



Intraspecific diet shift in *Talitrus saltator* inhabiting exposed sandy beaches

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ARTICLE INFO

Article history:

Received 26 February 2009

Accepted 22 June 2009

Available online 27 June 2009

Keywords:

stable isotopes
stranded algae
food sources
diet shift
sandy beaches
Talitrus saltator
Sargassum muticum
Galician coast

ABSTRACT

Talitrid amphipods are the most abundant herbivores on exposed sandy beaches. Despite their important role as trophic intermediates between macrophytes and higher levels (i.e. insect and bird) of beach food webs, very little information is available on their feeding patterns. The main aim of this study was to investigate intraspecific differences in the feeding behaviour of *Talitrus saltator*. We tested the hypotheses that: (1) adult females and males showed different isotope signatures and therefore relied on different sources of food; and (2) patterns of variation of isotope signatures of juveniles differed from those of adult specimens, evidencing a diet shift during the development. We used stable isotope signatures and tested for differences upon the level on the shore, times of the year and beaches experiencing similar morpho-dynamic and environmental conditions. Finally, we investigated the trophic significance of macrophyte detritus in the diet of males, females and juveniles. Results showed that adult males had a more variable diet than females and juveniles (inferred from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values). Dual-isotope graphs suggested that *Sargassum muticum* and *Cystoseira baccata* wrack could be among the main food sources for both juvenile and adult stage.

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1. Introduction

On exposed sandy beaches of temperate regions, the major sources of food are often marine macrophytes (macroalgae, sea-grasses) because little primary production occurs on the beach itself (e.g. Brown and McLachlan, 1990; Dugan et al., 2003). Hence, macrofaunal assemblages of exposed sandy beaches depend largely upon allochthonous inputs from the coastal ocean that arrive as stranded wrack (e.g. Kirkman and Kendrick, 1997; Colombini and Chelazzi, 2003; Lastra et al., 2008). This benefit may also extend beyond the beach itself. For example, wrack deposited along shorelines is consumed by detritivores and scavengers, which in turn are important food sources for vertebrate predators such as shorebirds, seabirds, lizards, rodents, marine mammals, and fishes (Polis et al., 1997). Despite the role of wrack as food subsidy for the macrofauna inhabiting sandy beaches, its trophic significance has proved difficult to evaluate in the field (e.g. Griffiths and Stenton-Dozey, 1981; Jedrzejczak, 2002).

Talitrid amphipods are some of the most abundant sand inhabitants on exposed beaches (e.g. Dugan et al., 2003; Lastra et al., 2006) and important consumers of wrack (Dugan et al., 2003). Their rate of consumption may be affected by several processes, such as competition with other consumers, physico-chemical and morphological characteristics of the macrophyte species, and availability of wrack (Van Alstyne et al., 2001; Orr et al., 2005). For instance, abundance, and identity of the consumers and the spatial and temporal variability of wrack composition could influence the processing and availability of macrophyte wrack and as a consequence, abundance and feeding behaviour of amphipods (Dugan et al., 2003).

Accumulating evidences suggest that benthic invertebrates might change their diet as they grow (Bergman and Greenberg, 1994; Polis et al., 1997; Hentschel, 1998; Rossi et al., 2004). Ontogenetic shifts in diets can have dramatic effects on the structure and composition of benthic assemblages (e.g. Cohen et al., 1993; Hentschel, 1998). For example, size-specific competition for food resources may limit population densities of deposit-feeding species (Hentschel and Jumars, 1994). Thus when an ontogenetic change in diet occurs, descriptions of food webs should distinguish among the size classes or life cycle stages on that species (Cohen et al., 1993). In addition, sex-related differences in diet have been reported as a fairly common phenomenon in marine organisms

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(e.g. Forero et al., 2002; Guerra-García et al., 2004; Bearhop et al., 2006; Schmidt et al., 2006; Hoeninghaus and Davis, 2007). Thus, female and male of the same consumer species may show resource repartition and different feeding behaviour.

Exposed sandy beaches on the Galician coast (northwestern Spain) support a high diversity of species and rich assemblages (Lastra et al., 2006). High productivity linked to phytoplankton biomass and wrack deposits are likely to be in part responsible for such patterns (Lastra et al., 2006). Despite the importance of wrack on sandy beaches very little is known about composition of assemblages or trophic interactions among species colonizing wrack deposits (but see Olabarria et al., 2007; Rodil et al., 2008). This information is essential to a better understanding of processes shaping structure of macrofaunal assemblages on exposed sandy beaches along the Galician coast.

This study investigated whether there were differences in the feeding behaviour of *Talitrus saltator* related to the sex and the development stage. We used stable isotopes to examine whether: (1) adult females and males showed different patterns of variation of isotope signatures and therefore relied on different sources of food; and (2) patterns of variation of isotope signatures of juveniles differed from those of adult specimens, evidencing a diet shift during ontogeny. We tested for differences upon the levels on the shore, times of the year and beaches experiencing similar morpho-dynamic and environmental conditions. Finally, we explored the importance of macrophyte detritus for the diet of males, females and juveniles. We employed stable isotope methods, since they have been revealed as a useful tool for identifying the diet of consumers inhabiting sandy beaches (e.g. Adin and Riera, 2003; Ince et al., 2007).

2. Materials and methods

2.1. Study site

Samples were collected from two exposed sandy beaches, Barra (42° 15' N, 8° 51' W) and Viñó (42° 15' N, 8° 50' W) located on the Galician coast, northwestern Atlantic coast of Spain. These beaches, about 400 m apart, were randomly chosen from a pool of six beaches (located in an area of approximately 7 km) with similar morpho-dynamic conditions and where talitrid amphipods were quite abundant. Both are backed by dunes and separated by a rocky platform. The beaches are ~1 km in length and experience mixed semi-diurnal tides with an approximate range of 2–4 m. The intertidal width (dune base to low swash level) ranges from ~30 to 80 m. Although the composition of wrack is very variable spatially and temporally both beaches receive mainly large inputs of brown algae such as *Fucus vesiculosus*, *Sargassum muticum* and *Laminaria ochroleuca* and the seagrass *Zostera marina*, as well as small quantities of other brown, red and green algae species from rocky shores located just offshore (personal observation).

2.2. Sampling collections

Animals were collected at two different levels on the shore, i.e. the strandline and 3 m above the strandline (hereafter low and upper zone, respectively) in December 2007, March and May 2008. In each zone, eight pitfall traps about 2 m apart were placed at both levels on the shore and beaches in the afternoon the day before collection. At least four adults and four juvenile individuals of *Talitrus saltator* were picked randomly from four chosen pitfalls at each sampling date. 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.

In the laboratory, animals were sorted alive and cleaned after relaxation with 10% MgCl. Animals were divided into juveniles, adults, females and males, based on their size (Scapini et al., 1997) and morphology (Lincoln, 1979), respectively. We considered juveniles the individuals smaller than 5 mm. Animals were dried at 60 °C for 48 h and then frozen (–20 °C). Adults were large enough to be analyzed individually, but juveniles had to be pooled into groups of two to three individuals to obtain sufficient tissue for chemical analyses. The detrital macroalgae and seagrass were rinsed with filtered seawater to clean off epibionts and then dried (60 °C) for 48 h. Subsequently, samples were ground into fine powder using a mortar and pestle, and then kept frozen (–20 °C) until isotopes analyses. Prior to analyses all samples were acidified with 10% HCl. The presence of inorganic carbon in amphipods can alter the carbon isotopic signature. The process of acidification is, therefore, necessary in sample preparation, mainly working with small organisms where it is not possible to dissect and remove the carbon structures (Vizzini and Mazzola, 2003).

2.3. Analytical technique

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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, where

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{reference}} \right) - 1 \right] \times 10^3,$$

with $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen, and reported relative to the Vienna Pee Dee Belemnite standard (PDB) for carbon and to air N_2 for nitrogen. Precision in the overall preparation and analysis was $\pm 0.13\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

2.4. Analysis of data

To test the hypothesis that adult females and males as well as juveniles of *Talitrus saltator* showed different spatio-temporal patterns of variation in their diets, the isotopic composition $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analysed separately with three-factor mixed model of analyses of variance (ANOVA). Level on the shore (two levels: low and upper zone) was a fixed factor and beach (two levels: Barra and Viñó) and date (three levels: December 07, March 08 and May 08) were random factors. In order to have a balanced design, individuals from the four pitfall traps were pooled and then, ten adults and six juveniles were randomly chosen from each beach, level on the shore and date of sampling. Data were not transformed whether or not variances were heterogeneous because the analysis of variance is robust to heterogeneous variance when there are balanced data and number of replicates is relatively large (Underwood, 1997). When significant differences among treatments and their interactions were found, Student–Newman–Keuls (SNK) test was done as a posteriori comparison (Underwood, 1997). When ANOVA analyses showed significant patterns, i.e. stable carbon and nitrogen isotope values of males, females or juveniles varied spatially or temporally, Spearman's rank correlations were used to test whether there were relationships between patterns of male and female adults, and adults and juveniles. We would expect non-significant correlation if isotopic signatures of different stages or sexes were independent from each other (e.g. they feed on different sources).

To investigate the role of wrack species as food sources for adults and juveniles, we plotted data of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for consumers and wrack species in a dual-isotope graph and considered a mean trophic enrichment of 1‰ for $\delta^{13}\text{C}$ (Rau et al., 1983;

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