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Original Articles

Niche segregation amongst sympatric species at exposed sandy shores with contrasting wrack availabilities illustrated by stable isotopic analysis

Filipa Bessa*, Alexandra Baeta, João Carlos Marques

IMAR-CMA Marine and Environmental Research Centre, Department of Life Sciences, University of Coimbra, 3004-517 Coimbra, Portugal

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ABSTRACT

Wrack supplies (macroalgae, seagrasses and carrion) are a common feature of sandy beaches worldwide. These allochthonous inputs are a potential high-quality food subsidy for beach fauna, but little is known about the feeding ecology and niche segregation strategies of these species in beaches with limited wrack availabilities. We used stable isotopic ratios of nitrogen and carbon to examine the diets and niche segregation among three sympatric crustaceans, the amphipods *Talitrus saltator* and *Talorchestia brito*, and the isopod *Tylos europaeus*, in two temperate beaches, Cabedelo and Quiaios, on the Portuguese Atlantic coast, with contrasting wrack availabilities, over winter and summer. In the beach with limited wrack (Quiaios), consumers showed significantly different interspecific and temporal isotopic signatures, suggesting a distinct foraging habitat and niche differentiation. Mixing models outputs (SIAR) revealed in this case a seasonal shift in the diet of consumers from terrestrial sources in winter towards marine-based sources (phytoplankton) in the summer. In contrast, at Cabedelo, consumers showed clear overlap in isotopic signatures, with similar contributions of the available wrack to their diets. As a whole, an opportunistic and generalist feeding behaviour was described for these species, namely for *T. saltator*. Isotopic profiles support the occurrence of spatial overlap during summer but different foraging strategies of the three species in these beaches during winter. Our results show that on temperate beaches with ephemeral wrack supplies, consumers might need to adopt different foraging strategies and niche segregation for their subsistence, and additionally illustrate the viability of using stable isotopes to capture subtle changes in trophic niches.

1. Introduction

Exposed sandy beaches form a highly dynamic interface between marine and terrestrial ecosystems that are generally characterised by little in situ primary productivity (McLachlan and Brown, 2006). These transitional habitats are mainly subsidised by allochthonous inputs of organic material from the coastal ocean (Colombini et al., 2003; Dugan et al., 2003; Griffiths et al., 1983), that vary from phytoplankton to beach-cast wrack, consisting of seagrasses, macroalgae, and carrion (Griffiths et al., 1983; Rossi and Underwood, 2002). This marine organic material is transported onshore by physical forces (e.g. wind, waves and currents), and accumulated in large volumes in the surf zones, being an important food resource to beach consumers—a trophic subsidy (*sensu* Polis et al., 1997).

The allochthonous inputs of nutrients for beach fauna are ubiquitous on exposed sandy shores worldwide and the pulse subsidies have multiple effects on food web dynamics on coastal areas (Heck et al., 2008; McLachlan and Brown, 2006).

One of the most important ecological roles of the invertebrates (as primary consumers) inhabiting sandy shores is the fragmentation and decomposition of beach-cast wrack as sources of energy and nutrients (organic matter) (Catenazzi and Donnelly, 2007; Colombini et al., 2003; Lastra et al., 2008; Salathé and Riera, 2012). In addition, the availability of wrack would influence the structure of these primary consumers (mainly crustaceans), which in turn supports the growth of consumers in higher trophic levels (e.g. shorebirds) resulting in the transfer of energy across coastal ecotones (review in Colombini et al., 2003).

The wrack deposits exported from the surrounding ecosystems such as rocky shores or seagrass beds are highly variable in space and time, and are also dependent on the beach type and the nearshore hydrodynamics (Gómez et al., 2013; Gonçalves and Marques, 2011; Orr et al., 2005). Beach fauna, commonly dominated by air-breathing scavenging crustaceans, face many challenges

* Corresponding author. Tel.: +351 239 836 386.
E-mail address: afbessa@uc.pt (F. Bessa).

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locating food resources and have likely evolved behavioural and physiological adaptations to live in this nutrient-limited environment (McLachlan and Brown, 2006). In general, most of these scavengers (namely talitrid amphipods and isopods) live buried between the drift line and the base of the foredunes during the day, emerging at night to feed and move across the shoreline (Scapini et al., 1997). Although these species have generally been regarded as essentially herbivorous, an opportunistic behaviour (detritivorous) has been described for these taxa (Adin and Riera, 2003; Porri et al., 2011).

The vertical distribution of available resources on sandy shores has been identified as the main factor driving population abundance and zonation of co-occurring mobile fauna (Ince et al., 2007; Jaramillo et al., 2006; MacMillan and Quijón, 2012; Rodil et al., 2008). Therefore, sympatric crustaceans need to partition both in situ and allochthonous marine resources to avoid direct competition for food resources on these systems (Huxel et al., 2002). Competition may, however, be lowered if species partition their niches by separating their surface activity (i.e. feeding in different zones), being active during different times of the day, or a combination of both spatial and temporal foraging strategies. In fact, differences in space and time partitioning of locomotor activities over the beach surface have been reported for several species of these brooding crustaceans (e.g. Jaramillo et al., 2003; Lastra et al., 2010; Scapini et al., 1992). Understanding foraging strategies of consumers inhabiting the same system is essential to understand their trophic relationships and ecological roles.

On exposed sandy beaches of temperate region, the abundant talitrid amphipods and oniscoidean isopods, are considered important wrack-deposit consumers (e.g. Gonçalves and Marques, 2011; Lastra et al., 2010; Rossi et al., 2010). Several studies highlighted the influence of beach wrack on the shore face as food resources for primary consumers (e.g. Crawley et al., 2009; Heck et al., 2008; Hyndes and Lavery, 2005; Rossi et al., 2010) and its role as an habitat for abundant beach invertebrates (e.g. Colombini et al., 2000; Duong and Fairweather, 2010; MacMillan and Quijón, 2012; Olabarria et al., 2007). The dietary wrack preferences of particular taxa (mainly amphipods) were also extensively studied, and while some studies showed similarly strong preferences for the brown algae (Adin and Riera, 2003; Crawley and Hyndes, 2007; Duarte et al., 2010; Olabarria et al., 2009), others showed that they are indiscriminate feeders (McLeod et al., 2013) and even not related with specific wrack species (Colombini et al., 2009; Porri et al., 2011).

In recent years, food web ecologists have been taken advantage of natural variation in isotope composition of food items to reconstruct the diets of several species (Boecklen et al., 2011; Peterson and Fry, 1987; Post, 2002). Stable isotopes ratios of carbon and nitrogen have been proved to be able to discriminate among various primary producers that did support the food web in several coastal regions (Baeta et al., 2009; Bergamino et al., 2011; DeNiro and Epstein, 1978, 1980). Stable isotope analysis (SIA) is currently among the most powerful tools for the study of trophic relationships and to estimate niche segregation among species in the marine environment (Cummings et al., 2012), and its use in characterising the food web structure of macrofaunal communities or consumers diets is relatively common on sandy beaches (e.g. Bergamino et al., 2011; Colombini et al., 2011; Olabarria et al., 2009; Rossi et al., 2010). However, on sandy shores with a low contribution of wrack, where organic material is typically composed of ephemeral algal fragments and vascular dune plants detritus, the feeding ecology and the niche segregation strategies of beach consumers are poorly understood.

Exposed sandy beaches are among the most common coastal ecosystems along the Western Portuguese coast (European Atlantic coast), but beaches here differ in the wrack availabilities (Gonçalves and Marques, 2011). Some of the most conspicuous representative species of these beaches are the talitrid amphipods *Talitrus saltator* and *Talorchestia brito*, and the oniscoidean isopod *Tylos europaeus*, widely studied in the central coast of Portugal (Gonçalves et al., 2005, 2009, 2013; Marques et al., 2003).

The aim of the present study was to determine if there is isotopic evidence for significant niche segregation among sympatric crustaceans living on exposed sandy shores with contracting wrack availabilities. We compared therefore the temporal isotopic signatures of primary consumers and potential food sources, the diets of consumers, and the pattern of distribution along the shore at two highly dynamic beaches on the European Atlantic coast (Portugal). Finally, we examined whether our findings based on stable isotope ratio analyses agree with previous descriptions of spatial surface activity segregation for these sympatric crustaceans.

2. Materials and methods

2.1. Study area

The study was carried out on two high energetic mesotidal sandy beaches: Cabedelo (40°07′32″N, 8°51′49″W) and Quiaios (40°12′21″N, 8°53′48″W) beaches, located on the European Atlantic coast (central Portugal) during the winter (January) and summer (July) 2011 (Fig. 1). This area is characterised by a maritime climate with mild winters and cool summers with the minimum average temperature of the coldest month of 4.8 °C and the maximum average of the warmest month of 24.2 °C (Danielsen, 2008). Both beaches present a high wave exposure environment and a mesotidal regime, with a mean spring tidal range of ca. 3.5 m (Gonçalves et al., 2009).

The Cabedelo sandy beach have a high recreational potential since it is located in a urban area while the Quiaios beach is located further north, about 8 km south of the Cape Mondego and more preserved from anthropogenic disturbances. The former beach is narrow (width approximately 80 m) and contains medium sediments, whereas Quiaios is wider (width approximately 100 m) and consists mainly of coarse sands (for more detailed description of the area, see Gonçalves et al., 2009). Quiaios beach is backed by a well-developed foredune, up to 2 m in height, which is vegetated with the dominant dune plants: *Ammophila arenaria* (L.), *Euphorbia paralias* (L.), *Elymus farctus* subsp. *farctus* (L.) and *Otanthus maritimus*.

At Cabedelo beach (touristic beach), local facilities located in the vicinity of the foredunes have partially damaged it and limited the local dune plants abundance and diversity (personal observations). However, this beach received large amounts of drift wrack (mainly macroalgae) that accumulate in the surf zone coming from rocky shores near the beach, while Quiaios is clearly more limited (Gonçalves and Marques, 2011).

The predominant wrack consumers are the semiterrestrial crustaceans amphipods *T. brito*, *T. saltator*, and the isopod *T. europaeus*. A full characterisation of the main physical features and macrofaunal communities of both beaches is provided in Gonçalves et al. (2009, 2013) and Marques et al. (2003).

2.2. Sampling design

Crustaceans (*T. brito, T. saltator and T. europaeus)* and potential food sources: Beach wrack (*Fucus* sp., *Ulva* sp., carrion) and dune plants detritus were collected (depending on their availability) along the sea-dune axis from Quiaios and Cabedelo beaches during both wet (winter, January) and dry (summer, July) seasons. In addition, seawater was collected from the swash zone of the beach for determination of suspended particulate organic matter (POM) as a proxy of phytoplankton.