

## HIGH INTRASPECIFIC VARIATION IN THE DIET OF THE FRENCH ANGELFISH *Pomacanthus paru* IN THE SOUTH-WESTERN ATLANTIC

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Grazing by reef fishes is among the most important biotic factors controlling the structure of benthic communities in coral reefs and tropical rocky shores (e.g., HIXON, 1983). Exclusion experiments have widely demonstrated that fish grazing is a key factor determining algal abundance, with direct and indirect effects on corals and other competing benthic organisms (e.g., SAMMARCO, 1983; LEWIS, 1986; HUGUES et al., 2007). Grazer exclusion reduces the resilience of coral reefs in face of disturbances such as hurricanes, bleaching events, and climate change (HUGUES et al., 2007; MUMBY, 2009). Underwater observations and palatability, caging and transplantation experiments indicate that grazing by reef fish also has strong influence on the abundance, distribution and shape of sponges (PAWLIK, 1998; WULFF, 2000; RUZICKA; GLEASON, 2009; LOH; PAWLIK, 2009).

Angelfishes (family Pomacanthidae) are very common and conspicuous reef fishes with a circum-global distribution on tropical and warm temperate reefs. Pomacanthids feed mainly on the structurally resilient and firmly attached benthic prey items avoided by most predators (KONOW; BELLWOOD, 2005). Sponges are the dominant item in the diet of several species of the genera *Holacanthus* and *Pomacanthus*, which are therefore often called spongivorous, while algae are usually a secondary item (e.g., RANDALL; HARTMAN, 1968; HOURIGAN et al., 1989; WULFF, 1994; VERDÍN et al., 2010). The diet of adult Western Atlantic angelfishes has only been studied in a few localities in the Caribbean (RANDALL; HARTMAN, 1968; HOURIGAN et al., 1989; WULFF, 1994; DUNLAP; PAWLIK, 1996; PAWLIK, 1998; SWEARINGEN; PAWLIK, 1998). In the South-western Atlantic only

juveniles have been studied (SAZIMA et al., 1999; ANDRÉA et al., 2007). Francini-Filho and Moura (2010) observed the feeding of adult *Pomacanthus arcuatus* and *P. paru* on the zoanthid *Palythoa caribaeorum* in Abrolhos, without giving any attention to other items of their diet. Ferreira et al. (2004) and Ruzicka and Gleason (2008) stressed the need to determine the extent of geographical variation in diet composition of spongivorous reef fishes, including angelfishes, to better understand the latitudinal variation of predation and herbivory intensity on Western Atlantic coral reefs. However, virtually nothing is yet known about the feeding habits of South-western Atlantic adult angelfishes.

The French angelfish *Pomacanthus paru* inhabits coral reefs and rocky shores from Florida (USA) to Santa Catarina State (Southern Brazil) (e.g., RANDALL; HARTMAN, 1968; FERREIRA et al., 2004). Due to its high abundance, colour pattern and large size, it is one of the most conspicuous and recognizable species of the family Pomacanthidae in the Caribbean (DELOACH, 1999). In Brazil *P. paru* is the most abundant angelfish and shows a patchy distribution, with peaks of abundance in Parcel Manoel Luís (0.52°S), Abrolhos (17.20°S), and Arraial do Cabo (23.0°S) (FERREIRA et al., 2004). In the South-western Atlantic, juveniles of *P. paru* have been reported as fish cleaners in Abrolhos, North-eastern Brazilian coast (SAZIMA et al., 1999), but a great diversity of sponges was also detected in their gut contents in Salvador, Bahia State (ANDRÉA et al., 2007). No data are available on the diet composition of adult *P. paru* or any other angelfish on the Brazilian coast, which represents approximately half of the latitudinal distribution of the most common Western Atlantic angelfishes. Here we investigated the

intraspecific variation in diet composition of *Pomacanthus paru* by means of gut content analysis in three localities along the Brazilian coast.

Fieldwork was conducted from January to July 2005 at Atol das Rocas ( $3^{\circ}52'S-33^{\circ}42'W$ ), Abrolhos Archipelago ( $17^{\circ}58'S-38^{\circ}42'W$ ) and Ilha Grande ( $23^{\circ}04'S-44^{\circ}19'W$ ) (Fig. 1). Detailed descriptions of these sites can be found elsewhere (KIKUCHI; LEÃO, 1997; VILLAÇA; PITOMBO, 1997; MORAES et al., 2003; CREED; OLIVEIRA, 2007). Samples were collected in two large tidal pools at Atol das Rocas (Barretinha and Barreta Falsa), one fringing reef in Abrolhos (Portinho Sul), and one rocky coast on Ilha Grande (Lagoa Verde) (Fig. 1).

Fifteen specimens of the French angelfish with standard length varying from 33–46 cm were sampled through spear fishing ( $n=5$  per locality). Stomachs were removed and fixed in 70% ethanol. The fish were fixed in 4% formaldehyde and deposited at the fish collection of Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil. The guts were dissected and stomach contents were separated under a stereomicroscope and fixed in 70% ethanol; intestinal

contents were not included in the analysis because they were too degraded for identification. Algae were identified under a stereomicroscope; sponges were dehydrated and placed in paraffin to prepare transversal sections for identification under a light microscope. Only fragments that could be sectioned were identified; isolated spicules and the smallest (approximately  $< 1\text{mm}^3$ ) or highly digested fragments, which could not be identified with certainty, were considered “undetermined”. Other invertebrates (tunicates and cnidarians) were identified only to higher taxonomic levels. The percentages (in volume) of sponges and algae per stomach were determined on a grid under a stereomicroscope. One-way ANOVA was used to compare the percentages of both sponges and algae in angelfish diet among the three sites. Data were examined *a priori* for normality and homoscedasticity using Kolmogorov-Smirnov and Levene Tests, respectively, and the *post-hoc* Tuckey test was used to determine which sites were significantly different (ZAR, 1999). All statistics were calculated using Vassar online software (<http://faculty.vassar.edu/lowry/VassarStats.html>).

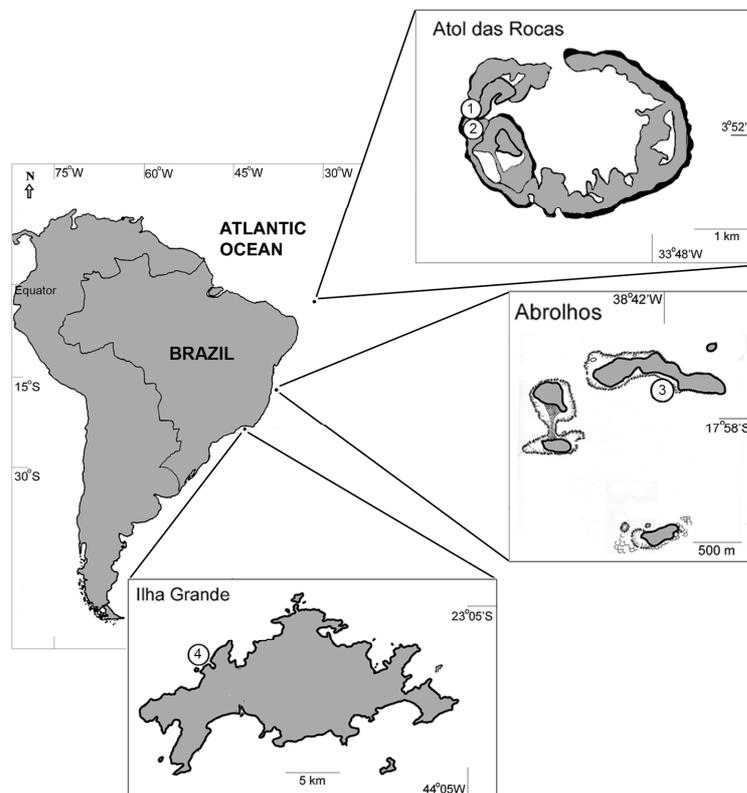


Fig. 1. Location of the collection sites (encircled numbers) in the three localities studied: Atol das Rocas (1, Barretinha; 2, Barreta Falsa Pool); Abrolhos (3, Portinho Sul); and Ilha Grande (4, Lagoa Verde).

Gut length data were obtained from freshly killed specimens right after collection. Viscera were excised from each specimen and extended to measure the gut from the posterior-most point of the stomach to the vent. Gut lengths were compared with total lengths to calculate the relative gut length index.

Considering the three sites altogether, algae represented 63.2±32.1% of the total gut contents of *P. paru* in Brazil, followed by sponges (31.5±32.1%), undetermined material (4.0±7.4%), tunicates (0.9±1.3%) and cnidarians (0.4±1.1%). A total of 36 sponge species (Table 1) and 26 species of algae (Table 2) were found in gut contents. Intraspecific variation of diet contents was high: the ratio of algae to sponges in individual fish varied from 0.05 to 23.75 (Fig. 2). Algae composed 5–95% of the gut contents in each individual examined, and 11 fish (73.3%) had 50% or more of their gut content composed of algae. The percentages of algae and sponges varied significantly among the different locations: algae were the main food item at Atol das Rocas and Abrolhos (91.0±4.4% and 70.0±24.2%, respectively [mean ± SD]) but comprised only 28.6±22.1% of the diet on Ilha Grande (ANOVA, d.f.=2, F=13.83, p= 0.000767). In contrast, sponges were the main group consumed by *P. paru* on Ilha Grande (69.8±22.0% of gut contents), but were significantly less predated on Abrolhos (18.8±16.2%) and Atol das Rocas (6.0±2.2%) (ANOVA, d.f.=2, F=22.73, p<0.0001; Fig. 3). The relative gut length index was 5.27±0.96 (n=15).

All algae and most sponge species were eaten at only a single site each. *Tedania ignis*, *Spirastrella hartmani*, *Aaptos* aff. *aaptos* and *Halichondria* sp. were eaten at two sites, and *Chondrilla* aff. *nucula* was the only species eaten in all three localities (Table 1). These results indicate a high geographical variation in the qualitative composition of the diet of *P. paru* that is probably related to the limited distribution of most prey species, which may be absent or rare in some areas. Although some of the above-mentioned species are among the most abundant and widely distributed sponges in Brazil, our qualitative data do not allow us to determine feeding preferences of *P. paru* for any prey species. It is remarkable, however, that *Tedania ignis*, *Chondrilla nucula* and species of *Spirastrella* (*S. coccinea*, *S. hartmani*, *Spirastrella* sp.) were also eaten by adult *P. paru* in the Caribbean and by juveniles in Salvador, Brazil (RANDALL; HARTMAN, 1968; WULFF, 1994; PAWLIK, 1998; SWEARINGEN; PAWLIK, 1998; ANDRÉA et al., 2007). This may indicate that *P. paru* has a preference for these species and actively searches for them, but experimental evidence is needed to test this hypothesis.

Table 1. Presence of sponges in gut contents of *Pomacanthus paru* in three localities in Brazil.

Sponges	Atol das Rocas	Abrolhos	Ilha Grande
<i>Chondrilla</i> aff. <i>nucula</i>	+	+	+
<i>Aaptos</i> aff. <i>aaptos</i>	+	+	
<i>Spirastrella hartmani</i>	+	+	
<i>Acervochalina</i> sp. 4	+		
<i>Amphimedon</i> aff. <i>compressa</i>	+		
Clionidae unidentified	+		
<i>Plakortis microrhabdifera</i>	+		
<i>Halichondria</i> sp.		+	+
<i>Tedania ignis</i>		+	+
<i>Acervochalina</i> sp. 2		+	
<i>Acervochalina</i> sp. 3		+	
Chalinidae unidentified 2		+	
<i>Cliona varians</i>		+	
Niphatidae unidentified		+	
Petrosiidae unidentified		+	
Suberitidae unidentified 2		+	
<i>Tedania</i> sp.		+	
<i>Tethya</i> sp.		+	
Thorectidae unidentified		+	
Spongiidae unidentified		+	
<i>Acervochalina</i> sp. 1			+
<i>Amphimedon</i> cf. <i>viridis</i>			+
Callyspongiidae unidentified			+
Chalinidae unidentified 1			+
<i>Clathria</i> ( <i>Microciona</i> sp.)			+
<i>Desmapsamma anchorata</i>			+
<i>Dragmacidon reticulatum</i>			+
<i>Dragmacidon</i> sp.			+
<i>Dysidea janiae</i>			+
cf. <i>Leucandra</i> sp.			+
<i>Mycale</i> sp.			+
<i>Mycale</i> cf. <i>angulosa</i>			+
<i>Mycale microsigmatosa</i>			+
<i>Polymastia janereinsis</i>			+
Suberitidae unidentified 1			+
<i>Terpios</i> cf. <i>fugax</i>			+

Table 2. Presence of algae in gut contents of *Pomacanthus paru* in three localities in Brazil.

Algae	Atol das Rocas	Abrolhos	Ilha Grande
<i>Botryocladia</i> sp.	+		
<i>Bryopsis pennata</i>	+		
<i>Caulerpa verticillata</i>	+		
<i>Codium</i> sp. 1	+		
<i>Gelidiella acerosa</i>	+		
<i>Hypnea spinella</i>	+		
<i>Laurencia</i> sp.	+		
<i>Siphocladus</i> sp.	+		
<i>Callithamniella</i> sp.		+	
<i>Caulerpa cupressoides</i>		+	
<i>Caulerpa mexicana</i>		+	
<i>Dictyopteris</i> sp.		+	
<i>Dictyota</i> sp. 1		+	
<i>Jania capillacea</i>		+	
<i>Spyridia</i> sp.		+	
<i>Udotea</i> sp.		+	
Udoteaceae		+	
unidentified			
<i>Caulerpa sertularoides</i>			+
<i>Caulerpa</i> sp.			+
<i>Champia</i> sp.			+
<i>Codium</i> sp. 2			+
<i>Dictyota</i> sp. 2			+
Gelidiaceae			+
unidentified			
<i>Hypnea cervicornis</i>			+
Rhodophyceae			+
unidentified			
<i>Sargassum</i> sp.			+

In the Caribbean, the French Angelfish *Pomacanthus paru* is usually classified as spongivorous, indicating that sponges are the major component of its diet (RANDALL; HARTMAN, 1968; WULFF, 1994). In contrast, our results show that in Brazil *P. paru* is an omnivorous benthic feeder, with a diet composed mainly of algae and rather secondarily by sponges. Tunicates and cnidarians are also eaten but in very low proportions. There was great geographical variation in the diet composition of *Pomacanthus paru*, which therefore may play a role of herbivore rather than carnivore in some areas, such as North-eastern Brazil. The relative gut length index of the species ( $5.27 \pm 0.96$ ) is comparable to that of 'robust omnivore' pomacanthids such as *Pygoplites diacanthus* and *Chaetodontoplus duboulayi*, and intermediate between spongivorous and herbivorous species of *Pomacanthus* (KONOW; BELLWOOD, 2011).

The intraspecific variability of *P. paru* diet observed here may have been biased by limitations of the study design such as low sample size, lack of quantification of the benthic communities, and analysis of only stomach, not whole gut contents, which could mean that only the last ingested preys were represented. However, ANOVA showed that within-site variation was significantly lower than between-site variation, indicating that spatial differences in the benthic community between sites are also important to determine the extent of variability in angelfish diet.

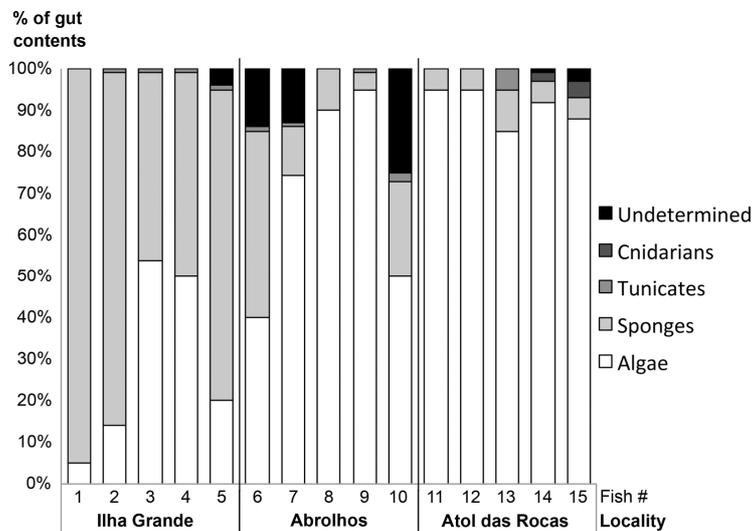


Fig. 2. Percentages (in volume) of taxonomic groups and undetermined material in gut contents of 15 adult specimens of *Pomacanthus paru* (numbered # 1–15) from three localities in Brazil: Fish # 1–5, Ilha Grande; # 6–10, Abrolhos Archipelago; # 11–15, Atol das Rocas.

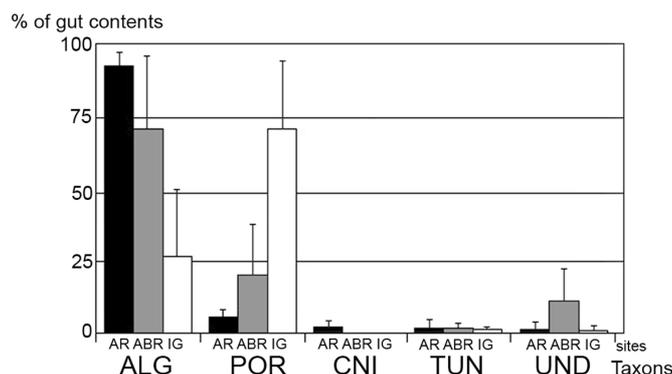


Fig. 3. Percentages (average and SD) of taxonomic groups and undetermined material in gut contents of *Pomacanthus paru* in three sites in Brazil: Atol das Rocas (AR, black bars), Abrolhos Archipelago (ABR, grey bars) and Ilha Grande (IG, white bars). Taxons: ALG, algae; POR, poríferans; CNI, cnidarians; TUN, tunicates; UND, undetermined material.

Intraspecific variation in diet composition was also found in the closely related species *Pomacanthus zonipectus* and *Holacanthus passer* from the Eastern Pacific, which may behave as omnivorous with adaptations to herbivory (PÉREZ-ESPAÑA; ABITIA-CÁRDENAS, 1996) or as spongivorous (VERDÍN et al., 2010). This variation appears to be related to the differences in local food availability (VERDÍN et al., 2010). In Brazil, algae are the most abundant organisms on the shallow reefs of Atol das Rocas and Abrolhos (KIKUCHI; LEÃO, 1997; MORAES et al., 2003; VILLAÇA; PITOMBO, 1997), where they are the main food of the French angelfish. The low similarity in qualitative composition of the diet between the three sites further supports the idea that diet composition is correlated to the composition of the benthic community, which varies in different localities. However, the adequate quantitative data on the structure of the benthic communities at each site needed to test this hypothesis is still lacking. An omnivorous strategy allows the grazer to change its diet according to local prey availability, but a balance between animal and vegetal food sources is often necessary to fulfil the dietary requirements of omnivorous fishes (e.g., RAUBENHEIMER et al., 2005). Furthermore, the high within-site variation in diet contents on Abrolhos and Ilha Grande indicates that other factors beyond food availability (e.g., age, sex, genetic variation, individual behaviour; e.g., SINGER; BERNAYS, 2003) are also important in determining angelfish diet and its variations.

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