



Fate and processing of macroalgal wrack subsidies in beaches of Deception Island, Antarctic Peninsula



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ABSTRACT

Drift macroalgae detached from rocky substrate frequently strands on the shore line, driving a number of ecological processes, such as degradation, consumption, habitat supply and biogeochemical processing. The algal subsidies received by beaches of Foster Bay, in Deception Island, were evaluated in terms of the spatio-temporal dynamics of wrack deposits. Predominance in the strands of a single red blade species, *Palmaria decipiens*, points toward an equivalent abundance in the subtidal macroalgal beds, accompanied by *Desmarestia menziesii* and *Desmarestia antarctica*, among others. Biomass measurements and wrack grooming along the intertidal range over time indicate that an instantaneous stock of 39.9 MT of algal debris strands on the shore line of Foster Bay, with more than 50% of these materials being renewed at each tidal cycle. Estimates of macrophyte production fluxing to the bay ecosystems suggest that only a small fraction (2.8%) of the detached material within the bay accumulates as wrack along the intertidal zone. Variability in the amount of algae along the shore is significantly affected by wind direction or coastal orientation, with larger strandings when sea–land winds prevail. The degradative process of algal wrack was analyzed through a litter bag experiment where pre-weighted fragments of *P. decipiens* and *D. menziesii* were sequentially removed from the drift line along 14 days. Degradation of wrack biomass occurs within the first days of decaying, losing up to 41.3% of its initial weight (*D. menziesii*), with remarkable variability among the two species tested. Higher feeding rates of amphipods were obtained with *P. decipiens* compared to that on *D. menziesii*, which can be mediated by its low content in deterrents and its blade shape, as well as being the most abundant species in the Deception Island and in many coastal areas of the Antarctic Peninsula. Globally, the consumer species assayed could process through consumption $0.73\% \text{ day}^{-1}$ of the instantaneous stock of algal deposits along the shore of Foster Bay. This study attempts to identify different linked processes poorly understood in the ecology of Antarctic shores, as the stranding, degradation and consumption of large amount of macroalgal subsidies from highly productive submerged rocky substrates toward low productive intertidal sedimentary shores.

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1. Introduction

Accumulation of allochthonous organic debris, also known as wrack, is a common event in the intertidal sedimentary coastlines worldwide. These external inputs of detrital macroalgae and/or animal cast can strongly influence ecological features and functioning of the receiver ecosystems by supplying food and habitat, frequently boosting abundance and biodiversity of primary and secondary consumers (e.g. Crawley et al., 2009; Cross et al., 2006; Dugan et al., 2003; Ince et al., 2007; Spiller et al., 2010; Wilson and Wolkovich, 2011). Influence of algal wrack is more relevant where a highly productive coastal environment (such as subtidal rocky shores) interfaces with and exports materials to the relatively less productive exposed sedimentary shores, such as boulder or sandy beaches, normally devoid of aquatic macrophytes (McLachlan and Brown, 2006).

Beach ecosystems are generally characterized by low in situ primary production (McLachlan and Brown, 2006), frequently subsidized by allochthonous biomass from the coastal ocean, rocky shores, sea grasses and salt marsh areas (Colombini and Chelazzi, 2003; Dugan et al., 2003; Griffiths et al., 1983; Orr et al., 2005). Beach consumers are therefore supported primarily by subsidies such as phytoplankton, macroalgae, vascular plants, carrion and other debris in different stages of decay (Griffiths et al., 1983; Lastra et al., 2008; Soares et al., 1997). In areas where the production of reef macroalgae is high (e.g. upwelling areas), input of drift material to the intertidal beach is commonly massive (Dugan et al., 2003; Hayes, 1974; Stenton-Dozey and Griffiths, 1983).

At tropical and temperate latitudes, following deposition on the beach, macroalgae detritus is subjected to a variety of processes, including desiccation, in situ macrofaunal consumption, microbial degradation, and export by tides and currents (Griffiths and Stenton-Dozey, 1981; Inglis, 1989; Jędrzejczak, 2002; Orr et al., 2005). The spatial distribution across the tidal range of stranded

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wrack (namely zonation), determines the exposure time to physical fractioning and biological consumption (Rodil et al., 2008). Wrack stranded at the upper part of the beach during spring high tides will desiccate and degrade for several weeks or months. Close to the swash zone, mats of wrack are driven by hydrodynamic forces of waves and currents during the entire tidal cycle.

Wrack decomposition is a complex process, depending on the beach characteristics (Orr et al., 2005), the amount of wrack stranded and the physicochemical, morphological and nutritional features of the macroalgae (Barreiro et al., 2013; Mews et al., 2006). Spatial and temporal variability in wrack accumulation and biomass may affect composition, abundance and demographic rates of consumers (Dugan et al., 2003; Olabarria et al., 2007). On the other hand, abundance, composition and structure of the consumer community can influence the processing of the algal subsidies, and this has been proven both in temperate (Dugan et al., 2003; Lastra et al., 2008) and polar latitudes (Urban-Malinga and Burska, 2009). Final stages of algal decomposition are associated with leaching of nutrients to the interstitial environment, and subsequently to the coastal waters. Dissolved nutrients fertilize the shore through the tidal beach runoff with nitrate, nitrite, ammonia and phosphorous, which have been studied in temperate (Dugan et al., 2011) and Antarctic shores (Nedzarek and Rakusa-Suszczewski, 2004; Sturz et al., 2003).

Biological processing through consumption by crustaceans and insects is a paramount pathway of the wrack subsidies in beaches of low and temperate latitudes. Amphipods are frequently the most abundant herbivore taxon, comprising up to 90% of the beach macrofauna (Stenton-Dozey and Griffiths, 1983). These primary consumers are important intermediates between macrophyte supply and higher trophic levels, as avian consumers (Dugan et al., 2003; Griffiths et al., 1983). In polar regions, ice scouring excludes all macrofaunal primary consumers and macroalgal growth from the mid and upper intertidal range (Dayton et al., 1969; Pugh and Davenport, 1997; Thrush et al., 2006). Therefore, only highly resistant meiofaunal organisms with supercooling adaptations (e.g. Collembola and Nematods) colonize the wrack material (Bock, 1982; Sømme, 1986), directly consuming algal tissues or the associated fungi and bacteria community (Burn, 1984).

Amphipods are one of the most conspicuous taxa that inhabit the saturated low intertidal and shallow subtidal in the Antarctic shores. Herbivorous and omnivorous behavior is common characteristics of this macrofaunal group, thus feeding on multiple food sources, including macroalgae (Huang et al., 2006; Nyssen et al., 2005; Richardson and Whitaker, 1979). There are few studies on the trophic relevance of the amphipods in the coastal ecosystems of the ice-free Antarctic shore (Dauby et al., 2001). However, some analyses on its significant role in transferring primary production towards upper trophic levels, including penguins and marine terns, have been published (e.g., Jazdzewski, 1981; Jazdzewski, and Konopacka, 1999).

Along the Antarctic coastline, large aggregations of macroalgae occur in the subtidal bottoms, either in open or sheltered shores, reaching down to 100 m deep. Studies on some critical embayments, such as Admiralty Bay in King George Island, indicated that around 30% of the subtidal bottoms are covered by macroalgal beds, comprising a biomass between 0.2 and 14 kg m⁻² wet weight (Quartino et al., 2001; Zielinski, 1990). The flux of biomass from macroalgal life stocks to the neighbor ecosystems, roughly equilibrate the summer primary production. This shows that marine benthic macroalgae are a significant energy source that probably supports a large fraction of the secondary production in the Antarctic coastal ecosystems (Quartino and Boraso de Zaixo, 2008). The ecological relevance of Antarctic macroalgae for submerged benthic communities, including fishes, is well documented (Gutt et al., 1998; Iken et al., 1997; Tatian et al., 2004). Unlike the subtidal, information on the fate and functional role of algal detritus in the intertidal environment, is scarce and punctual (Alkemade and van Rijswijk, 1993; Quartino and Boraso de Zaixo, 2008; Rakusa-Suszczewski, 1995).

The overall goal of this study was to investigate processes that potentially influence the amount of wrack stranded in Antarctic shores. Specifically, we assess 1) the rate at which macroalgal deposition occurs along the intertidal range on beaches of Foster Bay, 2) the role of wind direction on algal drifting and deposition, 3) the wrack decay process once stranded on the beach, 4) the potential impact of amphipods feeding on macrophyte stranded biomass, as a proxy of the macroalgal production flux towards upper trophic levels.

To fulfill these objectives, lab/field experimental manipulations were performed in Foster Bay, Deception Island, North of Antarctic Peninsula. As a semi-enclosed system, Foster Bay exchanges a small part of its total volume with the Bransfield Strait. This enhances the predictability of quantitative processes that take place within the system, such as connectivity between marine environments, material transferring, resource consumption and degradation.

2. Material and methods

2.1. Study site

Field sampling and experiments were carried out in a boulder beach at Deception Island, in the South-western limit of the South Shetland Archipelago, North of Antarctic Peninsula (Fig. 1). Deception Island is a young and active volcano rising 542 m above the sea level. The collapsed and flooded crater shapes an inner bay (forms Foster Bay) of 160 m maximum depth, 38 km² in surface, 3500 hm³ of volume and 30 km of shoreline, 80% of which is made of volcanic boulder and gravel beaches. Gray et al. (2003) described gravel and coarse sediment from 0 to 80 m depth, while silt and clay dominate bottoms deeper than 80 m. The Neptune's Bellows is the narrow channel (250 m) on the southeast side of Deception Island forming the connection between Foster Bay and the Bransfield Strait (Fig. 1).

Study site was a narrow bluff-backed beach (Fig. A.1) in the vicinity of the Antarctic Spanish Base Gabriel de Castilla (62° 58' 53" S, 60° 39' 10" W). The intertidal width of the beach (bluff base to low swash level at low tide) ranges from 27 to 37 m, depending on the lunar cycle, experiencing mixed semi-diurnal tides of 12.42 h, with ca. 2.2 m maximum range at spring tide (Vidal et al., 2011). Beach slope was uniform, ranging between 1/21 and 1/16. Surface substrate was very coarse, with pebbles (>4 mm) accumulating more than 50% of the sediment structure.

2.2. Litter bag experiment

The decomposition rates of two algal species were compared. The issue was to check for inter-specific differences in the decay process, that eventually affect the fate of macroalgal biomass stranded in the intertidal. A manipulative experiment took place along a stretch sector of beach, 100 m long (site A) (Fig. 1) during 14 days in February 2010. Wrack decay process was evaluated in terms of weight loss and decomposition rate. Fresh endemic Rhodophyte *Palmaria decipiens* (Reinsch) Ricker 1987 (hereafter *Palmaria*) and the Phaeophyta *Desmarestia menziesii* Agardh 1848 (hereafter *Desmarestia*) were collected from the shallow subtidal zone in the proximity of the study site. In the laboratory, all macroalgae were washed with water to clean any organisms and sediment attached, and then oven-dried at 60 °C for 48 h. Mimicking the natural macroalgae decomposition process in the intertidal, macroalgae fragments of 5 ± 0.5 g dry weight (DW) were introduced in 15 × 20 cm litter bags made of fine plastic mesh with a light diameter of 15 mm. The aperture size was chosen to prevent aeolian dispersion and to avoid any artifact effect on the macroalgae fragments due to the litter bags artificial composition ("screen" effect). There were no significant differences among the initial weights of all the macroalgae fragments utilized ($F_{3,32} = 0.1, P > 0.05$). A total of 40 litter bags were placed haphazardly on the highest drift line of the beach. Initial date was that of maximum high tide position along the lunar

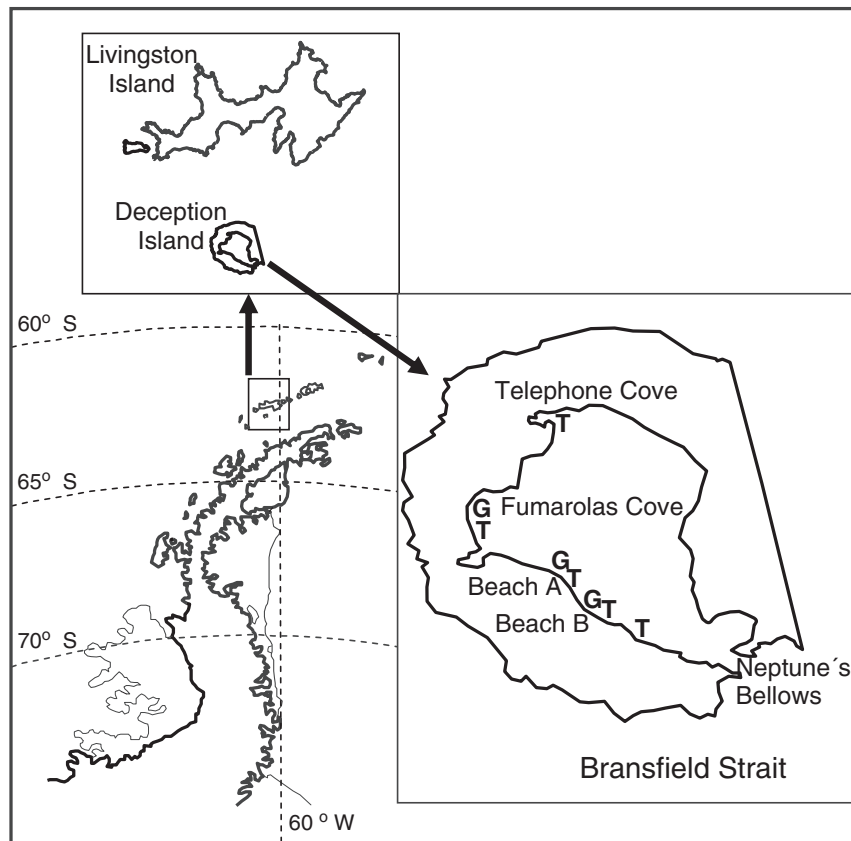


Fig. 1. Map of Antarctic Peninsula showing location of sampling and experimental sites in Foster Bay, Deception Island. G-letters are stations where algal wrack was groomed. T-letters indicate stations where amphipods were captured by trawling.

cycle, on February 5th 2010. Thus, tidal inundation of the experimental site or algal loss by wave action was eluded. Litter bags were placed parallel to the shoreline, approximately 0.5 m apart, and fixed to the sediment using long metal camping sticks. Algal material was re-hydrated with filtered seawater at the start of the experiment. On days 3, 5, 7 and 14, five litter bag replicates of each macroalgae species were collected into separate plastic bags and transported to the laboratory. The entire content of each bag was thoroughly washed with tap water over 0.5 mm sieve. Cleaned algal fragments were then oven-dried at 60 °C for 48 h and weighed.

Decomposition data derived from the wrack decay experiment were expressed as the difference between the initial and final dry weight (i.e., dry mass weight loss). The change in *P. decipiens* and *D. menziesii* dry weight over time, served as a measure of wrack decomposition inter-specific differences. Decomposition data from the two algal species were expressed as the percentage of initial dry weight loss, and then evaluated with a single exponential decay model (following Jędrzejczak, 2002):

$$W_t = W_0 e^{-kt}$$

where, W_t is the dry weight (g) of a litter sample remaining after time (t). W_0 is the initial dry weight (g) of a litter sample. k is the decay coefficient (day^{-1}) and t is the time (days).

This simple model does not discriminate between soluble and refractory material, nor does it distinguish microbial contributions (Jędrzejczak, 2002; Wieder and Lang, 1982). The decay coefficient (k) is a useful tool to compare decomposition rates between different macroalgal species over time. Finally, the differences in the decomposition rates between *Palmaria* and *Desmarestia* were analyzed using a 2-factor orthogonal analysis of variance. Types of wrack (two levels) and time (four levels) were considered fixed factors. Before analysis, the

homogeneity of variances was evaluated with Cochran's test and data were transformed when necessary.

Mean temperature during the experimental period was 1.4 °C, ranging between −2.5 and 6.1 °C (data from Spanish Meteorological State Agency).

2.3. Stranded wrack and turnover rate

A manipulative field experiment was conducted at two stretch sectors of the beach, 100 m long (sites A and B), 400 m separated (Fig. 1). Algal biomass, wrack zonation and turnover rate of stranded deposits, were calculated to describe the algal wrack dynamics in Foster Bay. Six shore-perpendicular transects were haphazardly distributed along the 100 m stretch at each site, from the bluff base to the low swash level (Fig. 2). A table of random numbers was used to set the distances between transects, with 5 m minimum spacing. Wrack coverage was measured along each transect at low spring tide using the line-intercept method (Dugan et al., 2003). The experiment started at spring low tide on January 4th 2011, with 37.5 m maximum beach width at site A, and 30 m at site B. Initially (at t_0), all wrack macroalgae stranded within a 1 m wide strip of beach centered on each transect, were groomed. All material was oven-dried at 60 °C until constant weight and weighed. Fresh weight (FW) of the algal wrack deposits was not measured, but a 10:1 ratio in wet/dry weight (Quartino and Boraso de Zaio, 2008) was assumed. Total stranding biomass at t_0 was estimated for each site as the average of the 6 transects (g DW m^{-1}). To evaluate spatial variability and average weight of wrack deposits in the intertidal sedimentary shores of Foster Bay, the 12 transects groomed at the initial day (t_0) in sites A and B were used, together with 6 transects groomed in Fumarolas beach, a 2.5 km long beach, 4 km West from the experimental sites (Fig. 1).

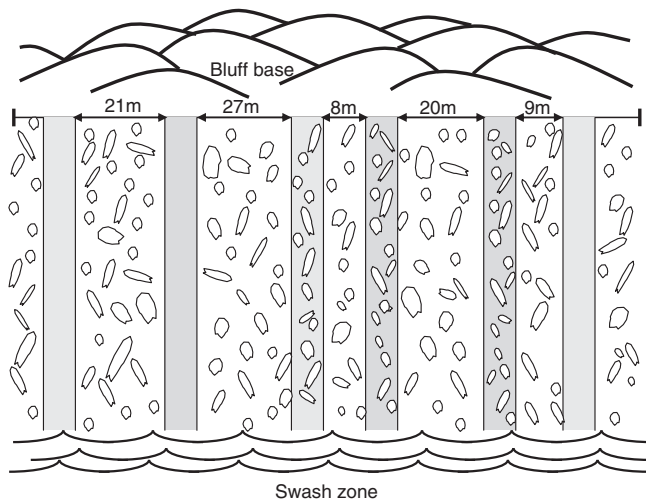


Fig. 2. Sampling design for the stranded wrack and turnover rate experiment during 5 consecutive days. Shaded strips are the 6 transects, 1 m wide, running from the bluff base to the swash zone at low tide. Empty shaded strips are the 3 transects where measurement of wrack coverage and grooming was carried out daily. Covered shaded strips are the 3 un-groomed transects where wrack coverage was measured daily, but not removed. Transects were distributed at random along 100 m stretch of the beach. Distances between transects are indicated for site A (as example).

Macroalgal deposits were tracked during 5 consecutive days (t_1 to t_5) at both sites (A and B). Wrack coverage at day 1 was measured at maximum low tide along the 6 transects. After which, three of these transects were randomly chosen for total grooming according to the above protocol, while the remaining three stayed as un-groomed controls (Fig. 2). This protocol was repeated until day 5 using fixed groomed and un-groomed transects. Collected material was oven-dried (60 °C) and weighed in the laboratory for dry-weight calculations. An ulterior sampling (t_6) was performed on January 13th to increase the time lapse of the study.

Turnover rate (%), as an estimate of the wrack amount that is replaced between two consecutive low tides, was calculated as the averaged difference between wrack biomass in groomed vs. un-groomed (control) transects along 5 consecutive days, from t_1 to t_5 . Wrack biomass at un-groomed profiles was estimated through linear regression analyses, using the biomass vs. coverture data from the groomed transects: $\text{Wrack Biomass (g DW m}^{-1}\text{)} = -0.031 + 0.007 \text{ Coverture (\%)}$, ($R^2 = 0.792$; $P < 0.001$). Wrack reaching the beach was calculated as the algal amount stranded at groomed transects plus the daily difference (either positive or negative) in algal deposits in the un-groomed transects, from t_0 to t_5 ($\text{g m}^{-1} \text{ day}^{-1}$).

Difference in the position of algal deposits across the beach between groomed and un-groomed transects was evaluated. Beach width and dry weight of algae across the beach were standardized at each transect as percentage. Next, each transect was divided into 5 equally sized distances across the beach to facilitate contrasting. Wilcoxon test for paired data (Zar, 1996) was used to check differences in averaged wrack biomass between groomed and un-groomed transects at each distance.

Wrack dynamics was analyzed using a three-factor orthogonal analysis of variance. Beach site (2 levels: A and B), time (7 levels: t_0 – t_6) and transect treatment (2 levels: groomed vs. un-groomed) were considered as fixed factors. The homogeneity of variances was examined with Cochran's test. Student–Newman–Keul's test (SNK) was used as a posteriori analyses to specify significant differences.

Regression was used to investigate the influence of wind direction as the variable potentially responsible for drifting macroalgae and stranding on the intertidal range. Data on wind direction (Spanish Antarctic Base Meteorological Reports) were split in sea-land and shore-parallel

directions, and then transformed into Cartesian co-ordinates (sin and cosine) by making the x-axis shore-parallel and y-axis sea-land orientated (Fallaci et al., 1999).

2.4. Wrack consumption

The potential consumption of two species of herbivores feeding on *Palmaria* and *Desmarestia* was quantified by means of lab experimental assays. Two common Antarctic amphipods from shallow subtidal environments were used in the trials: *Gondogeneia antarctica* (Chevrerux 1906) (hereafter *Gondogeneia*) and *Cheirimonon femoratus* (Pfeffer 1888) (hereafter *Cheirimonon*). *Gondogeneia* is widely distributed along the western Antarctic Peninsula, where it is one of the most abundant herbivores present in the shallow littoral benthic communities (Huang et al., 2003; Jazdzewski et al., 2000). *Cheirimonon* is an opportunistic species frequently featured as necrophagous, which inhabits from the lower intertidal (Jazdzewski et al., 2000) down to several hundred meters depth (Krappa et al., 2008).

Feeding trials were carried out for two size classes, juveniles and adults. Sex mature adult stages in *Gondogeneia* start at ca. 9 mm body length (Huang et al., 2006), while in *Cheirimonon*, sex maturity is reached at 6.5 mm in males and about 8 mm in females (Bregazzi, 1972). Individuals were measured from the tip of the rostrum to the base of the telson.

To estimate consumption rates ($\text{mg algae} \times \text{mg amphipod}^{-1} \times \text{day}^{-1}$), fresh amphipods were collected using hand nets in the shallow subtidal for *Gondogeneia*, and using baited traps for *Cheirimonon*. Before feeding assays, individuals were starved during 12 h into experimental containers (15 cm diameter, 12 cm height), filled with 8 cm of Millipore HA (0.45 μm) filtered and constantly oxygenated seawater. Later, separated groups of 20 juveniles or 10 adults were installed in containers filled with filtered and continually oxygenated seawater. One pre-weighed fragment of *Palmaria* was introduced in each container and removed after 24 h. The same protocol was used with fragments of *Desmarestia*. Every trial was replicated three times, each time with fresh algae and new individuals, to avoid pseudoreplication. All macrophyte portions were composed of fresh material that was harvested from the field. Macroalgae were always supplied in excess of anticipated consumption (generally 0.3–0.6 g wet weight). Fragments were extended in blotting paper during 5 min to remove excess of water and weighed to the nearest 0.001 g, prior to addition in the containers. To control for a possible weight change of the algal fragments independent of feeding by amphipods (e.g., water content increase, microbial degradation), three controls consisting of containers with water and pre-weighed algal fragments, but without amphipods, were prepared for each experimental trial. At the end of each experiment, the remaining food was removed, blotted to eliminate excess water, and weighed to the nearest 0.001 g.

The two amphipod species tested have a putative opportunistic feeding behavior (Bregazzi, 1972; Doyle et al., 2012). Thus, together with the algal feeding trials and using the same protocol, a test was conducted where the food choice was fish muscle, specifically hake (*Merluccius* sp.), as a proxy of an animal carrion supply. Food fragments (including controls) in the containers ranged between 1.5 and 3 g wet weight.

Experiments were placed in an outdoor exposed chamber. Water temperature in the containers were tracked every 10 min by using T-data loggers. Temperatures ranged between 0.21 and 3.6 °C, being always within the range measured in the shore sites where individuals were captured (Lastra, unpublished data). The total length of each amphipod used in the treatments was measured to the nearest 0.1 mm with a graded lens under stereo-microscope. Consumption rates were calculated as mg of food consumed per mg of amphipod during 24 h ($\text{mg} \times \text{mg}^{-1} \times \text{day}^{-1}$), using the formula: $(W_i(C_f/C_i) - W_f) / W$; where W_i and W_f are the initial and final blotted wet

weights of food in the treatment; Ci and Cf are the initial and final weights of the controls; and W = total biomass (DW) of the individuals in each treatment (e.g., Taylor and Brown, 2006). Consumption rates at each replicated trial were expressed per mg dry-weight of amphipod, using the following weight–length relationships developed from a subset of 300 individuals.

$$\begin{aligned} \text{Gondogeneia Dry weight} &= 0.00078 e^{0.219 \text{ Length}} \quad (R^2 = 0.811, P < 0.001). \\ \text{Cheirimedon Dry weight} &= 0.00037 e^{0.301 \text{ Length}} \quad (R^2 = 0.883, P < 0.001) \end{aligned}$$

We tested for treatment effects using 3-factor analysis of variance, with species (two levels), age class (two levels) and food type (three levels) as fixed factors. If the main effects were significant, the SNK test was used to identify differences among treatments. Before analysis, the homogeneity of variances was checked with Cochran's test.

The potential transferring of algal subsidies towards upper trophic levels was estimated through population abundance and body size of the two amphipod species along the shore line. Population density and size class distribution of *Gondogeneia* and *Cheirimedon* were assessed at 5 different sites around Foster Bay (Fig. 1). At each site, three replicated 20 m long-shore transects in the shallow subtidal were hand trawled by pushing a bottom aquatic Kick net 40 × 20 cm rectangular frame 1 mm mesh size (Water Mark®).

3. Results

3.1. Litter bag experiment

Maximum weight loss was observed at day 7 for *Palmaria* fragments (22.5%) and at day 5 for *Desmarestia* (41.3%). *Desmarestia* showed a faster weight loss over time compare to that of *Palmaria* ($F_{1,32} = 26.9$; $P < 0.001$) (Fig. 3A). Likewise, the decay coefficient (k) showed different pattern between the two macroalgal species along the study period (Fig. 3B), with decomposition rate being significantly higher in *Desmarestia* ($F_{1,32} = 27.2$; $P < 0.001$). A slower and consistent decay was observed in *Palmaria*, with almost no variation since the third day of the experiment. *Desmarestia* significantly increased the decomposition rate (in terms of k) after day 3, with the higher rate at day 5, switching into a more stable decay for the rest of the experiment (Fig. 3B). As expected, no macrofauna was found in none of the litter bags during the time of the study.

3.2. Wrack stranding and turnover rate

Close to 100% of the wrack collected along the intertidal shore in Foster Bay was *P. decipiens*, with a minor contribution of the similar red blade species *Iridaea cordata* (Turner) Bory, as well as *Desmarestia* spp. and *Desmarestia antarctica* RL Moe and PC Silva, among others. Initial standing crop (t_0) was similar in the two experimental sites (site A vs. site B; $F_{2,15} = 3.22$, $P = 0.068$), and also when comparing at a broader spatial scale: site A $219.27 \pm 107.12 \text{ g m}^{-1}$; site B $179.64 \pm 87.16 \text{ g m}^{-1}$, Fumarolas Beach $99.73 \pm 40.43 \text{ g m}^{-1}$ (DW). Averaged wrack biomass for the sampled shore was $0.166 (\pm 0.93) \text{ kg m}^{-1}$ (dry weight), which roughly means 1.66 kg of fresh algae per running meter of beach.

Average deposits in groomed transects from t_1 to t_6 were $42.36 \pm 44.09 \text{ g m}^{-1}$ and $61.11 \pm 41.81 \text{ g m}^{-1}$ (DW) in sites A and B, respectively. Wrack amount at ungroomed profiles averaged $68.41 \pm 26.88 \text{ g m}^{-1}$ for site A, and $85.83 \pm 54.34 \text{ g m}^{-1}$ (DW) for site B. The beach line profile covered by stranded material averaged $0.503 \text{ m}^2 \pm 0.534$ in site A and $0.602 \text{ m}^2 \pm 0.506$ at site B, which roughly means between 1.5 and 2.5% of the beach surface. Coverture (m^2) to biomass

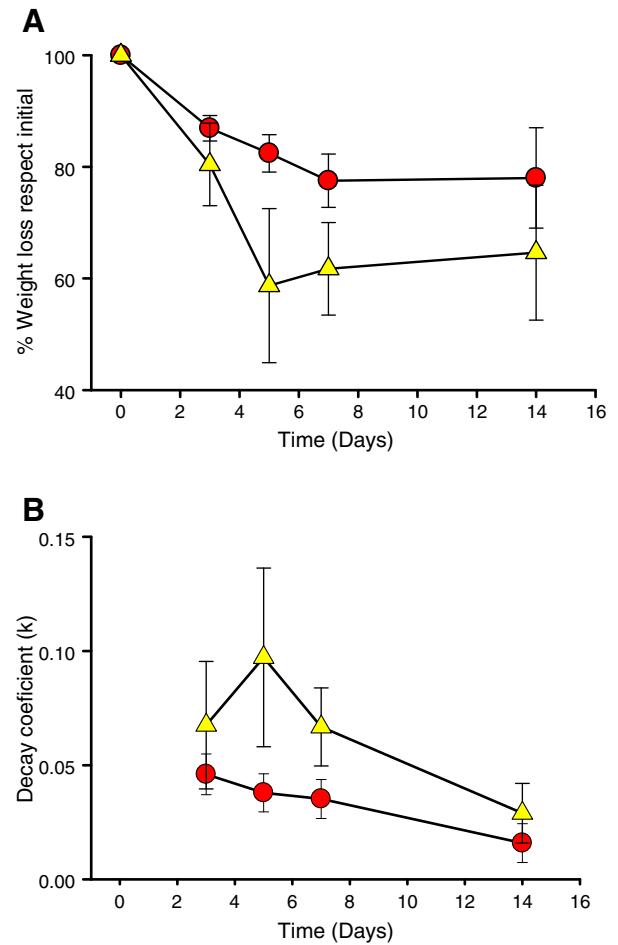


Fig. 3. Changes in the mean dry weight (A) and decay coefficient k (B) of *P. decipiens* (circles) and *D. menziesii* (triangles) in the wrack patches through time (\pm SE, $n = 3$). *Palmaria* (Dry weight = $99.8 - 4.76 \text{ day} + 0.23 \text{ day}^2$, $R^2 = 0.99$; $P < 0.01$), *Desmarestia* (Dry weight = $100.5 - 9.52 \text{ day} + 0.5 \text{ day}^2$, $R^2 = 0.94$; $P = 0.05$).

(DW) relationship increases linearly (Biomass (g DW m^{-1}) = $20.454 + 112.989 \text{ Coverture} (\text{m}^2)$; $R^2 = 0.792$, $P < 0.001$).

A decreasing pattern in the amount of algae stranded on the beach over time was observed (Fig. 4), in both the groomed and the ungroomed transects. This trend was consistent among experimental sites (three-way Anova: site \times time \times treatment interaction, $F_{6,56} = 1.21$, $P = 0.312$) (Table 1). Thus, data from the two beach sites were pooled to increase robustness for further analyses. The change over time in algal deposits (g DW m^{-1}) was evaluated with a single exponential decay model (Jędrzejczak, 2002): Groomed transects:

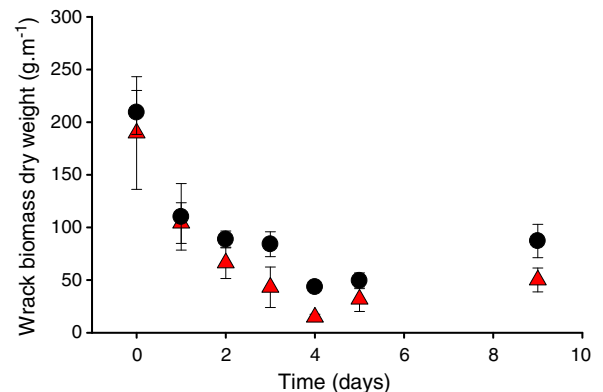


Fig. 4. Changes in the mean dry weight (\pm SE, $n = 6$) of stranded macroalgae on groomed (triangles) and ungroomed transects (circles). Data from sites A and B have been pooled.

Table 1

Three factors ANOVA analyses of stranded algal biomass dynamics in groomed and ungroomed transects along the study period; Mean squares (MS) Degrees of freedom, (df), F value and Significant coefficient (P) are shown.

Source	MS	df	F	P
Site	2033.58	1	0.83	0.365
Time	22953.26	6	9.41	0.000
Treatment (groomed vs. ungroomed)	796.36	1	0.33	0.570
Site × time	4070.79	6	1.67	0.145
Site × treatment	842.62	1	0.35	0.559
Time × treatment	18368.03	6	7.53	0.000
Site × time × treatment	2961.40	6	11.21	0.312
Residual	2438.41	56		
Total		83		

$y = 51.74 + 137.95 e^{-1.21x}$, $R^2 = 0.392$, $P < 0.001$; Ungroomed transects: $y = 77.12 + 132.1 e^{-x}$, $R^2 = 0.534$, $P < 0.001$. Mean turnover rate according to differences between groomed and ungroomed transects was 56.19 ± 17.69 . Average algal amount reaching the beach at each tidal cycle was $23.85 \pm 33.34 \text{ g m}^{-1}$ (DW), which means c.a. $0.24 \text{ kg m}^{-1} \text{ day}^{-1}$.

Wind conditions had a significant effect on the amount of algae stranded on the beach (Groomed: Wrack biomass (g DW m^{-1}) = $89.01 + 97.20$ wind direction; $R^2 = 0.51$, $P = 0.071$; Ungroomed: Wrack biomass (g DW m^{-1}) = $89.01 + 97.20$ wind direction, $R^2 = 0.607$, $P = 0.001$). Larger deposits were measured when sea wind blew perpendicularly to the shoreline (Fig. 5).

Spatial distribution across the beach of stranded macroalgae in groomed and ungroomed transects was similar along the study period (Fig. 6). Wilcoxon test for paired data did not find significant differences in wrack zonation in none of the groomed vs. ungroomed treatments from t_0 to t_6 .

3.3. Wrack consumption

The body size of the amphipods used in the feeding trials varied between the two species (Fig. 7), probably in relation to different maximum sizes and population structures. For *Gondogeneia*, mean length ranged from 4.59 to 5.65 mm in juvenile stages, and from 10.18 to 12.73 mm, for adults. For *Cheirimon*, mean length in juveniles ranged from 6.0 to 8.33 mm, and from 10.15 to 11.45 mm in adults. Natural population density of *Gondogeneia* in the swash and shallow subtidal zone was $30 \pm 43 \text{ ind. m}^{-2}$; for *Cheirimon*, it was $177 \pm 447 \text{ ind. m}^{-2}$. Mean sizes of the field captured individuals were $10.05 \pm 3.09 \text{ mm}$ for *Gondogeneia* and $8.24 \pm 2.58 \text{ mm}$ for *Cheirimon*.

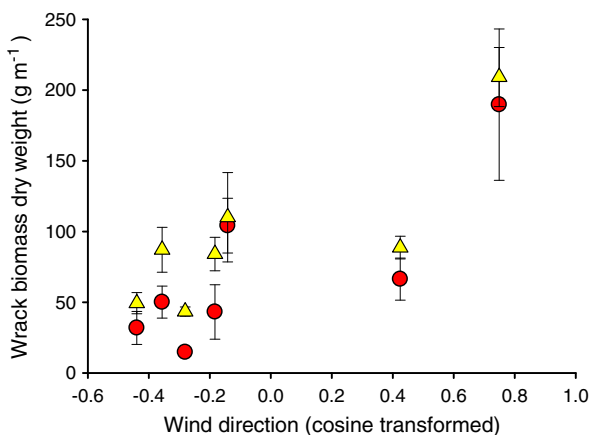


Fig. 5. Algal biomass stranded on groomed (triangles) and ungroomed transects (circles) in relation to sea-land and shore-parallel wind direction. Wind data ($n = 6$) were transformed into Cartesian co-ordinates (sin and cosine) by making the x-axis shore-parallel and y-axis sea-land orientated (Fallaci et al., 1999). Data from sites A and B have been pooled.

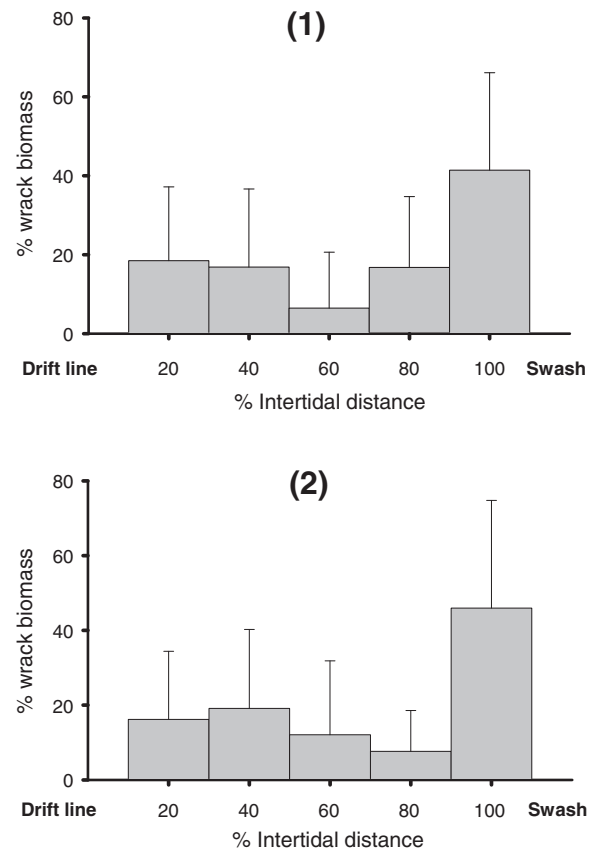


Fig. 6. Algal deposits distribution along the intertidal range in groomed (1) and ungroomed transects (2) (\pm SE, $n = 18$). X and Y values are distances and dry weight biomass standardized as percentages. Data from beach sites A and B have been pooled.

Feeding rate per mg of body mass of *Gondogeneia* was higher than that of *Cheirimon* (Species: $F_{1,24} = 10.23$, $P = 0.004$) (Table 2) (Fig. 7). Differences in feeding behavior were observed between small and large individuals, depending on the food supplied (Food × Size class interaction; $F_{2,24} = 5.22$, $P = 0.0013$). Juvenile individuals fed on fish muscle tissue and *Desmarestia* at a higher rate than that measured on adults (SNK test: $P < 0.01$). Adults fed on *Palmaria* blades at a higher rate than that of juveniles. Adults fed on fresh *Palmaria* at a faster rate than that on fish muscle (SNK test: $P < 0.05$).

Species to species contrasts were inconsistent against different food sources (i.e., three-way Anova: species × food × size-class interaction, $F = 0.59$, $P = 0.563$). Adult individuals of *Gondogeneia* fed on *Palmaria* at a higher rate than on *Desmarestia* (SNK test: $P < 0.01$) (Fig. 7). Juvenile individuals of both consumer species fed on *Desmarestia* at a higher rate than the adults, but this was only statistically significant for *Gondogeneia* (SNK test: $P < 0.01$). Fish muscle was consumed at a faster rate by *Gondogeneia* than by *Cheirimon*, but this was only statistically significant for juveniles (SNK test: $P < 0.05$).

4. Discussion

4.1. Wrack deposition and turnover rate

The averaged deposits of $1.66 \pm 0.93 \text{ kg}$ per running meter of shore line, mean that there was an instantaneous standing stock of 39.9 metric tons (MT) of algal wrack along the tidal beaches of Foster Bay. Extending the stranding rate of $0.24 \text{ kg m}^{-1} \text{ day}^{-1}$ (FW) along the ice-free period (Smith et al., 2003), results in 1545.48 MT of detached macroalgae reaching the beaches from early November through late July. Results of calculations were similar to those observed in neighbor bays of South Shetland Archipelago. Intertidal beaches of Admiralty

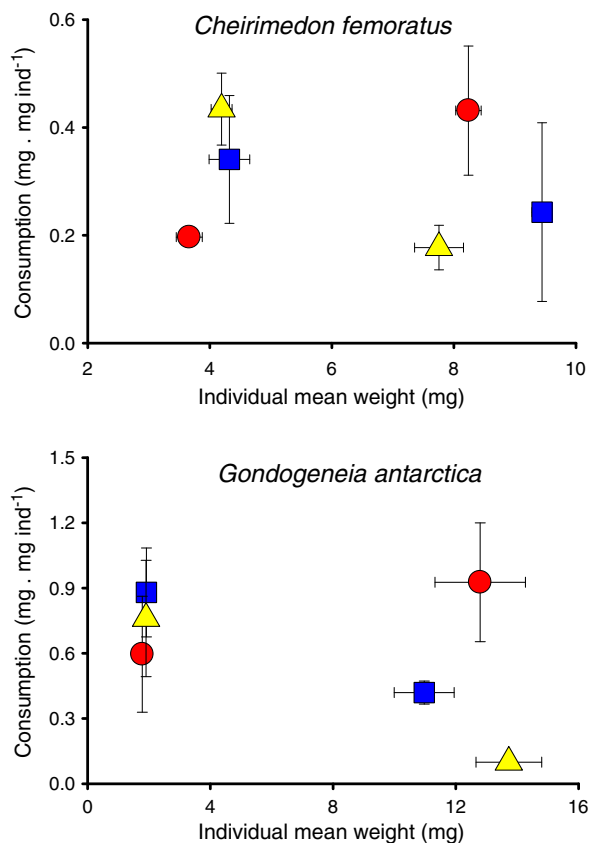


Fig. 7. Feeding rate ($\text{mg} \cdot \text{mg ind}^{-1}$ fresh weight) of the two amphipods species used in the trials in relation to food type supplied and the individual body mass of juvenile and adult stages (mg dry weight). *P. decipiens* (circles), *D. menziesii* (triangles) and hake muscle tissue (*Merluccius* sp.) (squares) were offered at satiety.

Bay in King George Island accumulate 2790 MT of stranded macroalgae along the 19.2 km of shore line from February to November (Rakusa-Suszczewski, 1995), involving deposition rates of $0.22 \text{ kg m}^{-1} \text{ day}^{-1}$. Annual input of stranded biomass for the Antarctic shores seems to be low, compared to that of highly productive areas in temperate latitudes. For example, estimated supplies of up to $1800 \text{ kg m}^{-1} \text{ yr}^{-1}$ (FW) have been cited for South African beaches (Griffiths and Stenton-Dozey, 1981). Giant kelp *Macrocystis pyrifera* is a major component of the macrophyte subsidies that strand on beaches in southern California (Dugan et al., 2003), with inputs exceeding $450 \text{ kg m}^{-1} \text{ yr}^{-1}$ (FW) (Hayes, 1974). The total annual amount of fresh wrack in the NW coast of Spain varies between 3.65 and $2398 \text{ kg m}^{-1} \text{ yr}^{-1}$ (FW) (Barreiro et al., 2013).

Variability in wrack supply is necessarily associated with environmental drivers, such as unequal source environments (e.g. surrounding rocky shore), coastal currents and wind-transport (Gomez et al., 2013; Orr et al., 2005). Coastal orientation and wind direction appear to be

critical in explaining the algal supply to the tidal zone. Orthogonal landward winds tend to accumulate maximum wrack biomass on the shore. Within similar wind conditions, beaches should receive different amounts of drifting macroalgae depending on their different cartesian orientation of the shoreline. Orientation of the two beaches included in the grooming experiment differ in 20° , which does not seem to induce significant variability in the amount of wrack received, nor in the spatial distribution of deposits at local scale. Patches were distributed all along the beach face, with highest piles stranded close to the swash zone and secondarily in the high tide drift line. Therefore, algal deposition occurs throughout the process of outgoing ebb tide. This pattern denotes that wrack distribution across the tidal zone is related to physical processes (mainly hydrodynamics) and beach characteristics. Wrack zonation can occur over shore parallel strips overlapped with drift lines (Marsden, 1991; Ochienga and Erfemeijer, 1999) or in patches across the tidal beach profile (Colombini et al., 2000; Marsden, 1991). Our findings partially differ from Orr et al. (2005), who explains how the slow retraction of the waterline during the first 90 min of outgoing ebb tide results in an increase of the wrack deposition in the upper part of the beaches. Measurements that agree with Gomez et al. (2013), demonstrate that sheet-like species without buoyant structures, as *Palmaria*, tend to strand in the lower intertidal, and this trend remains consistent regardless of the wrack biomass reaching the beach.

Macroalgae aggregations occupy approximately one-third of subtidal bottoms of bays and inlets of South Shetland Archipelago. About 2 kg m^{-2} occupies 31% of the bottom surface of Admiralty Bay, with an estimated live stock of 73,800 MT (Zielinski, 1990). Algal densities of 14 kg m^{-2} (FW) occupy 24.6% of the submerged environment in Potter Cove, King George Island, which means 37.4% of the bathymetry between 0 and 30 m (Quartino et al., 2005). Subtidal macroalgal beds of Foster Bay were not evaluated in the present study, but material cast up on the shore suggests that *P. decipiens* was an extremely dominant taxa on the algal beds during the austral spring–summer period. *Palmaria* has been cited as the most abundant seaweed at bays and coves of King George and Half Moon Islands, either in the shallow subtidal or stranded on the drift line, where it accumulates 10.31 kg m^{-2} of mean wrack biomass (FW) (Neushul, 1965; Oliveira et al., 2009; Westermeier et al., 1992). Live *Palmaria* averaged 0.230 kg m^{-2} (FW) in subtidal beds of Potter Cove, frequently attached to boulders and hard substrates (Quartino and Boraso de Zaixso, 2008). *Palmaria* is considered a “season anticipator”, able to optimally use the period of high light conditions in spring (Weykam et al., 1997). A further explanation of the spatial dominance and effective space occupation of *Palmaria* in Antarctic shores is its resistance to ice scouring (Neushul, 1965), which can be an advantage for a rapid growth after ice melting. Its bathymetric distribution ranges between 0 to lower than 70 m depth, albeit light requirements limit its significant aggregations between 0 and 30 m (Gomez et al., 1997; Lüder et al., 2001; Quartino et al., 2001; Westermeier et al., 1992). Approximately 10% (10.1 km^2) of the bathymetry of Foster Bay ranges between 0 and 30 m (UKHO Admiralty Chart 3202); thus, extrapolating from bottom surface covered by macroalgal beds in Potter Cove at this depth (37.4%), as well as *Palmaria* mean density (0.230 kg m^{-2}), means that 3.77 km^2 of the submerged bottoms of Foster Bay could harbor a live stock of 864.8 metric tonnes (MT) (FW) of *P. decipiens*. This prediction probably underestimates the amount of *Palmaria* in Foster Bay, as extrapolated data from areas with a high diverse macroalgal community, therefore subjected to strong interspecific competition (Klöser et al., 1994; Quartino et al., 2005).

To link live biomass of algal beds to detached biomass stranded on the shore, is challenging. There is a general lack in information on the proportion of algal net production that detaches from hard substrates and decomposes in the water column, accumulates in depth, or strands on the shore. Duarte and Cebrian (1996) reported that after being fragmented or detached, macroalgae export between 24.3 and 43.5% of the net primary production to neighbor or distant ecosystems,

Table 2

Three factors ANOVA analyses of amphipod consumption; Mean squares (MS) Degrees of freedom, (df), F value and Significant coefficient (P) are shown.

Source	MS	df	F	P
Species	0.8204	1	10.23	0.004
Food	0.0773	2	0.96	0.395
Size class	0.2294	1	2.86	0.103
Species \times food	0.0744	2	0.93	0.409
Species \times size class	0.1290	1	1.61	0.217
Food \times size class	0.4190	2	5.22	0.013
Species \times food \times size class	0.0471	2	0.59	0.564
Residual	0.0471	24		
Total	0.0802	35		

depending on coastal hydrodynamics. The amount of algal decay residing into the semi-enclosed system of Foster Bay can be inferred from the renewal time of the basin and the primary production of the algal live stock. Water volume exchange of Foster Bay varies between 1.1 and 2.2% over each tidal cycle, with a mean replacement time of 82 days (Vidal et al., 2011). Although primary production of algal live stock was not gauged in the present study, macrophyte growth in polar regions is strongly seasonal, with little or no specific growth during the winter and/or sea-ice cover period. Ice cover in Foster Bay starts in late July and is intermittently visible through early November (Smith et al., 2003). For the spring–summer 2010–11, sea ice completely disappeared on November 28 (personal observation). Specific growth rate of *P. decipiens* starts in October and last until late summer, ranging between 0.01 and 0.03 g g⁻¹ of daily production (Gomez et al., 1997; Weykam et al., 1997). Assuming an initial live stock of 864.8 MT, Foster Bay received 1414.7 MT (FW) of macroalgal decay from the ice cover melting to the start of our field work. Only 39.9 MT (2.82%) of these macroalgal subsidies was stored as wrack on the tidal zone, pointing that 1374.8 MT (97.18%) of the algal fragments remained within the bay basin or was flushed to open waters. Specifically, attending to an average volume replacement of 1.15% (Vidal et al., 2011), 232.2 kg of drifting algae was flushed out to the Bransfield Strait through Neptunes's Bellows at each tidal cycle.

4.2. Algal wrack weight loss

Wrack stranding is a very dynamic process. Frequent events of resuspension and redeposition may complicate the estimates of algal supply. A number of hydrodynamic factors drag algal amounts from the intertidal back to the water column or transport them to settle in different positions along and/or across the tidal zone. Furthermore, the duration of the ice free period in Antarctic shores determines the quantity of wrack reaching the beach along the year cycle. Stranding rate calculated at Foster Bay (0.24 kg m⁻¹ day⁻¹ FW) means that 0.4% of the algal fragments floating into the basin reached the shore at each tide cycle during the summer period. Even though *P. decipiens* is characterized by a low specific growth from December to August, the pattern of fronds fragmentation and export to the intertidal might well last for several months, according to the belated decomposition rate observed in the subtidal beds of Antarctic macroalgae. Decomposition rates based on weight loss after 20 days of the Antarctic red blade seaweed *Iridaea* sp., ranged between 14% and 87%, with an average of 35% over different substrates and intertidal conditions. These results agree with the values obtained in the present study, where maximum weight loss was 22.5% for *Palmaria* and 41.3% for *Desmarestia*. Manipulative experiments in subantarctic islands showed that degradative processes occur at much faster rates when consumed by insects and amphipods cooperate in wrack decay (Crafford and Scholtz, 1987). Field experiments with *Desmarestia anceps* Montagne indicated that decomposition process in the sublittoral is slow and based on physical fragmentation; i.e., fronds started to decay from day 144 at 0.24% per day, with an overall decomposition time of around 1 year (Brouwer, 1996). This is much slower than the decomposition rate calculated in our study for the intertidal deposits. Likewise in similar experimental designs in temperate latitudes (Rodil et al., 2008), most of the wrack weight loss occurs within the first 5–6 days, showing a relatively intensive initial wrack breakdown. In a functional approach, these results indicate that intertidal wrack deposits in the Antarctic can be considered as biogeochemical “hot spots” (sensu McClain et al., 2003), thus accelerating biomass processing and speeding the release of organic matter and nutrients to the coastal environment. Once initial loss in algal biomass occurs, decay processes tend to become steady; thus, deposits can last for several weeks when settled at the upper shore during spring high tides. Uneven weight loss of stranded *Palmaria* and *Desmarestia* implies that the breakdown depends on the macroalgal species. This introduces heterogeneity in the food supply available for different organisms in the

intertidal (Mews et al., 2006; Rodil et al., 2008), as well as variability in nutrient leaching to the coastal environment (Nedzarek and Rakusa-Suszczewski, 2004; Urban-Malinga and Burska, 2009).

We did not find macrofaunal consumers into the litter bags during the 14 day experiment. Consequently, the most important degradation processes were related to desiccation, physical fragmentation, meiofaunal consumption, mainly colembola (Sømme, 1986; Urban-Malinga and Burska, 2009) and microbial activity (Reichardt and Dieckmann, 1985). Kinetics of bacterial degradation of macrophytes in the Antarctic environment is specially adapted to cold temperature regime, whereby the detritus-based food web plays a similar role as in temperate latitudes (Reichardt and Dieckmann, 1985). In a leaching experiment reproducing natural decay of Antarctic macroalgae, Nedzarek and Rakusa-Suszczewski (2004) calculated that nutrients released from the red blade species *Curdia racovitzae* Hariot, *Myriogramme mangini* (Gain) Skottsberg and *Sarcodia cf. montagneana* (Hooker and Harvey), averaged 14.04 (±6.9) g total N kg⁻¹ (DW) and 7.43 (±2.3) g total P kg⁻¹ (DW), with a mean weight loss of 59.9% (±6.9). According to this, the 39.9 MT of algal wrack stranded along Foster Bay could release 11.2 kg of N and 5.9 kg of P over cycles of ca. 14 days. In a study on dissolved nutrients in different environments in Foster Bay, Sturz et al. (2003) measured concentrations of 1.17 ± 2.2 mg kg⁻¹ of N and 0.17 ± 0.13 mg kg⁻¹ of P in interstitial water of beaches, presumably leached from decaying organic matter, which has a clear effect on shore waters by significantly increasing nutrient concentration.

4.3. Wrack consumption by amphipods

The spatial distribution of wrack also limits its uses as food source. In the Antarctic intertidal shore line, where macrofaunal herbivore is excluded, consumption necessarily occurs once the swash flow reaches the position of algal deposits along the beach face. According to results of consumption experiments, *P. decipiens* is highly preferred as food for amphipods, compared to *D. menziesii*. This agrees with feeding trials conducted by Huang et al. (2006) and Aumack et al. (2011) for *G. antarctica* and *Proteobingia gracilis* Chevreux employing fresh algal tissues. In those studies, *Palmaria* was consumed more rapidly than other seven species of algae, including *D. menziesii*, which seems to be related to the algal palatability and the apparent lack of chemical deterrents in *Palmaria* (Huang et al., 2006). When the availability factor was examined, the most abundant species along many areas of the South Shetland Archipelago and the Antarctic Peninsula (Becker et al., 2011) was also the most preferred algal species. This raises the possibility that food availability rather than food quality influences the feeding behavior of the consumers, as proposed by Emlen (1966) in his model for the balance between energy vs. availability in the efficient exploitation of food resources. In any case, the consumption measured in our study agrees with the trend obtained by Paine and Vadas (1969), who stated that the rank order of food value for consumers in terms of energy in macroalgae Classes is Chlorophyta > Rhodophyta > Phaeophyta. Data of amphipod abundance in the field determine that the potential consumption of *Palmaria* by *Gondogeneia* and *Cheirimedon* was 92.01 and 203.7 kg day⁻¹ (FW), respectively. This is approximately 0.73% day⁻¹ of the instantaneous wrack stock along the shore.

Consumption rate for fish muscle was lower than for *Palmaria* and higher than that for *Desmarestia*, both for *Gondogeneia* and *Cheirimedon*. Caloric value (kcal g⁻¹) of the food offered was not measured, but studies on energy content of a large number of algal species conducted by Paine and Vadas (1969), averaged 0.69 ± 0.32 kcal g⁻¹ (FW) of 22 taxa of Rhodophyta; meanwhile, that for 15 Phaeophyta was 0.46 ± 0.17 kcal g⁻¹. Animal tissue largely surpassed the energy supplied from feeding on fresh algae, with values for fish muscle (*Merluccius* sp.) reaching to 1.1 kcal g⁻¹ (FW) (Montecchia et al., 1990). This kind of resource is scarce and unpredictable in beaches of Foster Bay.

Our study suggests that research conditions in Foster Bay are suitable for studies to quantify the connectivity between coastal

ecosystems. Unlike typical opening of marine environment, reduced water exchange between Foster Bay and Bransfield Strait, allows to assess internal processes such as export/import of primary production, biomass fluxes, subsidies and degradative pathways, among others. These enhance the relevance of future studies in Deception Island focused on primary producer distribution within the bay, life biomass quantification, dynamics of primary and secondary consumers, trophic cascades and biogeochemical processes within the interstitial environment of the sedimentary shores.

5. Conclusions and further directions

Our study is a pioneer in analyzing the dynamics of macroalgal wrack subsidies in Antarctic shores. Analyses of the interaction between highly productive macroalgal beds of shallow rocky substrates and the ice free sedimentary shores indicate that only a small fraction of the detached material strands in the shore, while most of it remains in the water column and is exported towards neighboring coastal areas. The variability of the wrack deposits at local scales is high (56% replacement at each tidal cycle), as well as the similarity of the zonation across the beach face of algal deposits. High variability also occurs in the amount of wrack that strand at the shore, which is partially explained by the interaction between wind direction and coastal orientation. Predominance of a single macroalgal species in the wrack deposits denotes an equivalent composition in the source-community. Further decomposition of wrack deposits takes place within the first days of the decay process, which suggest that intertidal wrack deposits in the Antarctic can be considered as biogeochemical “hot spots” that accelerate biomass processing and the releasing of organic matter and nutrients to the coastal environment.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2013.12.011>.

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