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Trophic niche shifts driven by phytoplankton in sandy beach ecosystems

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ABSTRACT

Stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) together with chlorophyll *a* and densities of surf diatoms were used to analyze changes in trophic niches of species in two sandy beaches of Uruguay with contrasting morphodynamics (i.e. dissipative vs. reflective). Consumers and food sources were collected over four seasons, including sediment organic matter (SOM), suspended particulate organic matter (POM) and the surf zone diatom *Asterionellopsis guyunusae*. Circular statistics and a Bayesian isotope mixing model were used to quantify food web differences between beaches. Consumers changed their trophic niche between beaches in the same direction of the food web space towards higher reliance on surf diatoms in the dissipative beach. Mixing models indicated that *A. guyunusae* was the primary nutrition source for suspension feeders in the dissipative beach, explaining their change in dietary niche compared to the reflective beach where the proportional contribution of surf diatoms was low. The high C/N ratios in *A. guyunusae* indicated its high nutritional value and N content, and may help to explain the high assimilation by suspension feeders at the dissipative beach. Furthermore, density of *A. guyunusae* was higher in the dissipative than in the reflective beach, and cell density was positively correlated with chlorophyll *a* only in the dissipative beach. Therefore, surf diatoms are important drivers in the dynamics of sandy beach food webs, determining the trophic niche space and productivity. Our study provides valuable insights on shifting foraging behavior by beach fauna in response to changes in resource availability.

1. Introduction

Exposed sandy beaches constitute physically stressful environments with strong spatial and temporal dynamics (McLachlan and Brown, 2006). Interactions between sand, waves, and tides produce a wide range of beach morphodynamic types ranging from narrow and steep, with coarse sediments and no surf zone (reflective) to wide and flat, with fine sediments and a large surf zone (dissipative) (Short, 1999; Finkl, 2004). Abiotic factors, including grain size, beach slope and swash processes, are usually considered the main drivers regulating the abundance and distribution of the resident fauna, whereas biological factors appear to have less influence (Defeo and McLachlan, 2005; McLachlan and Brown, 2006). However, understanding the role that biotic interactions can play in structuring sandy beach ecosystems is increasingly important, elemental and challenging (Defeo et al., 1997; Dugan et al., 2004; Ortega Cisneros et al., 2011; Rodil et al., 2012). In this context, the examination of the variability in space and time of food web structure and trophic interactions can improve our understanding of functional response to environmental variation and disturbance (Tewfik et al., 2016).

Sandy beach food webs are fuelled by marine derived organic matter, including surf zone phytoplankton, carrion, seagrasses and macroalgae (wrack), supporting a diverse community (McLachlan and Brown, 2006; Schlacher et al., 2008). However, food web structure markedly differs between beaches with contrasting morphodynamics (Bergamino et al., 2011). Particularly, reflective beaches are mainly subsidized, processing organic material inputs from the sea and land (McLachlan and Brown, 2006). By contrast, high diatom accumulations in the surf zone is a characteristic

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feature of dissipative beaches with high wave energy, defined as semi-closed ecosystems (*sensu* McLachlan, 1980), which are usually longer than 4 km and have an associated well-developed dune systems (Campbell, 1996). In these ecosystems, surf diatom concentrations reach high biomass and primary production rates (500–2000 g C m^{-3} yr^{-1}; McLachlan and Brown, 2006). Surf diatom densities are mainly controlled by onshore winds that generate high wave energy that resuspends cells and concentrates them in the surf zone (Odebrecht et al., 1995; Rörig and Garcia, 2003). The production of mucus may help them to attach to the foam in the surf zone, and during calm conditions promote their association with sand grains, increasing their sedimentation (Talbot and Bate, 1988; Du Preez and Campbell, 1996).

Dissipative sandy beaches placed on the Southwestern Atlantic along 630 km of sandy coast located between Atlântida (Brazil) and Barra del Chuy (Uruguay) hold conspicuous accumulations of the surf zone diatom *Asterionellopsis glacialis* (Odebrecht et al., 2014), recently described as *Asterionellopsis guyunusae* (Kaczmarska et al., 2014). This species may reach high abundance levels (10^8 to 10^9 cells L^{-1}; Bayssé et al., 1989) resulting in chlorophyll *a* concentrations as high as 1647 μg L^{-1} (Odebrecht et al., 1995). Previous observations suggested that *A. guyunusae* is the main energy source of coastal benthic filter feeders throughout the year, with high biomass occurring concurrently with diatom blooms (Garcia and Gianuca, 1997; Odebrecht et al., 2010, 2014). However, we still have much to learn about how changes in energy sources may alter trophic groups and food web structure in order to understand sandy beach ecosystem dynamics and function.

The importance of surf zone diatoms as food source is difficult to evaluate using traditional methods such as gut content analysis, because the material is finely triturated, hindering the identification of food items. This limitation enhances the importance of stable isotope analysis to examine spatial variability of consumers and their potential sources in coastal areas (Mortillaro et al., 2014; Schaal et al., 2016), because they provide time-integrated information on consumers' diet (Fry, 2006). The stable carbon isotope ratio ($\delta^{13}C$) in the tissues of a consumer reflects that of its prey with a slight modification (0–1‰), and therefore reflects the dietary composition of consumers (Fry, 2006). The stable nitrogen isotope ratio ($\delta^{15}N$) in the tissues of a consumer generally increases by 2–4‰ compared with that of its prey, and therefore can be used to delineate the trophic position of consumers in the food web (McCutchan et al., 2003; Caut et al., 2009).

The trophic niche space is a fundamental concept related to food web structure analyses (Cohen, 1978). Previous studies have shown the utility of stable isotopes to characterize the trophic niche width of a species because isotopic axes of $\delta^{13}C$ and $\delta^{15}N$ provide information on resource (bionomic) and habitat (scenopoetic) factors of the niche (Newsome et al., 2007; Rodríguez and Herrera, 2013; Marchese et al., 2014). Furthermore, novel quantitative approaches using circular statistics provide a powerful tool to compare differences in food web structure across time and space (Schmidt et al., 2007), but empirical studies using this approach are scant (Rodríguez and Herrera, 2013). In sandy beaches, previous studies have analyzed the food web functioning, including a variety of food sources and multiple species such as terrestrial organic matter derived from river discharges (Schlacher and Connolly, 2009; Bergamino et al., 2012), invasive seaweed (Rossi et al., 2010), macroalgae (Lastra et al., 2008; Ruiz-Delgado et al., 2014), terrestrial benthic invertebrates (Colombini et al., 2011), and fish species (Lercari et al., 2010; Bergamino et al., 2011). Investigations that provide insights about the existence of feeding strategies, including trophic niche shifts of beach consumers, are less common (Bessa et al., 2014).

The aim of this study was to assess the role of surf zone diatoms in the trophic niche of macrofaunal species in two sandy beaches with contrasting morphodynamics located in the Southwestern Atlantic Ocean coast of Uruguay. It is hypothesized that the trophic niche of the consumer species differs between beaches, owing to differences in the sources of organic matter available. The stable isotopes methodology and the isotopic niche space concept (Newsome et al., 2007) were used to characterize spatio-temporal patterns in nutritional resources utilization by invertebrates and to investigate trophic niche properties (Jackson et al., 2011) in sandy beaches.

2. Materials and methods

2.1. Study area

The study was conducted in two exposed sandy beaches with contrasting morphodynamics located in the Atlantic coast of Uruguay (Fig. 1): Barra del Chuy (33°45′S, 53°27′W) and Arachania (34°36′S, 53°44′W). Barra del Chuy is a dissipative with fine to very fine well sorted sand (mean grain size = 0.20 mm; sorting = 0.70 mm), a gentle slope (3.53%), heavy wave action, a wide surf zone and the highest macrofauna richness (21–29 species), abundance and biomass among all Uruguayan beaches (Lercari and Defeo, 2006, 2015). Arachania is a reflective beach with coarse sediments (grain size = 0.56 mm), steep slope (7.80%), and macrofauna richness 5 times lower than Barra del Chuy.

2.2. Sample collection and stable isotope analysis

At each sandy beach, macrofauna was collected in four consecutive seasons along three transects perpendicular to the shoreline and spaced 8 m apart, from the base of the dunes to the lower limit of the swash zone. Sampling units on each transect were extracted every 4 m with a sheet metal cylinder (27 cm in diameter and 40 cm deep), and the sediment was sieved through a 0.5 mm mesh. The retained organisms were transported to the laboratory, counted, identified to the species level (whenever possible) and used for stable isotopic analysis. Seawater was collected in a 5 L bottle from the swash zone of both beaches and then filtered onto ashed glass fiber filters (12 h at 450 °C) for determination of suspended particulate organic matter (POM). Zooplankton samples were obtained by towing a 190-μm mesh plankton net for 2 min. In addition, the pure surf diatom *A. guyunusae* was collected for isotopic analysis from the surf zone during a bloom episode that occurred in the dissipative Barra del Chuy (Fig. 1c), by filtering a water sample of 200 mL through a glass fiber filter Whatman GF/C. Samples of *A. guyunusae* were not collected in the reflective beach, because monospecific patches of this surf diatom are only found in the dissipative beach Barra del Chuy. In the reflective beach, *A. guyunusae* cells are found as a result of a passive transport by surface currents from dissipative beaches. Thus, the same isotopic values of *A. guyunusae* were considered for both beaches, assuming no differences between beaches for both $\delta^{13}C$ and $\delta^{15}N$ isotope values. This assumption could be valid for a comparative analysis of niche width under similar environmental constraints (see e.g., Careddu et al., 2015). Surface sediment organic matter samples (SOM) were collected at three different beach levels (i.e. supralittoral, intertidal and lowest swash level). All samples were stored at −20 °C until they were processed in the laboratory for isotopic analysis.

Samples of organisms, POM, SOM and pure surf diatoms were dried at 60 °C for 48 h. All tissue samples were individually homogenized using a mortar and pestle and finally 1 mg was weighed in tin capsule. We did not perform a lipid extraction in invertebrates, given the low C/N ratios that varied between 3 and 5,