

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



Thiago C. Mendes *, Cesar Augusto M.M. Cordeiro, Carlos Eduardo L. Ferreira

Laboratório de Ecologia e Conservação de Ambientes Recifais, Departamento de Biologia Marinha, Universidade Federal Fluminense, CP: 100.644, CEP: 24001-970, Niterói, RJ, Brazil

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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 macroalgal 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.

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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 macroalgal 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

* Corresponding author at: Institut de Recherche pour le Développement (IRD), UMR “Entropie”, Labex Corail, Université de Perpignan, Perpignan, 66000 – France.
E-mail address: tc Mendes@gmail.com (T.C. Mendes).

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* (Dubiascki-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 plagiogramma* 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

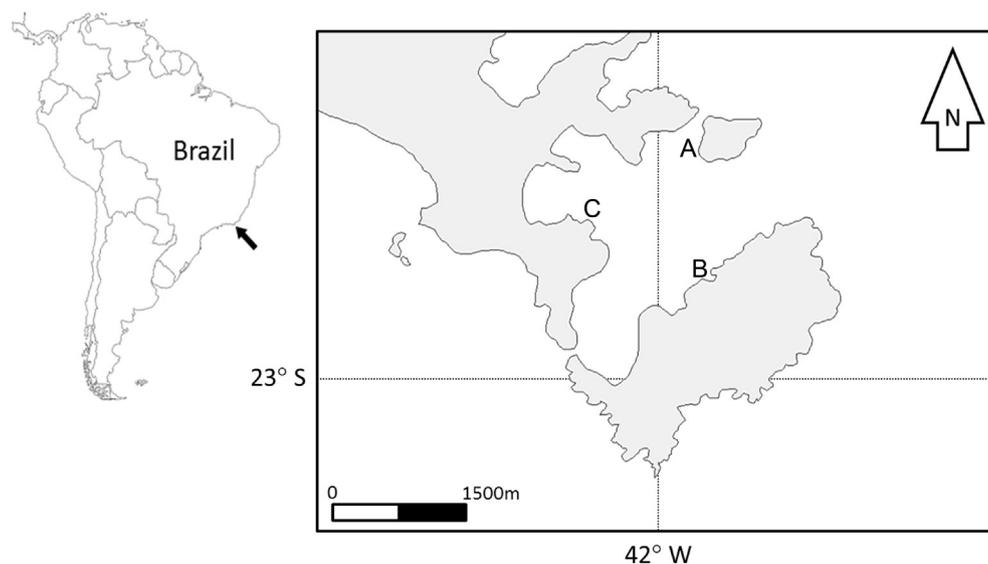


Fig. 1. Map of the study area at Arraial do Cabo, Southeastern Brazil, with the two study sites (A) Porcos Island and (B) Pedra Vermelha, as well as (C) Anjos Bay, where *P. brasiliense* and *D. plagiogramma* were collected.

used to evaluate mass variation in the absence of feeding activity by fishes (Fig. S1). Since no differences were found after 1 h intervals in the absence of herbivores (Table S1), reduction in algal mass during the experiment was attributed to consumption by fishes, with no need of controls (Roa, 1992). The multiple-choice feeding assays ($n = 48$) were performed on two different depth zones: shallower (between 2 and 4 m) and deeper (between 5 and 7 m) at both sites. Thus, the assays were equally distributed between the two sites and at different depth zones (12 assays per site and depth zone).

To assess the abundance and biomass of fishes potentially consuming macroalgae at the study sites, nominally herbivorous as well as omnivores were counted along underwater visual census (20×2 m) ($n = 15$ per site and depth zone). Each fish individual observed along transects was recorded and classified into species and length categories (10 cm interval size classes). Biomass was calculated using length–weight relationships available in the literature (e.g. Froese and Pauly, 2013).

2.4. Video analysis

All assays were filmed during their entire duration with a digital video camera Sony HDR-XR-100 on an underwater housing Equinox HD6 coupled on a tripod. The use of remote video has been widely used in reef ecology, since it offers some advantages for experiments that would otherwise require long periods of underwater observation, and allows feeding to be quantified in the absence of divers (Longo and Floeter, 2012). Afterwards, footage was analyzed and the number of bites of each fish towards each different macroalga was registered as well as the estimated size of each fish. In order to account for different body sizes, a mass standardized bite number was calculated as the product of fish body mass and number of bites per species (Hoey and Bellwood, 2009).

2.5. Macroalgal selectivity and data analysis

To evaluate macroalgal selectivity patterns of each nominally herbivorous species, the Strauss' Linear Selection Index (L) was used:

$$L = r_i - p_i,$$

where r_i is the percentage of bites towards macroalga i , in relation to the total number of bites from all macroalgae during each assay, and p_i is the percentage of the total algal mass presented at the beginning of every assay belonging to the macroalga i (Strauss, 1979). The Strauss' Linear Selection Index varies from -1 to $+1$, with positive values indicating positive selection, negative values indicating avoidance and near zero values indicating a random selection of the macroalgae offered (Strauss, 1979). To test their significance, a 95% confidence interval was calculated for each L value, thus intervals encompassing zero were considered not significant.

2.6. Data analysis

The use of multiple macroalgal species offered concomitantly to the fish assemblage implies that the consumption of each algae will be dependent on the consumption of the other algae presented. This experimental approach provides a dataset in which there is no independence among samples (macroalgae), what violates basic assumptions to run ANOVAs (Underwood, 1997). Thus, to test for differences in the consumption among the eleven macroalgae used, the Friedman's test was employed (Roa, 1992; Lockwood, 1998). When significant differences were found, Friedman's post-hoc multiple comparisons test was used to identify which algae were more or less consumed.

3. Results

3.1. Macroalgal consumption

No differences between total consumption of algae between sites or depths were detected, so hereafter the results were pooled. The eleven algal species used in the assays presented variable consumption rates by fish (Friedman Test, $\chi^2 = 182.371$, $p < 0.01$), with the two species with greatest consumption being the red algae *S. hypnoides* and *Amphiroa* sp., with an average $36.4\% (\pm 2.6 \text{ SE})$ and $35.5\% (\pm 2.2 \text{ SE})$ of mass consumed after 1 h (Fig. 2). Secondly consumed were *Ulva* sp. ($21.4\% \pm 3.4 \text{ SE}$) and *Dictyota* sp. ($19.8\% \pm 3.8 \text{ SE}$) followed by the other species, which had on average less than 15% of their mass consumed (Fig. 2). No relation between algal consumption and algal taxonomic group seems to exist since the huge variation on the distribution of consumption among algal groups. Although the two most consumed algae were Rhodophyta, *L. dendroidea* and *P. brasiliense* ranked among the three least consumed. Similarly, there was high variation in the consumption of species of Chlorophyta, with *Ulva* sp. being the third most consumed and *C. intertextum* the least consumed (Fig. 2).

3.2. Mass standardized bites and fish biomass

A total of eighteen fish species were recorded taking bites from the algae during the assays. These species represent 10 families and, although most of them are nominally herbivorous, some of them are omnivores, originally reported as invertebrate feeders (Ferreira et al., 2004). Only three species accounted for almost 70% of the total number of mass standardized bites: *Sparisoma tuiupiranga* (with 29.2% of the mass standardized bites), *Stephanolepis hispidus* (24.2%) and *Acanthurus chirurgus* (16.4%). Along with these, other species in decreasing order of importance were: *Sparisoma axillare* (8.4%), *Stegastes fuscus* (8.3%) and *D. argenteus* (4.1%) which together summed up to 90% of the total number of mass standardized bites (Table 1).

Among all the species observed feeding on the experiment, *S. fuscus* and *S. hispidus* presented the highest contribution to the total biomass according to the underwater visual censuses. Along with *S. tuiupiranga*, *A. chirurgus* and *A. bahianus*, these species represented almost 30% of the biomass of the whole fish assemblage in the region (Table 1).

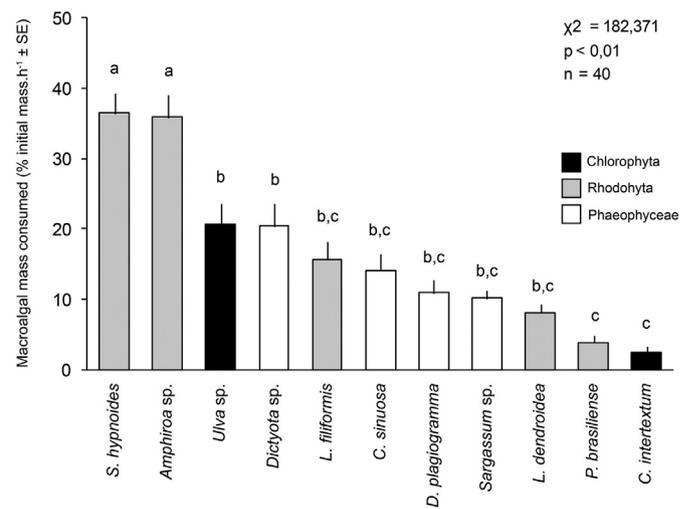


Fig. 2. Mean consumption rates of macroalgae by fish on multiple-choice feeding assays (percent mass consumed after 1 h). Black bars represent the Chlorophyta, gray bars are Rhodophyta, and white ones are Phaeophyceae. Error bars are standard error and letters above bars represent similar grouping in a posteriori Friedman's test.

Table 1

Fish species (with their related family and trophic classification) that feed on macroalgae offered on the assays with their respective relative mass standardized bite and relative biomass.

Species	Family	Trophic group	Stand. bites (%)	Biomass (%)
<i>Sparisoma tuiupiranga</i>	Labridae (Scarini)	Herbivore/detritivore	29.1	5.1
<i>Stephanolepis hispidus</i>	Monacanthidae	Omnivore	24.2	6.9
<i>Acanthurus chirurgus</i>	Acanthuridae	Herbivore/detritivore	16.4	4.6
<i>Sparisoma axillare</i>	Labridae (Scarini)	Herbivore/detritivore	8.4	2.7
<i>Stegastes fuscus</i>	Pomacentridae	Herbivore/detritivore	8.3	7.6
<i>Diplodus argenteus</i>	Sparidae	Omnivore	4.1	1.3
<i>Kyphosus sectatrix</i>	Kyphosidae	Herbivore	2.7	1.9
<i>Acanthurus bahianus</i>	Acanthuridae	Herbivore/detritivore	2.2	3.8
<i>Sparisoma radians</i>	Labridae (Scarini)	Herbivore/detritivore	2.1	0.1
<i>Pomacanthus paru</i>	Pomacanthidae	Omnivore	1.5	0.5
<i>Cantherhines pullus</i>	Monacanthidae	Omnivore	0.9	0.6
<i>Sparisoma frondosum</i>	Labridae (Scarini)	Herbivore/detritivore	0.7	0.9
<i>Chaetodon striatus</i>	Chaetodontidae	Invertivore	<0.1	1.9
<i>Sphaeroides spengleri</i>	Tetraodontidae	Invertivore	<0.1	<0.01
<i>Bodianus pulchelus</i>	Labridae	Invertivore	<0.1	2.3
<i>Cantherhines macrocerus</i>	Monacanthidae	Omnivore	<0.1	0.2
<i>Stegastes pictus</i>	Pomacentridae	Omnivore	<0.1	0.2
<i>Pseudupeneus maculatus</i>	Mullidae	Invertivore	<0.1	3.4

3.3. Feeding selectivity

All the species that interacted with the algal assays exhibited different patterns of selectivity and avoidance towards the macroalgal assayed. Although eighteen species have taken bites from the algae, only eight were abundant enough to have their selectivity patterns analyzed (Fig. 3).

The two most abundant Scarini species as well as the two most important Acanthuridae species (Table 1) presented very similar selectivity patterns. In general, these species selected only two algal species among eleven used in the assay while the patterns of selectivity and avoidance were nearly the same. The two most important parrotfishes, *S. tuiupiranga* and *S. axillare* presented similar selectivity patterns, as both selected the red algae *Amphiroa* sp. and *S. hypnoides* and avoided *C. intertextum*, *L. filiformis*, *P. brasiliense* and *C. sinuosa*. *S. axillare* also avoided *Ulva* sp. and *L. dendroidea*, while *S. tuiupiranga* was indifferent for both algae (Fig. 3). Similarly, the selectivity patterns of the surgeonfishes *A. chirurgus* and *A. bahianus* were basically identical: both selected *Amphiroa* sp. and *S. hypnoides* and avoided *Ulva* sp., *L. dendroidea*, *P. brasiliense*, *Sargassum* sp. and *D. plagiogramma*. Besides, *A. chirurgus* also avoided *L. filiformis* and *A. bahianus* avoided *C. intertextum* and *C. sinuosa* (Fig. 3).

The only species that selected the brown macroalgae *Sargassum* sp., *Dictyota* sp. and *D. plagiogramma* was *Kyphosus sectatrix*. Moreover, this species avoided all other algae with the exception of *Ulva* sp. and *S. hypnoides*. *D. argenteus* highly selected *Ulva* sp. and was indifferent to most other algal species with the exception of the avoided *Amphiroa* sp., *L. filiformis* and *C. sinuosa*. Although important in terms of percentage mass standardized bites, *S. fuscus* and *S. hispidus* consumed macroalgae in proportion to their availability, apart from *S. hispidus*, which avoided *C. intertextum* and *S. hypnoides* (Fig. 3). Results from the mean number of bites taken by each fish species towards the eleven macroalgae followed a pattern similar to their selectivity (Fig. S2).

4. Discussion

The present work highlights the elevated potential of nominally herbivorous and omnivorous fishes to consume macroalgal species in reefs in the Southeastern Atlantic, and a complex pattern of redundancy and complementarity in fish selection towards these algae. The remotely filmed assays revealed that only six fish species accounted for more than 90% of the mass standardized bites taken on macroalgae. Furthermore, while three among the four most important fishes displayed an unexpectedly elevated redundancy, a broad feeding complementarity

was observed among fishes with most species presenting different selectivity and avoidance patterns. Much debate exists on how redundant or complementary nominally herbivorous fish assemblages are in relation to their feeding ecology (Burkepile and Hay, 2011) and on the implications of these patterns to reef functioning (Rasher et al., 2013). Most studies to date were conducted on high diversity tropical coral reefs and have suggested the existence of a limited redundancy among nominally herbivorous fishes (e.g. Bellwood et al., 2003; Mantyka and Bellwood, 2007; Rasher et al., 2013). In this study, the depauperate Southwest Atlantic herbivorous fish assemblage presented a similar pattern to the one observed on tropical reefs elsewhere (Mantyka and Bellwood, 2007; Burkepile and Hay, 2011; Rasher et al., 2013), indicating that patterns may be similar across different reef systems.

It is important to note, however, that most of the fish species observed in our feedings trials ingest large amounts of detritus and filamentous algae naturally (which cannot have their consumption rates assessed with the methods used here) when feeding on macroalgae (Ferreira et al., 1998; Dias et al., 2001; Ferreira and Gonçalves, 2006). In fact, detritus within the epilithic algal matrix is a highly nutritious food source for these species, since it contains larger quantities of protein amino acids when compared to algae and thus may represent their primary nutritional source (Crossman et al., 2001). Nevertheless, although the approach used in the present work does not necessarily assess the real diet of nominally herbivorous fishes, it sheds light into the influence these organisms may have on the distribution of macroalgal communities on rocky shores based on their potential consumption rate and selectivity/avoidance patterns.

Numerous factors that can influence feeding selectivity by nominally herbivorous fishes have already been examined, such as algal nutritional quality (Pillans et al., 2004; Raubenheimer et al., 2005; Holzer et al., 2013; Goecker et al., 2005), food processing modes (Clements and Choat, 1997; Choat et al., 2004), presence of chemical and/or morphological defenses on algal thalli (Paul and Hay, 1986; Van Alstyne and Paul, 1990; Duffy and Paul, 1992; Hay et al., 1994), availability of the algal resource (Ferreira et al., 1998; Pérez-Matus et al., 2012), among others. Although not directly assessed in the present study, some of these factors can be used to infer the selectivity/avoidance patterns of nominally herbivorous fishes towards macroalgal species observed.

Both *S. hypnoides* and *Amphiroa* sp. were the most consumed algae and were selected by at least four fish species among the most important. In general, red and green algae tend to be favored in the diets of most herbivorous fishes due to their higher nutritional value when compared to brown algae (Zemke-White and Clements, 1999; Patarra et al., 2011), although the nutritional composition of algae is highly

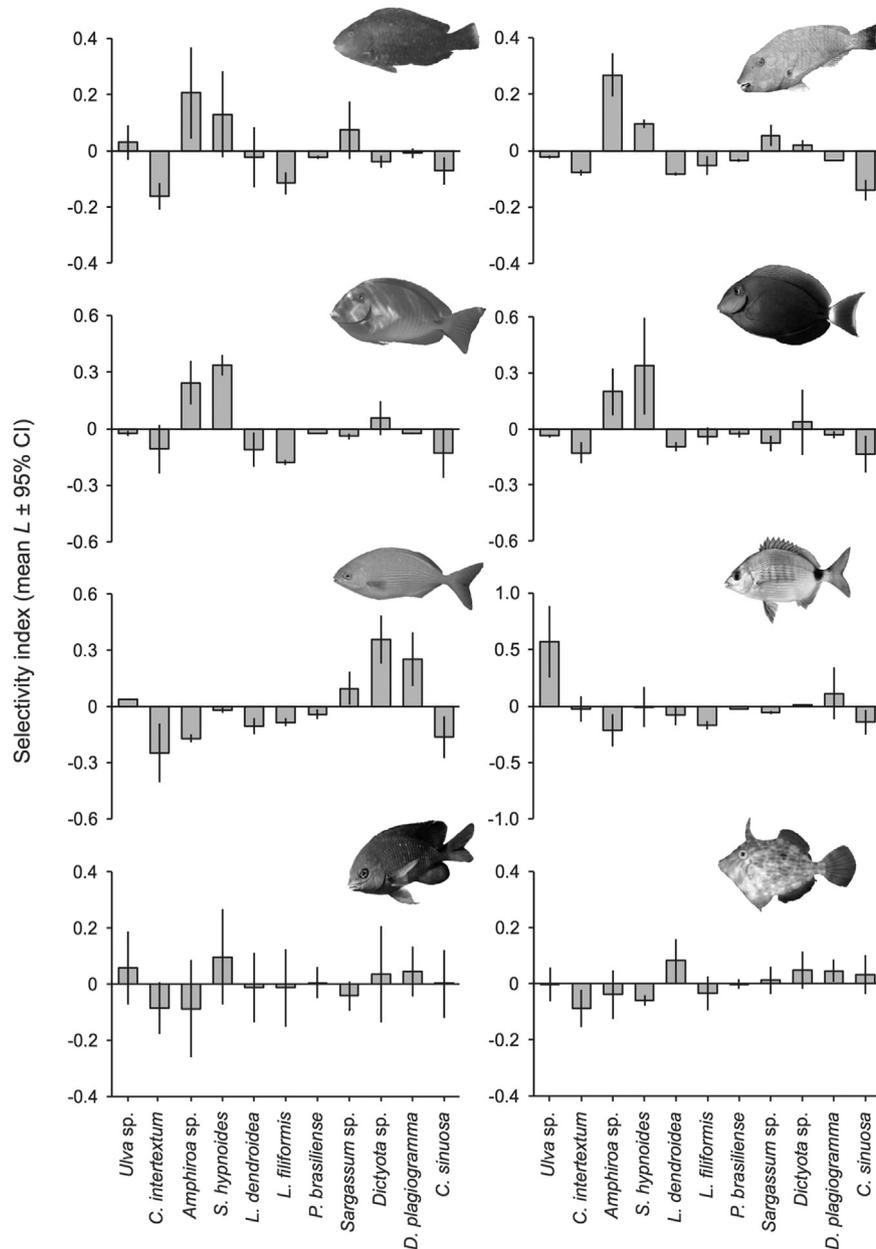


Fig. 3. Strauss' Linear Selection Index (L) for the eight most important fish species in terms of mass standardized bite. *Sparisoma tuiupiranga* (upper left), *Sparisoma axillare* (upper right), in descending order *Acanthurus chirurgus* (left), *Acanthurus bahianus* (right), *Kyphosus sectatrix* (left), *Diplodus argenteus* (right), *Stegastes fuscus* (bottom left), and *Stephanolepis hispidus* (bottom right). Error bars represent 95% confidence intervals.

variable and some brown algae have been shown to present high protein contents (Montgomery and Gerking, 1980; Kaehler and Kennish, 1996; McDermid and Stuercke, 2003). Apart from that, *S. hypnoides* has very soft and delicate thalli, what facilitates its digestion by fishes due to mechanical and/or chemical action (Zemke-White et al., 2000). On the other hand, *Amphiroa* sp. is expected to be of comparatively lower nutritional value due to its highly calcified thallus (Hay et al., 1994). *Amphiroa* sp. is one of the most conspicuous algae in the study area being the most abundant species within the epilithic algal matrix (Guimaraens and Coutinho, 1996; Ferreira et al., 1998). Indeed, the high abundance of *Amphiroa* sp. has already been used to explain its presence on the diet of local damselfishes (Ferreira et al., 1998). A further explanation for the selection of *Amphiroa* sp. lays on the possibility that their thalli were not totally devoid of detritus during the drying process due to their fragility. Consequently, the presence of detritus within the thalli of *Amphiroa* sp. may have served as an attractor to nominally herbivorous fishes, especially detritivorous scarids and

acanthurids, which rely on a protein-rich diet to meet their energetic demands (Crossman et al., 2005).

Numerous studies have described thallus calcification presented in *Amphiroa* sp. as well as in many other tropical algae from the genus *Halimeda*, *Galaxaura*, *Padina*, among others, as a strategy to escape herbivory (Littler et al., 1983; Hay et al., 1994). However, although calcification can deter some fish species (Lewis, 1985; Pillans et al., 2004), thallus calcification alone does not serve as a defensive strategy against some fish species, especially parrotfishes, as previous works have described an intense selection of calcified algae by different species (e.g. Schupp and Paul, 1994; Mantyka and Bellwood, 2007). In fact, gut content analyzes of a number of parrotfish species have revealed high quantities of calcium carbonate (Choat et al., 2002, unpublished data), which increase their gut pH (Lobel, 1981). Since parrotfishes rely basically on grinding by the pharyngeal teeth to break down the ingested material (Bonaldo et al., 2014), inorganic material may increase the efficiency of this mechanical mastication. This observation

is further supported by the fact that a number of parrotfish species feed on live coral colonies, ingesting great loads of their carbonate skeleton (Francini-Filho et al., 2008; Bonaldo and Bellwood, 2011). Similarly, both *Acanthurus* species observed feeding on the assays possess a thick walled gizzard-like piloric stomach, in which mechanical abrasion occurs. Calcium carbonate-rich *Amphiroa* sp. can be retained in this structure in order to help mechanical grinding of the ingested material. Thus, the selection of *Amphiroa* sp. by *Sparisoma* spp. and *Acanthurus* spp. can be explained by the digestive strategy these fishes possess, where inorganic material such as carbonate helps the mechanical trituration of various dietary materials.

The brown algae *Dictyota* sp., *D. plagiogramma* and *Sargassum* sp. were only selected by *K. sectatrix*. In general, these algae are not dietary to most nominally herbivorous fishes due to their highly refractory structural carbohydrates (Montgomery and Gerking, 1980). Nonetheless, most kyphosid species are known to harbor endosymbiont bacteria that promote the breakdown of these complex carbohydrates into assimilable short chain fatty acids (Clements and Choat, 1995), especially in the end of their intestines and in the hindgut chamber (when present). In general, most *Kyphosus* species are very important herbivorous fishes, consuming huge amounts of brown algae especially *Sargassum* spp. (Clements and Choat, 1997; Choat et al., 2002; Michael et al., 2013).

The green alga *C. intertextum* and the red algae *P. brasiliense* and both *Laurencia* species were largely avoided by most fishes, although they have thin thalli and some comparatively high nutritional contents. However, the presence of secondary metabolites may deter in some level the pressure by some fish species. A number of *Codium* species, including *C. intertextum* are known to possess dimethylsulfoniopropionate (DMSP), a substance that can decrease the activity of generalist feeders over their thalli (Van Alstyne and Puglisi, 2007). Similarly, *P. brasiliense* possesses halogenated monoterpenes (Vasconcelos et al., 2010) and *Laurencia* species produces elatol (Pereira et al., 2003), both of which prevent herbivore action towards these algae (Pereira et al., 2003; Vasconcelos et al., 2009).

From the eighteen fish species observed feeding on the trials, six (33.3%) are usually classified as omnivores. They accounted for 31.0% of the total number of bites observed on the assays and, among them, *S. hispidus* and *D. argenteus* corresponded to the second and sixth species in number of bites, respectively. The role of omnivores on algal consumption is usually regarded as of lower importance, and in many cases even disregarded. Bellwood et al (2006) highlighted the importance of omnivorous fishes on macroalgal consumption, especially for annual algae like *Sargassum* that are more likely to be consumed when senescent due to the higher epiphytes load. In general, omnivores are said to display limited selectivity towards different resources (Mantyka and Bellwood, 2007), since they would be able to ingest a large variety of food items (Raubenheimer et al., 2005; Pérez-Matus et al., 2012). This observation may be true to *S. hispidus*, that took a considerable amount of bites from the entire set of macroalgae offered and did not present any significant selectivity towards any algae. However, *D. argenteus* displayed a marked selectivity for *Ulva* sp. Indeed, *D. argenteus* presented a unique selectivity pattern, since it was the only species to select this alga. There is no standardized comparison of the omnivorous fishes influence on tropical and subtropical benthic communities. However, based on the amount of bites taken by these fishes on the present study, omnivores are likely to be more important in terms of algal consumption on subtropical than in tropical reefs.

In summary, this work tested whether a set of eleven of the most abundant macroalgal species in a subtropical rocky reef are susceptible to feeding by fishes and which are mostly prone to be selected or avoided by them. Herbivorous and omnivorous fishes possess a great capacity of consuming macroalgae with varying levels of selectivity, presenting elements of both redundancy and complementarity. Among the most abundant fishes four groups could be recognized

based on their selectivity/avoidance choices: (1) *Sparisoma* spp. and *Acanthurus* spp. which selected *S. hypnoides* and *Amphiroa* sp.; (2) *K. sectatrix* which selected only the brown algae *Dictyota* sp., *D. plagiogramma* and *Sargassum* sp.; (3) the omnivorous *D. argenteus* which highly selected *Ulva* sp.; and (4) *S. fuscus* and *S. hispidus* which did not selected or avoided any algae. The selectivity patterns presented by the different fish species seem to be driven by algal nutritional quality and presence of chemical deterrents as well as the food processing modes by these fishes. Future research may better elucidate the role of these traits on the feeding selection by these fishes to create a more thoroughly framework to predict patterns of fish feeding activity on Brazilian subtropical and tropical reefs.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2015.06.001>.

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