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An experimental evaluation of macroalgal consumption and selectivity by nominally herbivorous fishes on subtropical rocky reefs

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ABSTRACT

Herbivory is of great importance to reef system dynamics and structures because of the role primary consumers play in shaping benthic communities at various scales. In this work, the consumption and the feeding selectivity of the fish assemblage towards a set of macroalgae was evaluated through remotely filmed multiple-choice feeding assays. Macroalgal species showed a variable susceptibility to consumption, with *Spyridia hypnoides* and *Amphiroa* sp. being the most consumed and *Plocamium brasiliense* and *Codium intertextum* the least consumed among the 11 options. Eighteen herbivorous and omnivorous fish species were recorded taking bites from the feeding trial and only six were responsible for about 90% of the total number of mass standardized bites. Nominally herbivorous species (mainly *Sparisoma tuiupiranga* and *Acanthurus chirurgus*), as well as omnivorous species like *Stephanolepis hispidus* and *Diplodus argenteus*, were important in terms of macroalgal consumption. These observed patterns are likely to be driven by different food processing modes employed by fishes and nutritional and defensive properties of algae. Moreover, these results evidence a great potential for macroalgae consumption on subtropical rocky reefs and suggest the existence of elements of both redundancy and complementarity on macroalgal selectivity by herbivorous and omnivorous fishes in these environments.

1. Introduction

Nominally herbivorous fishes are usually among the most abundant and conspicuous components of the fish fauna in reef systems around the world (Horn, 1989; Choat, 1991; Ferreira et al., 2004; Cheal et al., 2013), where they account for a large proportion of the total reef fish biomass (Bouchon-Navaro and Harmelin-Vivien, 1981; Gust et al., 2001; Ferreira and Gonçalves, 2006). These species are known to be extremely important in shaping hard bottom benthic communities at various scales due to their grazing activity (Lewis and Wainwright, 1985; Carpenter, 1986; Polunin, 1988; Jesse and Wild, 2013). Indeed, a number of field and experimental studies have demonstrated the capacity of nominally herbivorous fishes to influence the distribution, standing crop, productivity and community structure of different algal groups on tropical reefs (Hatcher and Larkum, 1983; Carpenter, 1986; Klumpp and Polunin, 1990; Choat, 1991) and subtropical and temperate environments (Choat, 1982; Ojeda and Muñoz, 1999; Mendes et al., 2009; Taylor and Schiel, 2010).

Worldwide, the nominally herbivorous fish fauna encompasses species from different families, with distinct evolutionary histories, which present a huge variation in their feeding and food processing modes (Horn, 1989; Choat, 1991). These species are usually categorized into different functional groups based on their jaw mechanics and on the relative amount of macroalgae and detritus/sediment they ingest (Choat et al., 2002; Green and Bellwood, 2009). Understanding the selectivity patterns of different nominally herbivorous fish species towards multiple algal species is crucial to determine whether the local fish fauna is redundant or complementary in their potential algae consumption (Rasher et al., 2013). Moreover, the recognition of redundancy and complementarity patterns among consumer is vital to elucidate the role between diversity and ecosystem functioning at different scales (Duffy, 2009).

Most of the studies that have quantified consumption rates of macroalgae by herbivorous fishes, have utilized the genus *Sargassum* as a model (e. g. Hoey and Bellwood, 2009; Cvitanovic and Bellwood, 2009; Bennett and Bellwood, 2011; Vergés et al., 2012, among others). Although this approach can be useful in indicating the rates at which fishes are able to "remove" a late successional stage, habitat-forming algae from a reef, it does not take into account the fact that different macroalgae are consumed by different fishes (Choat et al., 2002; Ferreira and Gonçalves, 2006) and that different herbivorous fishes process food differently (Choat et al., 2004; Crossman et al., 2005). In this sense, the use of multiple-choice feeding trials typifies a more realistic scenario of macroalgae consumption by fishes, as well as their feeding choices (Lewis, 1985; Mantyka and Bellwood, 2007; Rasher et al., 2013).

The Southwest Atlantic harbors an impoverished fish fauna when compared to other biogeographic regions, like the Caribbean or the

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Indo–Pacific (Floeter et al., 2008), which reflects a smaller number of nominally herbivorous fishes (Ferreira and Gonçalves, 2006). Along the Brazilian coast, the most abundant roving herbivorous species belong to the families Acanthuridae, Kyphosidae and Labridae (tribe Scarini) (Ferreira et al., 2004). Other locally abundant species that are usually classified as omnivores can also ingest large quantities of algae, like the Sparidae *Diplodus argenteus* or the Pomacanthidae *Pomacanthus paru* (Dubiaski-Silva and Masunari, 2004; Batista et al., 2012). Thus, apart from the species classically identified as herbivores, several other species have also the potential to consume algae along the Brazilian coast.

The general focus of this paper is to experimentally assess macroalgal consumption by nominally herbivorous fishes and evaluate the selectivity feeding patterns of these fishes on a subtropical rocky reef in the Southwestern Atlantic. More specifically, the questions to be answered are: 1) What are the most important fish species interacting with (eating) macroalgae at subtropical reefs on Southwestern Atlantic?; 2) What is the consumption rate of different macroalgal species by these fishes?; 3) What algal species are selected or avoided by each of the most important fish? By answering these questions, it will be possible to better understand the role played by different nominally herbivorous fish species on subtropical rocky reefs and generate a baseline for predictions of the interactions between these fishes and their algal resources.

2. Material and methods

2.1. Study area

Fieldwork was conducted between December 2011 and January 2012 (Austral Summer) at Arraial do Cabo (22°57′ S, 42°01′ W) on the Southwestern Atlantic (Fig. 1). The region of Arraial do Cabo is of major ecological and biogeographic interest to the Southwestern Atlantic, since it represents the South distributional limit of some tropical reef organisms, and accumulates both tropical and warm temperate components (Ferreira et al., 2001, 2004). With annual average water temperatures of 22 °C (ranging from 18 to 25° at the study sites), the benthic cover of local rocky reefs includes corals (massive and milleporids) as veneer, with high cover of zoanthids, sponges, macroalgae and especially a rich epilithic algal community (Ferreira et al., 1998; Rogers et al., 2014).

Two sites with similar characteristics, protected from the prevailing NE winds and located approximately 2 km apart, were chosen for this study: Porcos Island and Pedra Vermelha (Fig. 1). These two sites harbor rocky reefs composed by flatten habitats in shallow, with boulders adding complexity, split over average depths, finally ending in sand bottoms about 9 m depth. Although these two sites are very similar in terms of both benthic and reef fish community, they were selected to evaluate possible spatial variations on the consumption patterns of macroalgae.

2.2. Macroalgal species

Eleven macroalgal species were chosen to evaluate the selectivity patterns of nominally herbivorous fishes: the Chlorophyta *Codium intertextum*, *Ulva* sp., the Rhodophyta *Amphiroa* sp., *Spyridia hypnoides*, *Plocamium brasiliense*, *Laurencia dendroidea*, *Laurencia filiformis*, and the Phaeophyceae *Sargassum* sp., *Dictyota* sp., *Dictyopteris plagiogramma* and *Colpomenia sinuosa*. These species were chosen because they are relatively abundant throughout the study area, encompass all three major macroalgal groups (Chlorophyta, Rhodophyta and Phaeophyceae) and possess different morphologies (*sensu* Steneck and Dethier, 1994). Most of the algal species are known to be dietary items to at least some fish in the region (Ferreira et al., 1998). All algal thalli used in the assays were collected at the same site in which each experimental plot was performed, except for *Dictyopteris plagyogramma* and *P. brasiliense*, which were collected at a nearby rocky shore in Anjos Bay (Fig. 1), where they attain much higher densities.

2.3. Multiple-choice assays

Care was taken when collecting macroalgae to minimize damage and ensure thalli physical integrity. Once collected, the thalli were transported to aquariums with aerated seawater and kept overnight prior the beginning of the assays. Each experimental assay consisted of one similar-sized piece of each macroalgal species tied to a rope (*ca.* 200 cm long) in a random order in a regular distance (*ca.* 15 cm). Each algae piece was weighted to the nearest 0.01 g before and after the experiment to assess the consumption rates after the trials. Each experimental assay was exposed to fish consumption during one hour. Pilot studies were performed to test the possible loss of algal mass related to experimental manipulations, in which exclusion nets were

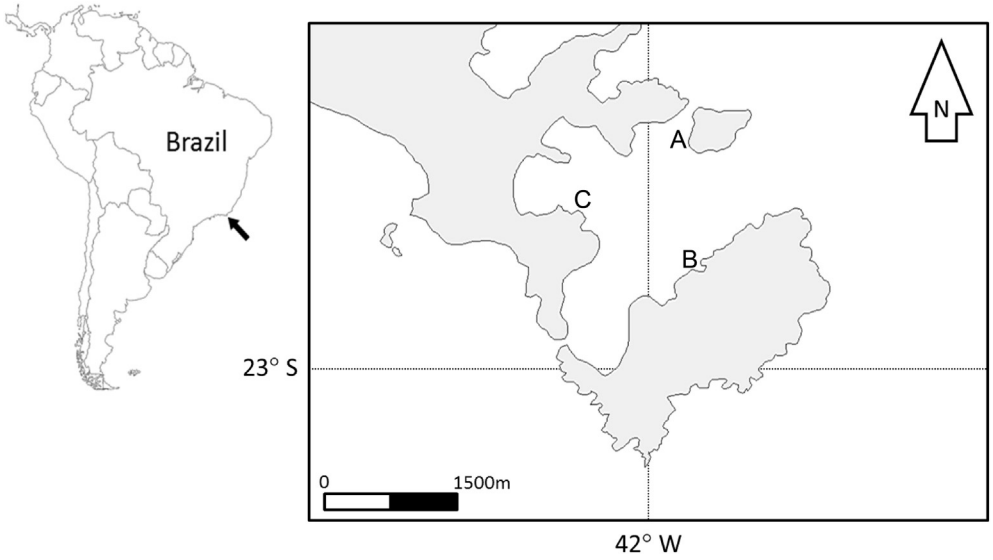

Fig. 1. Map of the study area at Arraial do Cabo, Southeastern Brazil, with the two study sites (A) Porcos Island and (B) Pedra Vermelha, as well as (C) Anjos Bay, where *P. brasiliense* and *D. plagiogramma* were collected.