Annual cycle of wrack supply to sandy beaches: effect of the physical environment

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ABSTRACT: Connectivity between ecosystems has been widely recognised as an important issue in ecological studies. Sandy beaches are very dynamic and open ecosystems, mainly supported by allochthonous subsidies of stranded organic matter (mostly macroalgae), also termed wrack supply. The magnitude and composition of algal wrack biomass throughout the annual cycle was assessed for 6 sandy beaches on the Galician coast, NW Spain. The effect of wave action and the topographical features of each beach in the wrack deposition process were investigated. Wrack species composition, biomass and coverage were measured monthly along 6 transects at each beach. Mean dry weight of wrack fluctuated from 14 ± 5.3 to 9189 ± 3594 g m^{-1} (along transects) between locations. Wrack was predominantly composed of brown algae, which accounted for 70% of the average biomass year round; the dominant species were *Cystoseira* sp. ($30.3 \pm 17.4\%$) and *Sargassum muticum* ($14.2 \pm 7.1\%$). A cyclical pattern in wrack composition, coupled with the life cycle of the predominant macroalgae, was observed. Wrack biomass and species composition were mostly explained by wave height and the ratio of beach length to beach area. Small, wave-sheltered beaches received the largest inputs of wrack, and had the lowest relative contribution of brown algae. These results provide evidence that variability in wrack supply on sandy beaches can be explained through interactions between wave exposure, coastal topography and seasonality.

KEY WORDS: Connectivity · Marine–terrestrial ecotone · NW Spain · Sandy beaches · Spatial subsidy · Wave exposure · Wrack

INTRODUCTION

Studies focusing on the linkages between habitats have increased in the last few decades, revealing the importance of ecotone zones and connectivity in the analysis of ecosystem functioning. These linkages involve the transfer of resources (e.g. nutrients, detritus and prey) from a 'donor habitat' to a 'recipient habitat' in a process termed 'spatial subsidy' (Polis et al. 1997). In this regard, several authors have shown how allochthonous subsidies of organic matter can greatly affect community structure, productivity and stability in a wide variety of marine and coastal ecosystems (e.g. Vetter 1994, Polis & Hurd 1996, Anderson & Polis 2004, Wernberg et al. 2006, Coupland & McDonald 2008, Crawley et al. 2009, Spiller et al. 2010).

The ocean–land interface occupies approx. 8% of the earth's surface (Ray & Hayden 1992). Primary production across the coastal ecotone is variable, ranging from 0 to ca. 3500 g m^{-2} yr^{-1} dry mass (Polis et al. 2004). Among the several classes of organic matter that have been linked to productivity in coastal environments, 2 are of paramount importance: macroalgae on rocky shores, and seagrasses in sheltered estuarine areas. Values from approx. 300 to 1900 g C m^{-2} yr^{-1} have been reported in kelp forest in different geographical areas (Mann 1973, Kirkman 1984, Foster & Schiel 1985). The productivity of seagrasses is comparable, reaching 1500 g C m^{-2} yr^{-1} (Mateo et al. 2006). Duarte & Cebrian (1996) estimated that, after being fragmented or detached, macroalgae and seagrasses export approx. 43 and

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24%, respectively, of the net primary production to neighbouring ecosystems.

Sandy beaches form a dynamic interface between marine and terrestrial ecosystems. Primary production on wave-exposed beaches is low, with values ranging from approx. 0 to 10 g C m^{-2} yr^{-1} (McLachlan & Brown 2006). Allochthonous subsidies support most of the beach food web (Griffiths et al. 1983, McLachlan & Brown 2006), also serving as habitat and refuge for the macrofaunal community (Ince et al. 2007). The amount of allochthonous subsidies on any beach firstly depends first on the production of the adjacent habitats. In many coastal regions, beaches near areas with high production of macroalgae and/or seagrasses receive extensive wrack inputs (e.g. Stenton-Dozey & Griffiths 1983, Hobday 2000, Mateo 2010). Parameters based on the edge-to-interior ratio are commonly used to evaluate habitat openness to such input (Polis & Hurd 1996). Fluxes between ecosystems are assumed to increase at higher edge-to-interior surface ratio because the higher this ratio is, the more edge is exposed to the donor ecosystem (Witman et al. 2004). However, fluxes between ecosystems depend on the permeability of the boundaries (Cadenasso & Pickett 2000, Witman et al. 2004), which, in the case of wrack supply to sandy beaches, means complex interactions among physical factors such as waves, currents, winds, coastal topography, etc. (Polis et al. 2004). Witman et al. (2004) concluded that, at decreasing flow velocities, deposition should be favoured.

Species composition and biomass of wrack inputs vary both spatially and temporally (e.g. Stenton-Dozey & Griffiths 1983, Marsden 1991, Dugan et al. 2003, Orr et al. 2005). Following deposition on the beach as wrack, drift materials are subjected to a variety of processes, including *in situ* consumption by beach herbivores, microbial degradation, desiccation and export by tides and currents (Griffiths & Stenton-Dozey 1981, Griffiths et al. 1983, Inglis 1989, Jędrzejczak 2002, Orr et al. 2005, Mews et al. 2006). These processes are dependent on the species composition of the wrack (Orr et al. 2005, Mews et al. 2006). For example, Orr et al. (2005) observed that the more buoyant species stranded on the beach were more likely to be resuspended during the following tide.

In order to understand the ecological implications of wrack subsidies, it is important to gauge both the magnitude and variability of the inputs at different spatio-temporal scales. The primary objective of this study, carried out on the coast of NW Spain, was therefore to evaluate changes of wrack supply on exposed sandy beaches over time and in space (i.e. from beach to beach). We hypothesized that (1) physical characteristics such as beach size, wave height and beach slope affect habitat permeability and thus the magnitude of

the inputs; and (2) time scales of variability in wrack supply depend on beach characteristics.

MATERIALS AND METHODS

Field sampling design. Six beaches on the NW coast of Spain (Fig. 1) were sampled monthly between December 2007 and November 2008: Balieiros (BA), Ladeira (LA), Samil (SA), Toralla (TO), Abra (PA) and America (AM). These beaches encompass an exposure range (McLachlan 1980) from very exposed to sheltered (Table 1). Tidal conditions were meso- macrotidal, with spring tides ranging from 3.5 to 4 m.

The following 6 environmental variables were recorded at each site: beach slope, estimated using Emery's profiling technique (Emery 1961); beach length; beach width, measured as the distance between the base of the dune and the lower swash level; wave height, estimated by measuring 30 breaking waves with gradu-
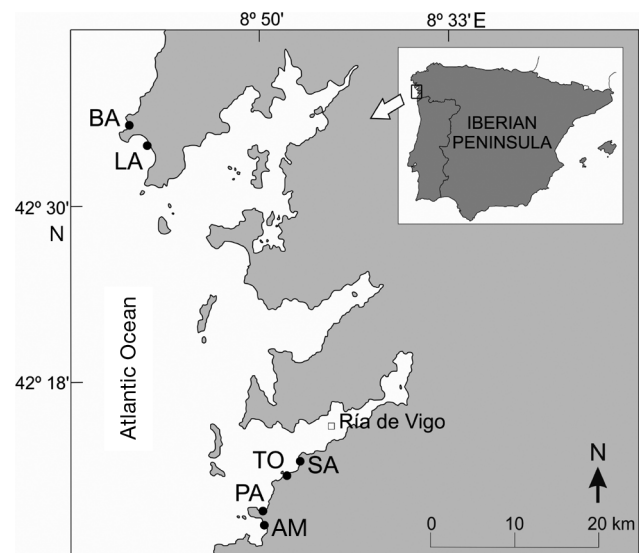

Fig. 1. Sampled beaches on the NW coast of the Iberian peninsula: America (AM), Abra (PA), Toralla (TO), Samil (SA), Ladeira (LA) and Balieiros (BA)

Table 1. Physical characteristics of studied beaches. Exposure index estimated according to the rating system of McLachlan (1980). See Fig. 1 for site abbreviations

Beach	Beach length (m)	Intertidal width (m)	1/slope	Exposure rate
PA	210	60	9.8	11 (exposed)
AM	2200	110	18.7	12 (exposed)
BA	840	100	10.9	18 (very exposed)
LA	5000	130	33.9	13 (exposed)
SA	1640	100	16.9	12 (exposed)
TO	100	60	13.8	10 (sheltered)

ated poles against the horizon; wave period, measured with a stop watch and calculated as the time interval between breakers; and beach area, calculated as the product of beach length and beach width.

Field sampling was carried out during low spring tides. Samples were collected from the base of the dune to the lowest swash level along 6 transects randomly spaced over a 100 m-long stretch in the centre of each beach. Coverage, specific composition and biomass of wrack were calculated along each transect. Coverage was measured using the line intercept method (Dugan et al. 2003). All wrack present on the sand surface within a 1 m wide strip of beach along each transect was collected to assess specific composition and biomass (Lastra et al. 2008).

Wrack species composition of wrack was determined to the lowest taxonomic level possible. Dry weight (wt) of each species was calculated after drying to a constant weight at 60°C. Due to the vast amounts of wrack stranded on PA and TO, 3 subsamples were taken from each transect at these sites to estimate the specific composition of the wrack.

Statistical analysis. *Beach characteristics and wrack deposition:* The relationship between beach characteristics and wrack composition based on biomass data was investigated using a non-parametric multiple-regression test, viz. distance-based multivariate analysis for linear model (DISTLM) (McArdle & Anderson 2001, Clarke & Gorley 2006). First, each environmental factor was analysed separately (ignoring any other factor) to evaluate the potential relationship between wrack composition and biomass (marginal test). Next, the abiotic factors were subjected to a best-selection procedure, where the amount of variability explained by each factor added to the model is conditional upon the factors previously included (sequential test). Both tests were based on the Bray-Curtis dissimilarity index. Data on the 6 transects at each location were averaged per month. The distance-based redundancy analysis (dbRDA) was used to represent the relationship between the multivariate data and the predictor variables. Differences in wrack composition among groups of beaches characterized according to the wave exposure and topographical factors in the dbRDA were tested with analysis of similarities (ANOSIM) (Clarke & Warwick 2001).

To analyse the specific composition of wrack on each beach, a non-metric multidimensional scaling (NMDS) was performed with the monthly relative biomass of each species per location. Prior to this, data were log-transformed to calculate the Bray-Curtis similarity index. Differences among groups of beaches were tested with ANOSIM. A similarity percentage (SIMPER) analysis was performed to find the species with the highest contribution to the similarity of each group.

Time-scale variability in wrack composition and biomass: The relative biomass of each wrack taxon per month was used to analyse the temporal variability of the wrack composition for all locations together, and for each beach individually. Data were log-transformed to calculate the Bray-Curtis similarity index. The cyclic-RELATE procedure (Clarke & Warwick 2001) was used to assess the monthly variation. This analysis computes the Spearman correlation between the corresponding pair of months in the similarity matrix; each pair of data points is then compared with a model of cyclicity. NMDS ordinations were performed to visualize the monthly relationship in wrack composition. A 2-way PERMANOVA was carried out with the relative biomass of each species; beach (6 levels) and month (12 levels) were fixed factors.

Temporal variability in total wrack biomass among beaches was calculated using a 2-way ANOVA, again with beach (6 levels) and month (12 levels) as fixed factors. *A posteriori* multiple comparison analyses were performed using Student-Newman-Keul's (SNK) tests ($\alpha = 0.05$).

Multivariate analyses were conducted with the package PRIMER v6 (Clarke & Gorley 2006). Univariate analyses were performed with WinGMAV (http://sydney.edu.au/science/bio/eicc).

RESULTS

Beach characteristics and wrack deposition

Multiple-regression analysis was performed to assess the extent to which the environmental variables selected affect wrack composition on each beach. Monthly data for species biomass (dry wt), length area ratio (*L:A*), wave height and 1/slope were included in the calculations (Table 2). Wrack biomass and composition were explained by *L:A* (24.7%, p = 0.001), wave height (23.0%, p = 0.001) and slope

Table 2. Tests for relationship between wrack composition and selected physical variables using the distance-based multivariate analysis for linear models (DISTLM) (p = 0.001). In marginal tests, each variable is analysed separately. In sequential tests, the amount of each variable added to the model (best procedure) is conditional upon variables previously included. % var = percentage of the multivariate variance explained by variable; % cum = cumulative percentage of variance explained; *L:A* = ratio of beach length to beach area; *H* = wave height (m)

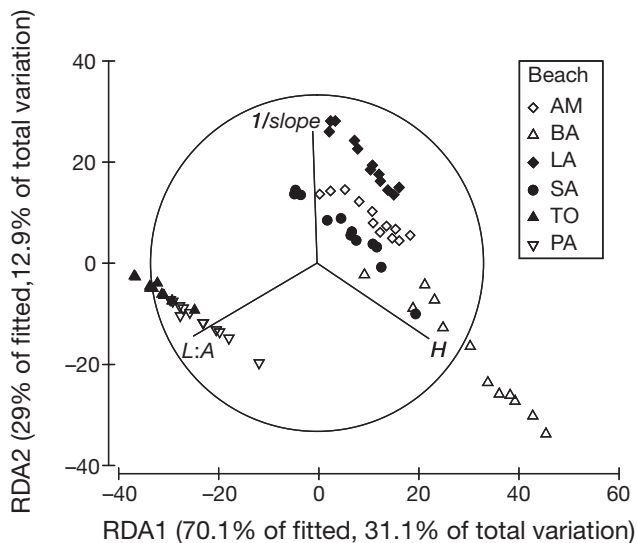| Variable	Marginal tests Pseudo-*F*	% var	Sequential tests Pseudo-*F*	% var	% cum
L:A	22.96	24.70	22.96	24.70	24.70
H	20.96	23.04	15.91	14.11	38.81
1/slope	8.92	11.31	6.69	5.48	44.29

Fig. 2. Distance-based redundancy analysis (dbRDA) ordination results for fitted model of wrack biomass and composition data (based on Bray-Curtis after log transformation) at each beach throughout the year versus explanatory variables. Beaches are grouped according to the environmental variables and wrack characteristics in: PA-TO, AM-LA-SA and BA. $L{:}A$ = ratio of beach length to beach area; H = wave height). See Fig. 1 for site abbreviations

(11%, p = 0.001). The sequential test explained 44.3% of the variability.

Beaches were divided into 3 groups, defined on the basis of topographical and wave exposure characteristics in the constrained dbRDA ordination (ANOSIM, global R = 0.61, p = 0.001) (Fig. 2). PA and TO were characterized by the highest $L{:}A$ ratios, low wave height and steep slope; AM, SA and LA were characterized by a low $L{:}A$, intermediate wave height and the flattest slope; BA was characterized by a low $L{:}A$, the greatest wave height and a steep slope.

Time-scale variability in wrack composition and biomass

The average monthly biomass of wrack varied widely in the beaches studied (Fig. 3), ranging (along the transects) from 14 ± 5 to 9189 ± 3594 g m^{-1} (mean ± SE) of dry wt in BA and PA, respectively. Average annual coverage fluctuated between 0.1 m^2 m^{-1} in BA (equivalent to 0.1% of beach width) and 9.7 m^2 m^{-1} in PA (equivalent to 16% of beach width). A significant correlation was obtained between wrack biomass and coverage throughout the year (r^2 = 0.81, p < 0.001).

A total of 38 species of macroalgae, 2 species of seagrasses and 1 specie of Cyanophyta were identified. Brown algae dominated the wrack with 19 species and accounted for 70% of the average annual biomass
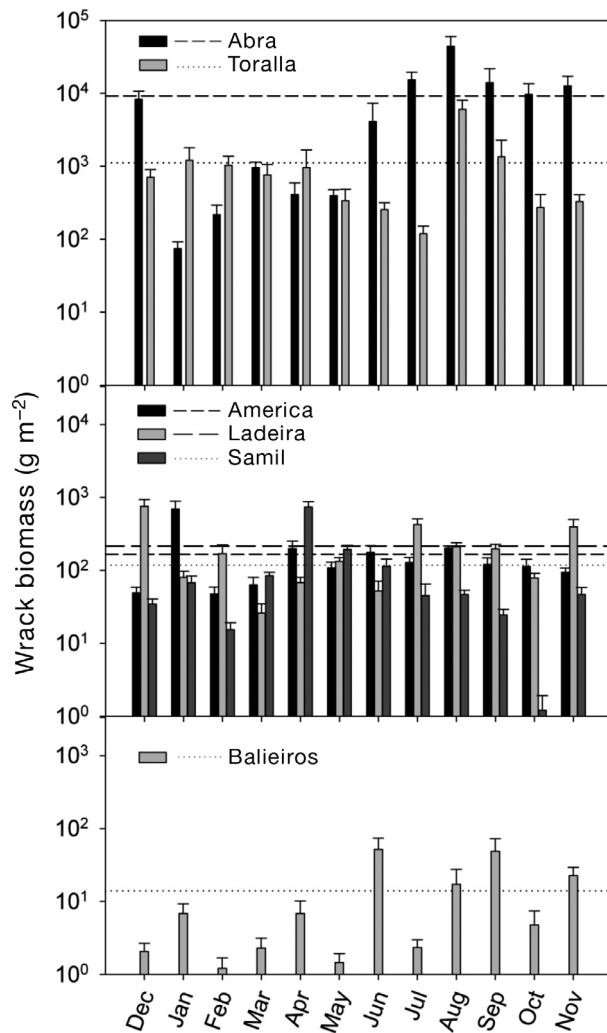

Fig. 3. Monthly variability in wrack input among and within the 3 beach groups throughout the year. Lines denote average monthly biomass at each beach. Error bars represent SE. *y*-axis is log scale

(Table 3). The number of species of red algae (16) was higher than that of green algae (3), although biomass values were more similar (3.5% and 5.3%, respectively). The contribution of seagrasses to total biomass was low. The group classified as 'remains' (amounting to 18.5% of the average annual biomass) corresponds to fragmented seaweeds that could not be identified due to their small size or excessively decomposed state. The main drift species, calculated on the basis of the total biomass of the 6 beaches, were *Cystoseira* spp., (30.3 ± 17.4%), followed by, *Sargassum muticum* (14.2 ± 7.1%), *Saccorhiza polyschides* (9.8 ± 8.6%), *Fucus* spp. (4.9 ± 4.0%), *Ulva* spp. (3.8 ± 4.6%), *Himanthalia elongata* (3.7 ± 6.9%) and *Halydris siliquosa* (3.3 ± 3.0%); contributions from other species amounted to less than 2%. Specific composition of wrack differed

Table 3. Total number of wrack species and mean % biomass ± SE (n = 12) of each taxonomic division at the studied beaches. See Fig. 1 for site abbreviations

Taxonomic division	No. species	PA	TO	AM	LA	SA	BA	Average
Heterokontophycophyta	19	57.2 ± 5.4	56.9 ± 7.3	73.7 ± 5.6	82.8 ± 2.2	74.0 ± 4.0	80.9 ± 6.1	70.9
Rhodophycophyta	16	11.2 ± 3.5	2.8 ± 0.4	0.3 ± 0.2	0.2 ± 0.1	0.5 ± 0.3	6.2 ± 1.6	3.5
Chlorophycophyta	3	5.0 ± 1.4	14.6 ± 3.1	2.9 ± 1.7	1.8 ± 0.5	6.6 ± 3.1	1.1 ± 0.7	5.3
Magnoliophyta	2	0.2 ± 0.1	1.1 ± 0.2	0.6 ± 0.2	2.0 ± 1.7	3.9 ± 1.4	2.8 ± 2.7	1.8
Remains	–	26.5 ± 5.6	24.6 ± 4.9	22.6 ± 6.0	13.3 ± 1.5	15.0 ± 3.3	9.0 ± 3.7	18.5

among the groups of beaches (see previous subsection) (ANOSIM, global R = 0.72, p = 0.001; Fig. 4). Of species appearing across several groups, *Cystoseira* spp. was the most abundant. Among beach groups, the largest influence of *Cystoseira* spp. was observed in the beaches exposed to intermediate wave action (AM, LA and SA); at these sites *S. muticum* and *Fucus* spp. also made their greatest contribution. In the more protected locations (PA and TO) a greater number of taxa were found; these beaches were characterized by the largest contribution of *S. polyschides* and *Ulva* spp. At the beach with the strongest wave action (BA), the contribution of *Zostera* spp. and *Ulva* spp. was lowest, and that of *H. elongata* relatively high (Table 4).

The monthly specific composition of wrack showed a cyclic correlation throughout the year both for all beaches combined (cyclic RELATE, $\rho = 0.798$; p = 0.001), and when each one was analyzed separately (cyclic RELATE: BA, $\rho = 0.419$; p = 0.001; AM, $\rho = 0.467$; p = 0.001; SA, $\rho = 0.315$; p = 0.001; LA, $\rho = 0.497$; p = 0.001; TO, $\rho = 0.502$; p = 0.001; PA, $\rho = 0.702$; p = 0.001) (Fig. 5).

The contribution of each taxon to the wrack composition shifted throughout the year, but this seasonal variation was different from beach to beach (PERMANOVA beach × month, Pseudo-$F_{55, 360} = 7.03$; p < 0.001). Despite the differences between beaches in each group, some trends were observed in the relative biomass of the dominant species (Fig. 6). In the more wave-protected locations (PA and TO) *Cystoseira* spp. reached the highest values toward September, October and November, *Sargassum muticum* during April and May and *Saccorhiza polyschides* in March, August and September; *Fucus* spp. showed low values throughout the year. In the beaches subjected to intermediate wave action (AM, LA and SA), the lowest relative biomass of *Cystoseira* spp. was recorded in April, May and June, coinciding with the upper limit of *S. muticum*; the highest proportion of *S. polyschides* was observed during January, February (at AM), and September and October (at LA); the input of *Fucus* spp. was low but consistent from month to month. In the beach affected by the strongest wave environment (BA), the relative biomass of *Cystoseira* spp. did not
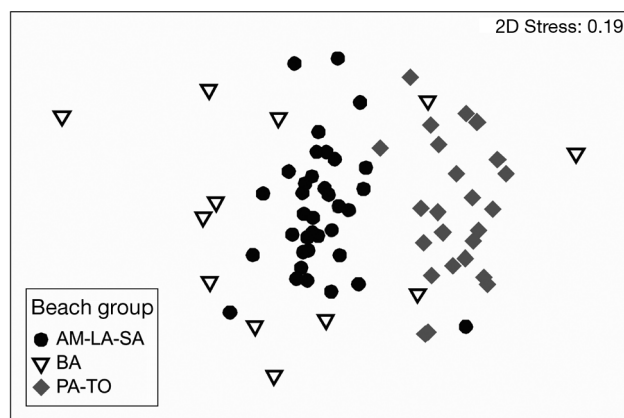

Fig. 4. Non-metric multidimensional scaling showing similarity of wrack species composition among and within beach groups, elaborated with standarized and log-transformed data. Average similarity across entire study: BA = 50.2% ; AM-LA-SA = 62.5% ; TO-PA = 61.9%. See Fig. 1 for site abbreviations

Table 4. Contribution to similarity (%) of the most abundant species stranded in each beach group. See Fig. 1 for site abbreviations

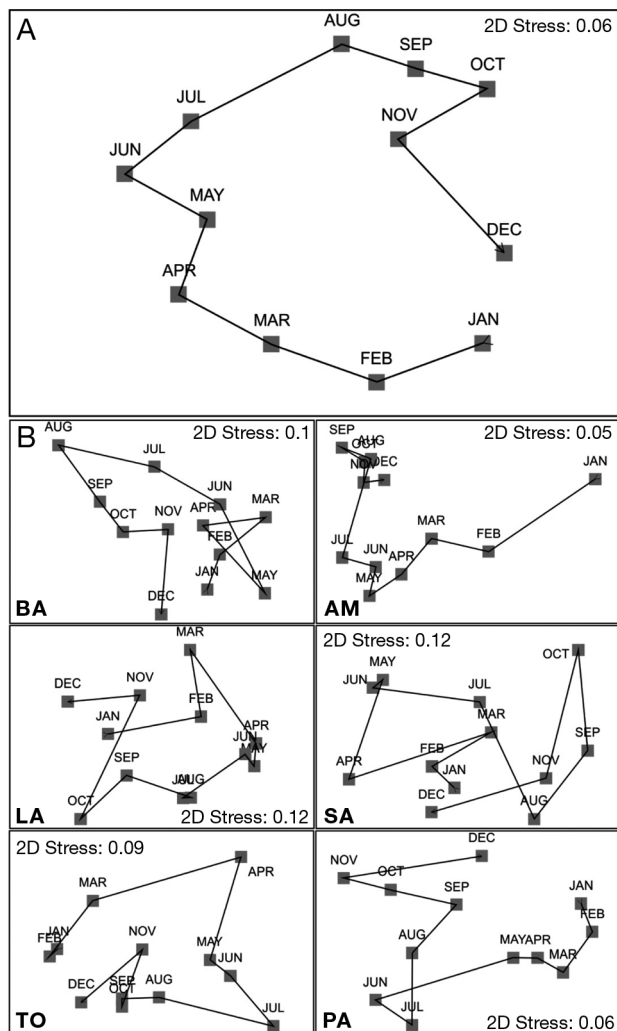| Wrack taxa	PA-TO	Beach group AM-LA-SA	BA
Chlorophycophyta			
Codium spp.	4.25	<1	<1
Ulva spp.	11.44	3.37	<1
Rhodophycophyta			
Asparagopsis armata	<1	<1	4.25
Gelidium spp.	<1	<1	3.78
Plocamium cartilagineum	1.76	<1	<1
Others spp.	3.82	<1	<1
Heterokontophycophyta			
Cystoseira sp.	19.1	46.45	28.31
Dictyota dichotoma	4.86	<1	<1
Dictyopteris polypodioides	3.85	<1	<1
Fucus sp.	3.16	12.96	11.7
Halidrys siliquosa	7.45	3.21	6.49
Halopteris sp.	1.72	<1	<1
Himanthalia elongata	<1	<1	19.18
Saccorhiza polyschides	17.72	<1	4.11
Sargassum muticum	9.64	22.72	13.06
Magnoliophyta			
Zostera spp.	2.2	3.62	<1

Fig. 5. Seasonal variability in specific composition calculated for standardized and log-transformed wrack biomass data, (A) with all locations included; and (B) for each beach independently. See Fig. 1 for site abbreviations

follow a clear pattern throughout the year. The highest proportion of *S. muticum* was recorded in April, the relative biomass of *S. polyschides* increased from July to September, and the highest value for *Fucus* spp. was observed in January.

Wrack biomass differed among beaches throughout the year (ANOVA beach x month, $F_{55,360} = 7.78$; p < 0.001) (Fig. 3). Wrack biomass was higher every month on beaches with the highest *L:A* and the lowest wave exposure (PA, TO or both) compared to beaches with more wave exposure, although during January, April and May, such differences were not significant (SNK test). The lowest biomass was measured on the most wave-exposed beach (BA). These differed significantly every month from the most sheltered beaches (PA and TO), but differences in biomass with intermediate *L:A* (AM, LA and SA) were not significant during June,

September, October or November (SNK test). Total biomass was significantly different within each beach throughout the year, although no similar pattern was observed when all locations were considered over time.

DISCUSSION

In the present study, which set out to quantify habitat openness and permeability, the life cycle of the predominant species of macroalgae, together with various quantifiable physical features, explained the substantial variability seen in wrack dynamics on sandy beaches.

Variability at a spatial scale (i.e. from location to location) in total wrack biomass was greater than that observed on a temporal scale, with values ranging from 0.2 to 110 kg m^{-1} among sites and 1 to 51 kg m^{-1} among months. Stranded biomass was greater on beaches with higher *L:A*. This ratio assesses the relationship between 'beach edge' and 'beach surface'. The higher it is the more edge is exposed to the donor ecosystem, therefore increasing the transfer of allochthonous materials. (Witman et al. 2004). In islands, for example, the amount of drift is a function of the length of the shoreline (Polis & Hurd 1996). Pocket beaches, or beaches inserted spatially along extensive rocky coasts (such as those in this study), could operate like island ecosystems with regard to volume of input received. Stranding of algae and seagrasses was greater in wave-protected environments than in exposed locations in the present study, which may be explained by a depositional process caused by a reduction in the flow of water that usually occurs around beach headlands (Komar 1998), or in rivers and streams (Witman et al. 2004). Low wave energy on the beach front causes a reduction in flow, which creates more favourable conditions for stranding wrack material.

The wide spatial variability in wrack biomass in this study is consistent with the extremely diverse data published on algae and seagrasses stranded on beaches: in South Africa, 2179 kg m^{-1} yr^{-1} (Stenton-Dozey & Griffiths 1983), 1200 to 1800 kg m^{-1} yr^{-1} (Koop et al. 1982) and 2920 kg m^{-1} yr^{-1} (McLachlan & Mc-Gwynne 1986) have been reported; 1000 to 2000 kg m^{-1} yr^{-1} have been reported in islands in the Gulf of California (Polis et al. 1997); 473 kg m^{-1} yr^{-1} in southern California, (Hayes 1974); 60 kg m^{-1} yr^{-1} in Canada (Wildish 1988); 0.7 kg m^{-1} yr^{-1} in Kenya (Ochieng & Erftemeijer 1999); and in Australia, from 360 to 2900 kg m^{-1} yr^{-1} for macroalgae and from 900 to 1800 kg m^{-1} yr^{-1} for seagrass (Hansen 1984). Besides the inherent geographical variability and the fre-
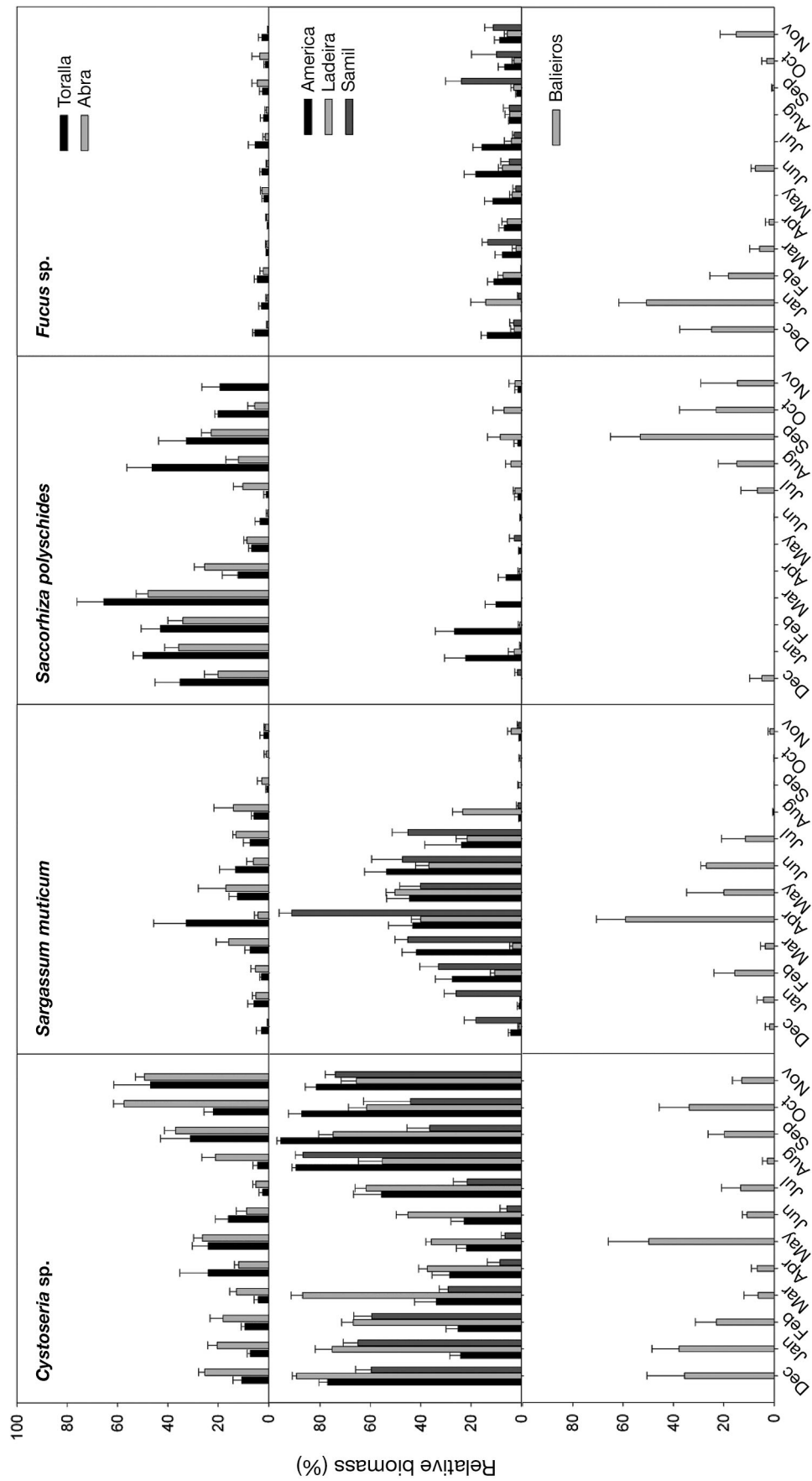
Fig. 6. Seasonal variability among predominant species found in wrack at each beach. Relative biomass of each species was average m^{-1} and per beach. Error bars represent SE (n = 6)

quency of resuspension and redeposition, which may complicate deposition rate estimates (Orr et al. 2005), we suggest that other factors such as wave exposure or the *L:A* ratio may help explain this variability.

Temporal variation in wrack biomass is a complex process. Some studies have registered a higher standing crop during winter (Koop & Field 1980, Stenton-Dozey & Griffiths 1983, Ochieng & Erftemeijer 1999), others in summer and autumn (Piriz et al. 2003, Kotwicki et al. 2005, Mateo 2010). We found significant differences in all the beaches over the course of the study. On the low-energy beaches wrack accumulations were higher during late summer (TO) and from summer to autumn (PA), but no clear trend was noted in stronger wave environments. This could indicate a more predictable scenario in the protected locations. We suggest that wrack accumulation on the low-energy beaches could mainly be determined by the life cycle of algae. During late summer and autumn senescence (e.g. *Saccorhiza polychydes*), branch decay (e.g. *Cystoseira baccata*) and increases in biomass of opportunistic drifted species (e.g. *Ulva* spp.) are common processes in the study area. However, with increasing wave exposure, biomass deposition may be more dynamic and sensitive to other factors, such as strong winds or heavy wave action.

All the primary producers in the surrounding ecosystems can potentially drift ashore. Indeed, large amounts of brown algae and seagrass stranded on beaches have been reported close to kelp forest and seagrass beds (e.g. Stenton-Dozey & Griffiths 1983, Mateo 2010). On the Galician coast, rocky shores are dominated by brown seaweeds (mostly of the orders Laminariales and Fucales; Bárbara et al. 2005) and *Zostera* beds in sheltered estuarine environments. The number of species of red algae in this area is 4 times higher than that of green algae (Bárbara et al. 2005). Throughout this study, wrack composition was dominated by brown algae, and the ratio between red and green algae on sandy shores was similar to that reported on rocky shores. Clear differences were noted, however, in the species-specific contributions from location to location, a phenomenon that cannot be attributed only to the availability of macroalgae in surrounding ecosystems. For instance, at beaches with intermediate and high exposure to wave action, wrack was dominated by algae with air bladders in their structure (e.g. *Cystoseira* spp, *Sargassum muticum*, *Fucus* spp.), a factor which, by increasing buoyancy, might assist in them drifting ashore. Buoyancy properties have been considered important in the supply of organic matter to sandy beaches (Orr et al. 2005). We suggest that buoyancy properties may be relevant in the stranding wrack episodes in beaches subjected to high-energy wave environments.

The greatest number of stranded species was measured on the more sheltered beaches. On the one hand, a lower-energy environment might facilitate algal deposition on the beach front, and, on the other hand, reduced wave energy on the sheltered rocky shore may promote the occurrence of annual opportunistic algal species (Kraufvelin et al. 2009), which can increase wrack biodiversity. Both effects may explain the larger number of species found in the more protected locations.

The specific composition of wrack showed a cyclical pattern throughout the year. This ongoing compositional change indicates that the wrack-stranding process is linked to the life cycle of algae and seagrasses. This cyclic trend implies that the variable arrival of resources to sandy beaches over a period of months is, to some extent, predictable. Focusing on the algae with the largest biomass supplied to the sampled beaches, viz. *Cystoseira* spp. and *Sargassum muticum*, we observed that the biomass contributed by these species to wrack is consistent with their life-cycle traits. These 2 algae have significant differences in their seasonal growth cycles, *Cystoseira* spp. showing a similar growth rate in summer and winter, and *S. muticum* showing a slow growth rate in winter, and a faster rate in the spring (Arenas et al. 1995). As the year progresses, these different traits produce dissimilar stocks of macroalgae in the rock habitat, which, once detached by waves and currents, can differentially subsidize sandy beaches over time. A further factor that has been suggested (in the population dynamics of *S. muticum*) is a 'self-thinning process', whereby the population becomes self-limiting as density increases (Harper 1977). The negative biomass–density relationship (as a measure of biomass accumulation-driven mortality) (Arenas & Fernández 2000), could increase the likelihood of occurrence of drifting *S. muticum* during the months with high growth rates (spring).

Our paper presents the first study on the temporal variability of wrack supply to sandy beaches over a range of environmental conditions. The results provide evidence that variability in such wrack supply can be explained through interactions between wave exposure, coastal topography and season. Differences in the source-community composition as well as differences in the buoyancy of macroalgae and seagrasses may influence wrack composition on beaches with different exposure rates (Orr et al. 2005). We did not quantify other potential factors, such as biomass in the donor areas, wind or currents. Our results provide evidence to support our initial hypothesis that smaller beaches, which have a higher *L:A*, namely a longer border with the donor ecosystem in relation to beach area, receive larger subsidies per unit surface area.

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