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The trophic significance of the invasive seaweed *Sargassum muticum* in sandy beaches

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ABSTRACT

Native and exotic seaweeds frequently lie on the beach and sustain part of the benthic food web. However, the role of exotic seaweeds as food sources for beach consumers has been poorly studied. We studied the temporal and spatial variability in the trophic significance of the invasive brown seaweed *Sargassum muticum* on sandy beaches. We measured the stable isotopes (δ^{13}C and δ^{15}N) in the tissues of *S. muticum* and of invertebrate consumers and estimated the dietary biomass proportion of *S. muticum* during four sampling dates at two beaches and heights on the shore. Samples were collected from eight pitfall traps placed at a distance of 2 m from each other. Detrital macroalgae and seagrasses were also collected by hand within an area of 30 cm around each pitfall trap. We measured the spatial and temporal variability in the isotope composition of the beach consumers and of *S. muticum* using different models of analyses of variance. We then calculated the biomass proportion of *S. muticum* to the animal diet with a two-isotopic mixing model. The invasive alga *S. muticum* seemed to be one of the main food sources for the amphipod *Talitrus saltator* and, to a less extent, for the isopod *Tylos europaeus*. The importance of *S. muticum* was however temporally variable and decreased during spring (in March and May), probably due to the availability of native macrophytes. The supply of invasive wrack to beach food webs thus deserves more attention if we want to understand their role in influencing food web dynamics.

1. Introduction

Marine seaweeds and seagrasses are often detached by waves or during storms and transported to nearby beaches where they accumulate for a variable amount of time and decompose (Inglis, 1989; Kirkman and Kendrick, 1997). These heaps of plant detritus, commonly referred as wrack, provide important, though ephemeral, spatial subsidies (*sensu* Polis et al., 1997) to sandy beaches (Griffiths et al., 1983). They may become a refuge from desiccation and predation (Buck et al., 2003; Lewis et al., 2007) as well as an important food source for a range of benthic consumers (Bedford and Moore, 1984; Polis et al., 1997; Bolam et al., 2000). Their role as food and nutrient supplier is of such an importance that they may become metabolic hotspots on poorly-enriched sandy beaches (Coupland et al., 2007). Furthermore, by providing allochthonous marine food sources to beach ecosystems, wrack becomes an important vehicle of carbon and nutrient exchange between different marine ecosystems and between marine and terrestrial ecosystems (Brown and McLachlan, 1990; Dugan et al., 2003; Colombini and Chelazzi, 2003; Schlacher and Connolly, 2009). Although it is often assumed that invertebrates are directly involved in the uptake of wrack, little is known about the role of this phytodetritus in subsidizing food to supralittoral beach communities (Bustamante and Branch, 1996; Mews et al., 2006). Such detection may be complicated by the existence of spatially and temporally variable sources of food. Different species of wrack may become available for a variable time and at different positions on the shore, depending on beach dynamics, macroalgal decomposition rate and life cycle, nutritional value or the presence of macroalgal species on the adjacent rocky shores (Orr et al., 2005). Furthermore, changes in environmental conditions such as temperature or desiccation may greatly affect macroalgal decomposition rates. Therefore, macroalgal availability could vary according to the time of the year, when macroalgae become available on the beach, or their position along the shoreline. For example, the higher the seaweed is located on the beach, the longer is supposed to be deposited (Orr et al., 2005). In addition, the beach consumers may greatly increase the spatial variability of beach food webs. Consumers might feed locally or move along the shore towards the food sources (Colombini et al., 2002). Such feeding patterns may vary within the same species as they may be a behavioral response to the availability of food and the need of refuge (Duffy and Hay, 1991; Pavia et al., 1999; Stachowicz and Hay, 1999; Cruz-Rivera and Hay, 2001).

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Very little attention has been given to the role of invasive seaweeds in providing food to these sandy beach consumers (Rodil et al., 2008), despite the fact that the arrival of invasive seaweeds and plants to new areas has become an increasing phenomenon during the last decades (Pauchard and Shea, 2006). According to the enemy release hypothesis, ERH, introduced plants should experience a decrease in regulation by herbivores due to the absence of their natural grazers (Keane and Crawley, 2002). Therefore, the detritus of invasive species could be less edible than the detritus of native seaweeds for beach inhabitants, and reduce the amount of wrack recycled in the food web. Under these circumstances, the presence of invasive seaweed detritus may even be a *cul-de-sac* for the flux of allochthonous organic matter into the beach food web.

The introduced Japanese brown alga *Sargassum muticum* (Yendo) Fensholt has invaded many intertidal habitats of Europe and North America (Britton-Simmons, 2004). *S. muticum* species invaded northern Spain in the 1980s and it was first observed on the Galician coast in 1986 (Fernández et al., 1990). Since then, it has successfully colonized most of the Galician estuaries increasing its abundance rapidly. Nonetheless, the trophic role of *S. muticum* has been poorly understood (Rodil et al., 2008).

This study investigated the role of this invasive seaweed as a potential food source for the invertebrates inhabiting sandy beaches on the Galician coast. In particular, we measured natural abundances of stable isotopes (δ^{13}C and δ^{15}N) of wrack and consumers, and estimated the biomass proportion of *S. muticum* contributing to the diet of the benthic consumers along two levels of the shoreline of two exposed sandy beaches at different times of the year. Shifts in the spatial and temporal isotopic composition of macroalgae and consumers may often occur (see Machás et al., 2006). Isotopic signature of macroalgal specimens might for instance vary according to the time of the year and the place where they grow. Furthermore, wrack isotopic composition varies during their decomposition rate according to environmental variables such as temperature, desiccation or beach dynamics. Thus, we expected changes in the isotopic signatures influenced by the origin of wrack and the different processes the wrack undergo (i.e.; dehydration, aging, fragmentation) at different shore levels and over time. Moreover, since isotopic signature of consumers reflects that of their food sources, we also expected that beach consumers would vary their isotopic composition following variations in their food sources. We tested the hypotheses that (i) the isotopic signatures of *S. muticum* and of consumers would show differences along the shore and through the year and that (ii) the variability in the isotopic signature of consumers would be influenced by that of *S. muticum*. Eventually, since macroalgae life-history traits and environmental conditions as well as consumer behaviour and energy requirements may greatly modify the availability of wrack as food for beach consumers, we estimated the biomass proportion of *S. muticum* contributing to the consumer diet and tested whether there would be differences along the shore and through the year.

2. Material and methods

2.1. Sampling and laboratory analyses

The study was done in the South part of the Galician coast (Northwest coast of Spain). We randomly chose two exposed sandy beaches, about 400 m apart, that presented similar morpho-dynamic conditions. Hereafter these beaches will be referred as Barra (42° 15′ N, 8° 51′ W) and Viñó (42° 15′ N, 8° 50′ W). We collected data on the natural abundance of stable isotopes (δ^{13}C and δ^{15}N) for sandy beach consumers and wrack in October and December 2007 and in March and May 2008. Eight pitfall traps made of plastic cups (15 cm, inner diameter) filled up with water were pushed in the sand and placed at a distance of 2 m from each other at two levels on the shore, i.e. the strandline and 3 m above the strandline (hereafter lower and upper zone, respectively). Pitfall traps were left overnight and the day after in the morning the content of each pitfall was collected and taken to the laboratory. Animals were picked directly from 4 randomly chosen pitfalls. Detrital macroalgae and seagrass were collected by hand within an area of ~30 cm around each pitfall trap. Additional detrital material deposited on the beach and located outside this area was also collected when it differed from that found inside the pitfall traps.

In the laboratory, animals were sorted alive and relaxed with 10% MgCl to be accurately cleaned of any residual debris and clean the stomach content. In total, 619 samples were analysed. Animals were then dried at 60 °C for 48 h. The detrital macroalgae and seagrass were rinsed with filtered seawater to clean off epibionts, dried (60 °C for 48 h) and ground to fine powder. All dried samples were stored frozen (−20 °C) until isotopic analyses.

The carbon and nitrogen isotopic composition of the samples was determined using a MAT 253 stable isotope ratio mass spectrometer. The carbon and nitrogen isotope ratios are expressed in the delta notation δ^{13}C and δ^{15}N, where $\delta X = [(R_{\mathrm{sample}}/R_{\mathrm{reference}}) - 1] \times 10^3$, with $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ for carbon and ${}^{15}\mathrm{N}/{}^{14}\mathrm{N}$ for nitrogen. Reference material was Vienna Pee Dee Belemnite standard (PDB) for carbon and air N_2 for nitrogen. Precision in the overall preparation and analysis was ±0.13% for both δ^{13}C and δ^{15}N. Samples were acidified before analyses by adding a drop of 10% HCl. Although acidification may introduce a bias in determining the natural abundance of δ^{15}N (Mateo et al., 2008), such treatment was necessary due to the large amount of carbonate in the wrack provided by coralline macroalgae and serpulid polychaetes. In addition, recent analyses on macrofauna consumers typical of intertidal flats revealed no differences between natural and acidified samples (Rossi F. unpublished).

2.2. Statistical analyses

To test for differences in the spatial and temporal distribution of stable isotopic signatures of *S. muticum* and benthic consumers (δ^{13}C and δ^{15}N), we used different models of analyses of variance (ANOVA). To test for differences in the δ^{13}C and δ^{15}N of *S. muticum*, we used a 3-way model ANOVA with sampling dates (random, 4 levels: October, December, March and May), shore (fixed, 2 levels: upper and lower zones) and beaches (random, 2 levels: Barra and Viñó) as orthogonal factors, and pitfall traps as replication units.

Talitrus saltator was the only consumer species to be analysed because it occurred in a sufficient number of traps at each shore level and beach to perform ANOVA (see *n* in Table 1). This species was however not collected in October and three sampling dates were used for detecting temporal fluctuations. To test for differences in the isotopic signatures (both δ^{13}C and δ^{15}N) of *T. saltator*, we used a 4-way model ANOVA with three orthogonal factors: sampling date (random, 3 levels: December, March and May), beach (random, 2 levels: Barra and Viñó) and shore (fixed, 2 levels: upper and lower zones) and one nested factor: pitfall traps. Animals collected within each pitfall were replicates. In order to balance the analyses of variance, three replicates traps and 6 animals per trap were used. Data were not-transformed whether or not variances of residuals were homogeneous because the ANOVA is robust to heterogeneous data when there are balanced data (Underwood, 1997). Factors were pooled when $P > 0.25$. When significant differences among main factors or their interactions were found, Student–Newman–Keuls (SNK) test was used as a posteriori comparison (Underwood, 1997). To test whether the differences observed in consumer isotopic signatures were due to the differences in *S. muticum*, we used a 3 factor analyses of covariance (ANCOVA), the same factors used for ANOVA and *S. muticum* isotopic signatures as covariate. Data were not transformed.

We calculated the contribution of *S. muticum* and the wrack species collected to the animal diet with a two-isotope mixing model (ISOSOURCE software, http://www.epa.gov/wed/pages/models.htm)

Table 1
Mean ± SD and sample numbers (*n*) of δ^{13}C and δ^{15}N at each beach (Barra and Viñó) and height on the shore (lower and upper zone) for each sampling date.

Barra Beach	October 2007			December 2007			March 2008			May 2008		
	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*
Lower zone												
Sargassum muticum	−18.4 ± 3.4	5.6 ± 0.6	4	−17.7 ± 1	5.2 ± 0.2	4	−20.4 ± 0.6	7.8 ± 0.5	4	−18.7 ± 1.2	5.9 ± 0.7	4
Ascophyllum nodosum							−17.4 ± 1.6	8.0 ± 0.8	3			
Colpomenia peregrina	−12.5 ± 3.4	6.5 ± 0.1	2									
Cystoseira baccata	−18.8	5.7	1				−19 ± 1.1	6.2 ± 2.2	3	−17.7 ± 0.7	6.4 ± 1	6
Fucus spp.				−14.3	8.6	1	−16.2 ± 1	9.6 ± 1	2			
Himanthalia elongata										−13.4 ± 0.8	7.2 ± 0.5	2
Codium sp.	−18.8 ± 7.5	6.9 ± 0.4	6	−13.6	6.9	1						
Plocamium cartilagineum				−22.9	7.4	1						
Ulva rigida	−12.5 ± 3.9	4 ± 3.6	2	−14.5 ± 1.4	7.6 ± 0.6	2						
Zostera marina	−10.1 ± 0.9	6.5 ± 1.1	3	−10.3 ± 1.3	6.8 ± 1.4	3	−11.2	6.3	1	−9.6 ± 0.9	7 ± 0.6	5
Aleochara sp	−19.1	10.2	1	−18.3	10	1	−22.3	11.1	1			
Arctosa variana				−26	2	1						
Formicidae										−24.9	3	1
Phaleria cadaverina							−16.2 ± 0.2	9.7 ± 0.9	2	−19.6 ± 2.3	10.6 ± 0.8	4
Larva *P.cadaverina*										−18	9.8	1
Talitrus saltator				−17.5 ± 0.8	8.3 ± 0.7	35	−17.4 ± 1.6	10.0 ± 1.7	26	−16.9 ± 1.0	9.3 ± 0.7	25
Trechus sp	−28.6	5	1									
Tylos europaeus	−18.1 ± 0.6	9 ± 0.6	3				−17.4 ± 3.5	9.9 ± 1.3	4	−13.3	9.6	1
Upper zone												
Sargassum muticum	−22.0 ± 6.1	6.6 ± 1	4	−17.9 ± 3.8	4.9 ± 1.2	4	−19.2 ± 0.6	7.1 ± 0.9	8	−17.7 ± 0.8	5.6 ± 0.7	3
Ascophyllum nodosum	−26.5	5.9	1	−14.6 ± 1.4	7.2 ± 0	2	−16.9 ± 0.9	8.7 ± 0.8	8	−16.6	8.5	1
Cystoseira baccata							−19 ± 1.3	5.6 ± 1.7	6	−18.9 ± 0.7	7 ± 0.7	2
Fucus spp.	−22.4 ± 0.4	8.1 ± 0.8	2				−15.7 ± 1	8.4 ± 0.6	7	16.0 ± 1.2	7.8 ± 0.8	3
Ceramium rubrum				−18.6	8.2	1						
Zostera marina	−19.9 ± 1.8	6 ± 2.1	4	−9.3 ± 5.5	7.8 ± 2.1	4	−11 ± 1	6 ± 0.5	4	−10.3 ± 0.3	7.8 ± 0.2	3
Arctosa variana	−20.9		1									
Diptera	−20.4		1									
Formicidae				−25.1		1				−25.4	5.8	1
Julidae							−21.1 ± 1	16.7 ± 3.7	4			
Ligia oceanica							−20.9	5.7	1			
Lycosidade							−21.4 ± 1.6	9.1 ± 1.8	3	−19 ± 3.1	9.7 ± 2.1	4
Phaleria cadaverina	−19.3 ± 2.5	13.1 ± 8.7	2				−22.6 ± 2	13.6 ± 7.4	26	−20.2 ± 1.5	8.6 ± 2.9	5
Phaleria sp.				−20.9	3.9	1						
Talitrus saltator				−16.5 ± 0.7	8.5 ± 0.9	40	−16.8 ± 0.9	9.8 ± 0.7	26	−16.8 ± 0.6	9.3 ± 0.6	26
Trechus sp.							−19.2	5	1			
Tylos europaeus	−17.7 ± 1.3	9.2 ± 0.4	13				−21.9 ± 1.1	8.0 ± 0.7	8			

Viñó Beach	October 2007			December 2007			March 2008			May 2008		
	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*
Lower zone												
Sargassum muticum	−23.4 ± 3.9	5.9 ± 0.8	6	−19 ± 0.5	4.5 ± 0.3	4	−19.3 ± 0.7	8 ± 0.4	4	−18.2 ± 1.9	6.7 ± 0.5	5
Ascophyllum nodosum										−17.4	5.0	1
Colpomenia peregrina	−8.1	1.1	1				−13 ± 0.6	6.7 ± 0.8	3			
Cystoseira baccata	−25.1	3.8	1				−18.7 ± 1.2	5.8 ± 0.9	2	−18.7 ± 2.5	6.8 ± 0.3	4
Fucus spp.				−14.2	9.8	1				−14.9	6.6	1
Himanthalia elongata										−10.3	6	1
Sacchoriza polyschides				−13.5	7.2	1						
Ceramium rubrum							−8.4	7.5	1			
Ulva rigida				−14 ± 3.4	7.3 ± 0.2	3	−16.5 ± 0	8.1 ± 0	1			
Zostera marina	−10.1 ± 0	9.0 ± 0	1	−10.1 ± 1.3	7.7 ± 0.6	4						
Aleochara sp										−18.1 ± 0.5	11.1 ± 0.3	8
Formicidae							−21	11.4	1			
Ligia oceanica							−17.3	10	1			
Lycosidade							−20.4	11.8	1			
Phaleria cadaverina							−21.7	9.3	1	−20.4 ± 1.8	10 ± 0.9	3
Talitrus saltator				−16.7 ± 1	8.5 ± 2	42	−16.5 ± 0.8	9.3 ± 0.9	27	−16.8 ± 1.0	9.0 ± 0.5	26
Tylos europaeus	−17.6 ± 1.4	9.2 ± 0.4	11	−13.5	9.1	1	−16.5	8.8	1	−15.6	9.5	1
Upper zone												
Sargassum muticum	−19.2 ± 2.1	5.4 ± 0.8	4	−19.1 ± 1.1	5.3 ± 0.3	4	−19.1 ± 1	7.8 ± 0.3	5	−18.5 ± 1.7	5.4 ± 0.8	3
Ascophyllum nodosum	−22.4	5.9	1									
Colpomenia peregrina							−11 ± 0.7	6.7 ± 0.1	5			
Cystoseira baccata							−20.9	6.6	1	−17.7 ± 1.1	5.5 ± 0.8	4
Fucus spp.				−15.2	5.9	1				−12.3	6.2	1
Himanthalia elongata										−10.5	6.5	1
Ceramium rubrum							−16.7	6.4	1			
Lomentaria clavellosa							−29.9	6.6	1			
Plocamium cartilagineum							−32.4	6.7	1			
Enteromorpha intestinalis	−17.5	6.6	1				−8.3	8.6	1			
Ulva rigida							−17.6 ± 1.1	6.7 ± 0.0	2			

Table 1 (*continued*)

Viñó Beach	October 2007			December 2007			March 2008			May 2008		
	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*	δ^{13}C	δ^{15}N	*n*
Upper zone												
Zostera marina	−14.9 ± 6.7	7.2 ± 0.4	5	−10.1	6.9	1				−10.1 ± 0.3	7 ± 0.7	5
Aleochara sp.							−17.4 ± 1.2	14.3 ± 9.9	4	−17.7 ± 0.4	11.2 ± 0.3	3
Diplopoda				−15	2.9	1						
Eurinebria complanata							−23.4	10.9	1			
Lycosidade				−21.2	8.4	1						
Phalangiidae				−23.3	5.9	1						
Phaleria cadaverina							−14.4 ± 0.4	10.1 ± 0.5	2	−21.2 ± 1	10.7 ± 1	9
Talitrus saltator				−17.9 ± 1.1	8.2 ± 0.8	43	−16.4 ± 1.5	10.1 ± 1.0	26	−16.6 ± 1.0	9.2 ± 0.7	26
Tylos europaeus	−16.9 ± 1.8	9.5 ± 0.2	3	−14.8	9.4	1	−16.4 ± 3.6	10.4 ± 0.9	14	−13.7 ± 0.7	9.7 ± 1.1	5

(Phillips and Gregg, 2001, 2003). The biomass fraction of each *i* food sources (f_{Si}) used by the consumer can be calculated following the equation:

$$\delta X_{\mathrm{consumer}} = \sum \delta X_{\mathrm{Si}} f_{\mathrm{Si}}$$

assuming that $\sum f_{\mathrm{Si}} = 1$

where $\delta X_{\mathrm{consumer}}$ represents the isotopic signature of the consumer and δX_{Si} that of *i* food source.

If we want to estimate the fractions for each food source, $f_{\mathrm{Si},}$ it is necessary to measure *n* isotope signatures to estimate $n+1$ biomass fraction. The ISOSOURCE mixing model software has been designed for situations in which *n* isotopes are being used and more than $n+1$ sources are likely to be contributing to a mixture. It is however advisable to use food sources that differ considerably in their isotopic signatures. In this study, when the isotope signatures of different wrack species coincided (e.g. differences were <1‰) species were aggregated (Phillips et al., 2005).

Furthermore, to apply the mixing model it is necessary to include in the model the fractionation that each isotope value undergoes during the digestion and assimilation process. Although fractionation is usually accepted to be relatively constant at each trophic level, amphipods and herbivores in general may show great variability (Vander Zanden and Rasmussen, 2001). We therefore applied two different fractionation values to our data. We first assumed the well-accepted positive fractionation of +1‰ for δ^{13}C and a mean trophic enrichment of +3.4‰ for δ^{15}N as a result of the assimilation of food (Adin and Riera, 2003). We then used the fractionation values proposed by Crawley et al. (2007). These researchers showed that the fractionation of the amphipod *Allorchestia compressa*, a species relatively similar to those species found in this study, may greatly vary depending on the macrophyte species. In *Sargassum* genus, they found negative δ^{13}C discrimination, with values in the consumers −2‰ depleted and a small positive δ^{15}N fractionation, with values +1‰ increased in the consumer. For other macroalgal species, including red and brown algae these authors measured average −3‰ and +1‰ in δ^{13}C and δ^{15}N, respectively. Moreover, when *A. compressa* was fed with seagrass detritus, fractionation values were −10‰ and +3 to 4‰. We therefore maintained the fractionation of 3.4‰ for the seagrass detritus.

The data corrected for fractionation can be represented graphically with a variety of methods. Here, we have reported the real signatures of both wrack and consumers as points and we have superimposed on the graph the wrack isotopic signatures corrected for fractionation as points delimiting a polygon (Fig. 1 and Results section). This graphical representation may also help to visually estimate the importance of each food source for each consumer. The consumer feeds on some of the collected food sources only when its isotopic signature is delimited by the polygon. The closer the isotopic signatures of the consumer are to one of the food source isotopic signatures delimiting the polygon, the larger is the biomass proportion of that food source used by the consumer (Phillips et al., 2005).

To test for differences in the biomass proportion of *S. muticum* assimilated by the consumers, we applied the previously described a 3-way ANOVA model on the mean dietary biomass proportion of *S. muticum* calculated by ISOSOURCE at each pitfall trap. Data were log-transformed to avoid the skewness from normal distribution generated when calculating ratios. We restricted our analysis to the sampling dates of December 2007 and March 2008, because at these sampling dates *S. muticum* signatures were clearly distinguished from other wrack species at any beach and shore level and the standard errors of the calculated means were relatively small.

3. Results

3.1. Isotopic composition

The δ^{13}C of *S. muticum* and *T. saltator* showed differences in the interaction sampling date × beach × shore (ANOVA, $F_{3,\ 32}=6.0$, $P=0.002$ and $F_{2,\ 24}=5.2$, $P=0.004$, respectively). The *a posteriori* SNK test done on this interaction term showed that the δ^{13}C values of *S. muticum* were depleted in October at the upper zone of Barra beach, whereas the δ^{13}C values of *T. saltator* were depleted in December at the upper zone of Viñó beach (SNK, $P=0.05$, Table 1). After eliminating the date of October, when *T. saltator* was not found, the δ^{13}C values of *S. muticum* were higher in March than December and May (ANOVA, $F_{2,\ 24}=6.9$, $P=0.004$).

There was also a significant interaction sampling date × beach × shore for the δ^{15}N of *S. muticum* ($F_{3,\ 32}=3.4$, $P=0.03$), which was ^{15}N depleted in December and ^{15}N enriched in March consistently at any beach and shore level (SNK performed on the interaction, $P=0.05$). The δ^{15}N of *T. saltator* varied among sampling dates (ANOVA, $F_{1,\ 16}=18.00$, $P=0.001$). The *T. saltator* tissues were δ^{15}N-depleted in December (SNK, $P=0.05$, Table 1). Such temporal differences were removed by adjusting the values to the influence of *S. muticum* (ANCOVA, $P>0.05$).

Overall, the isotopic values of the isopod *Tylos europeus* were fairly similar to those of *T. saltator* especially in March and May (Table 1, Fig. 1). Among the other taxa collected, which were found sporadically in the pitfall traps, the staphylinid *Aleochara* sp., Lycosidae, Formicidae and the tenebrionid *Phaleria cadaverina* had δ^{15}N values very variable, with δ^{15}N either above, close or below those of *T. saltator* or *T. europeus*, probably indicating feeding at different trophic levels. The isopod *Ligia oceanica* had instead isotopic signatures very close to those of *T. europeus*, whereas the other taxa (the staphilinid *Trechus* sp., the arachnids *Arctosa variana* and Phalangiidae, Diptera, Julidae milleped and the carabid *Eurynebria complanata*) were ^{13}C− or ^{15}N− depleted (Table 1, Fig. 1), which may indicate a diet based on terrestrial sources.

S. muticum was collected at any sampling occasion on both beaches and heights on the shore. We also collected six native brown macroalgae, variably present on the beaches (*Cystoseira baccata*, *Fucus* spp.,

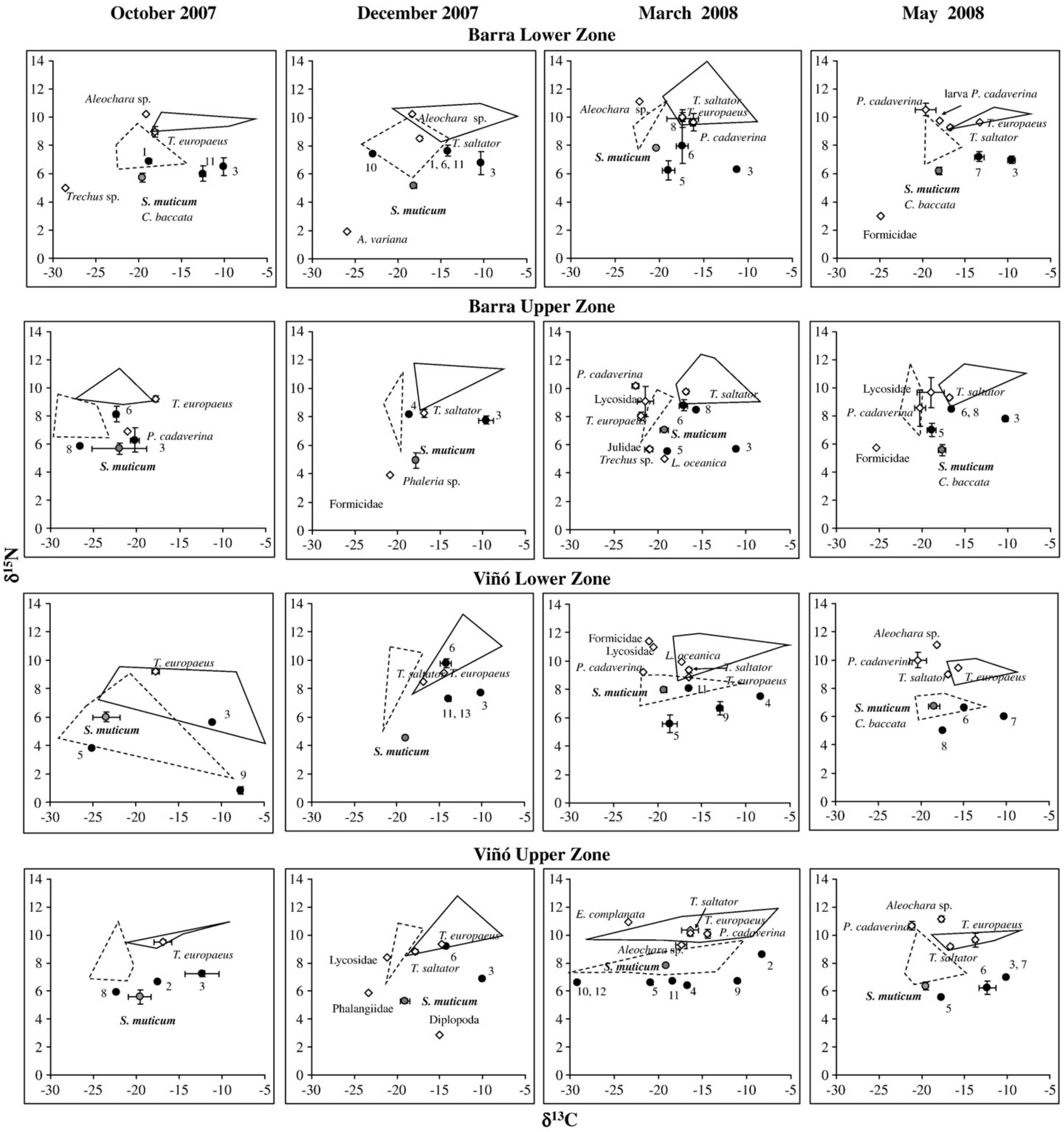


Fig. 1. Dual stable isotope plots for each beach (Barra and Viñó) and height on the shore (lower and upper zones) during October, December, March and May. Symbols refer to mean values (see Table 1 for Mean ± SD and *n*) of wrack (black circles) and consumers (open diamonds). *Sargassum muticum* is the grey circle. The polygons represent the projections of wrack signatures corrected for fractionation (see Material and methods). Continuous line indicates the correction according to the well-accepted fractionation of + 1 and + 3.4‰ for δ^{13}C and δ^{15}N, respectively (Adin and Riera, 2003). The polygon indicated as dashed line indicate the fractionation of − 2, − 3 or − 10‰ for δ^{13}C, 1 or 3.5‰ for δ^{15}N in *S. muticum*, other macroalgae and *Zostera marina*, respectively (Crawley et al. 2007). 1 = *Codium* sp.; 2 = *Enteromorpha intestinalis*; 3 = *Zostera marina*; 4 = *Ceramium rubrum*; 5 = *Cystoseira baccata*; 6 = *Fucus* spp.; 7 = *Himanthalia elongata*; 8 = *Ascophyllum nodosum*; 9 = *Colpomenia peregrina*; 10 = *Plocamium cartilagineum*, 11 = *Ulva rigida*, 12 = *Lomentaria clavellosa*, 13 = *Sacchoriza polyschides*.

Ascophyllum nodosum, *Colpomenia peregrina*, *Hymanthalia elongata and Sacchoriza polyschides*). Wrack was sometimes composed of red macroalgae (*Plocamium cartilagineum*, *Ceramium rubrum* and *Lomentaria clavellosa*) and green algae (*Enteromorpha intestinalis*, *U. rigida* and *Codium* sp.). The seagrass *Zostera marina* was often found mixed to the wrack seaweeds. These macrophytes had well distinguished isotopic

Table 2
Minimum and maximum dietary biomass proportion of wrack (ISOSOURCE) at each beach, height on the shore and sampling date.

Barra beach

Lower zone

			S. muticum	*S. muticum* + 5	3	5	6	7	10	11	1, 6, 11
October	*T. europaeus*	A		0.9–1	0–0.02					0–0.1	
December	*Aleochara sp.*	A	0–0.4		0–0.3				0.4–0.7		0–0.5
	T. saltator	A	0.7–1		0–0.1				0–0.2		0–0.1
		B	0–0.5		0–0.4				0–0.2		0.2–0.9
March	*P. cadaverina*	A	0–0.1		0.2–0.3	0.6–0.8	0–0.6				
	T. europaeus	A	0–0.3		0–0.2	0.5–0.9	0–0.1				
	T. saltator	A	0–0.4		0–0.2	0.5–0.9	0–0.2				
May	*P. cadaverina*	B			0.9–1			0–0.1			
	T. europaeus	A		0.4–0.7	0.2–0.5			0–0.4			
	T. saltator	A		0.8–1	0–0.1			0–0.2			

Upper zone

			S. muticum	*S. muticum* + 5	3	4	5	6	8
October	*T. europaeus*	A	0–0.03		0.9–1				
December	*T. saltator*	A	0.9–1		0–0.1	0–0.1			
March	*T. saltator*	A	0–0.7		0–0.2		0.2–0.7	0–0.4	0–0.3
May	*P. cadaverina*	B	0–0.5				0.04		0–0.6
	T. saltator	A	0.6–0.9		0–0.1		0–0.4		0–0.1

Viñó beach

Lower zone

			S. muticum	*S. muticum* + 5	3	4	5	6	9	11
October	*T. europaeus*	A	0.3–0.7		0.2–0.5		0–0.3		0–0.1	
December	*T. europaeus*	A	0.4–0.5		0.4–0.5			0–0.1		
	T. saltator	A	0.8–0.9		0–0.2			0–0.2		
March	*L. oceanica*	A	0–0.6			0–0.1	0.3–0.9		0–0.2	0–0.4
	P. cadaverina	B	0.9–1				0–0.1			0–0.1
	T. europaeus	A	0–03			0–0.1	0.8–0.9		0–0.2	
		B	0–0.6			0.1–0.5	0–0.2		0–0.5	0–0.7
	T. saltator	A	0–0.2			0–0.2	0.5–0.9		0–0.3	0–0.3
		B	0–0.1			0.3–0.4				0.5–0.7
May	*T. europaeus*	A		0.6–0.8				0–0.3		

Upper zone

			S. muticum	2	3	4	5	6	8	9	10, 12
October	*T. europaeus*	A	0–0.8		0–0.5				0–0.6		
December	*T. europaeus*	A	0.5–0.7		0.2–0.4			0–0.2			
	T. saltator	A	0.9–1		0–0.1						
March	*P. cadaverina*	A	0–0.5			0–0.9	0–0.5			0.1–0.8	0–0.2
	T. europaeus	A	0–0.7			0–0.9	0–0.7			0–0.7	0–0.3
	T. saltator	A	0–0.6			0–1	0–0.7			0–0.7	0–0.3
May	*T. europaeus*	A	0–0.6		0–0.5		0–0.7	0–0.7			
	T. saltator	A	0–0.9		0–0.2		0–1	0–0.2			

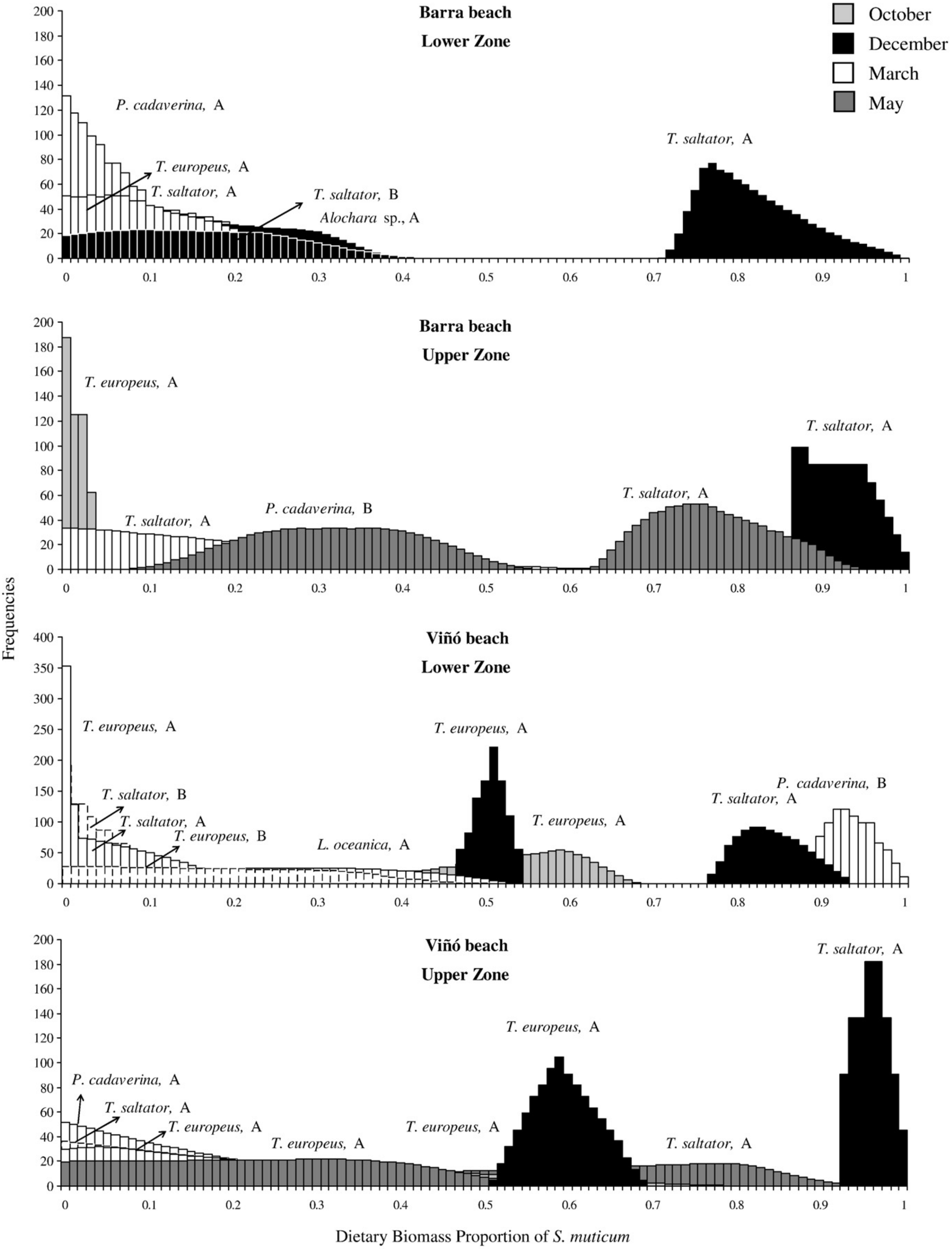
A: fractionation of +1 and +3.4‰ for δ^{13}C and δ^{15}N, respectively; B: fractionation of −2, −3, −10‰ for δ^{13}C and 1, 1, 3.5‰ for δ^{15}N in *Sargassum muticum*, other macroalgae and *Zostera marina*, respectively (see Materials and methods). 1 = *Codium* sp.; 2 = *Enteromorpha intestinalis*; 3 = *Zostera marina*; 4 = *Ceramium rubrum*; 5 = *Cystoseira baccata*; 6 = *Fucus* spp.; 7 = *Himanthalia elongata*; 8 = *Ascophyllum nodosum*; 9 = *Colpomenia peregrina*; 10 = *Plocamium cartilagineum*, 11 = *Ulva rigida*, 12 = *Lomentaria clavellosa*.

signatures, except *S. muticum* and *C. baccata* in May and in October, at the lower zone of Barra beach (see Table 1).

3.2. Mixing model

The dual-isotope plots (Fig. 1) showed that *T. saltator* and *T. europaeus* were included or very close to the polygon drawn by the wrack isotopic signatures using the classical fractionation of 1 and 3.4‰ (continuous line in Fig. 1), except at the lower zone of Viñó beach in May. These species were also included in the polygon drawn using the discrimination values from Crawley et al. (2007) (dashed line in Fig. 1) at the lower zones of Barra beach in December and of Viñó beach in March. The estimated dietary proportion of *S. muticum* decreased in March and May, except in the upper zone of Barra beach. In December, when both *T. europeus* and *T. saltator* were present, the proportion of *S. muticum* contributing to the diet of the former was smaller than that contributing to the diet of the latter (Table 2, Fig. 2). The biomass proportion of *S. muticum* assimilated by *T. saltator* decreased in March in both beaches, although differences were larger in Viñó than in Barra beach (ANOVA, significant interaction: sampling date × beach: $F_{1,\ 8} = 11.00$, $P = 0.01$; SNK done on the interaction at $P = 0.05$, Fig. 3).

The other consumers were rarely included within the polygons. *Aleochara* sp. was included at the lower zone of Barra beach in December, the isopod *L. oceanica* at the lower zone of Viñó beach in March and the tenebrionid *P. cadaverina* at Barra beach in March and May and at the upper zone of Viñó beach in March (Fig. 1). The estimated dietary proportion of assimilated *S. muticum* were low, except at the lower zone of Viño beach in March, when considering the discrimination values of Crawley et al. (2007) (Fig. 2).


Barra beach
Lower Zone
October
December
March
May
P. cadaverina, A
T. europeus, A
T. saltator, A
T. saltator, B
Alochara sp., A
T. saltator, A
Barra beach
Upper Zone
T. europeus, A
T. saltator, A
P. cadaverina, B
T. saltator, A
T. saltator, A
Viñó beach
Lower Zone
T. europeus, A
T. saltator, B
T. saltator, A
T. europeus, B
L. oceanica, A
T. europeus, A
T. europeus, A
T. saltator, A
P. cadaverina, B
Viñó beach
Upper Zone
P. cadaverina, A
T. saltator, A
T. europeus, A
T. europeus, A
T. europeus, A
T. europeus, A
T. saltator, A
T. saltator, A
Frequencies
Dietary Biomass Proportion of S. muticum
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
20
40
60
80
100
120
140
160
180
200
0
50
100
150
200
250
300
350
400

4. Discussion

Spatial and temporal variations in the isotopic composition of *S. muticum* may occur because waves and tides may continuously deposit plants that are detached from different areas, exposed to environmental processes that may affect the isotopic signature of macroalgae (Machás et al., 2006). For instance, ^{15}N enrichment in macroalgae often indicates an increase in the availability of human-derived nutrients (Carvalho et al., 2008) and differential decomposition among tissues may determine low δ^{13}C because lignine, the lowest decomposing part of plants is ^{13}C depleted (Benner et al., 1987). The ^{13}C depletion in *S. muticum* tissues at the upper zone is consistent with idea that wrack on higher levels on the shore is sometimes older than low on the shore (Orr et al., 2005), whereas there are several processes that could contribute to the increased values of δ^{15}N and δ^{13}C in March such as anthropogenic disturbance, different bacterial colonization or decomposition stage (Finlay and Kendall, 2007).

Consumers may integrate the isotopic changes in their food sources, when sufficient time allows the metabolic turnover of the ingested sources of food. We assumed that the isotope signatures of consumers integrated the isotopic signatures of the wrack collected at the same time. We sampled at a scale of months and the turnover for amphipods and, in general, arthropods are at a scale of 1–2 weeks (Crawley et al., 2007; Kaufman et al., 2008). We thus allowed a sufficient time to ensure that the isotopic signature of consumers did not resemble that of their food as collected at the previous sampling date. Rather, the consumers reflected the isotopic signatures of wrack deposited within 2 weeks before the sampling date. The temporal variation in the δ^{15}N of *T. saltator* in March, following that of *S. muticum* may thus suggest that this consumer fed on *S. muticum*. This explanation may hold even if we found inconsistent patterns of variability between the δ^{13}C of *S. muticum* and *T. saltator*. Marine invertebrates have difficulties in digesting structural carbohydrates as cellulose, though some talitrids may digest some complex polysaccharides (Crawley and Hyndes, 2007). Thus, they may assimilate carbon selectively feeding on tissues of the same wrack with less lignine. In addition, *T. saltator* may use different sources of carbon and nitrogen. On the beach, animals may move and forage at night low on the shore, returning to supratidal levels during the day or forage up and down on the shore during their tidal rhythms of activity (Brown and McLachlan, 1990).

The mixing model corroborated these findings that *T. saltator* may use *S. muticum* as a food source. The model also indicated that sometimes *T. saltator* might feed almost exclusively on *S. muticum*, whereas *T. europaeus*, fed on a mix of *S. muticum* and *Z. marina*. *T. europaeus* has been found burrowing beneath or near piles of kelp or *Zostera marina*, considered not only a refuge, but also a primary source of food ingested in order to assimilate the more labile and digestible biomass of the micro-epiphytes (Brown and Odendaal, 1994; Colombini and Chelazzi, 2003). The diversified diet of *T. europaeus* as compared to *T. saltator* in December might indicate a niche differentiation between these two ecologically similar species, a hypothesis that requires appropriate experimental work in the future.

It is also interesting to notice that other consumers, whose habitat is often the dune rather than the beach, such as scavenger staphylinid *Aleochara* sp. or the tenebrionid *P. cadaverina* seemed to forage on wrack and on *S. muticum* occasionally. Increased abundance of arthropods related to wrack deposition have been also found worldwide and explained assuming both a protection role, providing a shelter from desiccation and predators, and a trophic role of wrack (Ince et al., 2007). Olabarria et al. (2007) and Rodil et al. (2008) also observed that wrack attracted arthropods, including *Aleochara* and *Phaleria* on sandy beaches of the northwest coast of Spain. Our results suggest that such attraction effect of wrack is based on shelter provision and to a less extent on food supply.

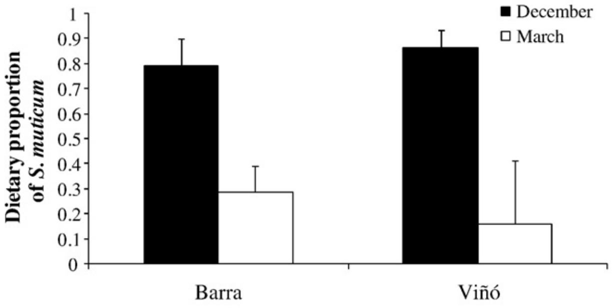


Fig. 3. Mean ± SE biomass proportion of *Sargassum muticum* (ISOSOURCE) contributing to *Talitrus saltator* diet.

The mixing model also showed that the dietary contribution of *S. muticum* was more important in October and December than in March and May and that the brown seaweed *C. baccata* became more important during spring. Consumers often show a feeding preference for brown algae over other macroalgae and seagrasses, even when the latter are equally or more abundant (Duffy and Hay, 2000; Pennings et al., 2000; Adin and Riera, 2003; Hyndes and Lavery, 2005; Crawley et al., 2007; Lastra et al., 2008), although brown algae produce numerous secondary metabolites that may prevent consumers (Jormalainen et al., 2001; Kubanek et al., 2004) and are of low nutritional value compared to green or red macroalgae (Duffy and Hay, 2000). Nonetheless, during desiccation and aging, brown algae may reduce secondary metabolite concentration and increase their nutritional value, through bacterial colonization (Cronin and Hay, 1996; Pennings et al., 2000; Norderhaug et al., 2003). In addition, the slowest decomposition rate among seaweeds guarantees longer availability on the beach (Buchsbaum et al., 1991; Kubanek et al., 2004; Crawley and Hyndes, 2007; Lastra et al., 2008), providing more permanent spatial subsidy than other seaweeds (Adin and Riera, 2003). Certain species may also adapt to high secondary metabolite concentration (Crawley and Hyndes, 2007) and take advantage from these deterrent metabolites, which may offer an additional protection from their predators (Duffy and Hay, 1991).

These findings do not explain why *T. saltator* would feed on *S. muticum* rather than other brown algae. The genus *Sargassum* has similar high levels of secondary metabolites and it does not decompose slower than other brown macroalgae (Crawley and Hyndes, 2007). Furthermore, adaptation to its secondary metabolites is less probable than for other seaweeds since *S. muticum* is an invasive species in the study area. There is also little evidence on feeding preference of amphipods for *S. muticum*. Although some amphipods may feed more on *Sargassum* than on other brown algae in the laboratory (Pennings et al., 2000), *T. saltator* may prefer *F. serratus* over other brown algae, including *S. muticum* (Adin and Riera, 2003). In addition, the amphipod *Allorchestia compressa* could consume the brown macroalgae *Ecklonia radiata* and *Sargassum* in equal proportions (Crawley and Hyndes, 2007).

Although we did not take any quantitative measurement of the biomass of the different algae within the strandline pool, the

Fig. 2. Frequency distribution of the dietary biomass proportion of *Sargassum muticum* (ISOSOURCE) at each beach and height on the shore for each sampling date. Data are reported only when isotopic signatures of *S. muticum* were distinguished from those of other seaweeds. The *Y*-axis indicates the number of times (over the total number of permutations done by ISOSOURCE) when a certain dietary proportion occurs. It does indicate the probability of occurrence of a given dietary proportion value (Phillips et al., 2005). A: fractionation of +1 and +3.4‰ for δ^{13}C and δ^{15}N, respectively; B: fractionation of −2, −3, −10‰ for δ^{13}C and 1, 1, 3.5‰ for δ^{15}N in *S. muticum*, other macroalgae and *Zostera marina*, respectively (see Material and methods).

availability of this invasive seaweed over the pool of other native brown seaweeds seems the most likely explanation. Indeed, the brown alga *C. baccata* that contributed to the consumer diet in March was not collected in December and other seaweeds were collected in a less number of times. Biomass of *S. muticum* on Galician sandy beaches, in fact, increases during summer and early autumn whereas biomass of *C. baccata* increases in mid-spring (C. Olabarria, personal observation).

In the mixing model we first assumed a fixed isotopic discrimination of +1 and +3.4‰ for δ^{13}C and δ^{15N}, respectively. Such values have been commonly used, also in beach ecosystems (Adin and Riera 2003). However, it has been recently demonstrated that when the most digestible compounds are ^{13}C-depleted, negative fractionation is likely (Crawley et al., 2007). We therefore also used the discrimination values calculated experimentally by Crawley et al. (2007). This alternative mixing model rarely identified wrack species as food sources for invertebrate consumers (6 *versus* the 27 times of the other model, Table 2) and called for alternative sources of food. However, wrack represents an important spatial subsidy for sandy beaches (e.g. Polis et al., 1997; Coupland et al., 2007) and it is very unlikely that beach inhabitants did not feed on wrack at all. Although our results cannot be conclusive and *ad hoc* experiments need to be done to identify discrimination values for each species and food source, we suggest that the values calculated in the laboratory for the amphipode *A. compressa* (Crawley et al., 2007) did not apply to our system.

5. Conclusion

Our study suggested that the invasive seaweed *S. muticum* could support the benthic food web based on *T. saltator*, one of the most numerous and widespread beach consumers, especially in December. In spring the ecological value of *S. muticum* appeared to be undertaken mainly by the native seaweed *C. baccata.* This species has a similar form and structure to that of *S. muticum.* In this case, a native and an invasive seaweed could play a similar role in supporting sandy beach food web alternating their role at different times of the year. Such temporal variability in providing the carbon and the nitrogen to the beach consumers was probably based on the differential availability of native vs. invasive brown seaweeds on the beach, rather than preferential choice of *T. saltator*. Therefore, by being one of the few brown species of seaweeds present on the beach during autumn, *S. muticum* could support a population of *T. saltator* otherwise absent or very reduced. How invasive seaweeds modify temporal food supply should be taken into account because it may have consequences for beach ecology and for the energy transfer in food webs.

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References

Adin, R., Riera, P., 2003. Preferential food source utilization among stranded macroalgae by *Talitrus saltator* (Amphipod, Talitridae): a stable isotopes study in the northern coast of Brittany (France). Estuarine Coastal and Shelf Science 56, 91–98.

Bedford, A.P., Moore, P.G., 1984. Macrofaunal involvement in the sublittoral decay of kelp debris — the detritivore community and species interactions. Estuarine Coastal and Shelf Science 18, 97–111.

Benner, R., Fogel, M.L., Sprague, E.K., Hodson, R.E., 1987. Depletion of 13C in lignin and its implications for stable carbon isotope studies. Nature 329, 708–710.

Bolam, S., Fernandes, G., Read, P., Raffaelli, D., 2000. Effects of macroalgal mats on intertidal sandflats: an experimental study. Journal of Experimental Marine Biology and Ecology 249, 123–137.

Britton-Simmons, K.H., 2004. Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic subtidal communities of Washington State, USA. Marine Ecology Progress Series 277, 61–78.

Brown, A.C., McLachlan, A., 1990. Ecology of sandy shores. Elsevier, Amsterdam. 328 pp.

Brown, A.C., Odendaal, F.J., 1994. The biology of oniscid isopoda of the genus *Tylos*. Advances in Marine Biology 30, 89–153.

Buchsbaum, R., Valiela, I., Swain, T., Dzierzeski, M., Allen, S., 1991. Available and refractory nitrogen in detritus of coastal vascular plants and macroalgae. Marine Ecology Progress Series 72, 131–143.

Buck, T.L., Breed, G.A., Pennings, S.C., Chase, M.E., Zimmer, M., Carefoot, T.H., 2003. Diet choice in an omnivorous salt-marsh crab: different food types, body size, and habitat complexity. Journal of Experimental Marine Biology and Ecology 292, 103–116.

Bustamante, R.H., Branch, G.M., 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196, 1–28.

Carvalho, M.C., Hayashizaki, K., Ogawa, H., 2008. Environment determines nitrogen content and stable isotope composition in the sporophyte of *Undaria pinnatifida* (Harvey) Suringar. Journal of Applied Phycology 20, 695–703.

Colombini, I., Aloia, A., Bouslama, M.F., ElGtari, M., Fallaci, M., Ronconi, L., Scapini, F., Chelazzi, L., 2002. Small-scale spatial and seasonal differences in the distribution of beach arthropods on the northwestern Tunisian coast. Are species evenly distributed along the shore? Marine Biology 140, 1001–1012.

Colombini, I., Chelazzi, L., 2003. Influence of marine allochthonous input on sandy beach communities. Oceanography and Marine Biology 41, 115–159.

Coupland, G.T., Duarte, C.M., Walker, D.I., 2007. High metabolic rates in beach cast communities. Ecosystems 10, 1341–1350.

Crawley, K.R., Hyndes, G.A., 2007. The role of different types of detached macrophytes in the food and habitat choice of a surf-zone inhabiting amphipod. Marine Biology 151, 1433–1443.

Crawley, K.R., Hyndes, G.A., Vanderklift, M.A., 2007. Variation among diets in discrimination of δ^{13}C and δ^{15}N in the amphipod *Allorchestes compressa*. Journal of Experimental Marine Biology and Ecology 349, 370–377.

Cronin, G., Hay, M.E., 1996. Within plant variation in seaweed palatability and chemical defenses: optimal defense theory versus the growth differentiation balance hypothesis. Oecologia 105, 361–368.

Cruz-Rivera, E., Hay, M.E., 2001. Macroalgal traits and the feeding and fitness of an herbivorous amphipod: the roles of selectivity, mixing, and compensation. Marine Ecology Progress Series 218, 249–266.

Duffy, J.E., Hay, M.E., 1991. Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72, 1286–1298.

Duffy, J.E., Hay, M.E., 2000. Strong impacts of grazing amphipods on the organization of a benthic community. Ecological Monographs 70, 237–263.

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. Estuarine Coastal and Shelf Science 58, 25–40.

Fernández, C., Gutierrez, L.M., Rico, J.M., 1990. Ecology of *Sargassum muticum* on the north coast of Spain — preliminary-observations. Botanica Marina 33, 423–428.

Finlay, J.C., Kendall, C., 2007. Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. In: Michener, R., Lajtha, K. (Eds.), Stable isotopes in ecology and environmental science. Oxford, United Kingdom, pp. 283–333.

Griffiths, C.L., Stenton-Dozey, J.M.E., Koop, K., 1983. Kelp wrack and the flow of energy through a sandy beach ecosystem. In: McLachlan, A., Erasmus, T. (Eds.), Sandy beaches as ecosystems. The Hague, The Netherlands, pp. 547–556.

Hyndes, G.A., Lavery, P.S., 2005. Does transported seagrass provide an important trophic link in unvegetated, nearshore areas? Estuarine Coastal and Shelf Science 63, 633–643.

Ince, R., Hyndes, G.A., Lavery, P.S., Vanderklift, M.A., 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. Estuarine Coastal and Shelf Science 74, 77–86.

Inglis, G., 1989. The colonization and degradation of stranded *Macrocystis pyrifera* (l) by the macrofauna of a new-zealand sandy beach. Journal of Experimental Marine Biology and Ecology 125, 203–217.

Jormalainen, V., Honkanen, T., Heikkila, N., 2001. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. Marine Ecology Progress Series 220, 219–230.

Kaufman, M.R., Gradinger, R.R., Bluhm, B.A., O´Brien, D.M., 2008. Using stable isotopes to assess carbon and nitrogen turnover in the Arctic sympagic amphipod *Onisimus litoralis*. Oecologia 158, 11–22.

Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17, 164–170.

Kirkman, H., Kendrick, G.A., 1997. Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: a review. Journal of Applied Phycology 9, 311–326.

Kubanek, J., Lester, S.E., Fenical, W., Hay, M.E., 2004. Ambiguous role of phlorotannins as chemical defenses in the brown alga Fucus vesiculosus. Marine Ecology Progress Series 277, 79–93.

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. Marine Biology 154, 163–174.

Lewis, T.L., Mews, M., Jelinski, D.E., Zimmer, M., 2007. Detrital subsidy to the supratidal zone provides feeding habitat for intertidal crabs. Estuarine and Coasts 30, 451–458.

Machás, R., Santos, R., Peterson, B., 2006. Elemental and stable isotope composition of *Zostera noltii* (Horneman) leaves during the early phases of decay in a temperate mesotidal lagoon. Estuarine Coastal and Shelf Science 66, 21–29.

Mateo, M.A., Serrano, O., Serrano, L., Michener, R.H., 2008. Effects of sample preparation on stable isotope ratios of carbon and nitrogen in marine invertebrates: implications for food web studies using stable isotopes. Oecologia 157, 105–115.

Mews, M., Zimmer, M., Jelinski, D.E., 2006. Species-specific decomposition rates of beach cast wrack in Barkley Sound, British Columbia, Canada. Marine Ecology Progress Series 328, 155–160.

Norderhaug, K.M., Fredriksen, S., Nygaard, K., 2003. Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation for food quality. Marine Ecology Progress Series 255, 135–144.

Olabarria, C., Lastra, M., Garrido, J., 2007. Succession of macrofauna on macroalgal wrack of an exposed sandy beach: effects of patch size and site. Marine Environmental Research 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.

Pauchard, A., Shea, K., 2006. Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8, 399–413.

Pavia, H., Carr, H., Aberg, P., 1999. Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae. Journal of Experimental Marine Biology and Ecology 236, 15–32.

Pennings, S.C., Carefoot, T.H., Zimmer, M., Danko, J.P., Ziegler, A., 2000. Feeding preferences of supralittoral isopods and amphipods. Canadian Journal of Zoology 78, 1918–1929.

Phillips, D.L., Gregg, J.W., 2001. Uncertainty in source partitioning using stable isotopes. Oecologia 127, 171–179.

Phillips, D.L., Gregg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136, 261–269.

Phillips, D.L., Newsome, S.D., Gregg, J.W., 2005. Combining sources in stable isotope mixing models: alternative methods. Oecologia 144, 520–527.

Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28, 289–316.

Rodil, I.F., Olabarria, C., Lastra, M., Lopez, J., 2008. Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. Journal of Experimental Marine Biology and Ecology 358, 1–13.

Schlacher, T.A., Connolly, R.M., 2009. Land-ocean coupling of carbon and nitrogen fluxes on sandy beaches. Ecosystems 12, 311–321.

Stachowicz, J.J., Hay, M.E., 1999. Reducing predation through chemically mediated camouflage: indirect effects of plant defenses on herbivores. Ecology 80, 495–509.

Underwood, A.J., 1997. Ecological experiments: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge. 504 pp.

Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. Limnology and Oceanography 46, 2061–2066.