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NOTE

Ecology of *Prognathodes obliquus*, a butterflyfish endemic to mesophotic ecosystems of St. Peter and St. Paul's Archipelago

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Abstract Chaetodontidae is among the most conspicuous families of fishes in tropical and subtropical coral and rocky reefs. Most ecological studies focus in the genus *Chaetodon*, while *Prognathodes* remains poorly understood. Here we provide the first account on the ecology of *Prognathodes obliquus*, a butterflyfish endemic to St. Peter and St. Paul's Archipelago (SPSPA), Mid-Atlantic Ridge. We studied the depth distribution and foraging behaviour of *P. obliquus* through technical diving, remote-operated vehicles and submarines. Also, we characterized its diet by analysing stomach contents. *Prognathodes obliquus* is mostly found below 40 m, with abundance peaking between 90 and 120 m and deepest record to date at 155 m. It forages mostly over sediment, epilithic algal matrix and complex bottoms formed by fused polychaete tubes, preying mostly upon polychaetes, crustaceans, hydroids and bryozoans. Branching black corals were rarely consumed and used mostly as refuge. In conclusion, *P. obliquus* is a generalist invertebrate feeder typical of mesophotic ecosystems of SPSPA.

Keywords Chaetodontidae · Diet · Deep reefs · Microplastics · Mid-Atlantic Ridge · St. Paul's Rocks

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Introduction

Chaetodontidae (butterflyfishes) is an iconic and diverse fish family inhabiting tropical and subtropical reefs. It contains approximately 130 species (Froese and Pauly 2019), most of them living in shallow coral ecosystems (SCEs; 0–30 m depth) and about 10% in the mesophotic coral ecosystems (MCEs; 30–150 m; Pratchett et al. 2014). Because they are easily identifiable to species and are closely associated with reefs (Reese 1975), Chaetodontidae is among the most studied families of reef fishes (Pratchett et al. 2014). However, most knowledge on their ecology is based on the genus *Chaetodon* from shallow tropical reefs of the Indo-Pacific and Caribbean (Pratchett et al. 2014).

Butterflyfishes are usually classified into four major trophic categories: hard-coral feeders, soft-coral feeders, non-coral feeders or generalists (Pratchett 2005). Here we consider "generalist" as those feeding on a variety of sessile and mobile invertebrates, without preference for specific taxonomic preys. In the Atlantic Ocean, ecological investigations were performed for only three species of *Chaetodon* and *Prognathodes aculeatus*, all generalist feeders (e.g. Randall 1967; Birkeland and Neudecker 1981; Liedke et al. 2016, 2018).

The genus *Prognathodes* includes 13 species, seven from the Atlantic Ocean (Copus et al. 2019), including three (*P. brasiliensis*, *P. guyanensis* and *P. obliquus*)

present in Brazil. All these latter species preferentially inhabit deep waters, with a few individuals recorded shallower than 15 m, mostly in oceanic islands (Pinheiro et al. 2015) or in subtropical areas affected by upwelling (authors pers. obs.). In Brazil, *P. guyanensis* and *P. obliquus* are associated with lower MCEs (80–150 m) and upper MCEs (150–180 m; Rosa et al. 2016; Francini-Filho et al. 2018), while *P. brasiliensis* is found both on shallow and MCEs (Pinheiro et al. 2015). The trophic ecology of this genus is still poorly studied, with the exception of *P. aculeatus* in the Caribbean (Randall 1967; Birkeland and Neudecker 1981) and *P. carlhubbsi* in Ecuador (Nalbant 1995). The lack of basic ecological information for most *Prognathodes* species is explained by the inherent logistical challenges of sampling depths > 30 m.

Prognathodes obliquus (Lubbock and Edwards 1980) is endemic to the St. Peter and St. Paul's Archipelago (SPSPA), Mid-Atlantic Ridge, Brazil. It is among the most common species in the MCEs (50–90 m) of the SPSPA, being particularly abundant in areas dominated by branching black corals (*Tanacetipathes* spp.) and encrusting sponges (Rosa et al. 2016), with rare sightings in waters < 30 m (Luiz et al. 2015). In this study, we characterized for the first time the vertical distribution, foraging behaviour and diet of *P. obliquus*.

Materials and methods

The SPSPA is located in the Mid-Atlantic Ridge, about 1000 km from the NE Brazilian coast (0°55.01′N; 29°20.76′W). Benthic assemblages over rocky reefs of the SPSPA are divided in three depth strata (Magalhães et al. 2015): (1) SCEs (< 30 m) dominated by *Palythoa caribaeorum*, *Caulerpa racemosa*, crustose coralline algae and *Bryopsis* spp., (2) upper MCEs (30–50 m) dominated by *Caulerpa* spp., two Scleractinia and algal turfs and (3) lower MCEs (50–90 m) dominated by sponges, black corals, bryozoans and intricate bottoms formed by fused polychaete tubes. Sampling occurred in eight expeditions between 2010 and 2018, using remote-operated vehicles (ROV), closed-circuit rebreathers and submarines (Triton and Deep Rover). All dives occurred during daytime (0900 to 1500 hrs) in depths between 0–600 m and sea temperatures were obtained by diving computers.

The behaviour of 37 haphazardly chosen individuals of *P. obliquus* (Fig. 1a) was video-recorded (footages obtained by divers = 35, footages obtained by ROV = 2). For each individual, we recorded a 30-s to 1-min video, totalling 30 min of footage. In each video, the individual recorded was engaging in foraging, but generally alternating with other behaviours, such as sheltering within black corals and engaging in agonistic interactions. All foraging records were obtained in the upper mesophotic zone (30–60 m). Data from ROV and submarine operations were used for understanding bathymetric distribution of *P. obliquus*. For diet analysis, 19 individuals were collected with hand spear and frozen at the end of the dive to avoid

Fig.1 **a** Individual of *Prognathodes obliquus*. **b** One individual hidden in the branches of Antipatharia black coral. **c** Feeding over sediment in 50 m. **d** Aggregation of 15 individuals (photographs **b** by R. Francini-Filho and **a**, **c**, **d** by L.A. Rocha)

enzymatic digestion of food items. Only adults were collected, as juveniles were never sighted. In the laboratory, total length was measured and individuals were dissected for obtaining stomach and intestine contents. The intestine total length was measured from the pyloric caecum to the anus. The relative intestine length was obtained as a ratio between intestine and body length (Berumen et al. 2011).

The fullness of each stomach was visually estimated and assigned to one of the following four categories: 0–25%, 25.1–50%, 50.1–75%, and 75.1%–100% (Liedke et al. 2018). Stomachs were then dissected in petri dish under stereomicroscope, and all food items were identified to lowest taxonomic level possible. Amorphous organic matter was analysed with an optical microscope to identify diagnostic structures, such as nematocysts and spicules (Liedke et al. 2016). The Digested Organic Matter (DOM) category was assigned when taxonomic identification was not possible. The Mixed Cnidaria category included DOM with cnidocytes from different groups (different forms of holotrichs and microbasic b-mastigophores).

Diet was quantified using the frequency of occurrence (%FO, i.e. how often a food item is present in the sampled stomachs) and volumetric index (*%V*, i.e. summed volume of each item pooled across individuals divided by the total volume of the sampled stomachs; Hynes 1950; Hyslop 1980). The volume of each food item, in each stomach, was measured through a millimetre petri dish where each item was placed between two 1-mm-thick coverslips and kneaded with a microscope slide, and then the number of 1-mm^3 grids were counted (Liedke et al. 2016). To determine the importance of each food category, we used the Feeding Index equation: $\%IAi = ((\%FOi \cdot \%Vi)/\sum(\%FO \cdot \%V)) \cdot 100$, whereas *%FOi* and *%Vi* are the frequency of occurrence and volume of the food category *i*, respectively (Kawakami and Vazzoler 1980; Liedke et al. 2016).

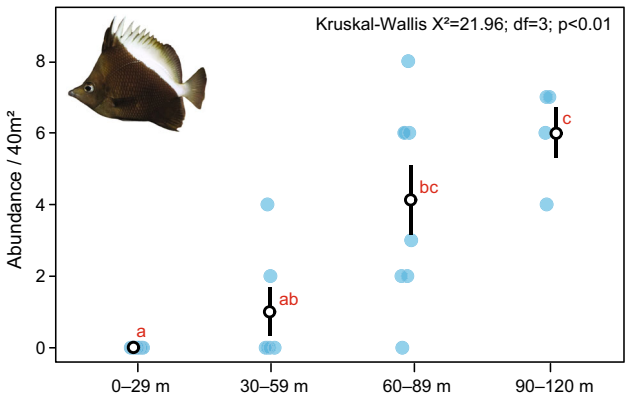

Fig. 2 Vertical distribution of *P. obliquus*. Blue dots are values for each transect. White circles and black bars represent the mean abundance (number of individuals per 40 m^2) and the standard error, respectively

To evaluate the abundance of *P. obliquus* across depth strata, we performed 31 underwater visual censuses (20 × 2 m transects), 13 transects < 30m depth; six between 30 and 59m; eight between 60 and 89; four between 90 and 120 using rebreathers (dives performed by LAR and HTP). Kruskal–Wallis and *post hoc* Dunn test were used to test for differences among depth strata. All analyses were performed in R software (R Core Team 2019).

Results and discussion

Of the 37 individuals recorded in the videos, 13 were sheltering among branches of black coral colonies (Fig. 1b); seven isolated individuals or in pairs were feeding on sediment and epilithic algal matrix (EAM) interspersed with polychaete tubes (Fig. 1c), and 17 were swimming close to the rocks, generally in pairs or in groups up to 15 individuals (Fig. 1d; https://www.youtube.com/watch?v=y-bDlM6ogyM). Despite black corals being abundant in the MCEs, no bites were recorded on them, suggesting that they are used as refuge instead of preferential prey.

The vertical distribution of *P. obliquus* starts with rare occurrences at 30 m but more regular sightings at 40 m, with abundance peaking in the lower MCEs (60–120 m; Fig. 2) and maximum depth recorded with submarines at 155 m. This species is thus restricted to mesophotic depths

Table 1 Diet of 19 individuals of *Prognathodes obliquus* in St. Peter and St. Paul's Archipelago

Food items	%FO	%V	%IAi
Polychaeta	84.21	30.08	41.93
Crustacea	63.16	16.74	17.50
Eggs	47.37	19.18	15.04
Hydrozoa	84.21	8.09	11.27
Bryozoa	42.11	13.26	9.24
Mixed cnidaria[a]	26.32	9.08	3.95
Digested organic matter[b]	15.79	1.27	0.33
Sediment	31.58	0.61	0.32
Algae	15.79	0.84	0.22
Plastic	31.58	0.21	0.11
Zoantharia	5.26	0.31	0.03
Organic detritus	10.53	0.09	0.02
Porifera	5.26	0.18	0.02
Nematoda	15.79	0.04	0.01
Antipatharia	10.53	0.03	0.01

Frequency of occurrence (%FO), volumetric index (%V), and feeding index (%IAi)

[a]Organic matter composed by different cnidocytes

[b]Organic matter without any identifiable structure

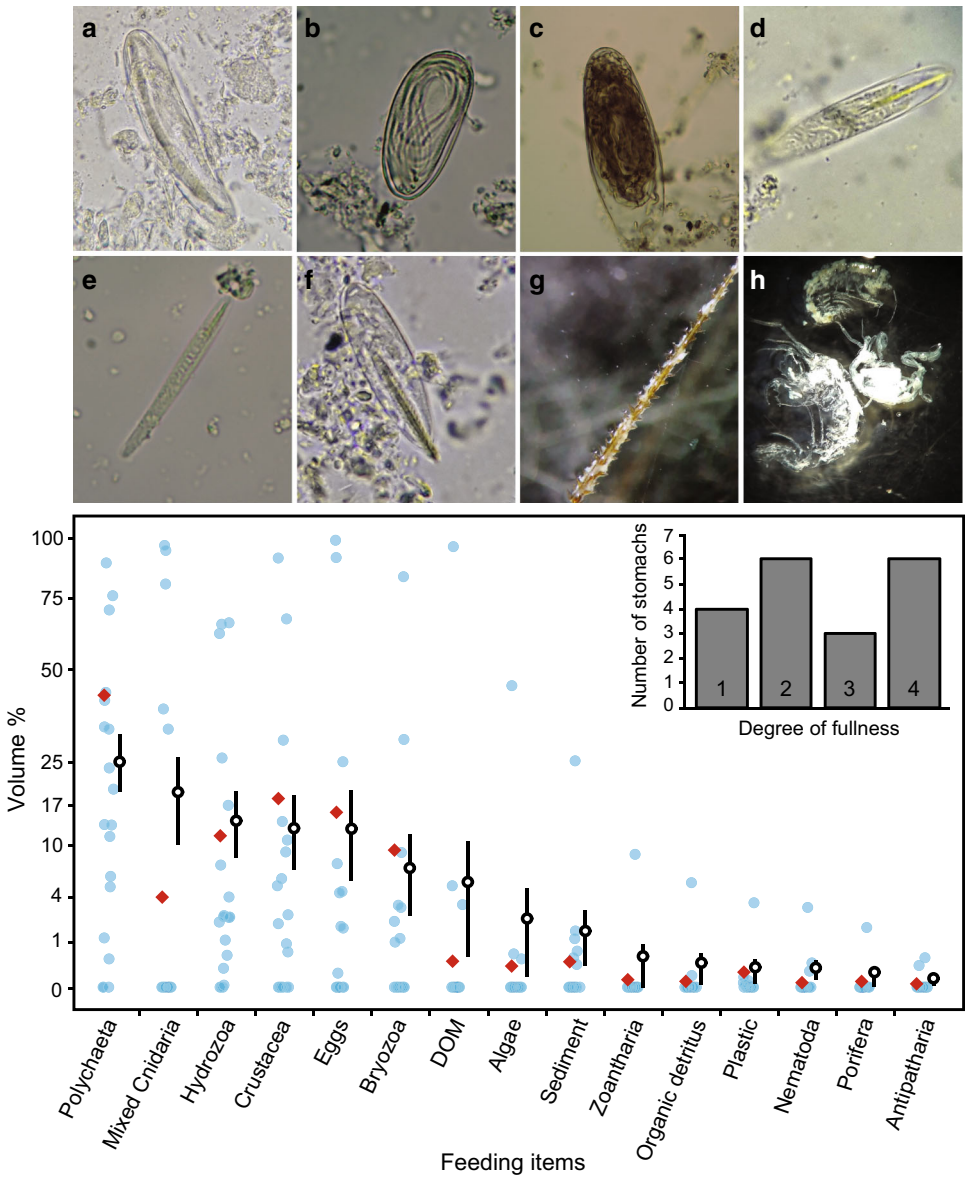

Fig. 3 The importance of feeding items in the diet of *P. obliquus*. Blue dots are the volume of each item for each stomach. Red diamonds represent the Feeding Index (%IAi). White circles and black bars represent the mean volume percentage of each item and the standard error, respectively. DOM = digested organic matter. Grey bars represent the stomachs' degree of fullness, in four categories: (1) 0–25%, (2) 25.1%–50%, (3) 50.1–75%, (4) 75.1–100%. Photographs of cnidocytes found in the mixed cnidaria: **a** p-mastigophore, **b** Holotrichous, **c** Ptychocyst, **d** p-mastigophore, **e** b-mastigophore, **f** b-mastigophore; and **g** *Tanacetipathes* spp., **h** Crustacea Amphipoda

around the SPSPA. A similar distribution pattern was found for the endemic *Prognathodes basabei* from the Hawaiian archipelago, which reaches 200 m of depth and presents a high abundance between 120 and 140 m (Pyle and Chave 1994; Pyle and Kosaki 2016). The vertical distribution of *P. obliquus* coincides with stratification in water temperature, with warmer waters between 0 and 30 m (26–30 °C), intermediate conditions between 30 and 60 m (18–26 °C), cold waters between 60 and 120 m (14–18 °C) and relatively colder waters below 150 m (< 14 °C). In fact, water temperature is an important determinant of species composition in mesophotic reefs (Simon et al. 2016). Anecdotally, we explored several habitats around SPSPA (i.e. exposed and sheltered, tidal pools, deep reefs) in different seasons, but never observed any juveniles, thus information about recruitment habitat and early life history remains unknown.

The 19 individuals collected for diet analyses had an average total length of 12.92 cm ± 1.87 (mean ± SE). The average relative intestine length was 2.32 ± 0.49, which is characteristic of fishes that eat both animal and plant material. Most of the stomachs were not completely full, but none were empty, which indicates that *P. obliquus* forages during the day, such as other Chaetodontidae species (Reese 1975). We identified 15 feeding items, 14 of which were animals (five of them: Polychaeta, Crustacea, Eggs, Hydrozoa and Bryozoa with summed importance > 95%), whereas algae were unimportant, occurring in only three individuals (IAi < 1%; Table 1; Fig. 3) and possibly ingested incidentally.

The incongruence between the omnivore intestine length and a carnivore diet could be explained by the relatively large amount of Cnidaria material ingested by *P. obliquus* (IAi = 14.47%). Cnidaria is a poor caloric resource (19.6 J mg^{-1}) compared to other invertebrates such as polychaetes (22.3 J mg^{-1}) and crustaceans (22.4 J mg^{-1}; reference values in Beukema 1997). The large intestine length found in hard-coral and soft-coral feeders could help them to deal with chemical defences (i.e. cnidocytes) and to improve the digestion/absorption of nutrients from cnidarians (Berumen et al. 2011).

Polychaeta was the most important item in the diet of *P. obliquus*, followed by Crustacea. A similar result was found for the diet of *P. aculeatus* in the Caribbean, which is composed mainly by Serpulidae Polychaeta (volume = 38.5%) and Crustacea (23.5%; Randall 1967). Due to decomposition, it was not possible to identify polychaetes to more precise taxonomic categories. Since we did not find tubes or radioles in the stomach content, which are characteristic of sessile polychaetes (Webb 1969), we believe material in *P. obliquus* stomachs were mobile polychaetes. These decomposed items could be better identified by using barcoding analyses in future studies (Leray et al. 2015). In contrast, Atlantic *Chaetodon* inhabiting shallow reefs eat more sessile polychaetes (e.g. Serpulidae and Sabellidae) and cnidarians (mostly Hexacorallia; Randall 1967; Liedke et al. 2018). Despite these differences, members of both genera in the Atlantic could be considered generalist feeders when compared to highly specialized hard-coral feeders of the Indo-Pacific, such as *C. baronessa* and *C. trifascialis* (Pratchett 2005).

Other animal items, such as sponges and black corals were probably accidentally ingested by *P. obliquus* given their low IAi values. This is a plausible explanation considering the high abundance of epibionts over sponges and black corals (M.R. Rosa et al., in preparation). Although there is no information about fishes eating ceriantharians in the Atlantic Ocean, we found cnidocytes of *Isarachnanthus* (Arachnactidae) in the diet of *P. obliquus*. This is the first record of a ceriantharian for the SPSPA, with the nearest record for this group in Rocas Atoll (Stampar et al. 2012). Surprisingly, even though this is a relatively deep-water species in a remote location, we found microplastics in six stomachs. Despite its geographical isolation, anthropogenic plastic pollution is prevalent in the SPSPA due to permanent human occupation and fishing activities. Great amounts of microplastic occur around the archipelago (Ivar do Sul et al. 2013) and fishing lines entangled in branching black corals are common (Francini-Filho et al. 2019), corroborating that pollution is an important threat to mesophotic reefs (Rocha et al. 2018).

In conclusion, we found that *P. obliquus* is a generalist carnivore, with diet composed mainly of sessile and mobile invertebrates, particularly Polychaeta and Crustacea. The first record of a ceriantharian in the SPSPA highlights the fact that trophic studies bring not only information about the studied species, but also about the environment where they live.

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Compliance with ethical standards

Conflict of interest We declare that there is no conflict of interest.

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