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Complex food webs of tropical intertidal rocky shores (SE Brazil) – An isotopic perspective

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ABSTRACT

Knowledge on food web structure, trophic links and energy pathways is essential for the understanding of complex and highly biodiverse tropical ecosystems. Emerging issues related to global change and species invasions call for an urgent advance on this topic. Isotopic analyses were applied to the tropical intertidal rocky shores of Southeastern Brazil, with the aim of 1) describing the general food web structure, 2) estimating food web length, 3) estimating the trophic level of the secondary consumers, and 4) their dependence on different energy pathways. An exceptionally high number of food web nodes (71) was analysed. The maximum trophic level (TL) was 3.3, similarly to what has been previously reported for temperate rocky intertidal ecosystems. Fish were the dominant top consumers (TL > 2.0), along with an important number of gastropods and crustaceans (both crabs and shrimp). Primary consumers were mostly crabs, gastropods and bivalves. Two invasive crustaceans were found among the top consumers, the Japanese peppermint shrimp, *Lysmata lipkei* (TL = 3.0), and the Indo-Pacific swimming crab, *Charybdis hellerii* (TL = 2.3). Among the primary consumers, one invasive bivalve was found, *Isognomon bicolor*. Mixing models showed that the top consumers depend mostly on the macroalgal and pelagic energy pathways. The food web currently established has low dependence on the benthic pathway. Given the important increase in precipitation predicted for this region and the increment in detritus it incurs, this food web is likely to suffer important alterations in the future.

1. Introduction

The tropics are home to high biodiversity and complex ecosystems. As the knowledge on global change increases, so does the awareness that tropical ecosystems are likely to be more sensitive than temperate ecosystems to the multiple pressures they will face over the next decades (e.g. Tewksbury et al., 2008; Somero, 2010; Sunday et al., 2011; Watson et al., 2013; Vinagre et al., 2016, 2018a,b). Yet, compared to their temperate counterparts, the ecological functioning of most tropical coastal habitats is still poorly studied.

Lying at the interface between the terrestrial and the marine realms, the intertidal zone of rocky shores is not only subject to changes in water temperature, but also to oscillations in air temperature, making this a physiologically challenging environment for marine organisms (e.g. Helmuth et al., 2006; Madeira et al., 2012; Vinagre et al., 2016). Tropical intertidal organisms live closer to their thermal limits than their temperate counterparts, being this way more vulnerable to the increase in mean and in extreme temperatures predicted for these areas (Stillman and Somero, 2000; Stillman, 2003; Vinagre et al., 2016, 2018a,b).

Rocky shores are, nevertheless, among the most productive ecosystems in the world, constituting an important link in the transfer of energy between the marine and terrestrial systems (e.g. Hori and Noda, 2001; Ellis et al., 2007), and providing refuge and nursery grounds to many commercial fish species and crustaceans (e.g. Turra and Leite, 2000; Barreiros et al., 2004; Cunha et al., 2008; Dias et al., 2014, 2016). Knowledge on the food web structure and energy pathways of tropical intertidal food webs is crucial for the understanding of their general functioning and to achieve their sustainable use and the conservation of biodiversity.

The intertidal rocky shorelines of Southeastern Brazil are predicted to be among the coastal areas of the world hardest hit by climate change, with an increase in temperature of up to 6 °C and an increase in rainfall of up to 60% by the year 2100 (PBMC, 2012). Besides a possible

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impoverishment of trophic interactions involving mobile consumers owing to exceedingly high thermal stress, a severe increase in rainfall will certainly lead to surplus terrestrial matter reaching coastal waters, likely fueling alternative energy pathways through nearshore pelagic and benthic compartments that may potentially disrupt present coastal food webs. Moreover, the rocky reefs in this region have been recently invaded by exotic species that have built very large populations, at times dominating seascapes. This is the case of sun corals *Tubastraea* spp (da Silva et al., 2014) in the subtidal and of the bicolored purse-oyster *Isognomon bicolor* in the intertidal zone (López et al., 2014). Other recent introductions included mobile consumers that may alter the structure of food webs through generalist epibenthic feeding (i.e. the peppermint shrimp *Lysmata lipkei;* Pachelle et al., 2016; Madeira et al., submitted) or through predation of higher-order prey (i.e. the Indo-Pacific swimming crab, *Charybdis hellerii*; Mantelatto and Dias, 1999). Corbisier et al. (2006) examined the rocky shore food web at a restricted area in Ubatuba (Flamengo sound), using stable isotopes and focusing on large trophic groups, 18 years before the present study, before the invasive species above have been detected in this ecosystem.

The aim of the present study was to conduct an in-depth analysis of the food web occurring in the tropical intertidal rocky shores of Southeastern Brazil, with the aim of 1) describing the general food web structure, 2) estimating food web length, 3) estimating the trophic level of the secondary consumers, and 4) their dependence on different energy pathways. Important attention was given to the new invading species given that their trophic role and dependence on energy pathways are entirely unknown in Brazilian waters.

Stable isotope analysis of δ^{13}C and δ^{15}N was applied in this investigation, since these two isotopes allow the estimation of the food sources, energy pathways and trophic levels of the organisms that compose the food web (e.g. Kwak and Zedler, 1997; Riera et al., 1999; Corbisier et al., 2006; Vinagre et al., 2015; Duarte et al., 2017). The δ^{13}C isotope is typically used to determine the origin and pathways of organic matter in food webs, an issue of crucial importance in the understanding of ecosystem's functioning, since it informs on the relative dependence of the organisms on the different energy pathways feeding the food web. This is possible when the primary sources (e.g. phytoplankton, macroalgae, detritus) are isotopically distinct, which often occurs in transition ecosystems, such as shallow coastal areas and estuaries (Hobson et al., 2002; Le Loc'h and Hily, 2005). Values of δ^{15}N increase by 2.5–4.5‰ from prey to predator making it a marker of trophic position (Owens, 1987; Peterson and Fry, 1987; Post, 2002). It can thus be used to understand the food web's basic topology.

2. Materials and methods

2.1. Study area

The southeast coasts of Brazil are characterized by basalt rocky shores punctuated by numerous sandy beaches, fringed by the Atlantic rain forest. The climate is wet tropical and summers are typically warm and wet, with frequent tropical storms. Ongoing climate change in the region is mostly caused by the poleward migration of the South Atlantic Convergence Zone, which is leading to heavier rainfall events (Zilli et al., 2018) and thereby increased inputs of terrestrial materials. Tree cover in the rainforest correlates with the number of rainy days during the wet season (Webb et al. 2005), thus forest fragmentation owing to human activity has ultimately also generated small-scale variation in precipitation. The numerous heavy rain showers (often more than once a day) mean that the input of terrestrial matter is highly variable on a fine temporal and spatial scale. This way, punctual collection of particulate matter (POM) for stable isotope analysis will necessarily result in highly variable δ^{13}C and δ^{15}N values. This also applies to phytoplankton and zooplankton. For this reason, sampling did not include POM, phytoplankton and zooplankton. Sampling was conducted in summer because it is the peak of biodiversity and biomass, ensuring that the highest possible variety of organisms was present. Sampling in summer in this area also allows direct comparison with the work of Corbisier et al. (2006), which also took place in summer (February 1999; 18 years before the current study, 65 km northeast from the study area).

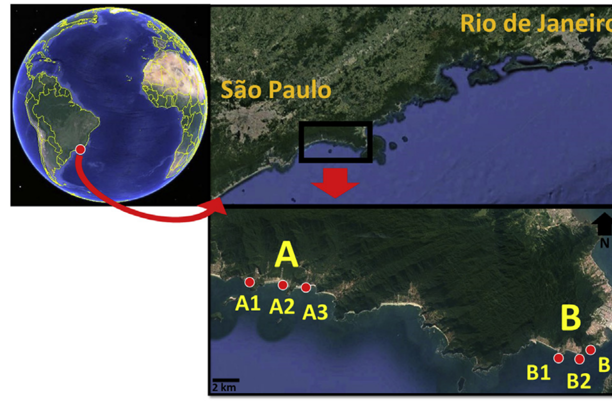

Fig. 1. Location of the study area in southeast Brazil. (A and B) indicate the two sampling sites. A1, A2, A3 and B1, B2, B3, indicate the location of the replicate sampling points within each site. Aerial photos adapted from Google Earth.

2.2. Sampling

Field work took place at low tide, during summer, in February of 2017, at two sites (A and B, Fig. 1), distanced approximately 40 km. At each site, three replicate points were sampled (Fig. 1, A1 – Barra do Sahy: 23°46′26″S; 45°42′09″W, A2 – Baleia: 23°46′47″S; 45°39′51″W, A3 – Camburizinho: 23°46′43″S; 45°38′46″W and B1 – Barequeçaba: 23°49′43″S; 45°26′29″W, B2 – Segredos: 23°49′45″S; 45°25′23″W, B3 – Cabelo Gordo: 23°49′33″S; 45°25′18″W). All points encompass mixed shallow habitats of rock and sand. Collection was conducted in the low intertidal area and infralittoral. Maximum depth at the sampling sites was 0.5 m. The spatial sampling design aimed at ensuring that the data encompassed spatial variability at a regional scale.

At each point, macroalgae, sessile and moving fauna were collected manually or with hand nets. At each point three sediment samples (3 × 60 ml) were collected. The number of replicates per sampling point was 3 for macroalgae and 3–6 for animals. Specimens of fauna were measured (total length for fish, shrimp, polychaeta and molluscs, carapace length for crabs and diameter for cnidarians) (Table 1). Samples were preserved on ice and taken to the laboratory at CEBIMar (Centre for Marine Biology of the University of São Paulo), where they were frozen at −20 °C and analysed within less than a week.

2.3. Isotope analysis

The isotopes analysed were δ^{13}C and δ^{15}N. These isotopes have been used worldwide for the description of food webs because they allow the estimation of the food sources used by organisms over time, allowing a characterization of their feeding habits and trophic levels (e.g. Peterson et al., 1985; Riera and Richard, 1996; Kwak and Zedler, 1997; Baeta et al., 2009; Vinagre et al., 2015).

Muscle tissue samples were dissected from fish, molluscs and crustaceans. For sponges and cnidarians, the whole animal was used, after cleaning of stomach contents. All samples were dried at 60 °C and ground to fine powder with a mortar and pestle.

The carbon and nitrogen isotopic composition of the samples was determined using a Flash EA 1112 Series elemental analyser coupled on line via Finningan ConFlo III interface to a Thermo delta V S mass spectrometer. The carbon and nitrogen isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰), a deviation from a standard material (PDB limestone for δ^{13}C and atmospheric