patterns and trophic relationships of invertebrate species living in decomposing

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organic matter. Mites, for example, form a large group of soil invertebrates that includes detritivorous, omnivorous, predaceous and parasitic forms. Beach-cast macrophytes may not be the only source of energy for supratidal consumers found in decomposing mats. Autotrophic organisms, such as diatoms, growing on the surface of decomposing particles may provide additional sources of food for algivores or detritivores.

The goal of this study was to evaluate the role of supratidal invertebrates in the decomposition rate of green algae of the genus *Ulva* on a shelly beach in central Peru. *Ulva* sp. is a conspicuous component of marine wrack that washes ashore in small- to medium-sized bays along the Peruvian coast (Koepcke & Koepcke 1952). We performed a 'litter bag' experiment, enclosing samples of algae of known mass in bags having different mesh sizes to control the colonization of *Ulva* sp. by species of supratidal invertebrates, and measured the rate of mass loss in algal samples during a 3 wk period. We hypothesized that the presence of large arthropods would accelerate the decomposition of algal samples. In addition, we used $\delta^{13}\text{C}$ to determine whether *Ulva* sp. was a significant source of carbon to supratidal invertebrates and $\delta^{15}\text{N}$ to infer the trophic position of supratidal invertebrates associated with decomposing algae.

MATERIALS AND METHODS

Study site. We conducted our study on a shelly beach of Paracas Bay, Peru ($13^{\circ}51'S$, $76^{\circ}16'W$) between 8 May and 8 June 2003. This beach is narrow (<20 m wide) and has a semi-diurnal tidal cycle (average tidal range, 0.58 m). Waters enclosed within Paracas Bay (~15 × 7 km) are calm because they are protected from winds and marine currents by a peninsula. Paracas lies close to one of the strongest upwelling centers along the Peruvian coast (Catenazzi & Donnelly 2007). The species identification of *Ulva* sp. was problematic; thus, we decided to refer to the broad-bladed *Ulva* sp. occurring in Paracas Bay by the generic name. The high oceanic productivity, along with shallow waters and the possible influence of industrial effluents from fishmeal processing facilities, favors the overgrowth of *Ulva* sp. in the bay. Drift input of other macroalgae was negligible compared with that of *Ulva* sp. throughout 2003 (Catenazzi & Donnelly 2007).

The beaches of Paracas Bay are bordered by one of the driest deserts on Earth (<2 mm annual rainfall). Temperatures are mild and range between an average of 22.9°C in February to 16.3°C in August. The desert is devoid of vegetation except for the halophyte *Sesuvium portulacastrum* that colonizes small supralittoral dunes. We worked along a sheltered beach composed

of empty shells, pebbles and decaying algal material. The shells originated from the erosion of a quaternary deposit located 10 to 20 cm beneath the ground. The subtidal zone along this segment was mainly composed of mud mixed with pebbles alternated with zones of rocky substrate.

Litter bags. We used litter bags with 5 mm, 1 mm or 80 μm mesh size to evaluate the role of different components of the supratidal invertebrate community during algal decomposition. These bags contained packs of 100 g portions of blotted dry thalli of *Ulva* sp. We performed 2 experiments for an original duration of 18 d. During the first experiment, bags were lost during a spring tide, limiting our data set to the first 9 d (8 to 16 May 2003). During the second experiment, all bags were recovered at the end of the 18 d period (22 May to 8 June 2003). Bags were collected at 1, 3, 9 and 18 d after initial placement on the beach.

We collected fresh samples of *Ulva* sp. floating near shore. In the laboratory, we rinsed algal samples to remove invertebrates and small bits of detritus. We prepared experimental litter bags 25 × 20 cm in size. We weighed 100 g portions of blotted dry thalli of *Ulva* sp. and enclosed them in separate bags of each of the 3 mesh sizes. We dried and weighed to constant mass ten 100 g portions of blotted dry *Ulva* sp. to estimate the initial dry weight value. Mesh size treatments were assigned randomly to *Ulva* sp. portions. We prepared 4 (Trial 1) and 5 (Trial 2) bags for each mesh size and sampling day, for a total of 36 (Trial 1) and 60 bags (Trial 2).

Bags were randomly positioned in 4 (Trial 1) or 5 sites (Trial 2). We placed a series of 3 bags of different mesh sizes at each site (distance between sites was ~100 m) during low tide at night in areas immediately above the mean high tide line. Most of the algal material washed ashore in Paracas Bay is periodically floated and deposited between successive tidal periods. All bags were covered with similar amounts of previously cleaned *Ulva* sp. to protect packs from desiccation.

After being recovered from the field, *Ulva* sp. packs were taken to the lab in sealed plastic bags. We processed bag contents through a 20 μm mesh sieve and transferred the contents to vials containing 70% ethanol. Invertebrates were sorted into taxonomic groups, identified to species level when possible and individually counted under a stereoscope. Unidentified species represented a negligible proportion of the overall number and biomass of invertebrates (Table 1). *Ulva* sp. thalli were removed from bags and individually cleaned to recover invertebrates that had remained attached to the algae. Cleaned *Ulva* sp. thalli were dried at 60°C and weighed until they reached constant mass. Invertebrate biomass was estimated by means of body-length–dry-mass relationships based

Table 1. *Ulva* sp.. Initial pack mass (m_0) and breakdown coefficients (k) of thalli in Paracas Bay, Peru, estimated by nonlinear regression analysis for bags with mesh sizes of 5 mm, 1 mm and 80 μ m. n = number of bags containing packs of 100 g blotted dry *Ulva* sp. ***p < 0.001, *p < 0.05

| Mesh size | $m_0 \pm$ SE (%) | $k \pm$ SE (d ⁻¹) | r ² | n |
|------------|------------------|-------------------------------|----------------|----|
| Trial 1 | | | | |
| 5 mm | 107.9 \pm 5.8 | 0.062 \pm 0.013 | 0.743*** | 12 |
| 1 mm | 85.4 \pm 5.6 | 0.041 \pm 0.014 | 0.482* | 12 |
| 80 μ m | 108.0 \pm 7.1 | 0.042 \pm 0.014 | 0.494* | 12 |
| Trial 2 | | | | |
| 5 mm | 75.6 \pm 3.1 | 0.022 \pm 0.005 | 0.561*** | 20 |
| 1 mm | 85.5 \pm 2.7 | 0.031 \pm 0.004 | 0.793*** | 20 |
| 80 μ m | 79.5 \pm 3.6 | 0.020 \pm 0.005 | 0.475*** | 20 |

on specimens collected at the field site. We used the average dry mass of 10 to 20 individuals for small invertebrates.

Stable isotope analyses. We used invertebrates collected from *Ulva* sp. packs in 5 mm mesh bags to explore natural variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. In addition to these invertebrates, we collected centipedes *Thindyla litoralis* and solifuges *Chinchippus peruvianus* that live in the intertidal zone where we conducted our experiment (Catenazzi & Donnelly 2007). We used carbon isotopic ratios to evaluate the source of carbon, whereas $\delta^{15}\text{N}$ was used to infer trophic position for the most conspicuous consumers (based on biomass data).

All samples were oven dried at 60°C for 48 h, ground with mortar and pestle and defatted with a dichloromethane:methanol (9:1) solution before stable isotope analysis. Isotopic analyses were conducted on a Finnigan MAT Delta Plus continuous flow isotope ratio mass spectrometer. We analyzed 3 to 4 mg of algal samples and ~0.4 to 0.7 mg of animal samples. Homogenized samples of consumers included 1 individual for large predators (rove beetle, solifuge, centipede), 5 to 6 individuals of the rove beetle *Carpelimus* sp., 10 to 15 individual flies, 50 to 60 individual mites and 400 to 450 individual springtails. We analyzed 5 replicates for each consumer. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are expressed relative to their respective international standards, Pee Dee belemnite and atmospheric air. We analyzed 16% of our samples in duplicate and calculated the average standard deviation (SD) on duplicated data to determine accuracy of our data. The average SD for replicate samples was 0.11‰ for $\delta^{13}\text{C}$ and 0.13‰ for $\delta^{15}\text{N}$.

Statistical analyses. Data on algal mass loss during breakdown were fitted to the exponential model:

$$m_t = m_0 e^{-kt}$$

where m_0 is the initial dry mass of algal packs, m_t is the remaining dry mass at time t and k is a breakdown rate coefficient, the daily rate of mass loss. The parameters of the model were calculated using nonlinear

iterative (n = 100) fitting procedures. Initial assumed values (i.e. $m = 100$ g at Day 0) were excluded from the model. The model assumes that the mass loss at any given time is directly proportional to the algal mass present (Hieber & Gessner 2002).

We used a repeated measures ANOVA to examine the effect of litterbag mesh size on the decomposition rate of *Ulva* sp. after 1, 2 and 9 d for Trial 1 and after 1, 3, 9 and 18 d for Trial 2. We compared weight loss patterns between the 2 trials and for each mesh size with analyses of covariance

(ANCOVAs) on log-transformed data. We compared the full model (different slope and intercept between the 2 trials) with 2 reduced models ('same slope, different intercept' and 'same slope and intercept') by using a General Linear Test (GLT). The GLT tests the null hypothesis that the regression coefficients for all additional variables are equal to zero. Temporal succession in the number and biomass of invertebrates was compared using ANOVAs for data from 5 mm bags only. Data from 1 mm and 80 μ m bags were not used because these bags contained subsets of the supratidal invertebrate fauna that were not representative of decomposition under natural conditions (i.e. they excluded invertebrates larger than 80 μ m or 1 mm). We used a 2-way ANOVA with d and mesh size as factors to evaluate differences in abundance and biomass of invertebrates in 5 mm and 1 mm bags (80 μ m bags were not used because some had many invertebrates larger than 80 μ m). Measurements of decomposition rates and number and biomass (on log(x+1)-transformed data) of invertebrates were tested for normality and homogeneity of variance before parametric tests were conducted. We ran all our statistical analyses in R (www.r-project.org). Data are reported as means \pm SE and differences were considered significant when p < 0.05.

We used stable isotope data to examine whether *Ulva* sp. was the main source of carbon for arthropods found in the litterbags and to estimate the trophic position of the main consumers. We addressed the first question by contrasting the $\delta^{13}\text{C}$ of consumers with the $\delta^{13}\text{C}$ of *Ulva* sp. with a Student's *t*-test. The values for consumers were corrected for different trophic fractionations by assuming an average trophic fractionation of 0.39‰ (Post 2002). We used $\delta^{15}\text{N}$ values to estimate the trophic position of consumers. We assumed that *Ulva* sp. was the basal resource for all invertebrates found in litterbags. Trophic position was estimated by using the formula (Post 2002):

$$\text{trophic position} = \lambda + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{Ulva}}) / \Delta_n$$

where $\lambda = 1$ is the trophic position of *Ulva* sp. and Δ_n is the estimated trophic fractionation, assuming a mean fractionation of 3.4‰ for each trophic level (Post 2002). We used average values (without SDs) of $\delta^{15}\text{N}_{Ulva}$ to simplify calculations.

RESULTS

Ulva sp. decomposition

Algal packs underwent substantial breakdown during the experimental period (Fig. 1). Breakdown coefficients varied between 0.020 and 0.062 d^{-1} (Table 1). The loss of initial weight was $37.54 \pm 2.27\%$ ($n = 27$) within 9 d for both trials combined and $46.51 \pm 1.92\%$ ($n = 15$) within 18 d in Trial 2. However, the exponen-

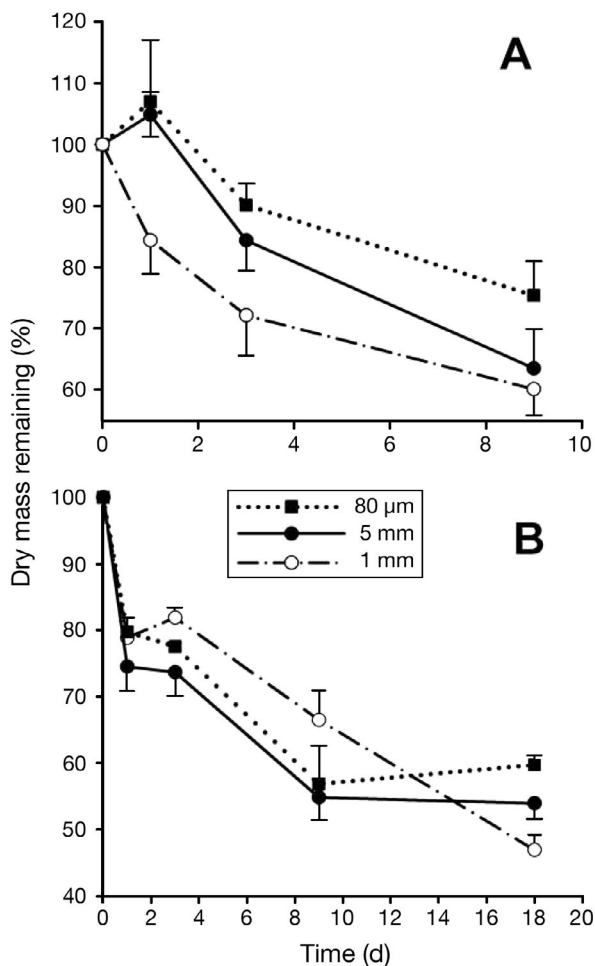


Fig. 1. *Ulva* sp. Dry mass remaining in bags with 80 μm (■), 1 mm (○) and 5 mm (●) mesh decomposing on a shelly beach in Paracas Bay during (A) Trial 1 (8 May to 16 May 2003) and (B) Trial 2 (22 May to 8 June 2003). Error bars indicate SE calculated from 4 (Trial 1) and 5 (Trial 2) replicate bags

tial breakdown model explained only 47 to 79% of the variation in decomposition rates of *Ulva* sp.

Patterns of weight loss were similar across bags of different mesh sizes and between the 2 trials (at least up to Day 9; Table 2). When any difference was found, a reduced model testing for same slope but different intercepts in the regression of weight against days was better than the full model testing for different slopes and intercepts. Similarly, mesh size did not affect the decomposition rate of *Ulva* sp. based on the repeated measures ANOVA (Table 3).

Table 2. *Ulva* sp. Analysis of covariance in weight loss pattern during decomposition under different invertebrate exclusion regimes and comparison of weight loss patterns between trials. Full models test for differences in slope and intercept terms, whereas reduced models test for differences in intercepts only. res. = residual, *** $p < 0.001$, ** $p < 0.01$

| Model | res. df | RSS | SS | F |
|---|---------|-------|-------|----------|
| Mesh size = factor, days = covariate | | | | |
| Trial 1 | | | | |
| Full model | 30 | 0.125 | 0.008 | 0.93 |
| Reduced model | 32 | 0.132 | 0.061 | 7.30** |
| Trial 2 | | | | |
| Full model | 54 | 0.184 | 0.020 | 2.87 |
| Reduced model | 56 | 0.204 | 0.009 | 0.28 |
| Trial = factor, days = covariate | | | | |
| 5 mm bags | | | | |
| Full model | 23 | 0.077 | 0.006 | 1.69 |
| Reduced model | 24 | 0.083 | 0.053 | 15.90*** |
| 1 mm bags | | | | |
| Full model | 23 | 0.070 | 0.003 | 0.98 |
| Reduced model | 24 | 0.073 | 0.004 | 1.38 |
| 80 μm bags | | | | |
| Full model | 23 | 0.091 | 0.001 | 0.69 |
| Reduced model | 24 | 0.091 | 0.073 | 18.71*** |

Table 3. *Ulva* sp. Repeated measures ANOVA for decomposition under different regimes of invertebrate exclusion during the 2 experiments ($n = 4$ replicates/mesh size for Trial 1 and $n = 5$ replicates/mesh size for Trial 2). Significant values are in **bold**

| Source | df | MS | F | p |
|-------------------------|----|-------|-------------|--------------|
| Trial 1 | | | | |
| Time | 3 | 7.67 | 3.78 | 0.033 |
| Mesh size | 2 | 12.86 | 2.81 | 0.107 |
| Time \times Mesh size | 6 | 1.79 | 2.06 | 0.087 |
| Trial 2 | | | | |
| Time | 4 | 53.63 | 5.96 | 0.002 |
| Mesh size | 2 | 3.71 | 3.14 | 0.080 |
| Time \times Mesh size | 8 | 1.47 | 2.10 | 0.054 |

Supratidal invertebrates in *Ulva* sp. packs

The invertebrate fauna in *Ulva* sp. packs included only a few species in each taxonomic group (Table 4). By far the most abundant taxon was the springtail *Paraxenylla peruensis* (1165.9 ± 309.3 ind. pack⁻¹), followed by 3 species of mites (82.9 ± 17.0 ind. pack⁻¹, of which 21.4 ± 5.8 ind. pack⁻¹ were from a species of Uropodidae) and the fly *Thoracochoaeta brachystoma* (23.6 ± 4.8 adults pack⁻¹). In terms of biomass, the most important invertebrates in the bags were the talitrid amphipod, *Transorchestia chiliensis*, (42.8 mg pack⁻¹), *Paraxenylla peruensis* (2.8 mg pack⁻¹) and mites (1.3 mg pack⁻¹).

Bags with mesh size of 80 μ m did not always exclude invertebrates larger than 80 μ m because one pack had 1383 mites and another pack contained 3445 springtails, despite the fact that bags appeared to be intact. However, in most 80 μ m bags, the total number of invertebrates was less than 150. Overall, the biomass of invertebrates in 80 μ m bags was significantly lower than the biomass of invertebrates in 1 mm and 5 mm samples (ANOVA, $F = 46.48$, $p < 0.01$; Tukey's test, $p < 0.01$).

Successional change in supratidal invertebrate communities

The number of invertebrates varied during the period of algal decomposition in 5 mm bags (Fig. 2). Log-transformed values for the total number of invertebrates for Trial 2 followed a polynomial curve where abundance = $(-0.010)d^2 + (0.181)d + 2.432$; the peak of this curve occurs for Day 9.335. In Trial 1, the number of invertebrates steadily increased between Day 1 and Day 9 ($F_{1,10} = 6.16$, $p = 0.03$). Total invertebrate biomass for *Ulva* sp. packs in 5 mm bags did not vary during algal decomposition in both Trial 1 ($F_{1,10} = 0.29$, $p = 0.60$) and Trial 2 ($F_{1,16} = 3.408$, $p = 0.083$).

In *Ulva* sp. packs that excluded large invertebrates (1 mm bags), the number of invertebrates did not vary during Trial 1 ($F_{1,10} = 2.25$, $p = 0.16$) and Trial 2 ($F_{1,18} = 0.03$, $p = 0.86$). Similarly, biomass did not vary during algal decomposition in either Trial 1 ($F_{1,10} = 2.21$, $p = 0.17$) or 2 ($F_{1,18} = 0.06$, $p = 0.80$). The number of invertebrates in *Ulva* sp. packs did not differ between 5 and 1 mm bags

Table 4. *Ulva* sp. Arthropods found in packs enclosed within 5 mm bags. Bags of smaller mesh size contained subsets of invertebrates found in 5 mm bags and did not include additional species not listed in this table. Species names (number of species found in parentheses) refer to adult forms unless otherwise specified; individuals is the sum of individuals from all collection dates (all 5 mm *Ulva* sp. packs for all dates in both trials)

| Taxonomic group | Species (no. of species) | Individuals |
|------------------------------|---------------------------------------|-------------|
| Oligochaeta: Enchytraeidae | Unidentified species (?) | 63 |
| Aranea: Ctenidae | Unidentified species (1) | 2 |
| Acarina: Mesostigmata | Unidentified species (2) | 1844 |
| | Uropodidae sp. (1) | 643 |
| Amphipoda: Talitridae | <i>Transorchestia chiliensis</i> | 635 |
| Geophilomorpha: Schendylidae | <i>Thindyla litoralis</i> | 1 |
| Collembola: Hypogastruridae | <i>Paraxenylla peruensis</i> | 34 978 |
| Coleoptera: Staphylinidae | <i>Cafius</i> sp. (1) | 42 |
| | <i>Carpelimus</i> sp. (1) | 13 |
| | Unidentified species | 1 |
| | Unidentified larvae | 20 |
| Coleoptera: Tenebrionidae | <i>Cordibates fuscus</i> | 17 |
| Coleoptera | Unidentified species (3) | 7 |
| Hymenoptera | Unidentified wasp (1) | 9 |
| Hymenoptera: Formicidae | <i>Solenopsis</i> sp. (1) | 4 |
| Diptera: Sphaeroceridae | <i>Thoracochoaeta brachystoma</i> (1) | 685 |
| Diptera | Other unidentified species | 3 |
| | Unidentified larvae | 114 |
| | Unidentified pupae | 470 |
| Diptera: Chironomidae | Unidentified species (1+) | 12 |

for either trial (2-way ANOVAs: $F_{1,18} = 0.18$, $p = 0.68$ for Trial 1 and $F_{1,32} = 0.74$, $p = 0.40$ for Trial 2).

The abundance and biomass of the most conspicuous groups varied through time in 5 mm bags during Trial 2 (Fig. 3). Numbers (although not biomass values) followed a polynomial curve for *Paraxenylla peruensis* (abundance = $[-0.014]d^2 + [0.288]d + 1.827$, peak at Day 10.148) and for mites (abundance = $[-0.008]d^2 + [0.114]d + 1.626$, peak at Day 4.021). The number and biomass of *Transorchestia chiliensis* ($F_{1,15} = 7.17$, $p = 0.017$ for abundance; $F_{1,15} = 7.73$, $p = 0.01$ for biomass) and *Thoracochoaeta brachystoma* ($F_{1,16} = 19.64$, $p < 0.01$ for abundance; $F_{1,16} = 17.41$, $p < 0.01$ for biomass) steadily decreased with time. At the same time, there was an increase in the number of pupae of *T. brachystoma* ($F_{1,16} = 8.07$, $p = 0.01$), but no variation in the number of larval forms ($F_{1,16} = 0.11$, $p = 0.74$). The number and biomass of the 2 species of rove beetles *Cafius* sp. and *Carpelimus* sp. did not vary during algal decomposition ($F_{1,16} = 1.86$, $p = 0.19$ for abundance; $F_{1,16} = 0.38$, $p = 0.54$ for biomass).

Food web of arthropods in decomposing *Ulva* sp.

Stable isotope analyses (Fig. 4) suggested that *Ulva* sp. was an important source of carbon for arthropods in litterbags because the average $\delta^{13}C$ values of most arthropods were not significantly different from those

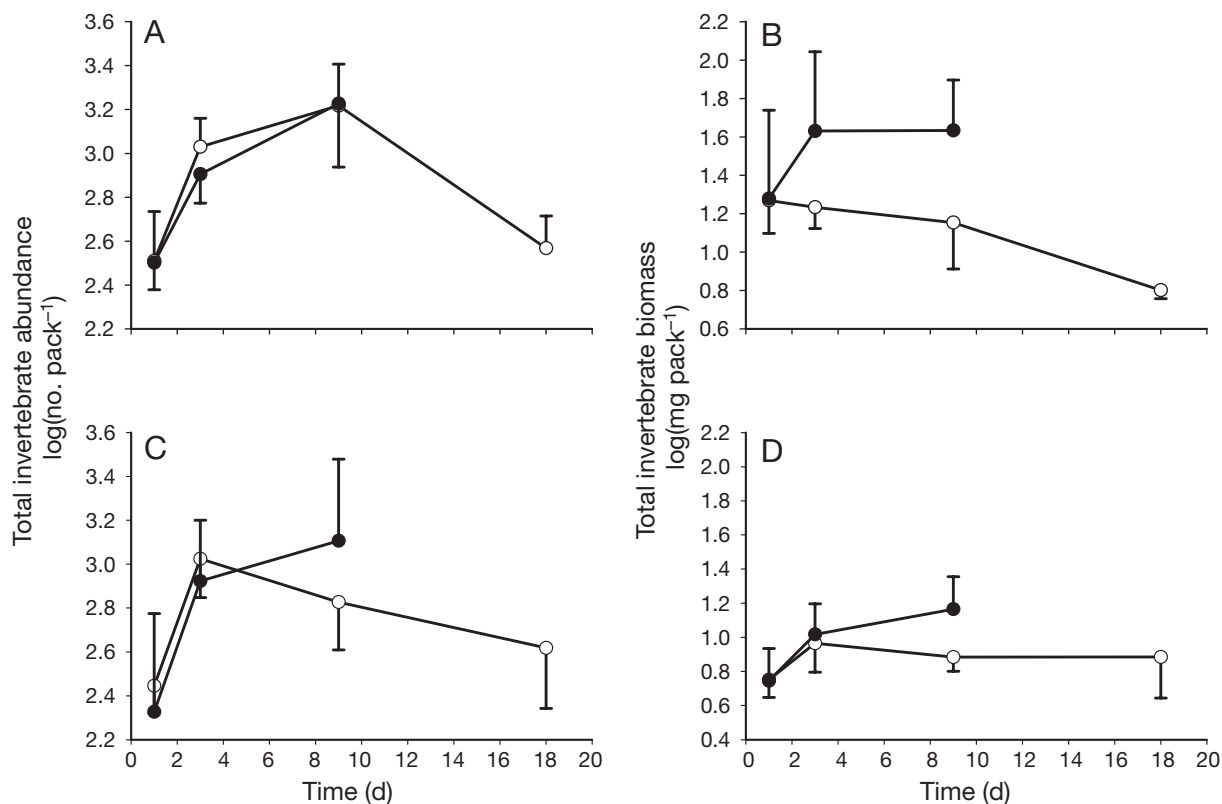


Fig. 2. *Ulva* sp. (A) Number and (B) biomass of invertebrates (no invertebrates excluded) decomposing in 5 mm bags during Trial 1 (●) (8 May to 16 May 2003) and Trial 2 (○) (22 May to 8 June 2003). (C) Number and (D) biomass of invertebrates (excluding invertebrates larger than 1 mm) decomposing in 1 mm bags during Trial 1 (●), and Trial 2 (○). Error bars indicate SE calculated from 4 (Trial 1) and 5 (Trial 2) replicate bags

of *Ulva* sp. (Table 5). Carbon isotopic values of the centipede *Thindyla litoralis* and the rove beetle *Carpelimus* sp. were significantly different from those of *Ulva* sp. only when we assumed that centipedes and the rove beetle *Carpelimus* sp. occupied the second and third trophic levels. Estimates of trophic position based on $\delta^{15}\text{N}$ values did not fully support these assumptions for *Carpelimus* sp., but supported the idea that centipedes were obtaining carbon from sources other than *Ulva* sp. (see next paragraph).

Arthropod consumers in decomposing *Ulva* sp. occupied 3 trophic levels above *Ulva* sp. (Table 6). A first group of consumers, with estimated trophic positions ranging from 1.39 to 1.53, included the beach flea *Transorchestia chiliensis* and the rove beetle *Carpelimus* sp., which probably feed exclusively upon *Ulva* sp. or epiphytic primary producers (e.g. diatoms). The second group included the largest number of consumers, ranging from predators (e.g. the solifuge *Chinchippus peruvianus*) to consumers that probably had a mixed diet (e.g. the springtail *Paraxenylla peruensis* and the fly *Thoracochoeta brachystoma*). The 'top' predators (trophic position between 2.53 and 2.62) in decomposing *Ulva* sp. were mites and centipedes.

DISCUSSION

The mass loss was extremely rapid for decomposing *Ulva* sp. in Paracas Bay and ranged at the higher end of reported values for beach-cast material decomposition. Green algae differ in physical and chemical properties from other algal and plant wrack deposited on beaches. Green algae should decompose faster than other algae under similar environmental conditions because they have reduced structural defenses (Padilla 1989, Duffy & Hay 1990), reduced antibiotic activity (Magallanes et al. 2003) and lower concentrations of phenolic and secondary compounds (Faulkner 1993, Targett & Arnold 1998) than kelp, rhodophytes and seagrass. This hypothesis is supported by typically slower breakdown rates in seagrass versus macroalgae (Ochieng & Erftemeijer 1999, Fourqurean & Schrlau 2003), but data comparing breakdown rates among different types of seaweeds are rare in the literature. Our measured decomposition rates are similar to values reported by Inglis (1989) for the kelp *Macrocystis pyrifera* along a New Zealand sandy beach.

Smith & Foreman (1984) compared the breakdown rate of submerged sample bags for 10 species of sea-

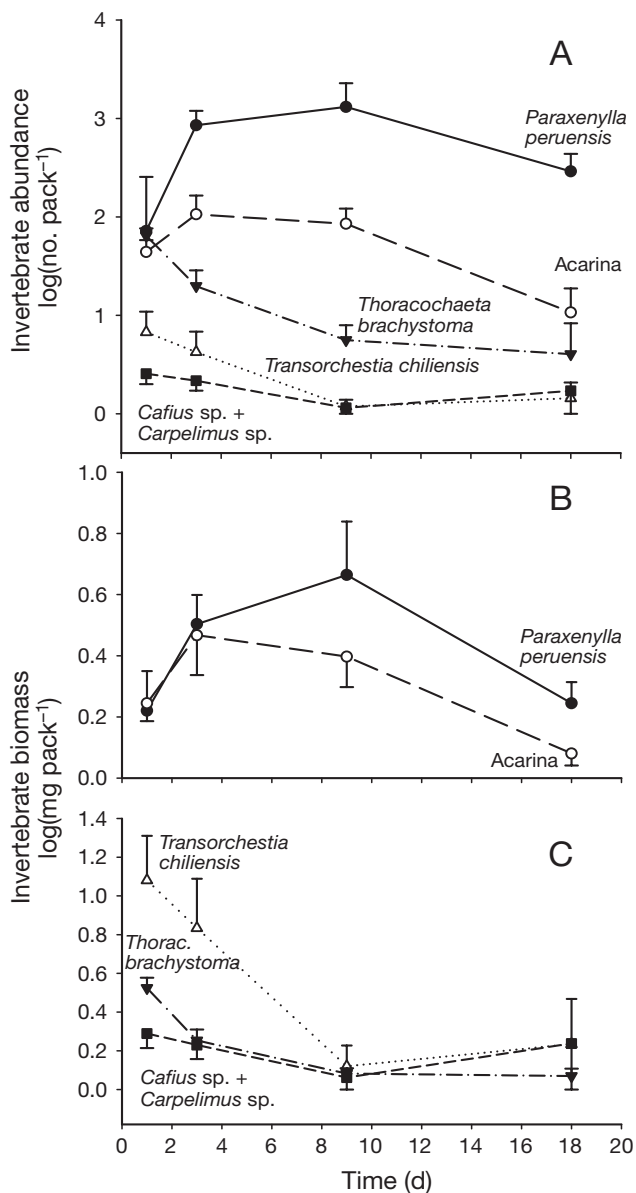


Fig. 3. *Ulva* sp. (A) Number (log-transformed data) of (●) *Paraxenylla peruensis*, (○) Acarina (unidentified species), (▼) *Thoracochaeta brachystoma*, (Δ) *Transorchestia chiliensis* and (■) rove beetles (one species of *Cafius* sp. and one species of *Carpelimus* sp.) found in *Ulva* sp. decomposing in 5 mm bags during Trial 2. (B) Biomass (log-transformed data) of (●) *P. peruensis* and (○) Acarina. (C) Biomass of (Δ) *Transorchestia chiliensis*, (▼) *T. brachystoma* and (■) rove beetles. Error bars indicate SE calculated for 5 replicate bags

weeds in the Strait of Georgia, Canada, and found that species with lower crude fiber content and decreasing particle size decomposed faster than other species. We do not have data on fiber content of *Ulva* sp. in Paracas Bay, but comparative studies at other locations showed similar or higher amounts of both crude and dietary fiber content in *Ulva* species with respect to other

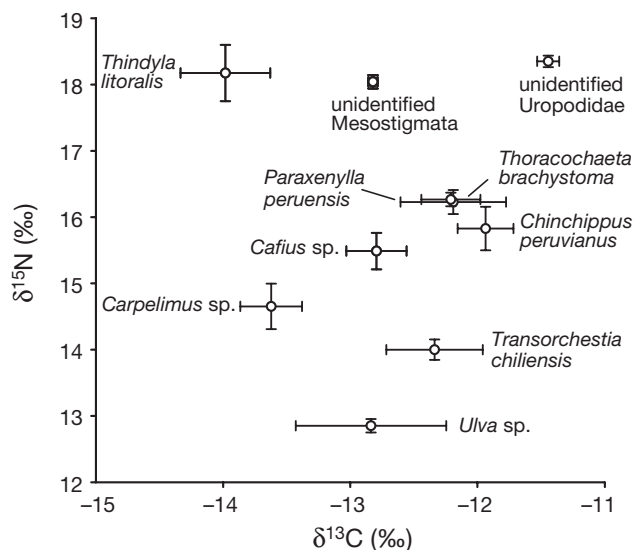


Fig. 4. *Ulva* sp. Average (mean \pm SE, $n = 5$ replicates) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the most important (by biomass) macro- and mesoinvertebrates found during the decomposition of beach-cast *Ulva* sp. The centipede *Thindyla litoralis* and the solifuge *Chinchippus peruvianus* are terrestrial predators that feed on supratidal invertebrates at the study site. See 'Materials and methods' for details on sampling and stable isotope analyses

green algae, kelp and rhodophytes (Ledesma et al. 1999, Carrillo et al. 2002). Invertebrate shredders could increase the seaweed decomposition rate by reducing the size of particles. A greater surface (relative to volume) in smaller particulate material exposed to microbial attack may explain the effect of particle size on decomposition rate (Colombini & Chelazzi 2003).

The decomposition of beach-cast green macroalgae has received relatively little attention, especially when compared with studies that considered stranded kelp. This is unfortunate because species of *Ulva* are characterized by a high growth rate and often dominate in eutrophic coastal waters (Viaroli et al. 2005), a condition that is becoming increasingly common (Morand & Briand 1996). A better understanding of processes controlling the decomposition of beach-cast *Ulva* sp. could prove useful in mitigating the effects of algal blooms upon intertidal and supratidal communities.

Role of and variation in supratidal invertebrate communities

Decaying *Ulva* sp. was quickly colonized by macro- and mesoinvertebrates. These groups were exclusively supra- and intertidal based upon our collections along a gradient from the intertidal to the supratidal and desert habitats (A. Catenazzi pers. obs.). A few desert arthropods were also found in the litterbags, such as

Table 5. *Ulva* sp. Results of Student's *t*-tests between $\delta^{13}\text{C}$ of *Ulva* sp. and $\delta^{13}\text{C}$ of invertebrates in packs for different trophic fractionations and assuming an average value of 0.39‰ for each trophic level. Tests were not computed if feeding patterns of a species do not support assumptions of a given trophic fractionation factor (e.g. *Thindyla litoralis* is predaceous and will not feed directly on *Ulva* sp.). Significant *t* and *p* values are in **bold**

| Consumer | $\delta^{13}\text{C}$ trophic fractionation | | | | | |
|-----------------------------------|---|----------|-------------|-------------|-------------|-------------|
| | + 0.39‰ | | + 0.78‰ | | + 1.17‰ | |
| | <i>t</i> | <i>p</i> | <i>t</i> | <i>p</i> | <i>t</i> | <i>p</i> |
| <i>Transorchestia chiliensis</i> | 0.50 | 0.63 | – | – | – | – |
| <i>Carpelimus</i> sp. | 1.84 | 0.10 | 2.44 | 0.04 | 3.05 | 0.02 |
| <i>Cafius</i> sp. | 0.54 | 0.60 | 1.15 | 0.28 | 1.77 | 0.11 |
| <i>Chinchipus peruvianus</i> | – | – | –0.19 | 0.85 | 0.42 | 0.68 |
| <i>Paraxenylla peruensis</i> | –0.36 | 0.73 | 0.18 | 0.86 | 0.72 | 0.49 |
| <i>Thoracochoaeta brachystoma</i> | –0.37 | 0.72 | 0.24 | 0.82 | 0.85 | 0.42 |
| <i>Thindyla litoralis</i> | – | – | 2.75 | 0.03 | 3.31 | 0.01 |
| Unidentified Mesostigmata | 0.63 | 0.55 | 1.29 | 0.23 | 1.94 | 0.09 |
| Uropodid mite | –1.68 | 0.13 | –1.03 | 0.33 | –0.37 | 0.72 |

Table 6. Estimated trophic position of intertidal invertebrates, assuming that *Ulva* sp. is the primary producer and that the trophic fractionation factor $\Delta = 3.4\text{‰}$

| Producer or consumer | Trophic position | SE |
|-----------------------------------|------------------|------|
| <i>Ulva</i> sp. | 1.00 | – |
| <i>Transorchestia chiliensis</i> | 1.39 | 0.07 |
| <i>Carpelimus</i> sp. | 1.53 | 0.10 |
| <i>Cafius</i> sp. | 1.78 | 0.08 |
| <i>Chinchipus peruvianus</i> | 1.88 | 0.10 |
| <i>Paraxenylla peruensis</i> | 1.99 | 0.05 |
| <i>Thoracochoaeta brachystoma</i> | 2.01 | 0.03 |
| <i>Thindyla litoralis</i> | 2.56 | 0.13 |
| Unidentified Mesostigmata | 2.53 | 0.03 |
| Uropodid mite | 2.62 | 0.03 |

the tenebrionid beetle *Cordibates fuscus* and a species of ant, *Solenopsis* sp. Macroinvertebrate abundance and biomass steadily declined in the period following colonization, similar to the situation observed by Inglis (1989) in decomposing kelp. The decrease in biomass was caused mainly by the decrease in the amphipod *Transorchestia chiliensis*, confirming a well-known pattern of amphipods as early colonizers of newly deposited beach-cast macroalgae (Griffiths & Stenton-Dozey 1981, Colombini et al. 2000). Another pattern characteristic of beach invertebrate succession was observed in the reproductive cycle of flies, with adult *Thoracochoaeta brachystoma* arriving early to lay eggs, a decreasing number of adults from Day 1 to Day 18, and a concomitant increase in the number of pupae. This cycle allows flies to reproduce before the arrival of the next spring tide (Dobson 1974).

Temporal variations in the invertebrate community may have been caused by changes in the nutritional quality of the algae, loss of moisture, greater exposure

to predators, or by the movement of consumers in and out of the litter bags. The movement of consumers is a likely source of variation in this system because beach organisms are known to adjust their movement patterns with daily variations in the tidal cycle (Jaramillo et al. 2000, but see Defeo & McLachlan 2005 for the relative independence of supratidal organisms to swash regimes in sandy beaches). The supratidal mesofauna of Paracas Bay differed from other studies because it was dominated by a springtail and because other groups, such as nematodes and oligochaetes, common in other locations (Inglis 1989, Ochieng & Erfteimeijer 1999, Jedrzejczak 2002) were numerically negligible in our

study system. The shelly substrate at our study beach provides suitable retreats for amphipods and springtails, but little sand for burrowing taxa such as enchytraeid oligochaetes.

The role of supratidal invertebrates in the decomposition of *Ulva* sp. seemed to be marginal according to the results of our experiment. Hieber & Gessner (2002) listed several caveats associated with the use of litter bags in estimating the effects of consumers on decomposition rates. However, Inglis (1989) did not detect any difference when testing for the effects of mesh size alone (without macro- and mesofauna) on the decomposition rate of seaweeds in the laboratory. Some of the alternatives proposed by Hieber & Gessner (2002) to litter bag experiments were to estimate feeding activity of consumers based on consumption rates measured in feeding trials in the laboratory. Zimmer et al. (2002) measured promotion of microbial respiration and amount of litter processed by supralittoral isopods and found that differences in isopod performance and contribution to litter breakdown were linked to changes in the chemical composition of the litter and species-specific differences in digestive capabilities and rates of net litter processing. In our study we decided to identify consumers that fed directly on *Ulva* sp. by using stable isotope analyses (see next section); the relative impact of these consumers on *Ulva* sp. material could be estimated by assuming feeding and growth rates for each invertebrate.

Food web in decomposing *Ulva* sp. and contribution to terrestrial consumers

The main source of energy for the consumers in litterbags was *Ulva* sp.. The slight shift of $\delta^{13}\text{C}$ of con-

sumers to the right of the value for *Ulva* sp. (Fig. 4) coincides with the expected variation, assuming a trophic fractionation of approximately 0.39‰ at each trophic interaction. However, we cannot exclude epiphytic diatoms with $\delta^{13}\text{C}$ similar to those of *Ulva* sp. as potential sources of energy to consumers because we did not collect and isolate these producers for stable isotope analysis. In the analysis of $\delta^{15}\text{N}$, estimates of trophic position agree well with what is known about the diet of consumers: talitrid amphipods, for example, occupy low trophic levels (Adin & Riera 2003), whereas predatory invertebrates, such as centipedes and solifuges, are near the top of the food web. One of the surprising findings was that springtails had a higher trophic position than solifuges. Consumption of heterotrophic microorganisms such as fungi and bacteria may explain the elevated $\delta^{15}\text{N}$ in springtails. The elevated trophic positions estimated for mites indicated that these were mainly predaceous and/or scavenging taxa. While sorting invertebrates in the laboratory, we often found hundreds of mites attached to carcasses of centipedes, suggesting that mites were feeding upon other predators.

Invertebrates associated with decomposing *Ulva* sp. in Paracas Bay are a significant source of food for terrestrial predators. These predators include sandpipers and other wading birds feeding on amphipods, flies and rove beetles (Duffy et al. 1981), lizards (Catenazzi et al. 2005), solifuges, geckos and scorpions (Catenazzi & Donnelly 2007), ghost crabs *Ocypode gaudichaudii*, spiders and predaceous beetles (A. Catenazzi pers. obs.). For desert consumers such as arachnids and lizards, the proportion of energy and nutrients derived from invertebrates associated with decomposing *Ulva* sp. exceeds the proportion obtained from other sources, with important consequences on the abundance and distribution of these predators (Catenazzi & Donnelly 2007). The dependence of predators on supratidal consumers is especially significant in Paracas Bay and much of the coastal desert of central and southern Peru because the extremely low levels of terrestrial primary productivity alone cannot support large populations of terrestrial consumers. Decomposition of *Ulva* sp. in Paracas Bay is one of the most important processes that make marine-derived resources available to terrestrial consumers.

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