Aquatic Botany 105 (2013) 25–33

Contents lists available at SciVerse ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

# Deposition patterns of algal wrack species on estuarine beaches

Marina Gómez*, Francisco Barreiro, Jesús López, Mariano Lastra, Rosario de la Huz

*Departamento de Ecoloxía e Bioloxía Animal, Facultade de Ciencias, Universidade de Vigo, 36310 Vigo, Spain*

ARTICLE INFO

*Article history:*
Received 6 June 2012
Received in revised form 4 December 2012
Accepted 6 December 2012
Available online 20 December 2012

*Keywords:*
NW Spain
Estuarine beaches
Intertidal levels
Algal wrack
Species composition
Spatio-temporal pattern

ABSTRACT

Wrack supply is a common feature of beaches around the world. The species composition and spatial distribution of wrack deposits have been widely recognized as two significant factors in the ecological role of macroalgae within beach ecosystems. These accumulation processes may be intensified by bloom events of opportunistic algae, which frequently occur in estuarine environments. For this study, wrack supply was assessed over 13 months in two estuarine beaches of the Galician coastline, NW Spain. Algal biomass and wrack species distribution were characterized, paying special attention to possible relationships between beach slope, tidal height and algal morphology. The results show that the average values in total monthly biomass of stranded macroalgae and seagrasses were similar for both beaches, but certain differences in temporal and spatial variability throughout the year's cycle were detected. Despite this, the distribution of algal species along the beach face was similar in both beaches: large amounts of sheet-like and thin branched species (e.g. *Ulva* spp., *Gracilaria gracilis*) dominated the wrack deposits on the low-tide terraces, whereas thick leathery species with positive flotation properties (e.g. *Fucus* spp., *Ascophyllum nodosum*) showed larger amounts in the upper foreshore zones. The relative contribution of the major morphological groups of algal wrack shifted throughout the year, suggesting an inverse relation between thick leathery group and sheet-like species, which could be associated with factors such as differences in macroalgae's life cycles and nutrient requirements of fast- and slow-growing species. This study demonstrates that beach topography, together with the morphology of macroalgae species influence the distribution of wrack deposits in estuarine beaches. Further research on the implications of wrack dynamics for sedimentary characteristics and faunal distribution is needed.



## 1. Introduction

Sandy beaches form a dynamic interface between marine and terrestrial ecosystems, and a great number of studies focussing on the connectivity between different components of a beach and their neighboring coastal environments have been conducted over the recent years (Polis and Hurd, 1996; Polis et al., 1997; Heck et al., 2008; Spiller et al., 2010; Mellbrand et al., 2011). One of the main linkages consists of allochthonous inputs of organic material, which sandy beaches receive in the form of beach-cast wrack, i.e. primarily macroalgae and higher plants/seagrasses (Rossi and Underwood, 2002). This wrack material, exported from surrounding ecosystems such as rocky shores or seagrass beds, may strand throughout the entire intertidal range. Algal wrack deposits are documented on different types of beaches over the world, and with extremely variable values (i.e. sandy beaches: Ochieng and Erftemeijer, 1999; Dugan et al., 2003; estuarine beaches: Piriz et al., 2003; Fox et al., 2008; Sousa-Dias and Melo, 2008).

Allochthonous organic material constitutes a complex, diverse and variable resource to beach consumers, both in time and space; its effects on trophic dynamics can follow multiple pathways up and down the food webs (Spiller et al., 2010). The degree to which this trophic subsidy (Polis et al., 1997) influence the distribution and abundance of macro- and meiofauna, depends both on the amount and species composition of the beach-cast wrack (Gonçalves and Marques, 2011).

Commonly, patches of algae are not evenly distributed along the beach, since the deposition pattern is highly influenced by the physical environment of a given beach (e.g. rate of exposure, beach slope, morphodynamic state and swash environment) and by the composition and buoyancy of the drifting wrack (Orr et al., 2005; McLachlan and Brown, 2006; Duong and Fairweather, 2011). The spatial distribution of the wrack debris along the beach profile depends on where the wrack strands during the ebbing time; therefore it may remain and be decomposed on the substrate, or instead be washed back into the sea with the next flooding tide (Orr et al., 2005). Thus, the specific habitat attributes of wrack accumulations change temporally as the organic material ages and experiences the physical dynamics of the beach environment. The spatial distribution of wrack on the beach may therefore affect the structure

* Corresponding author. Tel.: +34 986812588; fax: +34 986812556.
*E-mail address:* maringomez@uvigo.es (M. Gómez).

0304-3770/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.aquabot.2012.12.001

and function of animal assemblages and determine the taxonomic composition and turnover of macro and meiofauna species (Dugan et al., 2003; Olabarria et al., 2007; Pelletier et al., 2011).

Several studies highlight the influence of the amount and composition of wrack deposits on the decomposition process (Jędrzejczak, 2002), the incorporation of wrack into the trophic web (Crawley et al., 2009), its role as a habitat for beach invertebrates (Olabarria et al., 2007) and sedimentary processes such as accumulation and erosion (Nordstrom et al., 2007). Furthermore, the morphological and ecological features of the seaweed species involved in beach-cast deposits (e.g. levels of branching, toughness, nutritional values, decomposition rates) are important variables affecting the wrack-invertebrate interactions (Rodil et al., 2008a). The algal species which form the beach wrack are largely determined by the composition of the source community, the offshore marine environment, the prevailing wind and/or current direction, and the physical characteristics of the macrophyte detritus (e.g. buoyancy) (Ochieng and Erftemeijer, 1999; Orr et al., 2005; Barreiro et al., 2011).

Galician shoreline (NW Spain) is characterized by a set of prolonged inlets called *rías*. The internal areas of these embayments are frequently occupied by estuarine beaches, characterized by a steep foreshore zone and a wide, flat low-tide terrace, separated by a prominent change in beach-face slope (Nordstrom, 1992). Upper and lower zones are often featured by different swash-zone hydrodynamics, sediment transport and grain size (Jackson et al., 2002). According to this, significant differences in faunal densities and species composition have been highlighted (Rodil et al., 2008b).

Despite an extensive literature on the ecology of algal wrack deposits on beaches and other coastal environments, little attention has been given to the deposition pattern itself. Accumulations of algal wrack is a consistent feature of Galician sandy beaches (Olabarria et al., 2007); this depositional process is frequently intensified in estuarine and sheltered areas by bloom events of opportunistic algae (Villares and Carballeira, 2004). Consequently, this study attempts to examine the spatial and temporal patterns of wrack deposits on sheltered estuarine beaches on the Northwest coast of Spain. To achieve this goal, the wrack subsidies were characterized in terms of amount (biomass) and species composition along a tidal gradient in two sheltered beaches, paying special attention to possible relationships between species composition, beach slope and tidal zones. Three possible hypotheses were tested: (1) different tidal zones of estuarine beaches differ in wrack biomass and species composition; (2) Morphological characteristics of macroalgae affect its stranding position along the beach profile; and (3) There is a consistent pattern of wrack dynamics over the time and space among beaches.

## 2. Materials and methods

### 2.1. Study area

The study was carried out on the west coast of Galicia (NW coast of Spain) (Fig. 1). This coastline formed by a set of coastal embayments called *rías*, is characterized by a seasonal nutrient-rich deep water upwelling (Blanton et al., 1984) that typically fertilizes the shore from April to September, approximately coinciding with the dry season. This seasonal upwelling is mediated by north and north-east winds, switching to downwelling conditions during fall and winter (from October to February) when southerly and south-westerly winds dominate.

The *Ría de Arousa* (oriented in the SW–NE direction) is a large embayment with a surface area of 230 Km$^2$, 25 Km long and an average depth of 19 m (maximum depth 67 m at the ría's mouth) (Fig. 1). Hydrodynamic features of this system are given by an interaction between local and oceanic winds, together with the freshwater contribution, the upwelling event and the tide cycle effect (de Castro et al., 2000). The main freshwater input comes from *Umia River*, located in the southern shore of the ría, (with flow ranging between 5 and 73 m$^3$ s$^{-1}$); and *Ulla River* in the most internal area, with discharge volumes between 70 and 120 m$^3$ s$^{-1}$ in the summer and winter months respectively. The annual rainfall during the study period was between 19.8 and 295.8 L m$^{-2}$; the average air temperature was 14.5 ($\pm$1.1) °C; mean salinity and temperature at the water surface were 24.7 ($\pm$1.6)‰ and 14.9 ($\pm$0.8) °C. Oceanographic and meteorological information was supplied by the local meteorological office MeteoGalicia (www.meteogalicia.es).

Two similar sandy beaches located in the inner part of the ría were chosen in order to analyze the annual cycle of algal wrack subsidies in estuarine environments. Mañóns beach (MA: 42°37′50.57″ N–8°51′1.22″ W) is located 22 km inland from the open coast, with a southern orientation and a length and average width of 741 m and 286 m respectively. Arnelas beach (AR: 42°31′55.18″ N–8°52′8.05″ W) with eastern orientation, is located 13.5 km inland from the open ocean; beach length and width were 309 m and 169 m respectively (Fig. 1). Both sites are characterized by a low wave exposure environment and a mesotidal regime, with a mean spring tidal range of ca. 3 m. Both beaches were featured by an abrupt change in the slope in the across beach intertidal profile.

### 2.2. Sampling design

Samplings were carried out at a monthly base from January 2009 to January 2010 during spring low tides. Six transects were established along a designated central, shore-parallel stretch of 100 m on each beach; transects were randomly distributed at each sampling date, separated by at least 10 m. At each transect, 2 different zones were distinguished on the beach profile according with consistent changes in slope: upper zone (UP) delimited by the base of the dune and the prominent break in slope, and lower zone (LO) from the break in slope to the swash line (Fig. 2). To analyze specific composition and biomass, all wrack material stranded within a 1 m-wide band centered at each transects was collected (Lastra et al., 2008); wrack samples gathered at each tidal zone were collected in different bags for laboratory analysis. During the months when large amounts of wrack stranded on the beach, it was not feasible to collect all the material, thus three subsamples consisting of 25 × 25 cm quadrants were taken per level and transect; this subsampling method provided a good estimate of the mass and specific composition of the wrack (Barreiro et al., 2011). Wrack species were determined to the lowest taxonomic level possible. The dry weight of each species was calculated after drying the samples to a constant weight at 60 °C; algal biomass was expressed in g (dry weight) m$^{-2}$.

Beach profiles were measured during spring low tide, from the dune base to the lowest swash level, throughout the study period, according to Emery's method (Emery, 1961).

### 2.3. Data analysis

Paired-sample *t*-tests were used to compare beach slope of the two tidal levels throughout the year. Slope data collected at each sampling dates were used ($n$ = 13). K-S and Levene tests were done in order to test assumptions of normality and homogeneity of variances respectively. The statistical package SPSS 19 was used to perform these analyses.

Differences in wrack biomass were gauged using a 3-way ANOVA (WinGMAV software package; EICC, University of Sydney), with 'beach' (2 levels), 'tidal level' (2 levels) and 'month' (13 levels) as fixed factors. The six transects in each beach were used as replicates. Before statistical analysis, the homogeneity

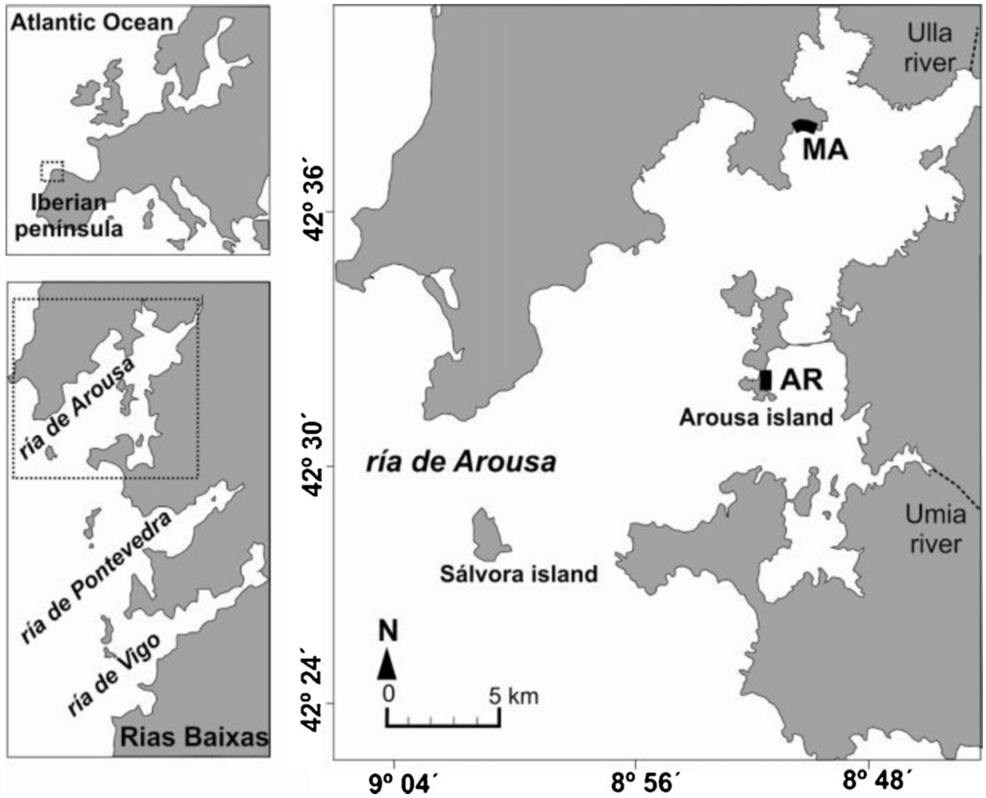


**Fig. 1.** Map of the study area. Location of the two estuarine beaches sampled on the NW coast of Spain: Mañóns (MA) and Arnelas (AR).

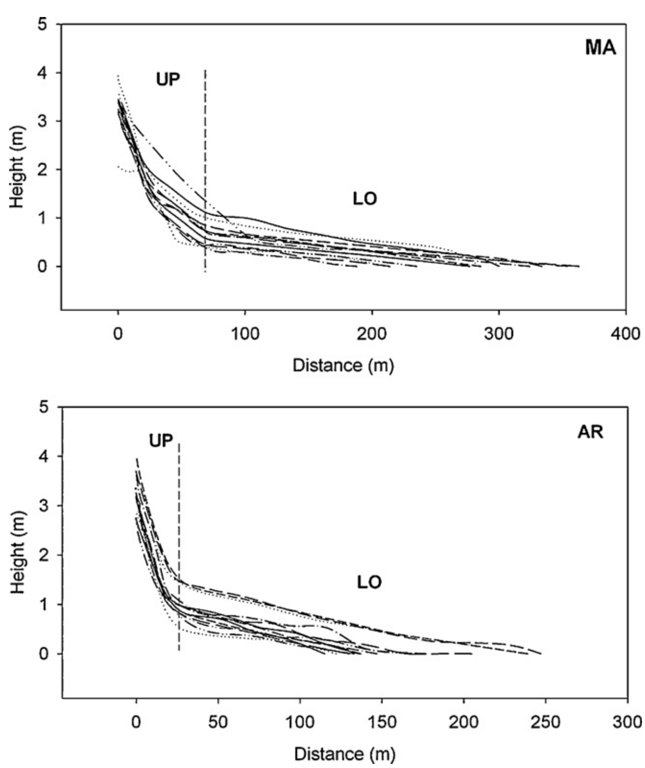


**Fig. 2.** Beach profiles. Monthly variability of the intertidal profiles at Mañóns (MA) and Arnelas beach (AR). Vertical dotted line marks the prominent break in slope that separated two defined tidal zones: UP (upper foreshore); LO (low-tide terrace).

of variances was analyzed using Conchran's test; the data were log transformed ($\log_{10}$) in order to meet assumptions of normality. Subsequent multiple comparisons were performed using Student–Newman–Keuls's (SNK) tests ($\alpha = 0.05$) (Underwood, 1997).

To analyze the specific composition of the samples, the mean monthly algal wrack biomass per transect was compared using 'PRIMER' (Plymouth Routines in Multivariate Ecological Research) software package. The data matrix was built in rows showing the different taxa, with the corresponding biomass values per transect, level, and month being expressed in columns. Similarity was calculated with the Bray–Curtis coefficient, using $\log(x+1)$ transformed data. Analysis of similarity (ANOSIM) was used to test the differences in wrack composition between the upper foreshore and low-tide terrace at both beaches. A graphic visualization of the distance between samples based on their similarities was performed throughout non-metric multi-dimensional scaling (nMDS). The similarity percentage test (SIMPER) was run to determine within-group similarities and between-groups dissimilarities. A high index of similarity within groups indicates group homogeneity, whereas a high dissimilarity between groups indicates distinct assemblages (Clarke and Gorley, 2006).

In order to evaluate the existence of any relationship between the morphology of stranded algae and their position on the beach face, a clustering approach by grouping together the species into 5 different functional groups was applied. This 'functional group' concept was based on algal morphology as follows: sheet-like species (e.g. *Ulva* spp., *Porphyra* sp. *Asperococcus* sp.), thin branched species (e.g. *Gracilaria gracilis*), coarsely branched species (e.g. *Chondrus crispus*, *Gigartina* sp.), thick leathery species (e.g. *Ascophylum nodosum, Cystoseira* spp., *Fucus* spp.) and seagrasses (*Zostera* spp.). This grouping does not crucially derive from the functional group concepts of other studies e.g. (Steneck and Dethier, 1994;

**Table 1**
Details of the 3-factor ANOVA test. Biomass values (g DW $m^{-2}$) were $Log_{10}$ ($x$) transformed. (df) degrees of freedom; (MS) mean square; (F) *F*-statistic.

| Source of variation | Biomass | | |
|---|---|---|---|
| | df | MS | *F* |
| Beach (B) | 1 | 0.0036 | $0.01^{ns}$ |
| Month (M) | 12 | 13.81 | $44.74^{*}$ |
| Level (L) | 1 | 15.88 | $51.44^{*}$ |
| B × M | 12 | 29.08 | $94.20^{*}$ |
| B × L | 1 | 62.11 | $201.17^{*}$ |
| M × L | 12 | 2.70 | $8.77^{*}$ |
| B × M × L | 12 | 12.19 | $39.51^{*}$ |
| Residual | 260 | 0.30 | |
| Total | 311 | | |

* $p < 0.001$
ns $p > 0.05$

Rubal et al., 2011). Interesting to note that species belonging to the thick leathery group usually presented gas-filled floats, known as pneumatocysts, which provide their positive buoyant properties (Denny and Gaylord, 2002), while sheet-like and thin branched species lacked them.

Non-parametric multivariate analysis of variance (PERMANOVA) was performed to test the hypothesis on differences in wrack composition between tidal levels during the study period using functional groups as level of aggregation. ‘Beach’, ‘tidal level’ and ‘month’ values were fixed factors in the model. Only the significant effects ($p < 0.05$) were further investigated through a series of pair-wise comparisons.

## 3. Results

The upper levels of both beaches were steeper than the lower terraces, and this feature was consistent over time (MA: $t = 14.343$, $p < 0.001$; AR: $t = 34.225$, $p < 0.001$) (Fig. 2). Average monthly values of 1/slope in Mañóns and Arnelas were 17 ± 2 and 9.3 ± 0.2 for the upper shore and 169 ± 57 and 113 ± 6 for the lower zone, respectively.

### 3.1. Wrack biomass

The average monthly wrack biomass recorded on Mañóns beach was 58 ± 22 g DW $m^{-2}$: 80 ± 7% located on the upper zone and 20 ± 7% on the low-tide terrace. A similar value of the average biomass (76 ± 33 g DW $m^{-2}$) was found in Arnelas beach; however, the wrack distribution across this beach differed: 47 ± 10% and 53 ± 10% were stranded on the upper and lower levels, respectively.

A high spatio-temporal variability was detected (ANOVA: beach × level × month interaction, $F_{12,260} = 39.51$; $p < 0.001$; Table 1), although some temporal trends can be described. The maximum values of wrack biomass in Mañóns occurred between April (208 ± 68 g DW $m^{-2}$) and July (227 ± 50 g DW $m^{-2}$), in coincidence with the dry and warm season, and the minimum in March and September, with 3.4 ± 0.5 and 4 ± 1 g DW $m^{-2}$ respectively (Fig. 3). Biomass dynamics on this beach throughout the year were consistent both in upper and lower tidal levels: wrack deposits on the upper beach were significantly higher than those on the lower beach throughout the year, except for May and June (SNK test; $p < 0.05$). By contrast, the highest values of biomass in Arnelas beach were recorded during the winter months (420 ± 70 g DW $m^{-2}$ in January 2009) and the lowest in summer (1.7 ± 0.4 g DW $m^{-2}$ in August) (Fig. 3). A similar annual pattern was observed on both tidal zones: wrack deposits on the lower beach were significantly higher than those on the upper zone during winter months; conversely, the upper zone showed higher values in spring (April, May and June). No significant differences were observed between tidal levels in late summer and fall (August–October).

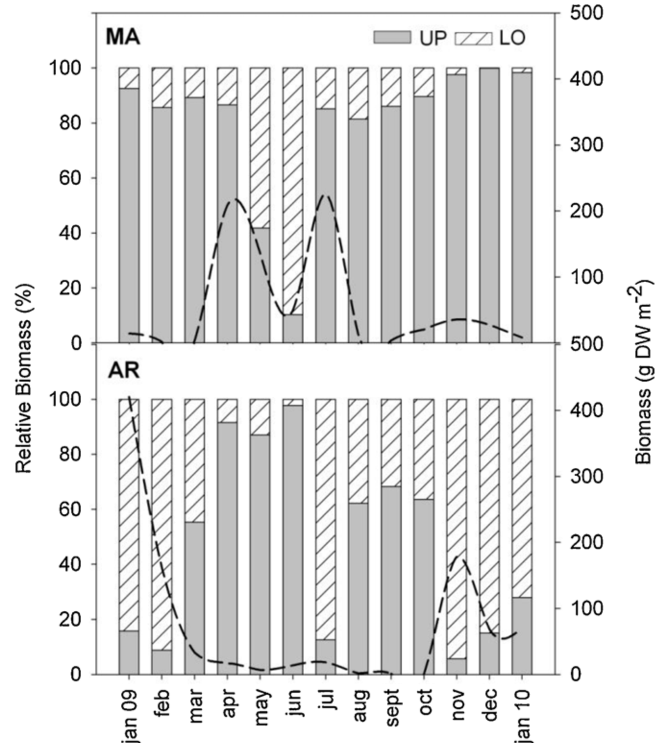


**Fig. 3.** Biomass of the wrack inputs. Monthly variability of wrack inputs on the beaches. Columns show relative biomass (%) of the two tidal heights; gray and white bars correspond to upper and lower levels respectively. Dotted lines represent the average monthly biomass (g DW $m^{-2}$).

### 3.2. Species composition

A total of 36 species of macroalgae (3 Chlorophycophyta, 15 Heterokontophycophyta, and 17 Rhodophycophyta) and one species of seagrass (Magnoliophyta) were identified and grouped into five functional groups (Table 2). The specific composition of wrack primarily included members of green algae (66.2% of the average annual biomass), with the genus *Ulva* spp. as most abundant taxa. Brown algae were the second most abundant wrack species (16.3%), dominated by *Fucus* spp., *A. nodosum* and *Laminaria* spp. Seagrass and red alga species had the lowest biomass (1.5% and 2.8% respectively), represented by *Zostera* spp. and *G. gracilis*, respectively. Fragmented seaweeds, classified as remains (13.2% of the average annual biomass), could not be identified due to their small size or excessively decomposed state.

Tidal level (UP and LO) was the most important source of variation in the specific composition. No significant differences were identified between beaches (Two-way ANOSIM routine; ‘Beach’ factor: global $R = 0.124$, $p = 0.07$; ‘Level’ factor: global $R = 0.303$, $p = 0.01$). These results were consistent with the two-dimensional nMDS ordination plot (Fig. 4). The low stress value (0.13) indicated that the plot was a satisfactory two-dimensional representation of the relationships between data-points. Samples from the upper zone tended to be grouped closer than those from the lower levels on both beaches; samples from Mañóns beach tended to be grouped closer than those from Arnelas (Fig. 4).

The results yielded by SIMPER analysis showed differences in species composition between beach levels. *Ulva* spp., *Fucus* spp. and remains fraction were the components with the highest contribution to discriminate between levels, with dissimilarity values

**Table 2**
List of the algal species collected during the study period on the two beaches and the functional group to which they were assigned: sheet-like (SH), thin branched (TB), coarsely branched (CB), thick-leathery (TL) and seagrass (SG).

| Wrack Taxa | Functional groups |
|---|---|
| Chlorophycophyta | |
| *Cladophora* sp. Kützing, 1843 | TB |
| *Codium* sp. Stackhouse, 1979 | CB |
| *Ulva* spp. Linnaeus, 1753 | SH |
| Heterokontophycophyta | |
| *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863 | TL |
| *Asperococcus* sp. J.V. Lamouroux, 1813 | SH |
| *Bifurcaria bifurcata* R. Ross, 1958 | TL |
| *Chorda filum* (Linnaeus) Stackhouse, 1797 | TB |
| *Colpomenia peregrina* Sauvageau, 1927 | CB |
| *Cystoseira* spp. C. Agardh, 1820 | TL |
| *Dictyopteris polypodioides* (A.P. De Candolle) J.V. Lamouroux, 1809 | CB |
| *Dictyota dichotoma* (Hudson) J.V. Lamouroux, 1809 | SH |
| *Fucus* spp. Linnaeus, 1753 | TL |
| *Halidrys siliquosa* (Linnaeus) Lynbye, 1819 | TL |
| *Himanthalia elongata* (Linnaeus) S.F. Gray, 1821 | TL |
| *Laminaria* spp. J.V. Lamouroux, 1813 | TL |
| *Padina pavonica* (Linnaeus) Thivy in W.R. Taylor, 1960 | CB |
| *Pelvetia canaliculata* (Linnaeus) Decaisne & Thuret, 1845 | CB |
| *Sargassum muticum* (Yendo) Fensholt, 1955 | TL |
| Magnoliophyta | |
| *Zostera* spp. Linnaeus, 1753 | SG |
| Rhodophycophyta | |
| *Ahnfeltia plicata* (Hudson) E.M. Fries, 1836 | TB |
| *Calliblepharis ciliata* (Hudson) Kützing, 1843 | CB |
| *Ceramium* sp. Roth, 1797 | TB |
| *Champia parvula* (C. Agardh) Harvey, 1853 | CB |
| *Chondracanthus acicularis* (Roth) Fredericq, 1993 | CB |
| *Chondracanthus teedi* (Mertens ex Roth) Kützing, 1843 | CB |
| *Chondrus crispus* Stackhouse, 1797 | CB |
| *Gastroclonium ovatum* (Hudson) Papenfuss, 1944 | CB |
| *Gelidium* sp. J.V. Lamouroux, 1813 | CB |
| *Gigartina pistillata* (S.G. Gmelin) Stackhouse, 1809 | CB |
| *Gigartina* sp. Stackhouse, 1809 | CB |
| *Gracilaria gracilis* (Stackhouse) M. Steentoft, L.M. Irvine & W.F. Farnham, 1995 | TB |
| *Gracilaria multipartita* (Clemente) Harvey, 1846 | CB |
| *Gracilaria vermiculophylla* (Ohmi) Papenfuss, 1967 | TB |
| *Laurencia obtusa* (Hudson) J.V. Lamouroux, 1813 | CB |
| *Lomentaria articulata* (Hudson) Lyngbye, 1819 | CB |
| *Plocamiun cartilagineum* (Linnaeus) P.S.Dixon, 1967 | CB |

of 30, 16 and 12%, respectively. Furthermore, dissimilarity between levels was also linked to species such as *A. nodosum* and *Zostera* spp. (with the highest biomass in the upper beach levels), together with *G. gracilis*, which mostly accumulate in the lower tidal zone. Only these 6 taxa, out of the 36 identified in this study, presented a total dissimilarity of c.a. 82%; while contribution of species like *Sargassum muticum*, *Cystoseira* spp. and *Asperococcus* sp. were lower than 3% (Table 3).

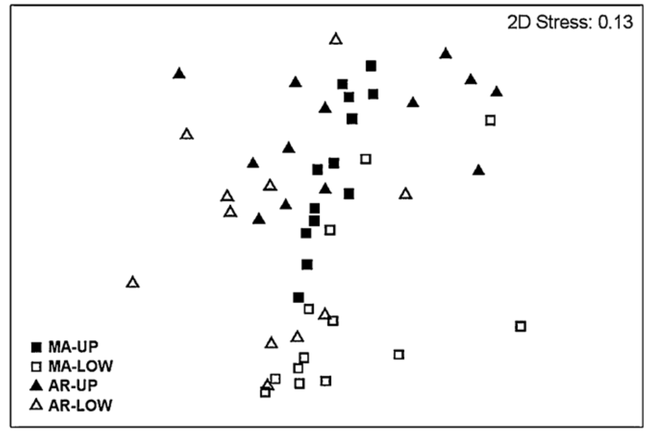

**Fig. 4.** nMDS plot. Non-metric multidimensional scaling (nMDS) showing similarity of wrack species composition among and within beaches.

Wrack deposits were mainly composed of a mixture of sheet-like opportunistic species, thin and coarsely branched, thick leathery taxa, as well as seagrass and the decay fraction. The thick leathery group (e.g. *Fucus* spp., *A. nodosum*, *S. muticum*, or *Cystoseira* spp.) showed the highest values in average biomass on the upper levels (25% and 36% in MA and AR respectively); while sheet-like species (e.g. *Ulva* sp.) and thin branched species (e.g. *G. gracilis*) presented the greatest accumulation on the lower beach (sheet-like: 94% and 74%; thin branched: 3% and 1% in MA and AR, respectively) (Fig. 5).

### 3.3. Temporal variability of algal wrack composition

The relative contribution of each functional group to the wrack composition of the two tidal levels shifted throughout the year, with seasonal variations among beaches and levels (PERMANOVA beach × level × month, $Pseudo\text{-}F_{12,260} = 16.207$; $p < 0.001$) (Table 4). The results of the pair-wise tests showed that the species composition of the deposits differed significantly between beaches ($p < 0.01$) throughout the year (excluding LO in April: $p = 0.134$). Large deposits of *Ulva* spp. occupied the entire lower level of Mañóns beach along the study period; thus wrack species composition differed between levels during most of the year (except in April, $p = 0.661$). Likewise, significant differences ($p < 0.01$) between tidal levels in Arnelas beach along the study period seemed to be linked with strong inputs of drifting *Ulva* spp. in the lower beach.

**Table 3**
Average biomass (g DW $m^{-2}$) of the most important taxa responsible for dissimilarity between levels and their individual contribution are shown. Biomass data previous log-transform and standardized (Mean ± SE; $n = 156$).

| | Av. Biomass (g DW $m^{-2}$) | | Contribution (%) |
|---|---|---|---|
| Species | UP | LOW | |
| *Ulva* spp. | 21.56 ± 1.55 | 53.09 ± 2.71 | 29.95 |
| *Fucus* spp. | 24.05 ± 1.44 | 9.79 ± 1.42 | 16.06 |
| Remains | 19.77 ± 0.98 | 7.75 ± 0.93 | 12.41 |
| *A. nodosum* | 11.47 ± 1.04 | 2.13 ± 0.58 | 8.75 |
| *Zostera* sp. | 7.98 ± 1.13 | 6.26 ± 1.39 | 8.64 |
| *G. gracilis* | 1.53 ± 0.28 | 8.29 ± 1.52 | 6.59 |
| *S. muticum* | 3.03 ± 0.46 | 1.61 ± 0.40 | 2.85 |
| *Cystoseira* sp. | 2.92 ± 0.36 | 1.73 ± 0.36 | 2.83 |
| *Asperococcus* sp. | 1.14 ± 0.49 | 2.53 ± 0.98 | 2.64 |
| Groups UP–LO (average dissimilarity = 67.20) | | | |

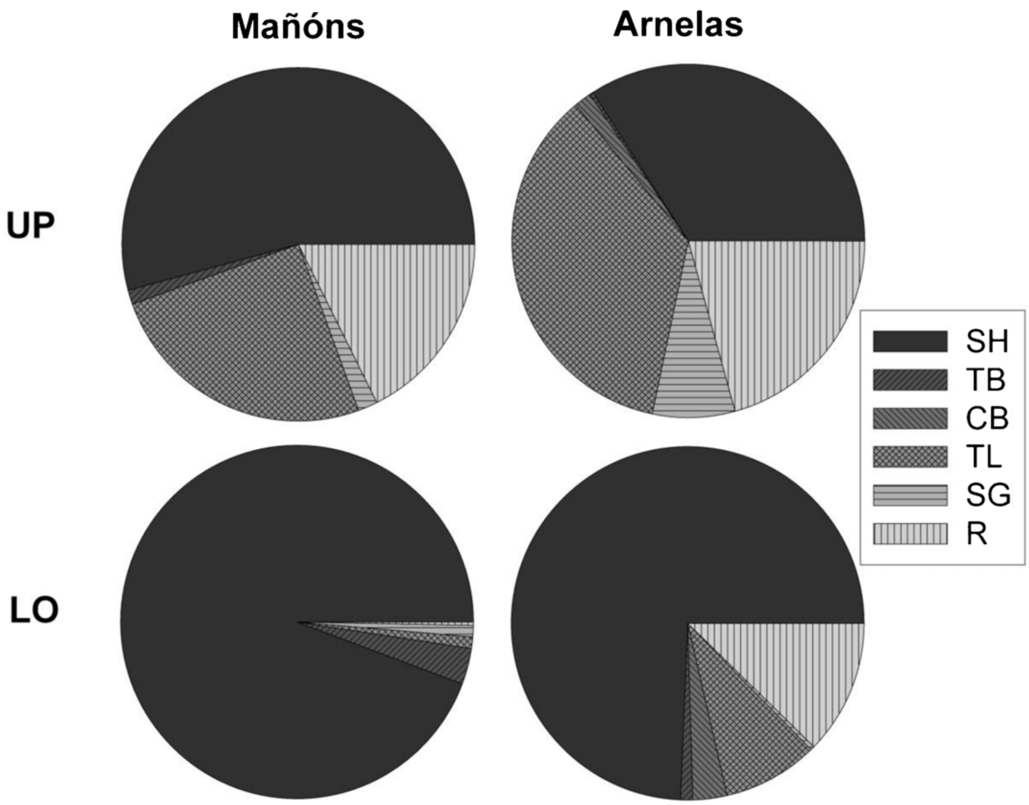


**Fig. 5.** Biomass of the functional groups of wrack. Mean annual biomass of the main functional groups of wrack collected on the beaches at the upper (UP) and lower (LO) tidal zones: sheet-like (SH), thin branched (TB), coarsely branched (CB), thick-leathery (TL), seagrass (SG) and remains portion (R).

Despite the high temporal variability, the spatial pattern of the dominant algal groups was similar throughout the year (Fig. 6). The dominance of sheet-like and thin branched macroalgae on the low-tide terraces of each beach prevailed throughout the year, whereas the seasonal cycle varied slightly between beaches. The highest relative biomass of sheet-like species in Mañóns was detected from spring to summer months (e.g.: 93.3% and 99.1% in May and September respectively), and from winter to spring months in Arnelas (e.g.: 99.3% and 99.9% in January and March). The relative biomass of the species included in the thick leathery group was higher on the upper levels in both beaches, with the largest accumulation from late summer to winter months (e.g.: 64.2% and 52.2% for October in MA and AR respectively), in coincidence with the lowest presence of opportunistic green algae. A single event of seagrass dominance was observed in May on the upper level of Arnelas beach (78.1%). The relative contribution of the decay fraction to the wrack biomass was quite stable throughout the year for both beaches, with the values on the upper levels higher than those recorded on the lower beach. The group of coarsely branched species exhibited the lowest biomass on both beaches during the study period (Fig. 6).

**Table 4**
Details of the 3-factor PERMANOVA test checking *beach*, *level* and *month* as fixed factors. Functional groups were considered as level of aggregation. (df) degrees of freedom; (MS) mean square; Pseudo-*F* statistic.

| Source | df | MS | Pseudo-F |
|---|---|---|---|
| Beach (B) | 1 | 38,673 | 69.352* |
| Level (L) | 1 | 90,760 | 162.76* |
| Month (M) | 12 | 14,258 | 25.569* |
| B × L | 1 | 11,056 | 19.826* |
| B × M | 12 | 12,084 | 21.669* |
| L × M | 12 | 4360 | 7.8186* |
| B × L × M | 12 | 4519.1 | 8.1039* |
| Res | 260 | 557.64 | |
| Total | 311 | | |

* $p = 0.001$

## 4. Discussion

The results of this study provide evidence of the variability in the deposition pattern of wrack species on estuarine beaches, both in time and space. Spatial differences in the species composition of the algal wrack in relation with beach morphology were consistent throughout the year. Sheet-like and thin branched species were stranded mainly on the lower tidal levels, while thick leathery and coarsely branched species dominated the drift-line and upper zones. These results indicate that the spatial variability in wrack composition on estuarine beaches might be explained through interactions between beach topography and species characteristics. Other putative environmental drivers, such as coastal hydrodynamics, adventives wind-transport and features of the swash-zone, are necessary contributors to observed patterns. Temporal variability in species composition were detected during the study period; data suggest that stranding period could be connected with factors such as life cycle and/or interspecific differences in nutrient requirement between opportunistic and slow-growing species.

### 4.1. Wrack biomass

The average monthly biomass values on both beaches (58 and 76 g DW m$^{-2}$ in MA and AR respectively) were comparable to those reported from northern European estuaries (Pihl et al., 1999; Anibal et al., 2007). Although both beaches showed similar values of stranded biomass, a different seasonal pattern of wrack supply was detected during the study period. This is in accordance with previous studies, which showed frequent temporal changes in

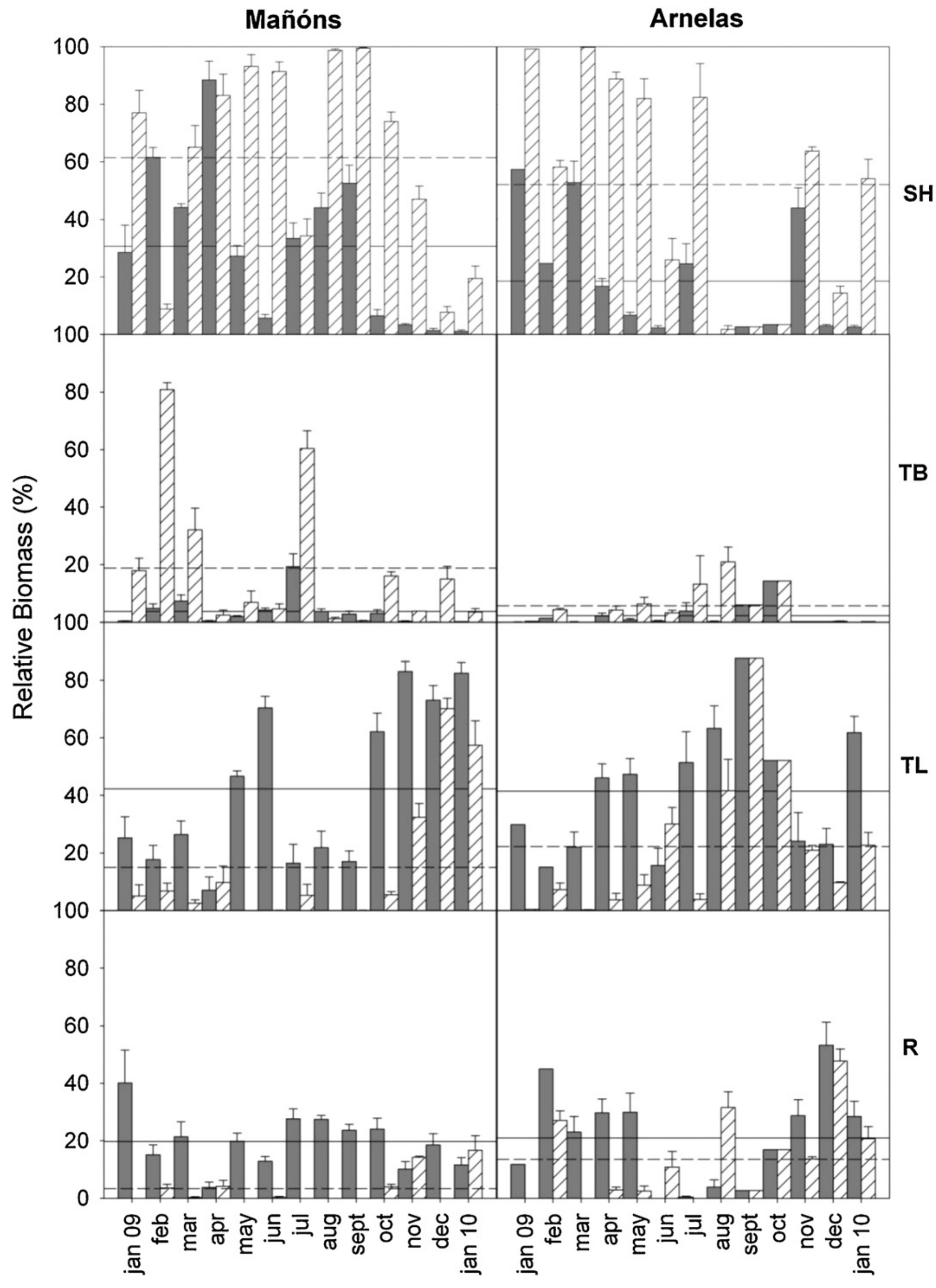


**Fig. 6.** Seasonal variability of the functional groups of wrack. Seasonal variability of the main functional groups of wrack collected on each beach. Gray bars indicate the relative biomass of each group for the upper level, and white bars for the lower ones. Monthly average biomass at each level ($n = 6$; ±SE). Solid lines line and dashed line denote average monthly biomass for the upper and lower zone respectively.

drifted macroalgae within and between sites (Bell and Hall, 1997). Differences in algal subsidies of the two studied beaches could be related to a number of factors, including unequal source ecosystems (surrounding rocky areas and sea-beds) and seasonal changes in hydrodynamic conditions at a local scale (currents and wave environment). The studied area is characterized by seasonal changes in the predominant wind direction, which affect transportation and translocation mechanisms of drift macroalgae. Moreover, coastal topography (Jackson et al., 2002) and intrinsic variability of water characteristics within the ría, such as differences in nutrient concentration (Fox et al., 2008), can potentially influence the amount of wrack that reach the beaches, thus contributing to the seasonal variability in algal biomass. The peak values of biomass stranded in Mañóns beach are probably associated with the algal bloom events that typically occur in the *Ría de Arousa* during summer period (Villares and Carballeira, 2004), linked with extended photoperiod, upwelling conditions and temperature increase; in contrast, the large deposits of wrack measured during the predominant rainfall period (winter) in Arnelas beach, could be linked with nutrient discharges of the nearby *Umia River*. Nutrients inputs supplied either by the upwelling events and the freshwater discharge may act as fertilization agents at different seasons of the year, thus promoting differences in productivity of source ecosystems (e.g. rocky areas) and heterogeneity in algal subsidies.

The distribution of the total wrack biomass differed among beaches; Mañóns accumulated a significant larger relative biomass on the upper level than that on the low-tide terrace for most of the year, while distribution of deposits on Arnelas beach was more variable over time. Although both beaches are sheltered and located in the interior of the estuary, differences in orientation toward open ocean and/or source environments might be responsible for the differences in the stranded wrack dynamics. Orientation within the estuary determines the effect of the prevailing winds (the strength and direction) and the type of waves reaching the beach (Nordstrom and Jackson, 2012). Previous studies showed that the strength and direction of the prevailing winds can influence the standing crop of wrack macroalgae (Lowthion et al., 1985); huge variations in the wave energy level may be found in sheltered environments within short distance alongshore, since variables such as orientation and distance from the mouth of the estuary are highly site-specific (Jackson, 1995).

### 4.2. Species composition

The Division Chlorophycophyta (mainly genera *Ulva*) dominated wrack species composition and represented the greatest contribution to the relative average annual biomass. This result provided evidences of the existence of blooms of opportunistic algae within the ría, which is in accordance with similar processes documented around the world (see Teichberg et al., 2010 and references therein). The huge accumulation of opportunistic algae in estuarine zones is related to their sheltered environment, higher water temperatures than in open waters, and certain episodic effluent events, which enhance the enrichment and nutrient concentration in the water column. Particularly, in the studied area, the wind driven upwelling events, which replenish nutrients, can be related with the occurrences of macroalgal blooms (Kiirikki and Blomster, 1996).

Brown macroalgae showed lower biomass than green macroalgae. This agrees with some studies which report a shift from slow-growing brown and red algae to fast-growing green algae in estuarine and sheltered areas (Lavery et al., 1991). Differences in wrack species composition between exposed and sheltered beaches could be explained by the specific source of the algal deposits. Wrack are mainly of local origin (blooms of green algae) at sheltered sites; while the drifted macroalgae on exposed beaches are supplied by surrounding areas (Berglund et al., 2003), where kelp and brown macroalgae dominate the rocky shore landscape of temperate latitudes.

The observed spatial pattern of wrack species composition was similar throughout the study period in the two different tidal zones. This agrees with other studies that stress the variation in wrack deposits composition during the different phases of the tidal cycle (Orr et al., 2005), thus resulting in the variation in the composition of the wrack deposits.

The remains fraction concentrates its biomass on the upper beach levels throughout the year, indicating a long exposure time of these deposits (from previous spring high-tide) to wind and solar radiation, as well as to faunal activity which promotes degradation and fragmentation. Macroalgae species with air bladders or structures with positive buoyant properties, e.g. *Fucus* spp., *A. nodosum*, *S. muticum*, or *Cystoseira* spp., showed the highest average biomass on the upper levels, while sheet-like species (e.g. *Asperococcus* sp. and *Ulva* spp.) and thin branched (e.g. *G. gracilis*) without buoyant structures mostly strand on the low tide terraces.

This pattern of spatial deposition is probably related with the hydrodynamic forces that operate in the swash zone throughout the tidal cycle. During the transition between flow and ebb at high tide, the steady swash zone on the upper foreshore concentrates the effect of the waves on the drift line level. Therefore, macroalgae and seagrasses floating in the water column remain in suspension until they strand in the upper edge of the wave up-rush. Additionally, air floating structures aid the species to strand once the tidal recession starts. The reduction in turbulence and swash energy associated with the beach profile at low tide, allows more algae to settle and accumulate on the low-tide terrace; in this way species without buoyant structures could be favored to strand on this part of the beach. We conclude that this pattern of wrack species deposition remains consistent regardless of the stranded biomass reaching a beach.

### 4.3. Temporal variability of algal wrack composition

Seasonal stranding of sheet-like species (mainly represented by the genus *Ulva*) was consistent with previous works reporting the highest biomass values during spring and summer months (Lavery et al., 1991; Villares and Carballeira, 2004). A number of biotic and physical factors such as wind transport, degradation and grazing (Lowthion et al., 1985; Pregnall and Rudy, 1985; Lastra et al., 2008), can be responsible of the minimum values of opportunistic species observed in Arnelas from August to October. Previous studies indicated that the advective wind transport for some periods often changed drastically the distribution of ephemeral algae and could purge an estuarine embayment completely (Salomonsen et al., 1999). Therefore, wind effect influences the seasonal succession of dominant species in shallow areas and a significant factor for the regulation of algal wrack biomass in estuarine beaches.

The biomass of macroalgal wrack recorded in this study suggests an inverse occurrence of thick leathery species and sheet-like species along the year cycle. This might be related to interspecific differences in nutrient requirements between fast and slow growing species (Martínez et al., 2012), as well as to differences in life cycles, producing dissimilar stocks in the rocky habitat, which can differentially subsidize the beaches once detached by waves and currents.

## 5. Conclusion

This study shows that beach topography, together with the morphology of macroalgae species, influence the distribution of stranded wrack along the beach face, which may in turn affect the distribution of benthic macrofauna.

The wrack species composition on the upper foreshore is similar to those deposits identified on exposed beaches (Barreiro et al., 2011), while lower tide terraces were dominated by macroalgae species characteristic of sheltered environments; thus, a heterogeneous distribution of the spatial and trophic niches available for beach macrofauna is identified. These distinct environments should not be overlooked in the ecological studies of estuarine beaches, but be instead explicitly incorporated into sampling effort. Further research on the implications of wrack dynamics in sedimentary characteristics and faunal distribution is needed.

## Acknowledgements

The authors thank L. Soliño, J. Hernández, J. Pascual, L. Gestoso, A. Serrano, L. García, A. Gómez, P. Otero and I.F. Rodil for help with field work. Thanks are also due to E.G. Mellado for fruitful help in the English writing of this manuscript. We are very grateful to the associated editor and two anonymous reviewers for critical review of the manuscript. This research was supported by the Ministerio de Ciencia e Innovación (BFU2010-16080) and the Xunta de Galicia (10PXIB312152PR).

## References


Anibal, J., Rocha, C., Sprung, M., 2007. Mudflat surface morphology as a structuring agent of algae and associated macroepifauna communities: a case study in the Ria Formosa. J. Sea Res. 57, 36–46.

Barreiro, F., Gómez, M., Lastra, M., López, J., de la Huz, R., 2011. Annual cycle of wrack supply to sandy beaches: effect of the physical environment. Mar. Ecol. Prog. Ser. 433, 65–74.

Bell, S., Hall, M., 1997. Drift macroalgal abundance in seagrass beds: investigating large-scale associations with physical and biotic attributes. Mar. Ecol. Prog. Ser. 147, 277–283.

Berglund, J., Mattila, J., Rönnberg, O., Heikkilä, J., Bonsdorff, E., 2003. Seasonal and inter-annual variation in occurrence and biomass of rooted macrophytes and drift algae in shallow bays. Estuar. Coast. Shelf Sci. 56, 1167–1175.

Blanton, J., Atkinson, L., de Castillejo, F., Montero, A., 1984. Coastal upwelling off the Rías Bajas, Galicia, northwest Spain. I. Hydrographic Studies. Rapp. P.Y. Reun. Cons. Int. Explor. Mer. 183, 79–90.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: user manual/tutorial, Plymouth.

Crawley, K., Hyndes, G., Vanderklift, M., Revill, A., Nichols, P., 2009. Allochthonous brown algae are the primary food source for consumers in a temperate coastal environment. Mar. Ecol. Prog. Ser. 376, 33–44.

de Castro, M., Gómez-Gesteira, M., Prego, R., Taboada, J.J., Montero, P., Herbello, P., Pérez-Villar, V., 2000. Wind and tidal influence on water circulation in a Galician ria (NW Spain). Estuar. Coast. Shelf Sci. 51, 161–176.

Denny, M., Gaylord, B., 2002. The mechanics of wave-swept algae. J. Exp. Biol. 205, 1355–1362.

Dugan, J.E., Hubbard, D.M., McCrary, M.D., Pierson, M.O., 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuar. Coast. Shelf Sci. 58, 25–40.

Duong, H.L.S., Fairweather, P.G., 2011. Effects of sandy beach cusps on wrack accumulation, sediment characteristics and macrofaunal assemblages. Aust. Ecol. 36, 733–744.

Emery, K., 1961. A simple method of measuring beach profiles. Limnol. Oceanogr. 6, 90–93.

Fox, S.E., Stieve, E., Valiela, I., Hauxwell, J., McClelland, J., 2008. Macrophyte abundance in Waquoit Bay: effects of land-derived nitrogen loads on seasonal and multi-year biomass patterns. Estuar. Coasts 31, 532–541.

Gonçalves, S.C., Marques, J.C., 2011. The effects of season and wrack subsidy on the community functioning of exposed sandy beaches. Estuar. Coast. Shelf Sci. 95, 165–177.

Heck, K.L., Carruthers, T.J.B., Duarte, C.M., Hughes, a.R., Kendrick, G., Orth, R.J., Williams, S.W., 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems 11, 1198–1210.

Jackson, N.L., 1995. Wind and waves: influence of local and non- local ocean waves on meso-scale beach behavior in estuarine environments. Ann. Assoc. Am. Geogr. 85, 21–37.

Jackson, N.L., Nordstrom, K.F., Eliot, I., Masselink, G., 2002. 'Low energy' sandy beaches in marine and estuarine environments: a review. Geomorphology 48, 147–162.

Jędrzejczak, M.F., 2002. Spatio-temporal decay 'hot spots' of stranded wrack in a Baltic sandy coastal system. Part I. Comparative study of the pattern: 1 type of wrack vs 3 beach sites. Oceanologia 44, 491–512.

Kiirikki, M., Blomster, J., 1996. Wind induced upwelling as a possible explanation for mass occurrences of epiphytic *Ectocarpus siliculosus* (Phaeophyta) in the northern Baltic Proper. Mar. Biol. 127, 353–358.

Lastra, M., Page, H.M., Dugan, J.E., Hubbard, D.M., Rodil, I.F., 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. Mar. Biol. 154, 163–174.

Lavery, P., Lukatelich, R., Mccomb, A., 1991. Changes in the biomass and species composition of macroalgae in a eutrophic estuary. Estuar. Coast. Shelf Sci. 33, 1–22.

Lowthion, D., Soulsby, P.G., Houston, M.C.M., 1985. Investigation of a eutrophic tidal basin Part I. Factors affecting the distribution and biomass of macroalgae. Mar. Ecol. Prog. Ser. 15, 263–284.

Martínez, B., Pato, L.S., Rico, J.M., 2012. Nutrient uptake and growth responses of three intertidal macroalgae with perennial opportunistic and summer-annual strategies. Aquat. Bot. 96, 14–22.

McLachlan, A., Brown, A.C., 2006. The ecology of sandy shores. Elsevier, Amsterdam.

Mellbrand, K., Lavery, P.S., Hyndes, G., Hambäck, P.A., 2011. Linking land and sea: different pathways for marine subsidies. Ecosystems 14, 732–744.

Nordstrom, K.F., 1992. Estuarine Beaches. Elsevier Science Publishers, New York.

Nordstrom, K.F., Jackson, N.L., 2012. Physical processes and landforms on beaches in short fetch environments in estuaries small lakes and reservoirs: a review. Earth-Sci. Rev. 111, 232–247.

Nordstrom, K.F., Jackson, N.L., Hartman, J.M., Wong, M., 2007. Aeolian sediment transport on a human-altered foredune. Earth Surf. Process. Landform 32, 102–115.

Ochieng, C.A., Erftemeijer, P.L.A., 1999. Accumulation of seagrass beach cast along the Kenyan coast: a quantitative assessment. Aquat. Bot. 65, 221–238.

Olabarria, C., Lastra, M., Garrido, J., 2007. Succession of macrofauna on macroalgal wrack of an exposed sandy beach: effects of patch size and site. Mar. Environ. Res. 63, 19–40.

Orr, M., Zimmer, M., Jelinski, D.E., Mews, M., 2005. Wrack deposition on different beach types: spatial and temporal variation in the pattern of subsidy. Ecology 86, 1496–1507.

Pelletier, A.J.D., Jelinski, D.E., Treplin, M., Zimmer, M., 2011. Colonisation of beach-cast macrophyte wrack patches by talitrid amphipods: a primer. Estuar. Coasts 34, 863–871.

Pihl, L., Svenson, A., Moksnes, P.O., Wennhage, H., 1999. Distribution of green algal mats throughout shallow soft bottoms of the Swedish Skagerrak archipelago in relation to nutrient sources and wave exposure. J. Sea Res. 41, 281–294.

Piriz, M., Eyras, M., Rostagno, C., 2003. Changes in biomass and botanical composition of beach-cast seaweeds in a disturbed coastal area from Argentine Patagonia. J. Appl. Phycol. 15, 67–74.

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of ecology: the dynamics food webs subsidized spatially. Annu. Rev. Ecol. Evol. Syst. 28, 289–316.

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

Pregnall, A.M., Rudy, P.P., 1985. Contribution of green macroalgal mats (*Enteromorpha* spp) to seasonal production in an estuary. Mar. Ecol. Prog. Ser. 24, 167–176.

Rodil, I.F., Olabarria, C., Lastra, M., Lopez, J., 2008a. Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. J. Exp. Mar. Biol. Ecol. 358, 1–13.

Rodil, I.F., Cividanes, S., Lastra, M., López, J., 2008b. Seasonal variability in the vertical distribution of benthic macrofauna and sedimentary organic matter in an estuarine beach (NW Spain). Estuar. Coasts 31, 382–395.

Rossi, F., Underwood, A., 2002. Small-scale disturbance and increased nutrients as influences on intertidal macrobenthic assemblages: experimental burial of wrack in different intertidal environments. Mar. Ecol. Prog. Ser. 241, 29–39.

Rubal, M., Veiga, P., Vieira, R., Sousa-Pinto, I., 2011. Seasonal patterns of tidepool macroalgal assemblages in the north of Portugal. Consistence between species and functional group approaches. J. Sea Res. 66, 187–194.

Salomonsen, J., Flindt, M., Geertz-Hansen, O., 1999. Modelling advective transport of *Ulva lactuca* (L) in the sheltered bay, Møllekrogen, Roskilde Fjord, Denmark. Hydrobiologia 397, 241–252.

Sousa-Dias, A., Melo, R.A., 2008. Long-term abundance patterns of macroalgae in relation to environmental variables in the Tagus Estuary (Portugal). Estuar. Coast. Shelf Sci. 76, 21–28.

Spiller, D.A., Piovia-Scorr, J., Wright, A.N., Yang, L.H., Takimoto, G., Schoener, T.W., Iwata, T., 2010. Marine subsidies have multiple effects on coastal food webs. Ecology 91, 1424–1434.

Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69, 476–498.

Teichberg, M., Fox, S.E., Olsen, Y.S., Valiela, I., Martinetto, P., Iribarne, O., Muto, E.Y., Petti, M.A.V., Corbisier, T.N., Soto-Jiménez, M., Páez-Osuna, F., Castro, P., Freitas, H., Zitelli, A., Cardinaletti, M., Tagliapietra, D., 2010. Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. Global Chang. Biol. 16, 2624–2637.

Underwood, A.J., 1997. Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.

Villares, R., Carballeira, A., 2004. Nutrient limitation in macroalgae (*Ulva* and *Enteromorpha*) from the Rías Baixas (NW Spain). Mar. Ecol 25, 225–243.