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Resource partitioning by two syntopic sister species of butterflyfish (Chaetodontidae)

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Resource partitioning is considered one of the main processes driving diversification in ecological communities because it allows coexistence among closely related and ecologically equivalent species. We combined three complementary approaches, i.e. the evaluation of foraging behaviour, diet composition and nutritional condition (RNA:DNA ratio), to assess feeding by two closely related (sister) butterflyfishes that are syntopic in Puerto Rico. Chaetodon capistratus *had a higher abundance and higher bite rate and selected octocorals and hard corals for feeding, whereas* Chaetodon striatus *fed preferentially on sandy substrates. Cnidarians and polychaetes were the most representative diet items for both species, but* C. capistratus *preferred the former (Feeding Index of 74.3%) and* C. striatus *the latter (Feeding Index of 60.4%). Similar RNA:DNA ratios for both species suggest that, although they differ in feeding rates and diet,* C. capistratus *and* C. striatus *have similar nutritional fitness. Therefore, these species are both zoobenthivores but show clear differences in their substrate selection. The differences in the use of foraging substrate by* C. capistratus *and* C. striatus, *despite their close phylogenetic relationship and similar diets, suggest that these species coexist by resource partitioning.*

Keywords: Chaetodontidae, co-occurring species, diet, feeding, habitat partitioning, nutritional condition, reef fish, stomach contents

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INTRODUCTION

Identifying the factors underlying species coexistence has been a major focus of ecological studies, as it may allow a better understanding of the processes that sustain biodiversity in natural ecosystems (Schoener, 1974; Wright, 1992; Levine & HilleRisLambers, 2010). Species can employ various strategies for coexistence, such as the differential usage of the available resources, in order to avoid direct competition (Schoener, 1974). Similar species, however, such as pairs of closely related species (hereafter called sister species) or ecologically equivalent species, may overlap in their spatial distribution to some degree (Hodge & Bellwood, 2016) and share some preferences for resources. Under such circumstances and when resources are limited, interspecific competition for resources tends to increase (Begon *et al*., 1996). In these cases, species coexistence is permitted by strategies that reduce interspecific competition, such as resource partitioning, in which species differ in their use of available resources, either because of differing preferences, or because they are driven to non-preferred resources by a superior competitor (Nagelkerken *et al*., 2009; Crow *et al*., 2010).

The butterflyfishes (Chaetodontidae) are one of the most speciose fish taxa in tropical reefs. They live closely associated with the substrate, feeding mostly on mobile and sessile invertebrates (Birkeland & Neudecker, 1981; Pratchett, 2005; Cole & Pratchett, 2014; Liedke *et al*., 2016), and represent one of the best models to study foraging by reef fish, as divers can easily identify individuals to the species level and record different feeding behaviours (Tricas, 1989). Therefore, several studies have questioned the extent to which resource use and food partitioning are important in butterflyfishes (e.g. Birkeland & Neudecker, 1981; Pitts, 1991; Nagelkerken *et al*., 2009). Some previous studies have found a high overlap in food items ingested by co-occurring butterflyfishes, thus suggesting only a low degree of resource partitioning (e.g. Cox, 1994; Pratchett, 2005). Corallivorous butterflyfishes in the Pacific, for example, may overlap in 30–70% of their diet (Cox, 1994; Pratchett, 2005). However, many of these studies provide a limited view of butterflyfish feeding either by classifying the organisms in their diets into broad taxonomic categories (e.g. Harmelin-Vivien & Bouchon-Navaro, 1983; Bouchon-Navaro, 1986; Zekeria *et al*., 2002) or by using only one approach to assess fish feeding (e.g. stomach content analysis or field observations), and there is a high likelihood of overestimating the level of diet overlap based on such limited studies (Pratchett, 2005; Nagelkerken *et al*., 2009).

Although butterflyfishes occur in tropical reefs worldwide, the vast majority of studies on feeding behaviour by these

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species have been conducted in the last few decades in highly diverse reefs in the Pacific (e.g. Berumen *et al.*, 2005; Pratchett, 2005; Berumen & Pratchett, 2006; Nagelkerken *et al.*, 2009; Cole & Pratchett, 2014; Madduppa *et al.*, 2014). This extensive body of literature has provided a better view of butterflyfish feeding ecology and of the potential mechanisms allowing species coexistence in various habitats. In the Atlantic, however, studies on butterflyfish feeding ecology were conducted before the 1990s, and although they have provided relevant information, most of those studies used methods based on either field or laboratory methods alone, without a combination of these approaches. Collectively, butterflyfishes in the Atlantic are considered more generalist than Indo-Pacific species because the former feed on a wide range of invertebrates, such as anthozoans, polychaetes and crustaceans (Birkeland & Neudecker, 1981; Pitts, 1991; Liedke *et al.*, 2016). Because of the differences in resource use by butterflyfishes between these regions, these species may also differ in other ecological features, such as the extent of resource overlap and the potential existence of resource partitioning in co-occurring species. For instance, given that butterflyfishes in the Atlantic are primarily generalists, co-occurring species in this region likely have higher overlap in resource use than species in the Indo-Pacific. Therefore, extrapolating conclusions from studies in the Pacific to the Atlantic may be misleading, and specific studies in the Atlantic are necessary for a better understanding of butterflyfishes in this region.

A next step in understanding the feeding ecology of butterflyfishes would thus be to investigate the use of food resources by multiple species in the Atlantic. Studies using different methods could provide a better view of food use and of the extent of resource partitioning by coexisting species. More specifically, studies on syntopic sister species could promote a better understanding of the mechanisms driving the coexistence of pairs of sister species of reef fishes and thus of the processes underlying diversity patterns in tropical reefs (Pitts, 1991; Pratchett, 2005; Bellwood *et al.*, 2006). The present study aimed to study the feeding ecology of two co-occurring sister butterflyfishes, *Chaetodon capistratus* Linnaeus, 1758 and *Chaetodon striatus* Linnaeus, 1758 (see Fessler & Westneat, 2007 for their phylogenetic relationship), in Puerto Rico by comparing their diets, foraging patterns and nutritional condition. We expect to find a large overlap in the resource use between both species, given the generalist diet of butterflyfishes in the Atlantic (in which they search for food items in different substrata), especially in comparison to species in the Indo-Pacific. This is the first comparative assessment of foraging patterns by these two species to examine levels of resource partitioning between them.

MATERIALS AND METHODS

Studied area

Fieldwork was conducted in coral reefs at 18–22 m depth around La Parguera, Puerto Rico (17°56′N 67°01′W) in March 2011. Underwater observations were performed using scuba during daytime, between 9:00 and 16:00 h, for 7 days, for a total of 50 h of sampling. Sea surface temperature was constant (27°C) during the period of data collection.

Diet

Analyses of stomach content were conducted to assess the diets of the studied species. A total of 55 butterflyfish specimens (25 *C. capistratus* and 30 *C. striatus*) were collected during daytime (10:00–14:00 h), by using a hand spear. Each fish was measured (total length, TL), and its stomach was removed and immediately stored in a plastic tube with ethanol. Additionally, the degree of fullness of each stomach was classified into one of the following four categories: $<25\%$, 25–50%, 50–75% and $>75\%$ (Mariscal, 1974). The food items were removed from the stomachs. Then, each item was identified to the most precise taxonomic category possible under a stereomicroscope, and its volume was estimated in mm^3 (methods in Liedke *et al.*, 2016). Because of the digestive process, some items could not be fully identified and were thus placed into one of the following five more general categories: (1) 'Actiniaria' or (2) 'Zoantharia' depending on the type of nematocysts in the item, (3) 'Corallimorpharia/Scleractinia' for items with undistinguished nematocysts, (4) 'digested organic matter' for items with identifiable elements of abundant organic matter, or (5) 'unidentifiable' for items with no identifiable elements.

The relative importance of each food item in the diet of each butterflyfish species was estimated using the Feeding Index (IA$_i$), calculated as follows:

$$\%IA_i = \frac{(F_i \cdot V_i)}{\sum_{x=1}^{n} (F_i \cdot V_i)},$$

in which F_i is the number of stomachs with a given prey type i in relation to the total number of stomachs and V_i is the volume of prey item i in relation to the total volume of all of the items in the diet of each species (Kawakami & Vazzoler, 1980).

Nutritional condition

We used the RNA:DNA ratio to assess oscillations in the physiological state of *C. capistratus* and *C. striatus* in response to diet (following Buckley & Szmant, 2004; Behrens & Lafferty, 2007). This metric was chosen for this purpose because RNA and protein synthesis fluctuates in response to energy demand (i.e. food availability and quality), whereas DNA is stable and fixed in each cell (Calderone *et al.*, 2001; Chícharo & Chícharo, 2008). RNA:DNA ratio values that are lower than one indicate physiological stress (Kono *et al.*, 2003; Behrens & Lafferty, 2007). For this analysis, white muscle tissue of each individual fish was removed, stored in RNALater solution (Qiagen) immediately after collection, and kept in a −20°C freezer. Nine samples from *C. capistratus* and 21 from *C. striatus* were thawed for assessment of the RNA and DNA concentrations using ethidium bromide fluorescence (Dahlhoff & Menge, 1996; see detailed methods in Liedke *et al.*, 2016). Each sample was taken from a different individual fish to ensure independence among samples.

Foraging behaviour and available benthic substrates

The foraging behaviour of the two studied species was quantified by using focal animal methodology (Lehner, 1996), in which divers followed haphazardly chosen adult individuals of *C. capistratus* ($N = 24$; 72 min of observations) and *C. striatus* ($N = 64$; 192 min) for 3-min periods. During these observational bouts, the divers counted the number of bites taken on each substrate type by each fish (see classification of substrate types below) and remained at a discreet distance from the fishes (1–3 m) in order to minimize disturbances to fish behaviour (Birkeland & Neudecker, 1981; Liedke *et al*., 2016). Additionally, before the counts, the divers spent a few minutes next to each individual fish to allow it to acclimate to the presence of the diver. This methodology has been applied in previous studies on butterflyfish feeding (Birkeland & Neudecker, 1981; Alwany *et al*., 2003; Liedke *et al*., 2016). At the end of each observation, the diver moved elsewhere within the site to avoid resampling the same individual fish (following Birkeland & Neudecker, 1981). The densities of *C. capistratus* and *C. striatus* at the study site were obtained from published online sources [100 m^2 (25 m × 4 m) belt transects NOAA, 2014]. We selected data (96 transects) that were collected on coral reefs in the same area and depth where the foraging behaviour was sampled.

Benthic assessments were conducted to compare the frequency of use with the relative cover availability of each substrate type at the study site. A total of 90 and 190 photographs were analysed for *C. capistratus* and *C. striatus*, respectively, for characterizing the available benthic community in the study area. Photos were randomly taken, from a distance of 80 cm from the substratum, around the entire reef area where the butterflyfishes were feeding, with each photoquadrat corresponding to an area of 40 × 60 cm (following Liedke *et al*., 2016). The photoquadrats are not paired with individual fish, but represent the whole of the feeding area for each species. For each photograph, 20 points were randomly added with the software Coral Point Count with Excel Extension (CPCe v3.5; Kohler & Gill, 2006), totalling 1800 points for *C. capistratus* and 3800 for *C. striatus*. The substrate immediately below each point was identified as belonging to one of 10 categories. These categories consisted of six algal-dominated substrates: (1) epilithic algal matrix (sensu Wilson *et al*., 2003), (2) crustose, (3) foliose, (4) leathery, (5) corticated and (6) articulated calcareous algae; two substrates that were dominated by anthozoans: (7) Octocorallia, (8) Scleractinia; and two other substrate types: (9) Porifera and (10) sand. Non-representative substrates, i.e. benthic cover $<5\%$, were not considered for the Resource Selection Function analyses (see below).

Data analysis

The fish density, bite rate and RNA:DNA ratio were compared between *C. capistratus* and *C. striatus* by using Student's t-tests for each variable. Before each comparison, data were examined for normality and homogeneity of variances using D'Agostino-Pearson and residual analysis, respectively. The data fulfilled the assumption of homoscedasticity but were log-transformed to meet assumptions of normality.

The selection of foraging substrate by each species was analysed using a Resource Selection Function (RSF; Manly, 1993, 1997; Manly *et al*., 1993). The RSF is a linear model approach that yields values proportional to probability of use of a certain resource unit (Boyce *et al*., 2002). It has several advantages over alternative widely used methods (e.g. Ivelev index (Jacobs, 1974) and Compositional analyses (Aebischer *et al*., 1993)) because it (1) can be solved using generalized linear models, (2) can include several resource layers and interaction terms (e.g. species, sites, individual covariates such as body mass and sex) and (3) can be used to quantify the importance of each resource layer in the same probabilistic selection process. Furthermore, it can specify different resource availability for each observation of use, and give the same statistical weight for each observed individual, approaching to a more mechanistically view of the choice process. Although the RSF allows specification of resource availability for each individual, we did not measure availability individually. We used RSF to individualize the use, and to model the resource selection by comparing species using a unique numerical step. On the other hand, alternative widely used indices aggregate all information (used and available) in a single package, ignoring differences of resource availability among individuals, mixing individuals with different features and biasing the indices values to those individuals with more observations.

The Resource Selection Function was built using the Conditional Logistic Regression (CLR) approach because our data consisted of direct observations of substrates on which different individuals foraged (bitten substrates, scored as 1) among a variety of available substrates (random sampling of unbitten substrates, scored as 0). We used 100 random substrate points (scored as 0) for each observed individual, which were taken from the relative substrate availability measured by pooling the photos taken in the entire reef area where each species was observed feeding (see 'Foraging behaviour and available benthic substrates' section). Actually, the substrate covers used in the analysis for each fish species are very similar (Supplementary Figure S1). The CLR was conditioned to individual identity. Species (*C. capistratus* and *C. striatus*) and type of foraging substrate (FS) were used as categorical variables in the model.

Our CLR model was thus represented by the following log-linear form of the logistic regression for each i substrate and j species: $\text{logit}(w_{ij}) = \beta_{1i} \times \text{FS} + \beta_{2ij} \times \text{FS} \times \text{Species}$, in which w depicts the selection strength based on the use/availability ratio and βs are model coefficients that indicate the odds ratio of each i substrate, consumed by j species, to be used in a different proportion of its availability. The CLR was solved using the *clogit* function in the *survival* package (Therneau, 2015) for R 3.3.1 for Mac OS (R Development Core Team, 2015). We fitted the CLR, clustering the bite observations within individuals to control pseudoreplication of correlated samples, and to allow us to calculate robust standard errors of the estimated coefficients in a very conservative way (Craiu *et al*., 2008). The general significance of each effect in the model (i.e. species, FS and the species × FS interaction) was assessed with Type III analysis of variance through partial likelihood ratio tests (Cox & Oakes, 1984). The raw data and an R code for data handling and RSF analysis are provided in the Supplementary material.

RESULTS

Chaetodon capistratus had a significantly higher mean density (3.1 ± 0.08 SE individuals per transect; $t_{210,90} = 12.46$, $P < 0.001$) and bite rate (3.36 ± 0.38 SE bites per min; $t_{59.77} = 5.78$, $P < 0.001$) than *C. striatus* (density: 1.5 ± 0.70 SE; bite rate: 1.38 ± 0.16 SE; Figure 1). We also observed

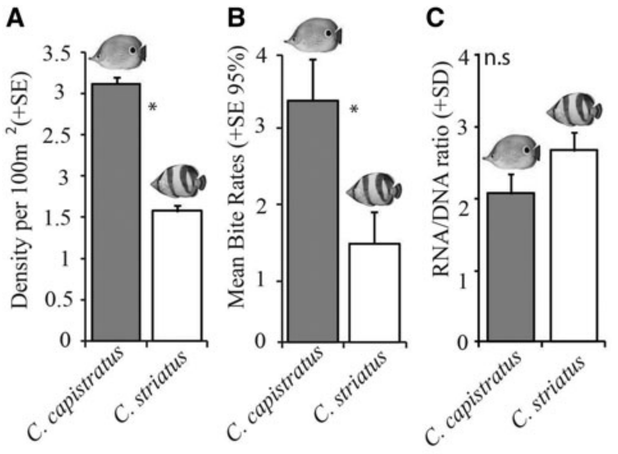

Fig. 1. Density of individuals (A), mean bite rates per min (B), and RNA:DNA ratios for *Chaetodon capistratus* (grey bars) and *Chaetodon striatus* (white bars) at La Parguera, Puerto Rico. Asterisks (*) indicate significant differences between species ($P < 0.05$).

differences in microhabitat use by the two species; while both species occurred in the outer reefs at ~18–22 m deep, only *C. capistratus* occurred in the centre of the large reefs, and *C. striatus* preferentially occupied the borders of the larger reefs (i.e. reef-sand interface) and the patch reefs interspersed with sand. The RSF indicated a global effect of foraging substrate (log-ratio $\chi^2_9 = 155.27$; $P < 0.001$) and a strong interaction between species and foraging substrate (log-ratio $\chi^2_{10} = 304.15$; $P < 0.001$). The estimated coefficients from the RSF and their respective 95% confidence intervals are provided in Supplementary Table S1. This interaction effect indicates that *C. capistratus* and *C. striatus* differ in their selection of foraging substrates (Figure 2). Indeed, although both species selected epilithic algal matrix, leathery algae, foliose algae, Scleractinia, Porifera and sandy substrates, Scleractinia was selected more often by *C. capistratus* than by *C. striatus*, and the opposite occurred for articulated calcareous algae and sand (*C. striatus* selected more articulated calcareous algae and sand than *C. capistratus*). Finally, the most conspicuous difference in substrate selection was detected for the Octocorallia substrate, as it was strongly selected by *C. capistratus* but used in accordance with its availability in the reef by *C. striatus* (Figure 2; Supplementary Figure S1).

More than 50% of the stomachs analysed for both species were more than 50% full. In total, 24 and 30 different items were found in the stomachs of *C. capistratus* and *C. striatus*, respectively (Table 1). The lists of diet items were similar between the species, but the relative contributions of some items differed. This was the case for Zoantharia and Octocorallia, for which the IA_i values were 19.8% and 9.3%, respectively, for *C. capistratus* but were lower than 0.5% for *C. striatus* (Table 1). Overall, cnidarians represented a total IA_i of 74.3% for *C. capistratus*, while polychaetes represented a total IA_i of 60.4% for *C. striatus*. Items with high representation in the diet of *C. striatus*, such as sabellid polychaetes ($IA_i = 26.6\%$), made up only 0.1% of the *C. capistratus* diet. However, the two species showed similar IA_i values for some items, such as 'Corallimorpharia/Scleractinia' and 'other' polychaetes (29.7% and 22.9%, respectively, for *C. capistratus* and 32.4% and 22.8% for *C. striatus*). The RNA:DNA ratio was 2.06 for *C. capistratus* and 2.6 for *C. striatus* with no significant differences between species ($t_{19.74} = -1.44$, $P = 0.166$; Figure 1).

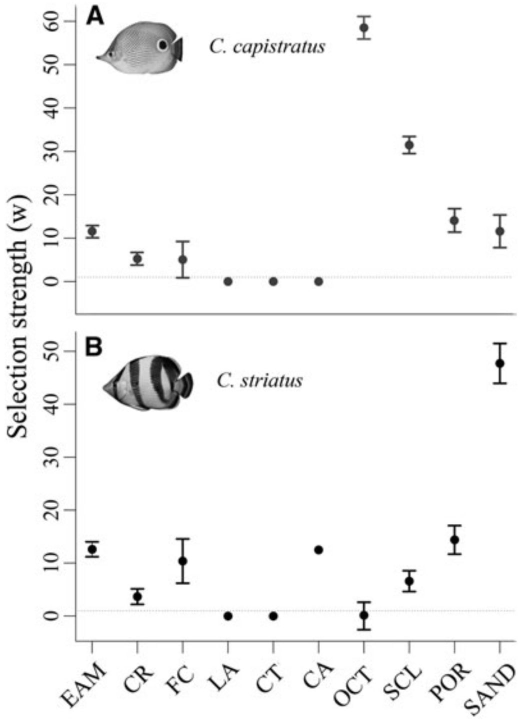

Fig. 2. Strength of the selection of foraging substrate by *Chaetodon capistratus* (A) and *Chaetodon striatus* (B) at La Parguera, Puerto Rico. Items with values crossing the dashed lines were used according to their availability (use/availability= 1); positive and negative values indicate selection and rejection, respectively. Acronyms for foraging substrates are as follows: EAM, epilithic algal matrix; CR, crustose algae; FC, foliose algae; LA, leathery algae; CT, corticated algae; CA, articulated calcareous algae; OCT, Octocorallia; SCL, Scleractinia; POR, Porifera; SAND, Sand.

DISCUSSION

This is the first study on reef fishes, to our knowledge, to combine three complementary approaches (the evaluation of foraging behaviour, diet and nutritional condition) to assess the use of food resources by sympatric sister butterflyfishes. We found that *C. capistratus* and *C. striatus* markedly differed in the use of foraging substrates and in the proportions of various dietary items. The differences in the selection of foraging substrates by *C. capistratus* and *C. striatus*, despite their close phylogenetic relationship and similar diets, suggest that these species coexist in Puerto Rico by resource partitioning.

Studies on resource use by sister species are particularly interesting because, provided that the species share a recent evolutionary history, such species are more prone to overlap in their distributions (Rocha *et al.*, 2008), behaviours and use of resources than unrelated species (Pratchett, 2005; Montanari *et al.*, 2012). In the Indo-Pacific, the sister species *Chaetodon ephippium* Cuvier, 1831, and *Chaetodon semeion* Bleeker, 1855, differed substantially in their diet composition and substrate use when sympatric. The former feeds preferentially on polychaetes and the latter on cnidarians, and they use different substrates to feed (Nagelkerken *et al.*, 2009). This pattern resembles our results where differences in the use

Table 1. Dietary items in stomach contents of *Chaetodon capistratus* and *Chaetodon striatus* in Puerto Rico: Frequency of occurrence (%, FO), Volume (%, V) and Feeding Index (%, IA_i).

Food item	***C. capistratus***			***C. striatus***		
	FO	**V**	**IA_i**	**FO**	**V**	**IA_i**
Algae	4.0	<0.1	<0.1	23.3	0.5	0.2
Cnidaria						
Hydrozoa				10.0	0.4	0.1
Octocorallia	48.0	7.1	**9.3**	6.7	0.1	<0.1
Zoantharia	28.0	25.9	**19.7**	3.3	1.0	0.1
Corallimorphalia/ Scleractinea	40.0	27.3	**29.6**	60.0	30	**28.9**
Other	28.0	20.7	**15.7**	33.3	16.6	**8.9**
Polychaeta						
Sabellidae	16.0	0.2	0.1	76.7	19.2	**23.7**
Serpulidae	44.0	0.7	0.8	56.7	6.5	**5.9**
Cirratulidae				6.7	1.1	0.1
Eunicidae				6.7	0.5	<0.1
Syllidae	32.0	1.1	0.9	6.7	<0.1	<0.1
Terebellidae	4.0	0.2	<0.1	3.3	0.2	<0.1
Others	76.0	11.1	**22.9**	90	21.2	**30.7**
Crustacea						
Amphipoda	12.0	0.1	<0.1	10.0	<0.1	<0.1
Isopoda				3.3	0.1	<0.1
Decapoda				6.7	<0.1	<0.1
Others	12.0	<0.1	<0.1	10.0	<0.1	<0.1
Eggs						
Mollusca	24.0	0.2	0.1	30	1.2	0.6
Crustacea				6.7	<0.1	<0.1
Others	8.0	<0.1	<0.1			
Others[a]	4.0	0.1	<0.1	26.7	<0.1	<0.1
Inorganic[b]	16.0	0.8	0.4	53.3	0.4	0.4
Digested organic matter[c]	4.0	4.3	0.5			
Unidentified	16.0	0.1	<0.1	33.3	0.7	0.4

Bold numbers highlight IA_i higher than 5.

[a] Fish scales, Foraminiferida, Ectoprocta, Porifera, Platyhelminthes, Nematomorpha, Nematoda, Echinodermata (Ophiuroidea and Holothuroidea) and Angiospermae.

[b] Fragments of silica and calcareous skeletons.

[c] Nematocysts, spicules and setae.

of food resources by *C. capistratus* and *C. striatus* were found both in diet composition and selection of substrate.

However, the mechanisms driving resource partitioning in these cases must be examined in detail, especially when interspecific competition is suggested as a main driver of this pattern (see also Bonin *et al.*, 2015). In our study, we could not assess whether limited resources cause competition between the species or confirm that this is the mechanism causing the differences in resource use by the two species. These differences may arise from other mechanisms such as differences in morphological and physiological requirements or in feeding preferences (Fulton *et al.*, 2001). Additionally, the current differences in the nutritional ecologies of these species may reflect past competition between the species that no longer exists, or even competition with other species (Begon *et al.*, 1996). Therefore, the mechanisms driving the observed differences between *C. capistratus* and *C. striatus* feeding remain to be tested, while further experimental studies would be necessary to verify whether the observed patterns are a consequence of interspecific competition (Sala & Ballesteros, 1997).

The higher abundance of *C. capistratus* in comparison to *C. striatus* in our study corroborates previously reported patterns of abundance for these species. *Chaetodon capistratus* is the most abundant and common butterflyfish in the Caribbean (Birkeland & Neudecker, 1981; Lasker, 1985) and occurs in a range of reef zones (Pitts, 1991) and reef patches, while *C. striatus* is less abundant in larger reefs and is mostly associated with reef patches (Pitts, 1991). This spatial partitioning may be a result of a strategy to reduce competition between the species or may reflect interspecific variation in preferred prey and individualistic responses to food availability (Bouchon-Navaro, 1981). At any rate, the similar values for nutritional condition for *C. capistratus* and *C. striatus* in the present study indicate that neither species is under physiological stress, such as starvation, at the studied site.

Contrasts in resource use by *C. capistratus* and *C. striatus* in the present study can also provide some explanation for the different distributions of these species in the western Atlantic. Although both species are broadcast spawners and have similar pelagic larval durations (B. Victor and L. Vigliola, personal communication), *C. capistratus* is restricted to the Caribbean, while *C. striatus* also occurs across almost the entire Brazilian coast, where it is the most abundant butterflyfish (Ferreira *et al.*, 2004; Liedke *et al.*, 2016). The wider geographic range of *C. striatus* suggests that this species has higher ecological plasticity and may thus survive under a wider variety of conditions than *C. capistratus*. Another non-mutually exclusive hypothesis for the differences in the distribution range of *C. capistratus* and *C. striatus* is the variation in availability of food items in Brazil and the Caribbean. In contrast to most butterflyfish species, *C. striatus* seems to prefer polychaetes to cnidarians (Pitts, 1991; Liedke *et al.*, 2016), while *C. capistratus* feeds mostly on Octocorallia (Pitts, 1991), and Octocorallia are much more abundant and diverse in the Caribbean. This fact likely explains, at least in part, the absence of *C. capistratus* from Brazilian reefs.

The use of multiple methodologies in our study complements previous studies on butterflyfishes in the Caribbean. As in our study, *C. capistratus* was more abundant and fed more on anthozoans than *C. striatus* in the Bahamas (Pitts, 1991). Additionally, *C. striatus* fed mostly on polychaetes and fish that occurred mainly in association with algae and sandy substrate in the Bahamas (Pitts, 1991), similar to the results in the present study.

Despite similarities between this and previous studies on *C. capistratus* and *C. striatus* feeding, some differences were also found. For example, the bite rates of both species were lower in our study. In St. Croix, the mean bite rate of *C. capistratus* was ~5 bites per min (Birkeland & Neudecker, 1981; Neudecker, 1985), while in the present study, the mean bite rate was 3.4 bites per min. On the Brazilian coast, where *C. capistratus* does not occur, *C. striatus* bite rates ranged between 1.5 and 3.6 bites per min (Bonaldo *et al.*, 2005; Liedke *et al.*, 2016), which were higher than the rates observed in the present study (1.4 bites per min). These differences in bite rates may be associated with a number of variables, such as differences in food resources, competition, and abiotic factors, because the fauna and environmental conditions of reefs in Puerto Rico differ from those in St Croix and Brazil (Liedke *et al.*, 2016).

In summary, our findings indicate that partitioning of food and foraging microhabitats by sister butterflyfishes is important in the Caribbean. Further studies on the use of resources by other sister species of butterflyfishes may improve our understanding of mechanisms driving species coexistence on coral reefs.

SUPPLEMENTARY MATERIAL

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