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Abundance, diet, foraging and nutritional condition of the banded butterflyfish (*Chaetodon striatus*) along the western Atlantic

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Abstract The feeding behaviour and diet plasticity of a given species are usually shaped by the relationship between species physiology and the quality and availability of resources in the environment. As such, some species may achieve wide geographical distributions by utilizing multiple resources at different sites within their ranges. We studied the distribution and feeding of *Chaetodon striatus*, the most widespread butterflyfish in the Atlantic, by assessing its density and foraging rates in eight sites enclosing 44° of latitude. We also evaluated the relationship between fish density and foraging rates with nutritional condition and diet across study sites, and the gut length relative to body size. Density and foraging rates did not differ among studied sites. In 169 stomachs analysed, we found 52 different items (12–23 per site). Polychaeta and Cnidaria were the most important items in seven study sites. Therefore, *C. striatus* may be considered as a non-coral generalist feeder, as it feeds on a wide variety of items and substrata along the studied range, with no consistent selectivity pattern for foraging substratum across sites. Individuals from all sites but Salvador (NE Brazil) had similar RNA/DNA ratios, suggesting that *C. striatus* nutritional condition is similar along its extensive distribution. Our findings highlight the importance of assessing different sites within the distribution range of generalist butterflyfishes, and different variables, to a better comprehension of the feeding ecology of these species.

Introduction

Diet and feeding behaviour are primarily important to the ecology, biology and evolution of organisms, as they are essential traits that affect species distribution and population structure (Brown 1984; Cole and Pratchett 2014). In this sense, the feeding behaviour and diet plasticity of a given species are usually shaped by the relationship

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between species morphology, physiology and the quality and availability of resources in the environment (Brown 1984; Lawton et al. 2012; Cole and Pratchett 2014). This relationship ultimately influences species distribution and density in a given location (Gerking 1994; Lawton et al. 2012). As such, some species may achieve high local abundance and wide geographical distributions by utilizing multiple resources at different sites throughout their ranges (Lawton et al. 2012).

The butterflyfishes (Chaetodontidae) include about 130 reef fish species that live closely associated to the substratum, and most of them consume a variety of benthic prey items, such as anthozoans, polychaetes and crustaceans (Randall 1967; Birkeland and Neudecker 1981; Sazima and Sazima 2001; Pratchett 2005). Butterflyfishes are generally classified into three major guilds according to their diet and feeding selectivity: obligate corallivores, facultative corallivores and non-coral generalist feeders. Most studies on butterflyfish feeding have been focused on Indo-Pacific corallivores, which usually have wide longitudinal and, in some cases, latitudinal distributions on tropical coral reefs (e.g. Hobson 1974; Irons 1989; Tricas 1989; Pratchett 2005; Gregson et al. 2008). Generalist corallivorous butterflyfishes with wide distributions in the Indo-Pacific may change their diet and foraging preferences over large spatial scales, in response to food availability (Berumen et al. 2005; Cole and Pratchett 2014) and intraspecific/interspecific competition (Cox 1994; Pratchett 2005). On the other hand, this variation is less noticeable in highly specialized corallivorous butterflyfishes in the Indo-Pacific, which are more sensitive to differences in the availability of their preferred prey species (Devictor et al. 2010; Cole and Pratchett 2014).

In contrast to corallivorous butterflyfishes, very few studies assessed feeding habits and dietary composition of non-coral feeder species (e.g. Randall 1967; Birkeland and Neudecker 1981; Bonaldo et al. 2005). Non-coral feeders differ from other butterflyfishes in their geographical distribution (Lawton and Pratchett 2012; Cole and Pratchett 2014), as their range is not only associated with coral reef habitats and may include temperate environments (Lawton and Pratchett 2012; Cole and Pratchett 2014). Non-coral feeder butterflyfishes also differ from other butterflyfishes in their morphology, as their gut length/body size ratio is usually intermediate to that of corallivores and planktivores (Berumen et al. 2011). However, little is known on the feeding ecology of non-coral feeder butterflyfishes and how their abundance and feeding habits respond to environmental differences within their distribution.

In the western Atlantic, the banded butterflyfish, *Chaetodon striatus*, is classified as a non-coral generalist feeder (also known as benthic invertebrate feeder sensu Cole and Pratchett 2014), as it feeds on a wide variety of prey items,

with only a small fraction of its diet, if any, represented by scleractinian corals (e.g. Randall 1967; Pitts 1991; Sazima and Sazima 2001; Bonaldo et al. 2005). *Chaetodon striatus* is the butterflyfish with the widest distribution range in the western Atlantic, which encompasses two biogeographic provinces (Caribbean and Brazil) and a diversity of environmental conditions, such as temperature (17–30 °C), habitat type (e.g. coral and rocky reefs), and food items/availability (Floeter et al. 2001). This diversity of environmental and biotic conditions may ultimately affect the abundance (e.g. via recruitment rates; Pratchett and Berumen 2008), diet, foraging selectivity (e.g. by changes in resource availability) and nutritional condition of *C. striatus* along its distribution range. However, given the apparent high feeding versatility and generalist habits of this species, it is possible that differences in prey availability do not exert a strong influence on local abundance of *C. striatus* along its distribution, especially in comparison with highly specialized corallivorous butterflyfishes.

We compared the abundance, diet and foraging rates and selectivity of *C. striatus* among eight distinct sites, spanning 44° of latitude, testing whether local variation in the availability of prey exerted an important influence on this seemingly generalist species. We particularly investigated whether fish density, foraging rates, foraging selectivity and nutritional condition varied along the studied gradient. We verified key dietary resources of *C. striatus* by validating in situ feeding observations using dietary analyses. We also assessed *C. striatus* gut length relative to body size, to verify whether this metric supported the food habit found for this species. As we show below, we found no differences in *C. striatus* density and foraging rates among sites. Also, our results suggest that *C. striatus* has high feeding plasticity, as it forages on a wide variety of food items and substrata along the studied sites, without clear differences in nutritional condition. Therefore, the present study reveals how wide-ranging species can be better understood using a plethora of complementary approaches.

Materials and methods

Study sites

The present study was conducted in eight sites distributed along the western Atlantic. These sites included three types of reefs: tropical biogenic reefs (one in Puerto Rico and three in Brazil: Tamandaré, Salvador and Abrolhos), volcanic rocky reefs (Trindade Island) and subtropical rocky reefs (Guarapari, Arraial do Cabo and Florianópolis; all situated in Brazil) (Fig. 1; Table 1). These eight sites were chosen because of their different reef formations and because they encompass a wide latitudinal range along
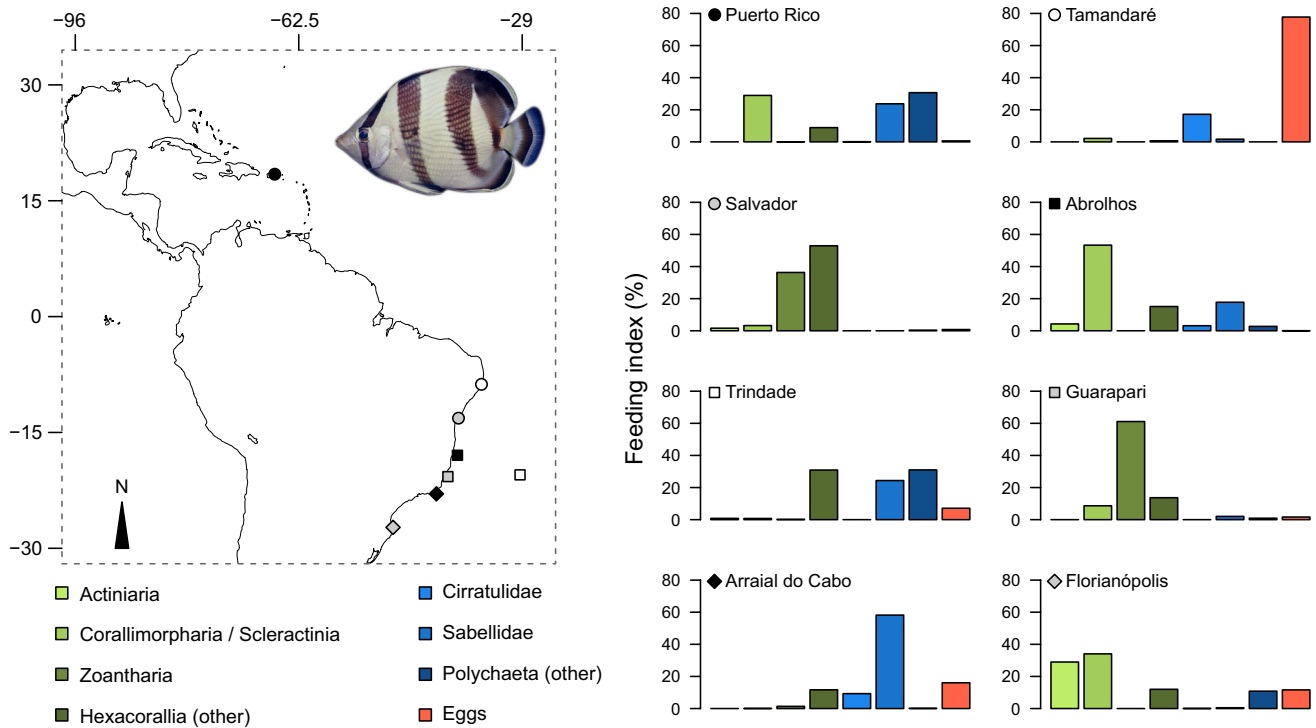
Fig. 1 Study sites along *Chaetodon striatus* distribution range (*left*); *Barplots* represent the feeding index based on stomach contents analysis of the most consumed items: Cnidarians and Polychaetes

Chaetodon striatus distribution in the western Atlantic. In fact, one of our sites, Florianópolis, is located on the Brazilian State that encloses the southernmost distribution limit of the species (Anderson et al. 2015).

Fieldwork was conducted between January 2010 and March 2012 on SCUBA. Underwater observations were done during daytime, between 9:00 and 16:00 h, in a total of 140 h of sampling, in depths ranging 2–16 m, which correspond to the range where rocky reefs were found at the study sites in Brazil. In Puerto Rico, however, the studied reefs were 18–22 m deep because we found no *C. striatus* individuals in shallow reefs. In each site, we sampled at least two different locations. We also compiled the yearly mean and minimum average water temperature for each site between 2003 and 2013 (Table 1; Selig et al. 2010). Sampling in Brazil was done during the austral summer and in Puerto Rico during boreal winter. Although data collection in Puerto Rico occurred during winter, water temperature was similarly warm across all study sites (Table 1).

Fish density

The density of *C. striatus* was assessed with a minimum of 30 belt transects per site (20 m long × 2 m wide = 40 m²; details in Floeter et al. 2007), except for Puerto Rico, where data were obtained from online published sources (data

collected in 100 m² belt transects at La Parguera; NOAA 2014). Samples of 13 additional sites along its distribution range were included for comparison (using the same transect size; 40 m²).

Foraging behaviour and benthic cover

We quantified the foraging behaviour of *C. striatus* by following haphazardly chosen individuals for 3-min periods (following Pratchett 2005; Cole and Pratchett 2011; Lawton and Pratchett 2012; Lawton et al. 2012). During each period, the observer counted the number of bites taken on each substratum type (see details below), keeping a distance of 1–3 m from the fish (Birkeland and Neudecker 1981). We observed a minimum of 49 individuals per site (Table 1) and, to minimize the risk of resampling the same fish individual, observers swam through the sampling site to search for individuals further away (following Birkeland and Neudecker 1981). Before each count, the observer waited a few minutes to minimize observer's effect on individual behaviour (Birkeland and Neudecker 1981). Only adult individuals were followed (total length generally >10 cm) to reduce variance attributable to ontogeny.

We used photoquadrats to estimate the relative abundance of each substratum type in each study site. Five photographs (covering an area of 40 cm × 60 cm; Krajewski

Table 1 *Chaetodon striatus* body size (cm, mean ± SE) and information on the study sites: temperature range (minimum and maximum mean temperature between 2003 and 2013; Selig et al. 2010), mean dive temperature (our data), geographic coordinates, coral species richness (Scleractinia/Octocorallia), main reef formation and cover, and the number of observed fishes in each site, number of transects and number of photographs analysed for each site

Study site	C. striatus size (cm)	Temperature range (°C)	Temperature dive (°C)	Geographic coordinate	Scleractinia/Octo-corallia	Reef type	Number of fish individuals observed	Number of transects	Number of photos of benthos
Puerto Rico	13.7 ± 0.8	26.0–30.3	27.0	17°56'N 67°01'W	117/99	Patchy coral reefs; sea whip	64	96	192
Tamandaré	8.5 ± 1.5	25.6–30.7	28.0	8°44'S 35°05'W	14/5	Rocky beach; urchin barrens and macroalgae	72	160	215
Salvador	8.8 ± 1.7	24.7–30.9	28.0	13°10'S 38°32'W	17/6	Rocky reef; mainly dominated by zoanthids	100	52	491
Abrolhos	10.7 ± 2.0	23.8–29.9	27.5	17°58'S 38°42'W	15/13	Coral reef; large reef complex; fringing reef; mainly dominated by scleractinians	82	164	309
Trindade	13.1 ± 0.2	22.8–28.4	–	20°30'S 29°20'W	11/2	Volcanic rocky reef; isolated oceanic island; mainly dominated by coralline algae	None	None	None
Guarapari	13 ± 1.9	22.0–29.0	23.0	20°S40'W	14/13	Rocky reef; mainly dominated by octocorals	72	30	251
Arraial do Cabo	10.7 ± 2.0	20.9–27.1	22.0	23°S 42°W	5/11	Rocky reef; sea fans	90	601	214
Florianópolis	12 ± 1.9	17.3–27.7	18.0	27°17'S 48°22'W	1/4	Rocky reef; macroalgae	49	420	154

and Floeter 2011) were taken in an area of approximately 2 m × 2.5 m (5 m^2) around the place where the last bite was taken by the observed individual (i.e. at the end of each 3-min observation period). However, because of logistical problems, we were not able to take photographs of all sampled individuals, but of about 60–98 % of them at each study site. Photographs were analysed with the software Coral Point Count with Excel Extension (CPCe v3.5—Kohler and Gill 2006), in which 20 points were randomly placed on each photograph. The benthic component immediately under each point was identified and placed into 11 categories, including six algae-dominated types (epilithic algal matrix, crustose, foliose, leathery, corticated and articulated calcareous), three Anthozoa (Octocorallia, Zoantharia and Scleractinia) and two others (Porifera and sand). Non-representative substratum types (<5 %) were excluded for RSF analyses (see "Materials and methods" section below). We analysed 154–491 photographs for each study site (Table 1).

Diet and relative gut length

For the analyses of diet, *C. striatus* adult individuals were collected with hand spear and had their stomach contents immediately stored in tubes with formaldehyde. We collected 17–30 fish individuals at each sampling site (total = 169 individuals). For each collected individual, we also assessed the relative gut length, by measuring the total length (TL) of each fish individual and the full non-stretched gut length, from the pyloric duct to the rectum. This measure can provide important information regarding the main type of diet in chaetodontids (Berumen et al. 2011).

The food items of each stomach were identified under a stereomicroscope to the most precise taxonomic category possible. The volume of each item was measured using a Petri dish, with a graph paper (each cell comprising 1 mm^2 of area) attached to the opposite side of the dish to serve as a counting grid (Hellawell and Abel 1970; Albrecht and Caramaschi 2003). Each food item was placed on the Petri dish and compressed to 1 mm of height with a histological glass. This limit was set with the help of two small glass slides 1 mm thick adjacent to the food item. The volume (mm^3) of each item was measured by counting the number of grid cells occupied by the item. The relative importance of each item in the diet of a given individual was analysed through the feeding index (IAi), which combines frequency of occurrence and volume of each item (following Kawakami and Vazzoler 1980; Lima et al. 2012).

Masses of organic material that seemed unidentifiable were analysed under a microscope to search for clue

elements, such as spicules and nematocysts. Contents were classified as "digested organic matter" when these elements were found mixed within organic matter. If nematocysts were recorded in high abundance within the organic matter, the item was placed into Cnidaria Hexacorallia Actiniaria or Cnidaria Hexacorallia Zoantharia category, according to the type of nematocyst found. As it was not possible to distinguish the nematocysts from Cnidaria Hexacorallia Corallimorpharia and Scleractinia, items with these nematocysts were thus classified as Cnidaria Hexacorallia Corallim/Scle. When nematocysts belonging to multiple orders were present, items were classified as Cnidaria Hexacorallia "other". When no identifiable elements were found, the material was classified as unidentifiable. Marine invertebrate taxonomists were consulted to confirm or identify dubious items.

Nutritional condition

Nutritional condition, which may be considered as a *fitness* measure, can be quantified through RNA:DNA ratio analyses (Behrens and Lafferty 2007). This index has been broadly employed as a fitness measure, since RNA protein synthesis varies with metabolic demand, i.e. fluctuates in response to food availability (quality), while DNA content per cell is fixed (Chícharo and Chícharo 2008). To determine RNA/DNA ratios, samples containing *C. striatus* white muscle from Puerto Rico, Salvador, Guarapari and Florianópolis ($n = 20, 19, 19$ and 20, respectively) were immediately stored in RNALater solution (Qiagen) after sampling and kept in a −20 °C freezer. Samples were thawed, and RNA and DNA concentrations of each sample were first assessed using ethidium bromide fluorescence (Dahlhoff and Menge 1996). We then weighted samples to 100 mg and homogenized them in replicates with 10 volumes of 2 mol NaCl. Samples were centrifuged for 1 min, and 5 μL of each sample was transferred into a microplate by adding 0.14 μL of solution containing 0.005 mg ethidium bromide and 0.15 mg proteinase K at 37 °C for 60 min. Following this initial incubation, we added 100 μL of buffer (80 mm Tris–HCl, pH 8.0 at 20 °C) and measured fluorescence at 365-nm excitation and 590-nm emission using a SpectraMax M5 spectrofluorometer. We assessed fluorescence attributable to RNA and DNA by sequential digestion of each nucleic acid using first 5 μL RNAse I (SIGMA), followed by 60-min incubation and then 5 μL DNAse I (SIGMA) and then by 30-min incubation. Finally, we estimated RNA and DNA concentrations based on standard curves of fluorescence, in which quantities of these nucleic acids are known.

Data analysis

Density data (i.e. discrete counts) are, by definition, better characterized by distributions such as Poisson and negative binomial. Therefore, an analysis of variance among multiple sites could be performed with generalized linear models (GLMs) assuming, for example, a Poisson distribution for the model error (Zuur et al. 2009). However, our density data presented a significant inflation of zeros (i.e. transects where no individuals were recorded), such that a GLM presented substantial overdispersion regardless of the choice of error distribution, hence hindering model interpretation. Therefore, to reduce the zero inflation, we adopted a bootstrap approach that entails the following three steps: (1) at each iteration ($n = 10,000$), for each site, 15 larger transects were drawn by pooling smaller original transects at random (with replacement) until a total area of 200 m^2 was achieved (i.e. 5×40 m^2 or 2×100 m^2); (2) at each iteration, a Bayesian Poisson GLM (using a log link; see Electronic Supplementary Material for details) was then fitted to estimate the average density/200 m^2 for each site; (3) these estimates of model averages (1002 MCMC steps per model fitting) were stored at each iteration to obtain a joint posterior distribution of random averages estimated from all the GLMs (total of 1000 iterations $\times$ 1002 MCMC steps per iteration = 1,002,000 estimates). Statistical significance between sites was assessed by the overlap (or lack thereof) between the 95 % confidence intervals of joint posterior distributions for average density/200 m^2.

Foraging rates among sites were compared using a GLM assuming a negative binomial distribution for the model error. An earlier model exploration indicated that the model was better fitted with a negative binomial distribution rather than Poisson (particularly, the gamma shape parameter $\theta \approx 1$).

Resource selection function (RSF) was used to evaluate foraging substratum selectivity, i.e. selection for preferred benthic substrata, at each of the seven study sites (Trindade was not included in this analysis, due to lack of data; see Table 1). Because our data consisted of direct observations of foraging substratum in which different individuals forage on (bitten substratum scored as 1), within a variety of available substrata (1000 random samples of unbitten substrata following observed availability proportion scored as 0), we applied a RSF using the logistic regression approach proposed by Manly (1993). The following log-linear form of the logistic regression represented our model:

$$\ln w = \beta_1 \times \text{Food} + \beta_2 \times \text{Site} + \beta_3 \times \text{Food} \times \text{Site} + \varepsilon,$$

where w depicts the selection strength based on the use/availability ratio, β_{1-3} represent model coefficients that indicate the effects of each variable, and ε is the model error. Sites and food (=foraging substratum) were entered as categorical

variables in the model. The significance of each parameter was assessed using type-III analysis of variance through partial likelihood ratio tests (Cox and Oakes 1984). We then refitted the significant model with observations of each fish individual being clustered to avoid pseudoreplication, which allowed estimating robust standard errors. RSF was conducted using the *survival* package version 2.8 (Therneau 2015) in R Software version 3.2.1 (R Core Team 2015).

One-way ANOVA was used to compare nutritional condition of *C. striatus* (measured as the natural logarithm of RNA/DNA) among sites. Tukey HSD was used to investigate pairwise differences among sites. Data met the assumptions for normality of residuals and homogeneity of variances for parametric tests (Underwood 1997; Zar 1999).

Data manipulation, statistical analyses and figures were coded in the R Software version 3.2.1 (R Core Team 2015) and can be fully reproduced assessing a free repository on GitHub (https://github.com/dbarneche/chaStri).

Results

Overall, density of *C. striatus* was not significantly different among most sites. However, density in Guarapari was significantly higher than in Puerto Rico (i.e. the 95 % confidence intervals from the posterior distributions do not overlap; Fig. 2a). Additional density data from other 13 sites support that *C. striatus* density in the Caribbean is generally lower than in the Brazilian coast (Fig. 2b).

Mean foraging rates of *C. striatus* differed among some sites, without a clear trend (Table 2; Fig. 3). *Chaetodon striatus* showed preferences for some substratum types over others [substratum effect (β_1): L.R. $\chi^2 = 161.08$, $df = 10$, $p < 0.0001$], but patterns of substratum selection and rejection were not consistent across sites [site effect (β_2): L.R. $\chi^2 = 706.57$, $df = 6$, $p < 0.0001$; Fig. 4]. Foraging substrata selected in some sites were avoided or used according to their availability in other sites [interaction term effect site–substratum (β_3): LR $\chi^2 = 1896.27$, $df = 60$, $p < 0.0001$]. No substrata were totally preferred or rejected across the seven sites, and *C. striatus* selected all substrata considered in at least one study site (Fig. 4). Articulated calcareous algae, for example, were positively selected in four out of seven study sites. In fact, in Florianópolis, this item was not recorded on the photographs (Fig. S1 in Electronic Supplementary Material). Anthozoa Octocorallia was selected in two study sites in Brazil. Moreover, in tropical sites in Brazil, such as Abrolhos and Tamandaré, *C. striatus* selected Anthozoa Scleractinia, differently from what was found in Puerto Rico, where hard coral was neither selected nor rejected. Epilithic algae matrix was slightly to substantially preferred in five out of seven sites (Fig. 4).
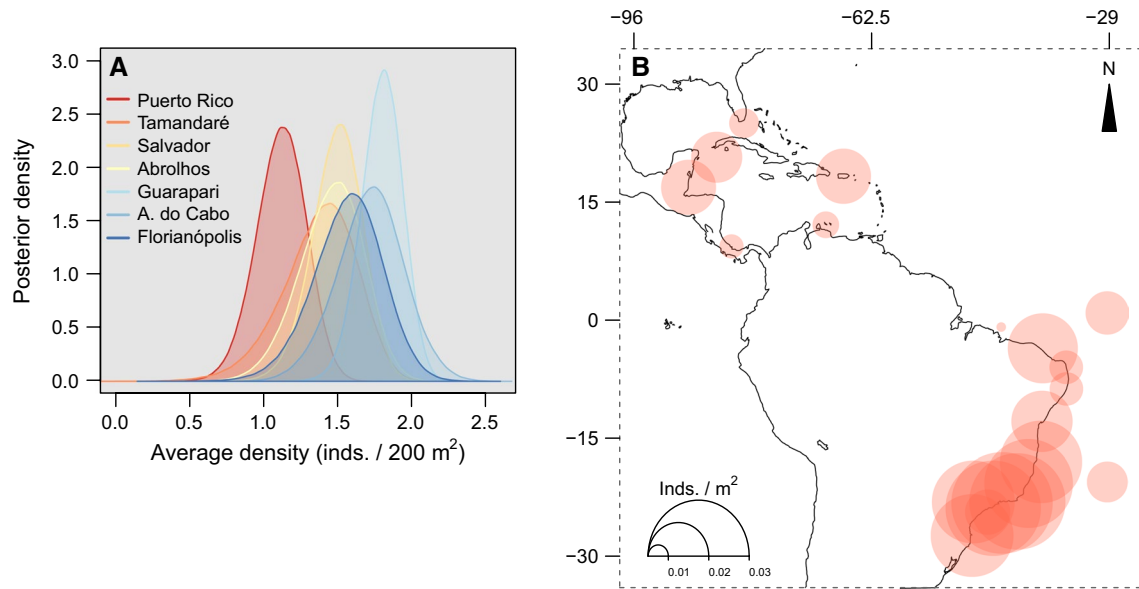
Fig. 2 a Average density of individuals in seven study sites and **b** density in additional sites along the distributional range of *C. striatus*. In (**a**), the curves represent the posterior density distribution of parameters (average densities of individuals in each site) summed across all MCMC chains ($n = 1,002,000$) as estimated using Bayesian methods in *JAGS*. In (**b**), *circles* represent the number of individuals per m²

Table 2 Average deviations in foraging rates (bites/3 min⁻¹) among sites

Reference level	Abrolhos	A. do Cabo	Florianópolis	Guarapari	Puerto Rico	Salvador
Arraial do Cabo	−0.299					
	(0.066)					
Florianópolis	−0.099	0.199				
	(0.611)	(0.296)				
Guarapari	**−0.540**	−0.241	**−0.440**			
	(<0.05)	(0.144)	**(<0.05)**			
Puerto Rico	0.187	**0.486**	0.286	**0.726**		
	(0.302)	**(<0.05)**	(0.167)	**(<0.05)**		
Salvador	**−0.550**	−0.251	**−0.450**	−0.010	**−0.736**	
	(<0.05)	(0.098)	**(<0.05)**	(0.950)	**(<0.05)**	
Tamandaré	−0.245	0.053	−0.146	0.294	**−0.432**	0.304
	(0.153)	(0.749)	(0.463)	(0.91)	**(<0.05)**	(0.060)

Estimates and *p* values (in parentheses) were estimated using a negative binomial GLM. Bold values indicate significant relationships (*p* value < 0.05)

Cnidaria and Polychaeta composed most of *C. striatus* diet in all sites (Table 3; Fig. 1). The number of items in all individuals combined per site ranged from 12 to 23 (the lowest diversity of items in Salvador and Tamandaré, the highest in Puerto Rico). Mollusca and/or Crustacean eggs were found in stomach contents in all sites, but in different proportions (Table 3). In terms of feeding index (*IAi*), sessile Polychaeta (mainly Sabellidae and Serpulidae) and Cnidaria Hexacorallia (0–58.2 and 2.8–94 %, respectively) were the dominant diet items across all sites, representing 4.5–94 % of the feeding index per site when combined (Table 3). Octocorallia was only found in stomach contents from Trindade (10 % frequency of occurrence—FO) and Puerto Rico (6.7 % FO), in both cases with *IAi* < 0.1 %.

Stomach length varied between 37.5 and 106 cm, with gut length relative to total length ranging 2.9–7.3 (mean 4.6 ± 0.26 SE; Fig. 5). *Chaetodon striatus* RNA/DNA ratio was similar among Puerto Rico, Guarapari and Florianópolis, but lower in Salvador (ANOVA: *p* < 0.01; Fig. 6).
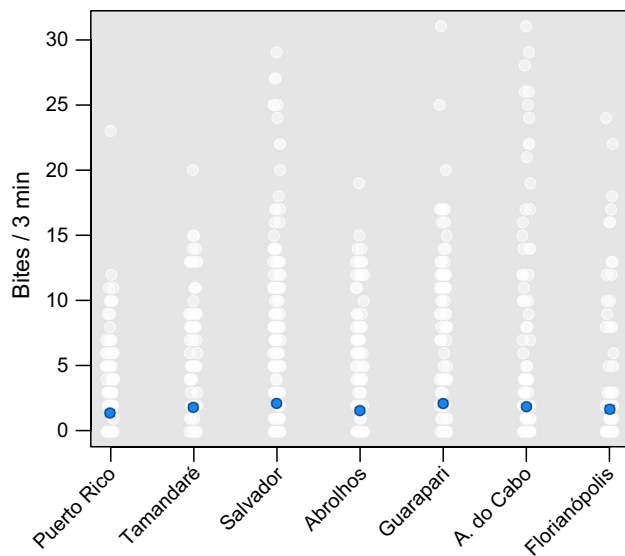
Fig. 3 Foraging rates (3 min⁻¹) of *C. striatus* at each studied site. *Blue circles* represent the average foraging rates as estimated by the negative binomial GLM, and *interval bars* (too small to be seen) represent model estimated average 95 % CI

Discussion

This study found that the abundance of *C. striatus* was not significantly different among most studied sites in Brazil, despite spanning 27° of latitude, and marked differences in local habitat structure, benthic composition and environmental conditions. However, densities in the Caribbean were generally lower than in Brazil. Our study shows that *C. striatus* is versatile and generalist, without strong patterns of selectivity of diet items and foraging substrata across sites. This fact, along with the similar density and nutritional condition of *C. striatus* within the studied range, indicates that the different reef formations and environmental conditions in the western Atlantic do not represent a major challenge to the maintenance of populations of this species in this area. Indeed, the high feeding plasticity of *C. striatus* is probably one of the factors explaining the species occurrence in so many markedly different reef ecosystems.

Despite the marked similar abundance and feeding versatility of *C. striatus* on reefs in the western Atlantic, its distribution terminates abruptly at 27°S in southern Brazil (Floeter et al. 2001; Ferreira et al. 2004; Anderson et al. 2015), the southernmost distribution limit for myriad tropical reef fishes within the Brazilian Province. In this area, there is an almost complete absence of suitable reef habitats, and temperatures stay below 17 °C for extended periods in winter, which constrain the occurrence of tropical reef species (Floeter et al. 2001; Ferreira et al. 2004; Anderson et al. 2015). As a consequence, even versatile
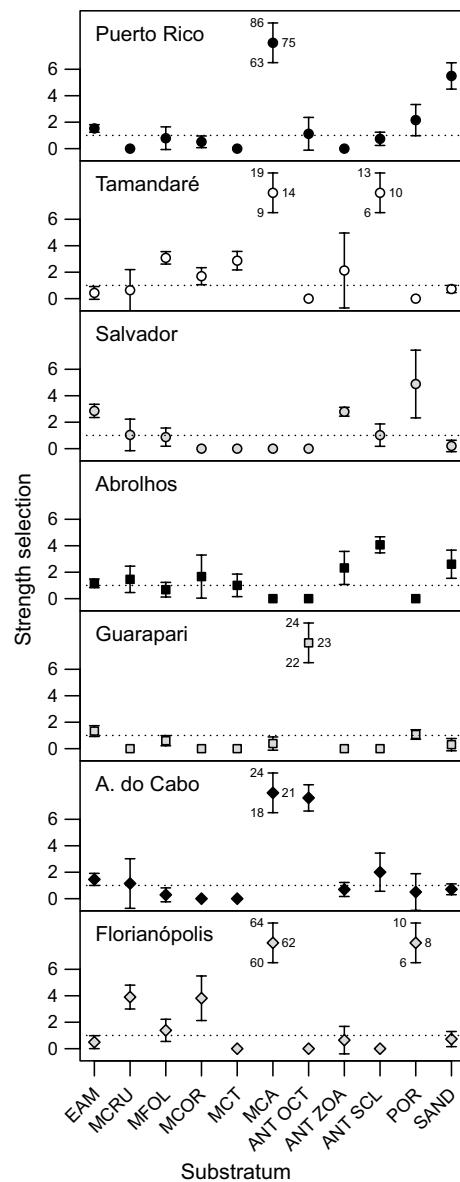

Fig. 4 Strength selection estimation for different food items consumed by *C. striatus* in each of the eight study sites. Food items with values crossing *dashed lines* were used according to their availability (use/availability = 1). Food items strength selection values above 1 were selected (use > availability), while values below 1 indicate avoidance (use < availability). Food acronyms are as follows: ALGAE: *EAM* epilithic algal matrix, MCRU, crustose; MFOL, foliose; MCOR, leathery; MCT, corticated; MCA, articulated calcareous; CORALS: Anthozoans: ANT OCT, Octocorallia; ANT ZOA, Zoantharia; ANT SCL, Scleractinia; OTHERS: POR, Porifera; SAND, Sand. *Numbers* depict data points above the maximum *y* axis value (i.e. 6)

species such as *C. striatus* may have their establishment and survivorship challenged by extreme environmental conditions.

Our diet analyses corroborated the classification of *C. striatus* as non-coral generalist feeder, as it ingested a large variety of benthic items. Polychaetes and cnidarians were

Table 3 Frequency of occurrence (%, FO), volume (%, V) in the diet and feeding index (%, IAi) of dietary items ("other" counting as one item) of *Chaetodon striatus* from populations in the eight study sites along the western Atlantic

Food items	Locality (no. of stomachs/no. of items)														
	Puerto Rico (30/23)			Tamandaré (17/12)			Salvador (21/12)			Abrolhos (20/17)			Trindade Island (20/19)		
	FO	V	IAi	FO	V	IAi	FO	V	IAi	FO	V	IAi	FO	V	IAi
Algae	23.3	0.5	0.2	5.9	<0.1	<0.1	4.8	0.2	<0.1	40.0	1.5	1.7	10.0	0. 3	<0.1
Cnidaria															
Hydrozoa	10.0	0.4	0.1	17.6	<0.1	<0.1	4.8	<0.1	<0.1	0	0	0	35.0	0.1	<0.1
Anthozoa															
Octocorallia	6.7	0.1	<0.1	0	0	0	0	0	0	0	0	0	10.0	0.4	<0.1
Hexac. Actiniaria	0	0	0	0	0	0	9.5	5.5	1.6	15.0	10.0	4.3	15.0	3.3	0.8
Hexac. Zoantharia	3.3	1.0	0.1	0	0	0	33.3	35.5	36.3	0	0	0	5.0	2.1	0.2
Hexac. Corallim./Scle.	60.0	30	28.9	29.4	5.6	2.1	9.5	11.1	3.2	45.0	41.7	53.3	15.0	3.0	0.7
Hexac. Other	33.3	16.6	8.9	17.6	2.9	0.7	42.9	40.2	52.9	25.0	21.2	15.1	65.0	29.3	30.9
Annelida: Polychaeta															
Sabellidae	76.7	19.2	23.7	47.1	2.7	1.7	0	0	0	55.0	11.4	17.8	85.0	17.7	2.4
Serpulidae	56.7	6.5	5.9	0	0	0	0	0	0	0	0	0	20.0	1.3	0.4
Cirratulidae	6.7	1.1	0.1	94.1	14.0	17.2	0	0	0	30.0	3.7	3.2	0	0	0
Eunicidae	6.7	0.5	<0.1	0	0	0	0	0	0	0	0	0	5.0	<0.1	<0.1
Syllidae	6.7	<0.1	<0.1	0	0	0	0	0	0	5.0	<0.1	<0.1	0	0	0
Terebellidae	3.3	0.2	<0.1	0	0	0	0	0	0	25.0	0.6	0.5	0	0	0
Other	90	21.2	30.7	0	0	0	14.3	0.9	0.4	25.0	3.8	2.7	95.0	20.1	31.3
Arthropoda: Crustacea															
Amphipoda	10.0	<0.1	<0.1	5.9	<0.1	<0.1	0	0	0	10.0	<0.1	<0.1	15.0	<0.1	<0.1
Isopoda	3.3	0.1	<0.1	0	0	0	0	0	0	0	0	0	0	0	0
Decapoda	6.7	<0.1	<0.1	0	0	0	0	0	0	5.0	<0.1	<0.1	15.0	0.1	<0.1
Other	10.0	<0.1	<0.1	17.6	<0.1	<0.1	4.8	0.3	<0.1	10.0	<0.1	<0.1	30	0.8	0.4
Eggs															
Mollusca	30	1.2	0.6	82.4	72.3	77.7	9.5	2.6	0.8	15.0	0.1	<0.1	45	9.7	7.1
Crustacea	6.7	<0.1	<0.1	0	0	0	0	0	0	0	0	0	0	0	0
Other	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Other[a]	26.7	<0.1	<0.1	17.6	<0.1	<0.1	14.3	<0.1	<0.1	5.0	<0.1	<0.1	20.0	<0.1	<0.1
Inorganic[b]	53.3	0.4	0.4	0	0	0	57.1	2.3	4	5.0	0.2	<0.1	55	0.2	0.2
Digested organic matter[c]	0	0	0	5.9	1.3	0.1	0	0	0	5.0	4.5	0.6	5.0	8.1	0.7
Unidentified	33.3	0.7	0.4	35.3	1.0	0.5	14.3	1.4	0.6	25.0	1.1	0.8	55.0	3.5	3.1

Food items	Locality (no. of stomachs/no. of items)								
	Guarapari (22/217)			Arraial do Cabo (19/17)			Florianópolis (20/14)		
	FO	V	IAi	FO	V	IAi	FO	V	IAi
Algae	9.1	<0.1	<0.1	26.3	0.3	0.2	25	0.2	0.2
Cnidaria									
Hydrozoa	36.4	0.3	0.2	15.8	<0.1	<0.1	60.0	0.6	1.0
Anthozoa									
Octocorallia	0	0	0	0	0	0	0	0	0
Hexac. Actiniaria	0	0	0	0	0	0	35.0	29.5	29
Hexac. Zoantharia	77.3	48.6	61.1	10.5	7.2	1.3	0	0	0
Hexac. Corallim./Scle.	50.0	10.6	8.6	5.3	0.7	<0.1	35.0	34.6	34.1
Hexac. Other	40.9	20.5	13.7	31.6	20.4	11.7	25.0	17.1	12
Annelida: Polychaeta									

Table 3 continued

Food items	Locality (no. of stomachs/no. of items)								
	Guarapari (22/217)			Arraial do Cabo (19/17)			Florianópolis (20/14)		
	FO	V	IAi	FO	V	IAi	FO	V	IAi
Sabellidae	45.5	2.8	2.0	89.5	35.9	58.2	15.0	1.2	0.5
Serpulidae	4.5	<0.1	<0.1	0	0	0	0	0	0
Cirratulidae	0	0	0	63.2	8.1	9.3	5.0	0.4	<0.1
Eunicidae	0	0	0	0	0	0	0	0	0
Syllidae	13.6	<0.1	<0.1	0	0	0	0	0	0
Terebellidae	9.1	1.0	0.1	0	0	0	0	0	0
Other	31.8	1.7	0.9	10.5	0.6	0.1	75.0	5.1	10.8
Arthropoda: Crustacea									
Amphipoda	40.9	0.3	0.1	57.9	0.5	0.5	10.0	0.1	<0.1
Isopoda	0	0	0	15.8	0.1	<0.1	0	0	0
Decapoda	0	0	0	21.1	0.7	0.3	0	0	0
Other	18.2	<0.1	<0.1	10.5	<0.1	<1.0	10	<0.1	<0.1
Eggs									
Mollusca	63.6	1.6	1.6	42.1	21.0	16.1	40	10.3	11.6
Crustacea	0	0	0	0	0	0	0	0	0
Other	18.2	0.5	0.2	0	0	0	0	0	0
Other[a]	40.9	2.1	1.4	47.4	2	1.7	5.0	<0.1	<0.1
Inorganic[b]	50	0.9	0.8	10.5	<0.1	<0.1	5.0	<0.1	<0.1
Digested organic matter[c]	0	0	0	5.3	1.6	0.2	0	0	0
Unidentified	63.6	8.8	9.2	31.6	0.7	0.4	35.0	0.8	0.8

[a] Composed by fish scales, Foraminifera, Ectoprocta, Porifera, Platyhelminthes, Nematomorpha, Nematoda, Echinodermata (Ophiuroidea and Holothuroidea) and Angiosperm

[b] Composed by fragments of silica and calcareous skeletons

[c] Composed by a mixture of nematocysts, spicules and setae
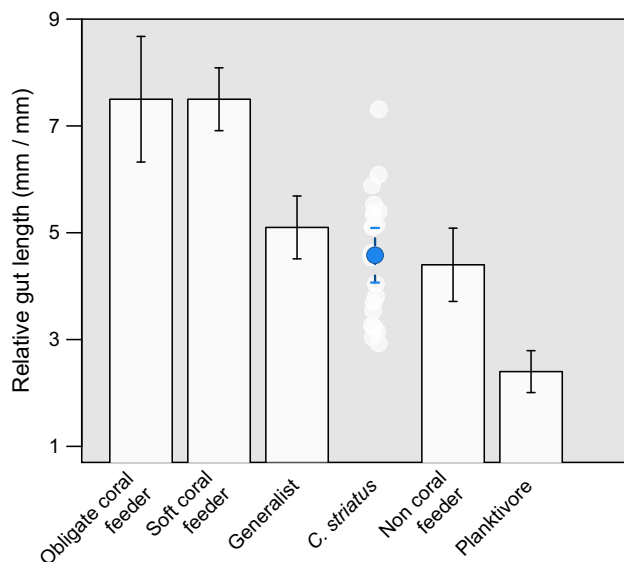
Fig. 5 Relative gut length of *C. striatus* in comparison with other butterflyfishes, grouped by feeding preferences (mean ± 95 % CI). Information displayed by *white bars* was extracted from Berumen et al. (2011)
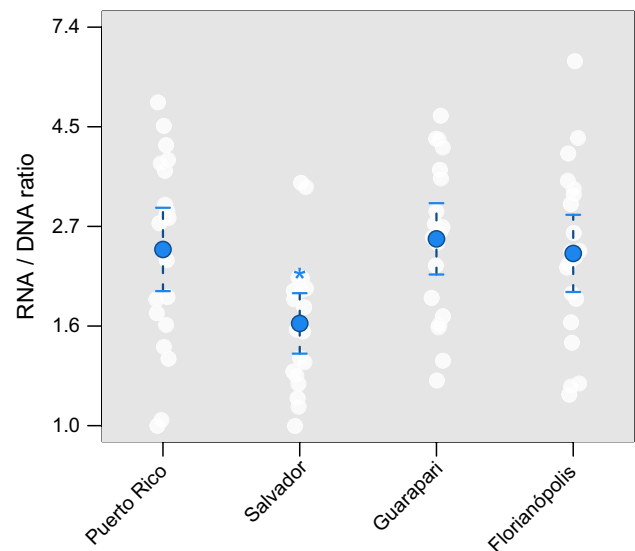
Fig. 6 RNA/DNA ratio (mean ± 95 % CI) for *C. striatus* individuals four study sites along the Brazilian coast. A total of 19–20 individuals were analysed per study site

the groups consumed in higher quantity in all study sites, as observed in a previous study in the Caribbean, in which polychaetes and anthozoans represented, respectively, 58.7 and 32.5 % of *C. striatus* stomach contents (Randall 1967). Similarly, a study in shallow reefs in Brazil found that *C. striatus* feeds mostly on cnidarians (Bonaldo et al. 2005). Polychaetes are an abundant food resource on reefs, with species associated with algae, sand, corals and sponges (Paiva 2006). This fact probably explains why, in the present study, *C. striatus* foraged mostly in substrata like algal patches and sand, where these invertebrates may occur in high abundances (Paiva 2006). Also, the great contribution of anthozoans in *C. striatus* diet was supported by field observations of foraging behaviour, as a high proportion of bites were taken in at least one anthozoan category in almost all sites.

The use of complementary diet and foraging behaviour data allowed us to have a broader view of *C. striatus* feeding patterns. In Arraial do Cabo and Abrolhos, for example, *C. striatus* frequently bit on octocorals, which were completely absent in stomach contents in these sites. Polyp sclerites of *Phyllogorgia dilatata* and *Plexaurella* spp, the main octocorals in Arraial do Cabo and Abrolhos, are usually fragile or absent (Castro et al. 2010; Medeiros personal communication), what probably explains their absence in stomach contents in these sites. In contrast, stomach contents in Florianópolis had high quantities of anthozoans (75.1 % *IAi*), which were not recorded as a foraging substratum in this site. Indeed, most bites were taken on algal-dominated substrata (Fig. 4 and Fig. S1 in Electronic Supplementary Material) in Florianópolis, where fish probably search for cryptic anthozoans, such as small anemones. These cases exemplify the importance of combining field observations and stomach content analyses for a better comprehension of the feeding ecology of a species.

Our study revealed a high diversity of food items in *C. striatus* diet, some with high frequency of occurrence but low volume, which resulted in low feeding index values. Some of these items probably represent important complementary resources, with high energetic value (Fyhn and Govoni 1995; Nagelkerken et al. 2009). This is the case for crustaceans, present in stomach contents from almost all sampling sites, but with low feeding index (<0.5 %), as well as egg mass, also with high frequency but with low volume (except at Tamandaré, which presented a feeding index of 77.7 %).

Some food items of low nutritional value, such as sand and calcareous skeleton, were probably ingested incidentally with invertebrates. Algal ingestion by *C. striatus* must also be incidental, since the frequency of this item in the diet of butterflyfish species feeding on algae is usually higher than the values recorded in the present study (e.g. Sano 1989).

The variation in gut length of *C. striatus* among individuals of similar total body length in the presented study (up to 30 cm) is expected, as gut morphology can vary among conspecific individuals (Raubenheimer and Bassil 2007). Also, Berumen et al. (2011) compared the gut length, relative to total body length, of 28 species of butterflyfishes, including obligate coral feeders, facultative coral feeders, generalists, non-coral feeders and planktivores. Our results of relative gut length in *C. striatus* fit within the subset of generalists and non-coral feeders (4–5 of relative gut length, Fig. 5), as proposed by the gut content analyses in the present study.

The similarities of RNA/DNA ratio indicates that most *C. striatus* populations sampled in the present study have similar nutritional condition. Although we did not analyse tissue samples for all study sites, our geographically extreme sites (Puerto Rico and Florianópolis) were included. In fact, nutritional condition was similar even considering Florianópolis, the southernmost limit of distribution of the studied species, where environmental conditions can be adverse for many tropical reef fish species. Also, although individuals from Salvador showed a lower RNA/DNA ratio, this value was higher than 1, considered as the indicative boundary of physiological stress, such as starvation (Kono et al. 2003; Behrens and Lafferty 2007). These relatively low values from Salvador may be explained by the higher contribution of cnidarians in *C. striatus* stomach contents (94 % *IAi*), in the bite rates (62.8 %), as well as in the benthic cover of this site (49.5 %) (Fig. S1 in Electronic Supplementary Material). Cnidarians provide relatively less energetic value and nutritional quality, probably because of chemical and structural defences (Birkeland and Neudecker 1981; Fox and Morrow 1981; Suchanek and Green 1981). Therefore, the relatively higher consumption of cnidarians by *C. striatus* in Salvador is a likely driver of lower RNA/DNA in this site.

Our results support the usual trophic classification of *C. striatus* as "sessile invertebrate feeder" (Ferreira et al. 2004), feeding on a wide variety of prey items (e.g. Randall 1967; Pitts 1991; Bonaldo et al. 2005), as in our study sessile invertebrates presented the highest feeding index (83 %) among all food items. Further, mobile invertebrates represented a substantial part of *C. striatus* diet (14 %) in our sites, which indicates that the species diet is more versatile than previously assumed. This fact is particularly relevant as polychaetes and crustaceans generally have higher caloric value (639 and 817 cal/g wet wt, Cummins and Wuycheck 1971) than anthozoans (494 cal/g, wet wt Cummins and Wuycheck 1971). Therefore, the mobile invertebrates may have a higher contribution in providing energy and nutrients to *C. striatus* than previously assumed. In terms of feeding behaviour, *C. striatus* could be considered as a generalist zoobenthivore that forages on multiple

substrata in tropical and subtropical reefs. This strategy seems successful along a wide variety of reef environments, temperature range and resource availability in which *C. striatus* occurs, as indicated by the absence of major differences in density and foraging rates across the studied reefs.

In summary, our study assessed different aspects related to *C. striatus* feeding, by using a combination of tools to identify potential drivers of the density and distribution of a wide-ranging reef fish species. In assessing different variables related to *C. striatus* feeding, we obtained a broad understanding of its feeding ecology, specifically by comparing data obtained from in situ observations (abundance, feeding rates, substratum selection) with laboratory analyses (diet composition, gut length relative to body size, nutritional condition). Our results show that *C. striatus* is evenly distributed along its range, with no major differences in foraging rates across sites encompassing a 44° latitudinal range. *Chaetodon striatus* also exhibits high feeding plasticity, with use of different diet items and foraging substrata throughout its distribution. This feeding plasticity was not related to major differences in nutritional condition across sites. This uniformity in *C. striatus* feeding is striking, especially considering the high differences in reef structure (tropical coral reef, temperate rocky reefs), benthic cover and fish community (Ferreira et al. 2004; Floeter et al. 2001, 2004) along the studied gradient. Therefore, the feeding versatility and plasticity of *C. striatus* seem to explain its wide latitudinal distribution, which encompasses two biogeographic provinces and a wide range of environmental conditions (Floeter et al. 2001). Our results thus highlight the importance of assessing a large geographical gradient within the distribution range of generalist species to better comprehend their feeding ecology.

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