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**Sandy beaches as biogeochemical hotspots: the metabolic role
of macroalgal wrack on low-productive shores¹**

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¹ Designed study: IFR, CO, ML; Performed research: IFR, CO, ML, JL Analyzed data: IFR; Contributed methods: IFR, ML, JL, APM, JPF, SVF Wrote the paper: IFR, CO, with editorial inputs from all the authors.

Abstract

Sandy beaches, which represent the most common type of land-sea interface, harbour distinctive biotic communities and regulate the flow of energy between marine and terrestrial ecosystems. Accumulations of sea wrack on sandy beaches are of crucial importance for recycling beach nutrients and for regulating trophic connectivity and coastal functioning. We investigated the role of beaches as biogeochemical hotspots by examining the metabolic activity in accumulations of different species of wrack on two exposed beaches affected by different levels of human pressure. Experimental wrack patches provided large amounts of different sedimentary nutrients over time due to remineralization of the algae. Unsurprisingly, the variation in the nutrients present in the beach sediments was related to the species of wrack considered. Macroalgal wrack was metabolically very active and supported high respiration rates represented by intense CO₂ fluxes. Importantly, we demonstrated that the wrack metabolic rate differed significantly depending on the algal species considered. Different macrofauna and bacterial assemblages were identified in the different wrack patches and on the different beaches. We suggest that human activities such as beach grooming can modify the wrack-associated communities, thus contributing to the variability in the biogeochemical processes and metabolic rates. Significant changes in the type and amount of wrack deposited on beaches can change fundamental processes related to the marine-terrestrial transfer of nutrients and energy and to the marine-atmospheric transfer of CO₂ emissions, with ecological consequences for nearshore environments.

Keywords: bacterial assemblages; benthic macrofauna; CO₂ emissions; metabolic hotspots; non-native species; nutrient inputs

1. Introduction

Sandy beaches are valuable ecosystems that provide ecological and socioeconomic services such as provision of harvestable resources, recycling of organic matter and nutrients, coastal protection and social recreation (Schlacher and others 2008). They are also natural habitats for many distinctive plants and animals, and as transition zones can be colonized by highly diverse and unique biological communities (Schlacher and others 2008). These different components interact in a large ecological network to create the open ecosystems of sandy beaches. Sandy beaches represent the main interface between marine and terrestrial ecosystems and regulate exchanges between these key systems, thus contributing to the normal functioning of both (e.g. Dugan and others 2003; Lastra and others 2008; Spiller and others 2010).

The spatial input of nutrients via the movement or deposition of organisms or material on shorelines around the world is of key significance for relatively unproductive coastal ecosystems such as exposed beaches. This pattern has been increasingly studied in recent years (e.g. Inglis 1989; Dugan and others 2003; Ince and others 2007; Lastra and others 2008; Crawley and others 2009; Rodil and others 2015a,b). Macrophytes become naturally detached from rocky shores and subtidal bottom habitats and transported to nearby beaches where they accumulate and decompose as wrack for variable amounts of time (Orr and others 2005; Mews and others 2006). Wrack deposits have the potential to provide rich and highly heterogeneous habitats for a range of organisms, including marine and terrestrial macroinvertebrates and also microbial communities (Colombini and Chelazzi 2003). Furthermore, by providing external food sources to beaches, wrack becomes an important vehicle of carbon and nutrient exchange between different aquatic ecosystems and between marine and terrestrial ecosystems (Dugan and others 2011; Spiller and others 2010). Wrack that is deposited across the entire intertidal range is moved by tides and waves

before being washed away. However, wrack accumulations may remain, age and decompose on the supratidal areas for several weeks and are often buried, thus affecting the physical and chemical characteristics of the sediments for a long period (Orr and others 2005). Wrack will thus decay and release nutrients into the sediment, stimulating the growth of bacteria, supplying organic matter for the macrobenthos and modifying oxygen exchange in the sediment (Dugan and others 2011). Typical benthic communities (i.e. bacteria, meio- and macrofauna) also play a key role in the decomposition and transformation of wrack through fragmentation, decomposition and remineralization (Lastra and others 2008; Dugan and others 2011). These processes will depend on the quantity and quality of the wrack as well as on the frequency and spatial distribution of the accumulations (e.g. Orr and others 2005; Mews and others 2006; Olabarria and others 2007; Rodil and others 2008). Most studies of beach wrack have focused on the surface of sediments, and the effects of buried wrack have received only incidental attention (e.g. Olabarria and others 2010; Pelletier and others 2011). Moreover, most studies have focused on the fauna, with little consideration given to the metabolism of the community thriving on these deposits, which is likely to be dominated by microbial communities. For example, bacteria are responsible for remineralizing most of the detritus back into nutrients, thus playing a key role in the functioning of nearshores (Koop and others 1982, Inglis 1989).

Interfaces between terrestrial and aquatic ecosystems have been recognized as biogeochemical hotspots (*sensu* McClain and others 2003), and recent evidence shows that sandy beaches fit this concept for nutrient cycling (Dugan and others 2011). Beach wrack deposits can be considered metabolic hotspots with high activity and rates of CO₂ flux relative to other marine and terrestrial habitats (Coupland and others 2007). Community respiration may be a good indicator of the flow of organic matter in ecosystems (Williams

and del Giorgio 2005). Thus, intense respiration reveals an active metabolic role of wrack material, whereas low respiration rates suggest that the material accumulated has a largely structural role (Coupland and others 2007). The metabolic activity of beach wrack has not been studied in detail, although it is the foundation for thriving life and the development of diversity in such environments characterized by low productivity (see Coupland and others 2007). The biogeochemical processes associated with wrack must be investigated in order to improve our understanding of the ecological role of these spatial deposits in supporting the basic processes of nutrient remineralization and beach functioning (Dugan and others 2011). The role of these processes may vary depending on the beach considered and on the intensity of human impact. For instance, wrack is often removed mechanically from tourist beaches, thus significantly reducing the amounts of organic matter in shoreline sediments, offshore nutrient concentrations, and microbial and macrofauna numbers in the terrestrial and aquatic parts of the beach ecosystem (e.g. Dugan and others 2003; Malm and others 2004; Russell and others 2014).

We considered whether two ocean-exposed sandy beaches act as biogeochemical hotspots (McClain and others 2003) by extending the hotspot concept to wrack deposits. We deliberately buried macroalgal detritus to test the fate and the respiration rates supported by beach wrack and to examine changes in the sedimentary biogeochemical composition. Specifically, we compared *in situ* respiratory CO₂ fluxes in four macroalgal species, and we described how the different types of wrack affected the nutrient composition and respiratory rates in the sediment over time. In addition, we examined the role of macrofaunal and bacterial assemblages in the wrack metabolic activity and nutrient remineralization by comparing the existing relationships between sedimentary changes and beach benthic communities. We performed the study on two sandy beaches affected by different types of human activity to examine different ecological responses associated with

different anthropogenic impacts.

2. Material and methods

2.1. Study sites, experimental design and set-up

The study was conducted at two nearby beaches: América (AM) and Abra (AB) beaches, which are typical of exposed sandy beaches on the NW coast of Spain. Both beaches are influenced by a mesotidal regime with a medium tidal range of ~3.5 m. AM beach (42° 7' 53" N, 8° 49' 83" W), which is about 1280 m long and 103 m wide (low spring tide), is located in an urbanized area that receives large numbers of tourists during weekends and summer. The beach has a well-developed seafront promenade, and a dune habitat rehabilitation project was initiated in 2005 in some areas between the promenade and the beach. The abundance of macroinvertebrates on AM beach is generally low, and supratidal macrofauna is rarely found (De la Huz and others 2005). AM beach is subjected to frequent mechanical grooming (i.e. daily during summer and holidays and occasionally during the rest of the year) to remove accumulations of detritus from the ocean, including wrack (pers. obs). AB beach (42° 9' 11" N, 8° 49' 49" W), which is about 225 m long and 40 m wide, is located in an urbanized area, but is relatively isolated from visitors. The dune habitat is non-existent and the space is occupied by old houses and a seawall. Invertebrates, such as amphipods, are abundant on the beach (pers. obs.). Mechanical grooming to remove debris is not currently carried out on the beach (pers. obs.).

Despite the difference in the dimensions, these two neighboring beaches are exposed to similar oceanographic conditions and receive similar deposits of algal wrack species (Barreiro and others 2011). Thus, wrack is naturally very abundant, diverse and variable on both beaches (supplementary material Figure S1), with patches mainly composed of brown algae spread through the beach shore (Barreiro and others 2011, 2013). Three days before the start of the experiment, entire fresh portions of four of the most abundant brown

macroalgal species found on this coastline (Olabarria and others 2009; Barreiro and others 2011, 2013) were collected. Two native species *Saccorhiza polyschides* (Lightfoot) Batters, 1902 (hereafter Sp) and *Cystoseira baccata* (S. G. Gmelin) P. C. Silva, 1952 (Cb), and two non-native species *Sargassum muticum* (Yendo) Fensholt, 1955 (Sm) and *Undaria pinnatifida* (Harvey) Suringar, 1873 (Up) were collected by hand from nearby rocky areas, transported to the laboratory, separated into patches of similar weight (1.0 ± 0.1 kg wet weight) and stored in bags while the decomposition process began. We used a standardized, manageable quantity of wrack that was sufficient to trigger both microbial degradation of the wrack and the macrofaunal colonization processes (Olabarria and others 2007; Rodil and others 2015a,b). We included non-native species because they are increasingly abundant on shores around the world, with important ecological and economic effects on coastal systems (e.g. Rodil and others 2008; Williams and Smith 2007; Suárez-Jiménez and others 2017).

The experiment began on 13 March 2015 (time 0) and lasted for 12 days, i.e. a sufficient length of time for the wrack degradation and community colonization process to occur (Olabarria and others 2007; Rodil and others 2008; Lavery and others 2013). Experimental patches of each algal species ($n = 4$) were placed in previously dug (10 cm depth), square holes (0.25 m^2) and were covered with a fine layer of sand (1-2 cm). The spacing between each patch was 2 m apart, and the location was determined by random distribution. On days 3, 6, and 12, four randomly chosen replicate patches were sampled on each beach. Thus, a total of forty-eight patches of wrack were placed on each beach at the highest mark of the drift line parallel to the shoreline (i.e. 4 algal species x 3 days x 4 replicates). Procedural sand controls (PC, $n = 4$), in which the sediment was disturbed but no wrack was added, were established. Wrack degradation, which rapidly affects sedimentary traits, nutrient recycling and community structure of beaches, is dependent on

the algal species (Lavery and others 2013; Rodil and others 2015a,b). On day 12, all wrack patches left on AB were washed away due to an extremely high spring tide (augmented by a solar eclipse and a *perigee* full moon).

2.2. Sediment and nutrient analyses

Sediment samples were randomly collected from underneath each wrack patch to measure sedimentary water content, organic matter and nutrient contents. The water content (%) of sediment samples (~80 g) was calculated as the difference between the initial wet weight and the final dry weight (60°C, 24 h). Total organic matter (OM, %) was measured as the difference in the weight of sediment (~ 50 g) before and after ignition (500 °C, 4 h). The inorganic dissolved nutrients in sediments (± 20 g) were filtered (2-4 μ m filter paper) to remove any particulate material and stored at -30°C . The nutrients were quantified by continuous flow analysis (CFA) in Auto-Analyzer (Bran Luebbe AA3). The Berthelot reaction was used to determine the ammonium concentration (NH_4^+) (absorbance at 660 nm); nitrites (NO_2^-) were determined by the sulphonylamide and N-1-naphthylethylenediamine dihydrochloride reaction (550 nm); nitrates (NO_3^-) were converted to NO_2^- and measured as above. Phosphates (PO_4^{3-}) were determined by the ammonium molybdate and ascorbic acid reaction (880 nm).

2.3. Wrack metabolic activity

Estimates of CO_2 effluxes ($\mu\text{moles m}^{-2} \text{ day}^{-1}$) were measured *in situ* in the middle of each wrack patch using a portable soil respiration gas analyzer (WEST Systems fluxmeter®). This device, which includes a metallic cylindrical respiration chamber (cover area 500 cm^2), allows measurement of fluxes in 2-3 minutes based on the rate of accumulation of CO_2 within the chamber. On days 0 (4 random replicates of freshly allocated algae), 3, 6 and 12 of the study, the chamber was inserted (approx. 2cm) into the

wrack deposit in each corresponding experimental patch by applying gentle pressure to the top of the chamber. Wrack temperature was simultaneously measured with an alcohol thermometer ($^{\circ}\text{C}$). The fluxes were always measured between 10:00 and 12:00 (solar time), because mid-day values of CO_2 efflux have been shown to be representative of daily averages (Xu and Qi, 2001). Immediately after the measurements, we excised the wrack area below the flux chamber (i.e. 500 cm^2) with a cutter. The excised portions were placed in plastic bags, transported to the laboratory and frozen (-20°C). All the macrofauna associated with the excised wrack portions were separated and preserved in ethanol (70%) for later identification. All the excised wrack portions were dried (60°C , 48 h) and weighed (g) to estimate the change in wrack biomass over time.

2.4. Wrack-associated bacterial community structure

Sediment samples were randomly collected to evaluate bacterial communities by Automated-rRNA Intergenic Spacer Analysis (ARISA). This technique exploits the variability in the length of the intergenic spacer (IGS) between the small (16S) and large (23S) subunit rRNA genes in the *rrn* operon (Ranjard and others 2001). The DNA was amplified using ITSf (5'-GTCGTAACAAGGTAGCCGTA-3') and ITSReub (5'-GCCAAGGCATCCACC-3') primer sets (Cardinale and others 2004), to amplify the ITS1 region in the rRNA. Total DNA was extracted from 1.0 g wet weight of homogenized subsamples by using the Power Soil Extraction Kit (Mo Bio Laboratories, Inc). PCRs were performed in triplicate 25 μL volumes containing between 5 and 50 ng of DNA, 400 mM of both primers, 0.3 mM dNTPs, 3 x Taq PCR buffer, 2.5 U Taq DNA polymerase, 2.5 mM MgSO_4 and 1 mg mL^{-1} serum albumin (BSA). A standardized amount of the product was diluted 1:5 and mixed with 0.5 μL of ROX-labelled genotyping internal size standard (ROX 1000, Applied Biosystems). The sample fragments were analyzed in a genetic analyzer (ABI3730 XL).

ARISA fragment lengths were analyzed using Peak Scanner Software (Applied Biosystems). Fragments that differed by less or equal to 2 base pair (bp) were considered identical, and fragments with Fluorescence Units below 50 were considered “background noise”. Fragments > 200 bp were considered too short ITS for bacteria and removed. The bacterial richness was estimated as the total number of unique operational technical units (OTUs) identified within each electropherogram (see supplementary material, Figs. S2-S3), where the number of peaks represented the species number (phylotype/genotype richness), and the peak height (fluorescence units) represented the relative abundance of each bacterial species. The Shannon–Wiener diversity index, which considers the number of species present and their relative importance within the assemblage, was calculated using the PRIMER S/W (Clarke and Gorley, 2006).

2.5. Wrack-associated macrofauna community

Samples of macrofauna were collected under each experimental patch with a 10-cm diameter corer ($n = 3$), penetrating 20 cm deep into the substratum. The samples were enclosed in individually labelled plastic bags, before being transported to the laboratory. The individuals were sorted, identified and counted to the lowest possible taxonomic level. Macroinfauna collected from the sediment and all the macrofauna associated with the excised wrack portions (see section 2.3.) were pooled to obtain total abundance (i.e. counts) and the number of taxa per experimental patch, and used as the main benthic community descriptors.

2.6. Statistical analysis

Changes in wrack temperature, biomass and metabolic activity (i.e. CO_2), and changes in sediment water content, organic matter and inorganic nutrient concentrations were analyzed using 3-way ANOVA models. A Type II Sum of Squares ANOVA

(Langsrud, 2003) was used to deal with unbalanced data (i.e. missing data from AB day 12). Beach (AM and AB), patch (Sp, Up, Cb, Sm, PC), and time (t3, t6, and t12 days, or t0, t3, t6 and t12 days for CO₂) were considered orthogonal fixed factors. Changes in bacterial richness (OTUs) were analyzed using the same models. The normality (Shapiro test) and the variance (Levene's test) of the residuals were evaluated, and Box-Cox power transformations were performed when necessary. Three factor non-parametric multivariate analysis of variance (PERMANOVA, PRIMER S/W) was used to examine differences between bacterial assemblages (Anderson and others 2008). The data were normalized by presence/absence before being analyzed using a Bray-Curtis resemblance matrix (4999 permutations). Significant effects identified were further investigated by pairwise comparisons. Non-metric multidimensional scaling (nMDS, PRIMER S/W) was used to visualize multivariate patterns in bacterial assemblages. Changes in macrofauna were analyzed by use of generalized linear models (G_zLM), due to the large number of zero values. *A posteriori* comparisons were performed using the least squares means (lsmeans) package (Lenth 2016) and Tukey's adjustment.

We used G_zLM to examine the relationships between the main benthic community descriptors (i.e. bacterial diversity, OTUs and macrofauna abundance) and the biomass, metabolic activity and nutrient release from the wrack. We included the same categorical factors as above and the main benthic community descriptors (as co-variables) as the predictor variables, and considered wrack biomass (i.e. dry weight), metabolic activity (i.e. CO₂) and sedimentary traits (i.e. water content, organic matter and inorganic nutrients) response variables. We first fitted maximal models using all the factors and descriptors (variance inflation factor < 2) to check for interactions between factors and continuous predictors. We simplified the models by removing non-significant interaction terms and non-significant explanatory variables. The Akaike's

Information Criterion (AIC) and the proportional increase in explained deviance (pseudo- R^2) were used to evaluate each model fit. *A posteriori* comparisons were performed by reassigning the “Intercept” term sequentially and using lsmeans. The following model assumptions were checked: (i) homogeneity, by examining plots of residuals against fitted values; (ii) normality, by examining quantile-quantile plots or histograms of the residuals; and (iii) data independence, by examining plots of residuals against each explanatory variable. All statistical analyses were performed with R software (R Development Core Team, 2016).

3. Results

3.1. Ambient conditions within experimental wrack patches

Wrack biomass decreased over time ($t_3 > t_6 > t_{12}$; $p < 0.001$), with significant ($p < 0.001$) differences between algal species ($Sm = Cb > Sp = Up$) (Figure 1a-b, Table S1). Wrack temperature varied significantly over time on AM beach ($t_3 < t_6 > t_{12}$), and it was higher ($p < 0.001$) in patches on AB than on AM (Figure 1c, Table S1). The sedimentary organic matter content was higher ($p < 0.001$) in patches of Up at t_{12} than in the patches of the other wrack species (Figure 1d, Table S1). Water sediment differed ($p < 0.001$) between beaches (AM > AB) and between patches (Up > Sp = Sm > Cb > Sand) (Figure 1e-f, Table S1).

3.2. Nutrient analysis of the sediments under patches

The concentrations of inorganic dissolved nutrients, i.e. NO_2^- , NO_3^- , NH_4^+ , and PO_4^{3-} , varied between patches, and patterns differed between beaches and over time (Figure 2, Figure 3, Table S2). Thus, the concentration of NO_2^- under Sp was higher ($p < 0.001$) than under any other patch, except for Up on AB (Figure 2a). The NO_2^- concentration increased significantly ($p < 0.001$) over time, only in the Sp patch ($t_3 < t_6 = t_{12}$; Figure

3a). The NO_3^- concentration differed significantly ($p < 0.001$) between patches on AM beach ($\text{Sp} > \text{Up} = \text{Cb} = \text{Sm} > \text{Sand}$) and on AB beach ($\text{Sp} = \text{Up} > \text{Cb} = \text{Sm} > \text{Sand}$) (Figure 2b). The concentration of NO_3^- under Sp increased significantly ($p < 0.001$) over time ($t3 < t6 = t12$) (Figure 3b). The concentration of NH_4^+ differed significantly ($p < 0.05$) between wrack and the bare sand (control) on AM beach (Figure 2c) and at t12 (Figure 3c). No significant differences in NH_4^+ concentrations were found on AB (Figure 2c). The concentration of PO_4^{3-} was significantly higher ($p < 0.001$) in the Up patches than in other patches on AM and AB (Figure 2d) on all sampling dates (Figure 3d). The concentration of PO_4^{3-} in the Sp and Sm patches on AM and in the Cb patches on AB were significantly higher than in the bare sand (Figure 2d). The concentration of PO_4^{3-} increased significantly ($p < 0.001$) over time in both the Sp ($t3 < t6 = t12$) and Sm ($t3 = t6 < t12$) patches (Figure 3d).

3.3. Wrack metabolic activity

The experimental wrack patches supported high metabolic activities, as reflected by the accumulated CO_2 fluxes: (mean $\pm$ SE) 3.5 ± 0.4 on AM and 4.2 ± 0.6 on AB ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), compared to the mean value of $0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the bare sand control (Table 1). The first wrack metabolic measurements ($t0$) already showed a significant response relative to bare sand (Figure 4, Table 2). The metabolic rates varied significantly ($p < 0.001$) between patches, between beaches and over time (i.e. triple interaction, $F_{8,105} = 4.8$) (Table S2). Thus, the metabolic activity in Sp was very high and increased significantly ($p < 0.001$) over time on AM and AB, although it was significantly lower ($p < 0.001$) at t12 in the Sp patch on AM (Figure 4, Table 2). The metabolic activity was higher in Up than in the other types of wrack (see t3 for both beaches) between patches ($p < 0.001$) and over time (Figure 4) on AM and AB (Table

2). The metabolic activity was lower in the Cb patches than in the other patches at all times (Figure 4). The metabolic rate in Cb patches on both beaches increased significantly ($p < 0.001$) after six days (Figure 4, Table 2). The metabolic rate in the Sm patches increased significantly ($p < 0.001$) after 12 days on AM and after 6 days on AB (Figure 4). The only significant difference ($p < 0.01$) between beaches in relation to the metabolic activity (AM < AB) was observed for Sm (AM: $0.528 \pm 0.066 \mu\text{moles m}^{-2} \text{s}^{-1}$ and AB: $1.467 \pm 0.229 \mu\text{moles m}^{-2} \text{s}^{-1}$; mean $\pm$ SE) at t3 (Figure 4, Table S3).

3.4. Wrack-associated communities: bacterial and macrofaunal characterization

Bacterial relative abundance and richness ranged respectively from 862 to 298 150 fluorescence units (peak heights) and from 11 to 268 OTUs (Figures S2-S3). The presence of wrack increased the richness ($F_{4,75} = 2.6$; $p < 0.05$) of bacteria relative to the bare sand. OTUs richness increased over time at AM (t3 < t6, t3 < t12; $p < 0.01$ and t12 < t6; $p < 0.05$) and AB (t3 < t6; $p < 0.001$) (Figure 5a, Table S4). The similarity in the wrack-associated bacterial assemblages between beaches was low, but significant (33.4%, $t = 4.2$; $p < 0.001$). The assemblages varied significantly between patches, between beaches and over time (pseudo- $F_{1,75} = 4.8$; $p < 0.001$). Thus, Sp and Up showed the lowest similarities on AM, and Sm showed the lowest similarities to the other patches on AB (Figure 6, Table S5). The bacterial assemblages within patches of the same wrack species showed lower similarity on AM than at AB over time (Table S5, Figure 6).

A total of 1,969 macroinvertebrates from 9 taxa were identified (Table S6). The number of taxa (AM: t3 = t6 < t12, AB: t6 < t12) and abundance (t3 = t6 < t12) associated with wrack increased significantly ($p < 0.001$) over time (Table S4). However, the number of taxa was significantly larger ($p < 0.001$) on AB than on AM (Figure 5b). Abundance differed significantly between wrack patches on AB (Table S4,

Figure 5c). Most organisms sampled on AM were dipteran larvae belonging to the Anthomyiidae family ($p < 0.001$), and most specimens from AB were amphipods (Talitridae family) ($p < 0.001$). The abundance of Anthomyiidae differed significantly ($p < 0.001$) between patches on AM (Sp = Cb > Up = Sm) and AB (Cb > Sp > Up = Sm) (Figure 5d), and it increased ($p < 0.001$) over time (t3 = t6 < t12). The abundance of Talitridae differed significantly between patches, but only on AB (Cb = Sm > Sp = Up = Sand; $p < 0.001$) (Figure 5e).

3.5. Relationships between wrack-related variables and community descriptors

Bacterial richness (OTUs) was significantly ($p < 0.01$) and negatively (Estimate = -0.003, $t = -2.9$; pseudo- $R^2 = 59.1$) related to wrack biomass ($F_{1,74} = 8.85$; $p < 0.01$) (Figure 7a). Bacterial diversity (Shannon-Wiener index) was significantly ($p < 0.05$) and positively (Estimate = 0.22, $t = 3.3$; pseudo- $R^2 = 24.1$) related to the sedimentary dissolved inorganic nitrogen (i.e. DIN = $\text{NO}_2^- + \text{NO}_3^- + \text{NH}_4^+$) under the wrack patches ($F_{1,73} = 11.2$; $p = 0.0013$) (Figure 7b).

Macrofaunal abundance was significantly and positively related to both organic matter ($F_{1,97} = 4.9$; $p < 0.05$) and NH_4^+ ($F_{1,99} = 7.3$; $p < 0.01$) concentrations in the sediment (Figure 7c-d). However, these relationships depended on the wrack species considered (i.e. wrack: abundance interaction, Table 3). Thus, the macrofauna-OM relationship ($F_{4,90} = 3.2$; $p < 0.05$) was stronger in Up than in the other types of wrack patches (Figure 7c, Table 3). The macrofauna- NH_4^+ relationship ($F_{4,88} = 6.5$; $p < 0.001$) was also stronger in Up than in the Cb and Sp patches (Figure 7d, Table 3).

4. Discussion

The role of beaches as metabolic hotspots and that of wrack as a source of CO_2 are poorly studied topics (Coupland and others 2007). Here we demonstrate the active

metabolic role of beach wrack and how different algal species support different wrack respiration rates.

4.1. Wrack degradation and metabolic activity

The biomass of all algae decreased rapidly throughout the study period, following a typical wrack decomposition pattern (e.g. Olabarria and others 2007; Rodil and others 2008). However, the algal biomass differed after 12 days, indicating a species-specific mass loss. Thus, the weight loss was greater in *S. polyschides* and *U. pinnatifida* patches than in *S. muticum* and *C. baccata* patches. Our results also showed that beach wrack was metabolically very active, and supported intense CO₂ fluxes, thus confirming the findings of a previous study also conducted on beach-cast metabolic rates (Coupland and others 2007). Thus, wrack supported higher respiration rates than bare sediments, with some patches showing higher rates than reported for other wrack species (Coupland and others 2007). Our findings indicate that beach wrack deposits act as metabolic hotspots, as observed in other major ecosystems around the world, including land communities, such as tropical rain forests, and seafloor communities, such as seagrass meadows (see Coupland and others 2007 for explicit comparisons). In contrast to the latter study, we show that wrack differing in species composition had different metabolic rates, indicating a differential species-specific metabolic activity. For instance, metabolically reactive *S. polyschides* and *U. pinnatifida* are structurally simple algal species with long, labile strap-like blades that stack up in layers on the sand and that degrade rapidly and become readily available for consumption. *S. muticum* and *C. baccata* are morphologically more complex algae with resistant leathery branches bearing secondary branches that slow down their degradation, so that they remain for longer on the beach. Some marine vegetation, such as seagrass, with large and robust structures and known to be resistant to degradation, contain refractory organic matter components that are resistant to degradation and microbial attack

(Trevathan-Tackett and others 2017). Similarly, wrack structure (shape and toughness) is important in relation to algal-specific biochemical composition (nutrients and phenols) and variable surface:volume ratio in the sediment (e.g. Duggins and Eckman 1997; Bucholtz and others 2014).

4.2. Effects of wrack patches on sedimentary nutrients and community structure

High levels of sedimentary nutrients associated with the remineralization of wrack were recorded, suggesting rapid leaching from the wrack (Dugan and others 2011). Nutrient variability in the beach sediments is often related to different types of accumulations found on the shore (Dugan and others 2011; Barreiro and others 2013). For instance, structurally simple algae with the potential to store large quantities of nutrients can cause rapid leaching of nutrient compounds during decay (Hanisak 1993; Barreiro and others 2013). Thus, *U. pinnatifida* provided the greatest amounts of organic matter, probably due to the rapid decay. Similarly, the greatest contributions of nitrate and nitrite (i.e. NO_x^- -N) were associated with *S. polyschides* and *U. pinnatifida*. High levels of NO_x^- -N suggest rapid nitrification of the NH_4^+ derived from remineralized wrack (Dugan and others 2011). Release of large amounts of PO_4^{3-} was also associated with *U. pinnatifida*. The rapid release of inorganic nutrients during algal mineralization is ecologically relevant because these compounds represent a main source of nutrients for microbes and macrofauna (Malm and others 2004; Ince and others 2007).

The decomposition of wrack and the consequent leaching of the organic matter into the underlying sediment require the joint action of microbial decomposers and detritivores (Koop and Griffiths 1982; Inglis 1989; Dugan and others 2003, 2011). For instance, the dissolved inorganic nitrogen (DIN) stored in the sediments beneath wrack may be associated with degradation and consumption of the wrack by respectively bacteria and macrofauna (Orr and others 2005). Thus, the strong positive relationship between DIN and

bacteria in the experimental wrack patches supports the role of bacteria as key decomposers of wrack (Koop and others 1982; García-Robledo and others 2008; Sosik and Simenstad 2013). In our study, large numbers of bacteria rapidly colonized the wrack, and bacterial assemblages varied significantly, possibly due to the specificity of bacteria associated with different algae (Barott and others 2011). The activity of bacterial strains consisting of several genera with diverse capacities poses an advantage in the presence of different wrack. Thus, the relationship between DIN and bacteria observed in the patches may reflect aerobic respiration by autotrophic bacteria (García-Robledo and others 2008). The rapid rate of degradation and greater nutrient releases from *S. polyschides* and *U. pinnatifida*, together with significant DIN-bacteria relationships, indicates the need for studies with higher sampling frequency (i.e. daily or even hourly). This type of studies would provide more accurate information on nutrient release and a more detailed response of the benthic community to the wrack biomass.

The beach macrofauna community is capable of quickly processing detritus and linking oceanic productivity to upper-trophic consumers (Dugan and others 2003). For instance, the organic matter and NH_4^+ concentrations under *U. pinnatifida* were significantly and positive related to the presence of macrofauna. This macroalgal species degrades quickly and is very rich in nutrients that are readily available to consumers and essential for various metabolic functions (Sánchez-Machado and others 2004; Park and others 2012). The beaches under study showed contrasting community structure and colonization patterns related to the beach life-history that affected the potential relationships between wrack biochemical composition and associated consumers. Thus, on AM the typical macrofauna were only found at the end of the experiment, and even then, the associated macrofauna assemblage was dominated by dipteran larvae. Conversely, typical wrack-associated talitrids were only present on AB, facilitating degradation of the wrack and

consequently the beach nutrient cycling. Talitrids were most abundant in the *S. muticum* and *C. baccata* patches on AB. This is probably related to the potential benefits provided by the structurally complex macroalgae (long-lasting refuge from predation and environmental stress) as an alternative habitat for the fauna (e.g. Cowles and others 2009).

AM beach is subjected to regular mechanical grooming that removes wrack and modifies the community, while no cleaning activities are carried out at AB. Beach grooming is known to modify the role of the beach microbial community through changes in bacterial production in the underlying sand and in the associated surf zone that can affect the microbial food-web and even the water quality (Malm and others 2004; Russell and others 2014). Removing wrack from beaches potentially alters local benthic communities (Dugan and others 2003). The lack of talitrids on AM, combined with regular and intense beach grooming, may have created a situation where the presence of wrack triggered the oviposition of dipteran larvae, leading to an increase in the presence of flies. This represents an important change in the beach community scenario from a typical beach fauna to a terrestrial community type.

4.3. Ecological implications

The role of detrital subsidies on sandy beach communities can be affected in a future scenario of global change. For instance, climate change may alter the amount and identity of the macroalgae growing offshore affecting how much, and the kind of wrack, is deposited on intertidal shores worldwide (e.g. Bishop and others 2010; Byrnes and others 2011; Krunhshal and Scheibling 2012; Rodil and others 2015a). As global climate change factors increase wrack production (Smetacek and Zingone 2013) and introduced algae spread worldwide (Williams and Smith 2007), unwanted piles of wrack will be cast ashore thus affecting coastal goods and services and challenging the coastal functioning. For instance, *U. pinnatifida* and *S. muticum* are highly invasive and colonize coastal areas

worldwide, thus potentially influencing benthic communities and food-webs on coastal shores (e.g. Rodil and others 2008; Suárez-Jiménez and others 2017). In some areas of the world, the increasing development of massive *Sargassum* spp. shore-accumulations (i.e. golden tides) is known to affect tourism-based economies (Smetacek and Zingone, 2013). However, moderate accumulations of specific species of wrack, including non-native species, may have a positive role on beach communities as trophic deposits (Olabarria and others 2009; Quijón and others 2017; Suárez-Jiménez and others 2017). Here, we show that wrack can represent an important source of beach metabolic activity, depending on the type of wrack that accumulates on the beach. Consequently, large wrack accumulations of specific algal species can promote high emissions of CO₂ (Coupland and others 2007; the present study), potentially affecting the functioning of land-sea interfaces. For instance, the high carbon-to-nitrogen ratio (50:1) of *Sargassum* spp. makes this alga a very efficient vehicle for sequestering carbon in the oceans (Smetacek and Zingone 2013). *U. pinnatifida* can also contribute to increasing the carbon export to nearby ecosystems and can alter the biomass export regime as it spreads across shallow coastal habitats (Tait and others 2015). Therefore, increasing accumulations of wrack emitting CO₂ into the atmosphere from intertidal shores can affect the role of macroalgae in marine carbon sequestration (Krause-Jensen and Duarte 2016). The potential influence of beach wrack in the global carbon balance, mainly during seasonal peaks in accumulation, has not generally been considered and deserves further detailed study. The capacity of beaches as metabolic hotspots and wrack as a source of CO₂ adds further value to the many ecological services provided by beach systems. Significant modifications in the quality (non-indigenous species) and quantity (beach grooming/seaweed tides) of beach wrack may change fundamental processes related to the marine-terrestrial transfer of nutrients and energy, and to the marine-atmospheric transfer of greenhouse gas emissions.

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661 **Table 1.** Summary showing the mean $\pm$ standard error of the metabolic activity ($\mu\text{mol CO}_2 \mu\text{m}^{-2} \text{s}^{-1}$) of all the wrack species (^awrack patches averaged
662 over time) and per sampling day (^btime averaged for all the wrack species) from the two study beaches (AM: América and AB: Abra). We also show
663 maximum and minimum values, and the cumulative sum of the CO₂ flux per sampling time (12 days for AM, 6 days for AB) and wrack species.

Beach	Wrack species ^a	Mean $\pm$ SE	Maximum	Minimum	Cumulative	Time ^b	Mean $\pm$ SE	Maximum	Minimum
AM	<i>S. polyschides</i>	3.4 $\pm$ 0.6	8.98	0.71	13.8	time 0	0.9 $\pm$ 0.1	1.65	0.04
	<i>U. pinnatifida</i>	6.5 $\pm$ 0.9	11.2	1.33	25.8	time 3	2.6 $\pm$ 0.7	9.94	0.04
	<i>C. baccata</i>	1.4 $\pm$ 0.2	2.26	0.51	5.5	time 6	4.2 $\pm$ 0.9	11.2	0.07
	<i>S. muticum</i>	2.7 $\pm$ 0.6	8.01	0.36	10.8	time 12	3.6 $\pm$ 0.6	8.01	0.07
	Sand control	0.07 $\pm$ 0.02	0.11	0.04	0.3				
AB	<i>S. polyschides</i>	4.7 $\pm$ 0.9	8.07	0.60	14.2	time 0	1.0 $\pm$ 0.13	1.90	0.10
	<i>U. pinnatifida</i>	8.3 $\pm$ 1.5	14.9	1.50	24.9	time 3	3.95 $\pm$ 0.9	12.0	0.10
	<i>C. baccata</i>	1.5 $\pm$ 0.2	2.40	0.80	4.5	time 6	5.1 $\pm$ 1.0	14.9	0.10
	<i>S. muticum</i>	2.1 $\pm$ 0.3	3.90	0.90	6.4	time 12	-	-	-
	Sand control	0.09 $\pm$ 0.03	0.13	0.05	0.3				

Table 2. *A posteriori* comparisons (posthoc tests, lsmeans) on the effects of wrack patches, beach (AM: América, AB: Abra) and time (0, 3, 6 and 12 days) on wrack metabolic activity (CO₂: $\mu\text{moles m}^{-2} \text{ day}^{-1}$) after a 3-way ANOVA analysis (see supplementary material Table S2).

Wrack patch	Beach	posthoc tests ($p < 0.001$)
<i>S. polyschides</i> (Sp)	AM	$t_6 > t_{12} = t_3 > t_0$
	AB	$t_0 < t_3 < t_6$
<i>U. pinnatifida</i> (Up)	AM	$t_0 < t_3 = t_6 = t_{12}$
	AB	$t_0 < t_3 = t_6$
<i>C. baccata</i> (Cb)	AM	$t_0 = t_3 < t_6 = t_{12}$
	AB	$t_6 > t_0 = t_3; t_3 = t_6$
<i>S. muticum</i> (Sm)	AM	$t_0 = t_3 = t_6 < t_{12}$
	AB	$t_0 = t_3 < t_6$
Sand control	AM	$t_0 = t_3 = t_6 = t_{12}$
	AB	
Time		
0	AM	$\text{Sand} < \text{Cb} < \text{Up} = \text{Sm}; \text{Cb} = \text{Sp}; \text{Up} = \text{Sm} = \text{Sp}$
	AB	
3	AM	$\text{Sand} < \text{Sm} = \text{Cb} < \text{Sp} < \text{Up}$
	AB	
6	AM	$\text{Sand} < \text{Sm} = \text{Cb} < \text{Sp} = \text{Up}$
	AB	
12	AM	$\text{Sand} < \text{Cb} = \text{Sp} < \text{Sm} = \text{Up}$

669 **Table 3.** Summary of the generalized linear models indicating the significance of macrofauna abundance on wrack-related response variables
670 (OM: organic matter (%), NH₄⁺: ammonium (μM)), including significant pair-wise contrasts between patches (Sp: *S. polyschides*, Up: *U.*
671 *pinnatifida*, Cb: *C. baccata*, Sm: *S. muticum*).

Regression-based models	Model summary (GzLM)						
	Coefficient	Estimate	t ^(p)	Contrasts	Estimate	t ^(p)	pseudo-R ²
OM ~ Patch:Abundance ^a	Cb:Abundance	0.001	0.67	Cb-Up	0.007	3.24**	29.2
	Sm:Abundance	0.0001	0.04	Sm-Up	0.007	2.5*	
	Sp: Abundance	0.001	0.69	Sp-Up	0.006	2.9*	
	Up: Abundance	0.01	4.35***				
NH ₄ ⁺ ~ Patch: Abundance ^a	Cb:Abundance	-0.22	-1.28	Cb-Up	1.5	4.8***	35.1
	Sm:Abundance	0.50	1.44	Sp-Up	1.1	3.3**	
	Sp: Abundance	0.20	0.80	Sm-Up	0.75	1.7 ⁺	
	Up: Abundance	1.30	4.9***	Cb-Sm	0.72	1.9 ⁺	

^aNegative binomial model distribution (log-link structure) to avoid overdispersion.

Proportional increase in explained deviance: pseudo-R².

Significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ⁺ $0.05 < p < 0.10$.

Figure captions

Figure 1. Mean (+SE) amount of (a) wrack biomass over time and (b) among algal species, (c) wrack temperature at the beaches over time, (d) sedimentary organic matter between patches and over time, (e) sedimentary water content at the beaches and (f) between wrack patches (time-accumulated). Beaches (América, AM, and Abra, AB), wrack (*S. polyschides* Sp, *U. pinnatifida* Up, *C. baccata* Cb, *S. muticum* Sm, and procedure sand control PC) and time (3, 6 and 12 days). Data are displayed per significant factors (non-significant factors are averaged, see Table S1).

Figure 2. Mean (+SE) amount of sedimentary NO_2^- , NO_3^- , NH_4^+ and PO_4^{3+} underneath the experimental wrack patches (*S. polyschides* Sp, *U. pinnatifida* Up, *C. baccata* Cb, *S. muticum* Sm, and procedure sand control PC) at the beaches (América, AM, and Abra, AB). Data are displayed per significant factors (see Table S2).

Figure 3. Mean (+SE) amount of sedimentary NO_2^- , NO_3^- , NH_4^+ and PO_4^{3+} underneath the experimental wrack patches (*S. polyschides* Sp, *U. pinnatifida* Up, *C. baccata* Cb, *S. muticum* Sm, and procedure sand control PC) over time (3, 6 and 12 days). Data are displayed per significant factors (see Table S2).

Figure 4. Mean ($\pm$ SE) wrack metabolic activity (i.e. CO_2) at the beaches (América and Abra) compared between wrack patches (*S. polyschides* Sp, *U. pinnatifida* Up, *C. baccata* Cb, *S. muticum* Sm, and procedure sand control PC) over time (0, 3, 6 and 12 days). Data are displayed per significant factors (see Table 2 and Table S2).

Figure 5. Mean (+SE) wrack-associated (a) bacterial richness (operational technical units), and (b) macrofauna taxa at the beaches over time, (c) total macrofauna abundance (counts), (d) Anthomyiidae abundance at the beaches (AM and AB) and (e) talitridae abundance between wrack patches (AB beach). Beaches (América, AM, and Abra, AB), wrack (*S. polyschides* Sp, *U. pinnatifida* Up, *C. baccata* Cb, *S. muticum* Sm, and procedure

sand control) and time (3, 6 and 12 days). Data are displayed per significant factors (non-significant factor are averaged, see Table S4).

Figure 6. Non-metric multidimensional scaling (nMDS) for differences in bacterial assemblages between beaches (América, AM, and Abra, AB), wrack (*S. polyschides* Sp, *U. pinnatifida* Up, *C. baccata* Cb, *S. muticum* Sm, and procedure sand control, PC), and over time (3, 6 and 12 days).

Figure 7. Responses of the (a) wrack biomass (dry weight) to bacterial richness (OTUs), (b) sedimentary total dissolved inorganic nitrogen concentration (DIN) to bacterial diversity (Shannon-diversity), and responses of the sedimentary (c) organic matter and (d) ammonium (NH_4^+) concentration to macrofauna abundance. Wrack patches: *S. polyschides*, Sp; *U. pinnatifida*, Up; *C. baccata*, Cb; *S. muticum*, Sm.

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