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The omnivorous triggerfish *Melichthys niger* is a functional herbivore on an isolated Atlantic oceanic island

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Abstract

This study evaluated the functional role of the highly generalist omnivore *Melichthys niger* in the remote St. Peter and St Paul's Archipelago (SPSPA), Brazil, where grazing herbivorous fishes are very scarce. We analysed patterns of distribution from zero to 30 m deep during three time intervals during the day and sampled different aspects of their feeding behaviour, including diel feeding rate, feeding substrate and diet. The density of *M. niger* increased with depth (26–30 m) and decreased by the end of the day. Although *M. niger* did not present a typical herbivore diel feeding pattern, they targeted the epilithic algal matrix as their primary feeding substrate, ingesting predominantly algae and detritus. The characteristic *Caulerpa racemosa* var. *peltata* from SPSPA was ingested only as detached fronds. We suggest that in the isolated SPSPA, the single species *M. niger* may perform a unique role as a link between benthic primary production and higher levels. Further studies on the trophic ecology of omnivorous species are necessary to better understand their roles in a reef system, especially in impoverished areas where they are likely to play a crucial role.

KEYWORDS
Balistidae, daily variation, feeding behaviour, herbivory, oceanic island, omnivory

1 | INTRODUCTION

Oceanic islands are often considered natural laboratories, where anthropogenic effects on native communities are absent or less pronounced than on continents (Sandin *et al*., 2008; Quimbayo *et al*., 2018). Features such as distance from the mainland and island size and age can affect colonisation and extinction rates on oceanic islands, driving patterns of richness and endemism in marine communities (Hachich *et al*., 2015; Pinheiro *et al*., 2017). The geographic isolation of these islands leads to impoverished taxonomic and functional richness, but relatively high richness of unique species (*i.e*., endemics; Robertson 2001; Allen 2008). Indeed, reef-fish assemblages from oceanic islands are taxonomically and functionally depauperate when compared with coastal regions, as only a subset of the coastal species are able to reach and establish themselves on these isolated systems (Bender *et al*., 2017). This scenario generates a pattern in which some functional groups are entirely absent or represented by very few species on oceanic islands. This absence may benefit generalist species because of their plastic diet.

Fish herbivory is considered an important process in marine reef environments as it can influence the distribution, diversity and productivity of different algal groups (Carpenter, 1986; Lewis, 1986),

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*In memoriam.

determining spatial patterns of benthic community organisation and dynamics (Aronson & Precht, 2000; Paddack *et al*., 2006; Smith *et al*., 2001). In tropical coral reefs, herbivorous fishes have received a disproportionate level of attention due to the notion that their feeding activity can mediate coral–algal interactions and maintain reef functioning through top-down mechanisms (Bozec & Mumby, 2015; Burkepile & Hay, 2006). More recently, the view that macroalgae are a natural component of healthy reefs with herbivorous fishes exerting little or no pressure on their dynamics has been widely reported (Bruno *et al*., 2014; Carassou *et al*., 2013; Russ *et al*., 2015; Suchley *et al*., 2016). Nevertheless, herbivorous fishes perform a key function on tropical reef systems as they constitute a major link between benthic productivity and higher trophic levels (Bascompte *et al*., 2005) and their removal from natural systems may hamper energy fluxes across trophic food webs (Bierwagen *et al*., 2018).

In regions where functional redundancy is lower, generalist species tend to be favoured and can establish themselves more readily (Parravicini *et al*., 2015). Species with plastic diets and habitat requirements are among the best candidates for filling empty niches and, due to their isolation and small area, oceanic islands are the habitats where these empty niches are particularly evident. Among reef fishes, omnivores can be considered generalists par excellence as most of them have highly variable diets and broad habitat requirements (Dubiaski-Silva & Masunari, 2006; Pratchett *et al*., 2011). These characteristics give omnivorous fishes the potential to perform various roles on reef systems, filling vacant niches in impoverished systems such as oceanic islands. Thus, the assessment and evaluation of the functional roles played by omnivores in isolated oceanic islands and the spatial variation of these roles, is a promising research avenue with the potential for novel findings.

The black triggerfish *Melichthys niger* (Bloch 1786) ranks among the most widespread and plastic fishes on tropical reefs. They can form large schools on oceanic islands (Kavanagh & Olney, 2006), particularly in the South Atlantic islands where they contribute substantially to the total reef-fish biomass (Longo *et al*., 2015; Morais *et al*., 2017). Among the features that enable *M. niger* to thrive in these harsh environments are an exceptionally long pelagic larval stage, a plastic diet and a voracious piranha-like feeding habit (Gasparini & Floeter, 2001; Kavanagh & Olney, 2006; Randall, 1967; Sazima *et al*., 2003). They can eat almost anything available, including recently spawned fish eggs (Sancho *et al*., 2000), dolphin faeces and vomit (Sazima *et al*., 2003), plankton material, as well as a wide array of benthic algae and invertebrates (Kavanagh & Olney, 2006; Randall, 1967; Sazima *et al*., 2003; Turingan *et al*., 1995).

Here, we evaluate the role of the *M. niger* at St. Peter and St. Paul's Archipelago, one of the smallest and most isolated tropical oceanic islands in the world (Figure 1). More specifically, we aimed to answer the following questions: (a) how does the abundance of *M. niger* vary with depth and across daylight hours, (b) how does the feeding behaviour of *M. niger* vary across daylight hours, (c) which substrata are frequently used by *M. niger* as feeding grounds, and (d) what is the composition of the diet of *M. niger*? This approach will yield an overall insight into the functional role played by this species in SPSPA.

2 | MATERIALS AND METHODS

All collections were performed under environmental and ethical permits of responsible agencies (ICMBIO permits #14611-1 and #20227-1).

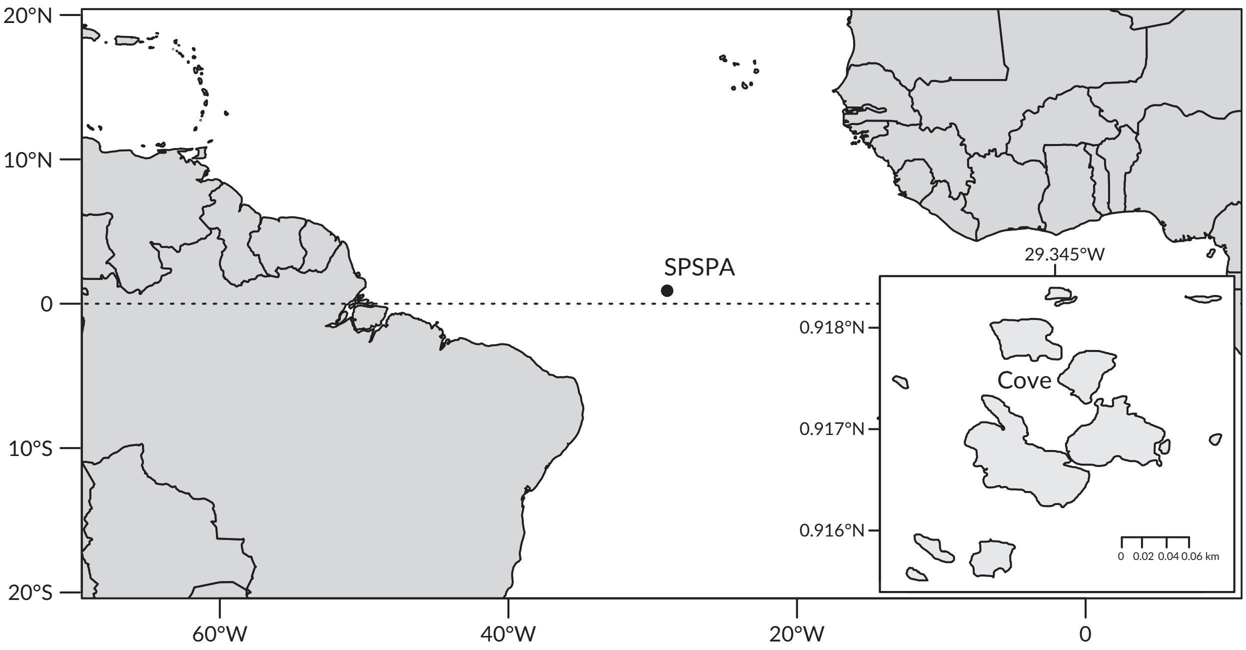

FIGURE 1 Map of the St Peter and St Paul's Archipelago (SPSPA) showing the Cove (inset) where *Melichthys niger* were sampled

2.1 | Study area

St. Peter and St. Paul's Archipelago (SPSPA) is one of the smallest and most isolated tropical archipelagos in the world (Edwards & Lubbock, 1983; Luiz *et al*., 2015). It consists of a group of 10 small and five larger barren islets, located in the equatorial Atlantic (0° 55′ N, 29° 22′ W), *c*. 1010 km off the north-east coast of Brazil and 1890 km south-west of Senegal (Figure 1). The archipelago is considered an important outpost between the Brazilian and the Tropical Eastern Atlantic biological provinces (Floeter *et al*., 2008). Given its isolation and small size, the SPSPA harbours the most depauperate fish fauna among all tropical oceanic islands with only *c*. 55 species recorded to date (Feitoza *et al*., 2003; Kulbicki *et al*., 2013; Lubbock & Edwards, 1981). The sea surface is influenced by the South Equatorial Current (SEC) from east to west, with an average velocity of 20 cm s^{-1}. At 50–100 m depth, the archipelago is influenced by the Equatorial Undercurrent (EUC) flowing from west to east with an average velocity of 100 cm s^{-1} (Edwards & Lubbock, 1983). Sampling was carried out during two expeditions in April 2008 and July 2009 in the cove, a small inlet protected from the prevailing currents with a gentle slope from 3 to 25 m deep followed by a steep wall (Figure 1). Sampling was restricted to this site as it is the single area in the entire archipelago with a considerable horizontal or near-horizontal bottom configuration, it is comparatively sheltered and the fish assemblage there does not differ from other sites in the archipelago (Luiz *et al*., 2015).

2.2 | Population density of *M. niger*

To assess *M. niger* population density, 120 stationary circular underwater visual censuses (UVC) were performed focusing on this single species. Each UVC involved a diver positioned in the centre of a 5 m radius circle (78.5 m^2) in which all *M. niger* individuals were counted. This method was chosen given the reduced reef area available in the habitat studied, which would preclude a large sample unit using strip transects. Moreover, circular UVCs can be rapidly replicated, being a good option for counting a single swarming species such as *M. niger*. UVCs were performed at three depth zones: shallow (0–10 m), middle (11–20 m) and deep (21–30 m) and on three periods of the day: morning (between 06:00 and 09:00 h), noon (between 11:00 and 13:00 h) and afternoon (between 16:00 and 19:00 h).

2.3 | Feeding behaviour

To assess the diel feeding pattern of *M. niger*, 207 individuals were followed during 3 min sessions from dawn to dusk in which the total number of bites was recorded. Sampling started at 06:00 h with the first rays of light and lasted until 18:00 h when the sun set. Observations were never performed from a distance <5 m from the focal individual to avoid human interference. Nevertheless, to avoid possible interferences on their behaviour, focal individuals were allowed to familiarise with the observer for *c*. 1 min prior to the beginning of each observation session. In addition, 30 individual *M. niger* were actively followed through the same procedure to determine preferences for feeding substrata. In this case, sessions ended when 10 bites were taken. Feeding substrate was classified in six broad categories: epilithic algal matrix (EAM), mats of *Caulerpa racemosa* var. *peltata*, mats of *Bryopsis* spp., rubble, rock covered with a thin microalgal biofilm and drift material (mainly composed of detached pieces of *Caulerpa*). EAM consists of a complex and variable assemblage of small filamentous and coralline algae, organic detritus (from dead algae, fish faeces and coral mucus) colonised by microorganisms, microalgae (cyanobacteria, diatoms and dinoflagellates), associated meiofauna and sediment (Wilson & Bellwood, 1997).

2.4 | Diet

Twenty-seven adult *M. niger* individuals were collected with a speargun to assess diet by gut-content analysis. Collection was carried out in the early afternoon to ensure fish had their stomachs full. Once collected, fish were removed from the water, killed by pithing if necessary, and had their stomach removed. The entire stomach content of each individual was stored in translucent plastic vials with 4% formalin and transported to the laboratory. In the laboratory, each sample was evenly spread on a Petri dish placed above a gridded paper with 50 marked points below. The food item above each point was identified and counted under x50 magnification on a stereoscopic microscope. Food items were identified to the lowest taxonomic level when possible and classified according to their taxonomic and morphologic structure (Steneck & Dethier, 1994) into the following groups: red articulated calcareous algae, red filamentous algae, red corticated algae, green filamentous algae, *Caulerpa*, fish egg, Crustacea, Gastropoda, zooplankton, detritus, sediment and others. *Caulerpa* was composed by the single stoloniferous species *C. racemosa* var. *peltata*. Detritus was defined as "dead and decaying primary producer material which normally becomes detached from the primary producer after senescence" (Lartigue & Cebrian, 2012) and consisted primarily of amorphous, opaque, flocculent material (*sensu* Wilson & Bellwood, 1997). Sediment comprised inorganic sediment present in the EAM that was probably ingested unintentionally.

2.5 | Data analysis

To examine the variation in the density of *M. niger* in different depths across daylight hours, we used a generalised linear model (GLM) with a Poisson distribution, considering depth (three levels: shallow, middle and deep) and period of the day (three levels: morning, noon and afternoon) as fixed factors. We used a model selection approach to assess the best models explaining the variation in density of *M. niger* among the following models: (a) full model with interaction between terms, (b) full model without interaction between terms, (c) only depth, and (d) only period of the day. Model selection was based on the Akaike information criterion (AIC).

We used a generalised additive model (GAM) to examine trends in bite rate of *M. niger* throughout the day using time of the day as a continuous factor (with 11 levels) and a Poisson distribution. The GAM was performed in R (www.r-project.org) using the package mgcv

TABLE 1 Generalised linear models results for predicting the population density of *Melichthys niger* in three depth zones and during three periods of the day in St Peter and St Paul's Archipelago

Model	df	AIC	ΔAIC	R^2
Time × depth	9	2748.8	0.0	0.52
Time + depth	5	2931.5	182.7	0.47
Depth	3	3143.1	394.3	0.41
Time	3	4336.4	1587.6	0.07

(Wood, 2011). Because data on feeding substrata and diet are based on repeated measures of individual fish, we fitted fish identity as a random factor. For this we used generalised linear mixed models (GLMM) to compare the proportion of feeding substrata used and the relative dietary contribution of different food items with a beta-binomial distribution using the package lme4 in R (Bates *et al*., 2015). Pairwise *post hoc* comparisons were performed using the package multcomp in R (Hothorn *et al*., 2008). Models were validated by visual inspection of residual plots.

3 | RESULTS

We observed an important interaction between depth and period of the day driving density of *M. niger* (Table 1). Overall density of *M. niger* was similar between shallow and intermediate depths but exhibited a 2.5 fold increase towards the deeper zone (Figure 2). While density decreased throughout the day in the first two depth zones, it was higher overall in the deeper zone and peaked in the noon (Figure 2). Period of the day was the least important factor for *M. niger* density which was highest in deeper zones (mean ± SD = 47.6 ± 19.5 individuals sample^{-1}), followed by intermediate (18.9 ± 8.41 individuals sample^{-1}) and shallow areas (16.9 ± 9.41 individuals sample^{-1}).

Bite rates of *M. niger* varied up to six-fold throughout the day (Figure 3a). Feeding activity increased abruptly from an average of 6.7 bites 3^{-1} min at 08:00 h to a peak of 24.8 bites 3^{-1} min at 11:00 h. Bite rate decreased to a plateau between 13:00 and 17:00 h and feeding activity decreased to 3.8 bites 3^{-1} min at 18:00 h until cessation (Figure 3a). The GAM model indicated a peak between 09:00 and 11:00 h followed by a slight decrease and a plateau until 17:00 h (Figure 3b). Overall, more than 60% of the total daily bites of *M. niger* were recorded in the morning. The six feeding substrata were used by *M. niger* in different proportions. More than 65% of the bites recorded were on the EAM, while rubble and drift material received 15.3% and 9.3% of the total number of bites, respectively. Mats of *Bryopsis* and *Caulerpa* were less important with only 4.3% and 4.0% of the bites, respectively (Figure 4).

The diet of *M. niger* was grouped into 12 categories but was largely dominated by algal items. Detritus was the most important food item and composed more than 36.3% (± 2.9 SE) of the diet of *M. niger* (Figure 5). Detached *Caulerpa*, red articulated calcareous (mainly *Jania* spp.) and green filamentous algae (mainly *Bryopsis* spp.) were of secondary importance in the diet of *M. niger*, whereas red and corticated filamentous algae, eggs and small crustaceans were of minor importance. Other items, such as sediment, gastropods and zooplankton were also present but in very small quantities and in just some specimens analysed (Figure 5). Although detritus was the single most important food category in the diet of *M. niger*, the sum of all algal groups accounted for 55.8% (± 3.6 SE) of its diet whereas animal material accounted for only 5.7% (± 1.2 SE).

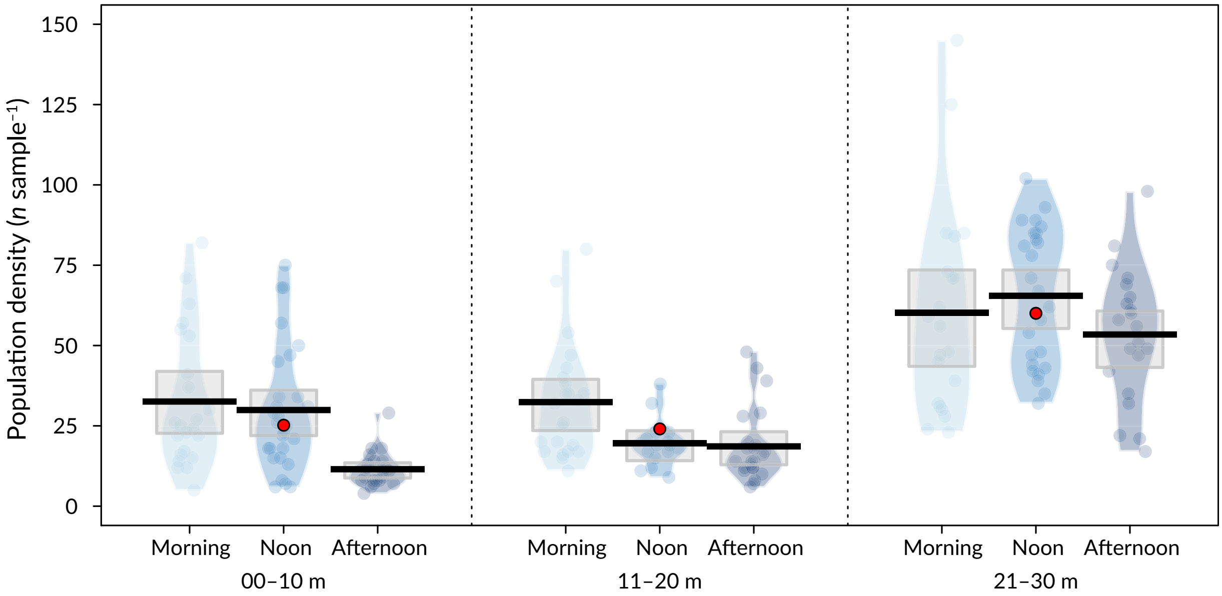

FIGURE 2 Population density of *Melichthys niger* at the St Peter and St Paul's Archipelago at three depth zones during three periods of the day: morning, 06:00–09:00 h; noon, 11:00–13:00 h; afternoon, 16:00–19:00 h. ●, Individual 5 m radius sample (78.5 m^2); ●, mean from each depth; ——, median; □, 25th–75th percentiles; ▬, range

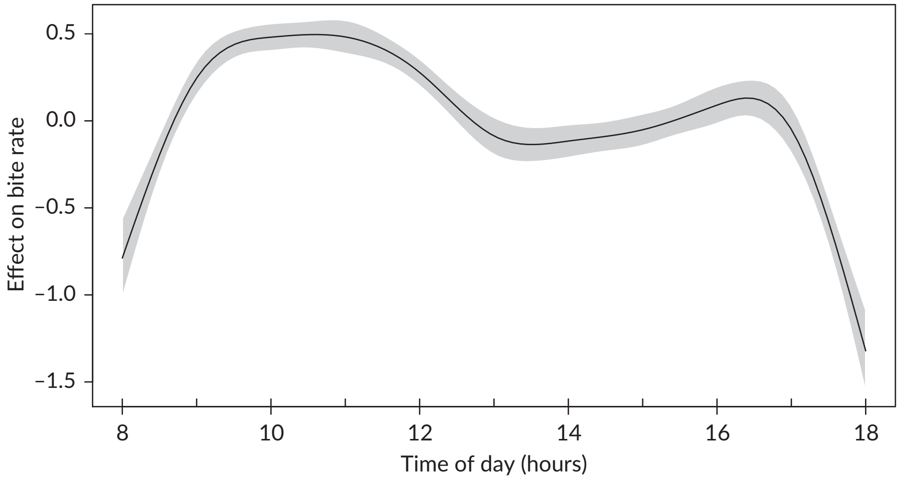

FIGURE 3 Diel feeding behaviour of *Melichthys niger* at the St Peter and St Paul's Archipelago. Results of generalised additive model (——) of bite rate as a function of time of day. ▬, 95% CI

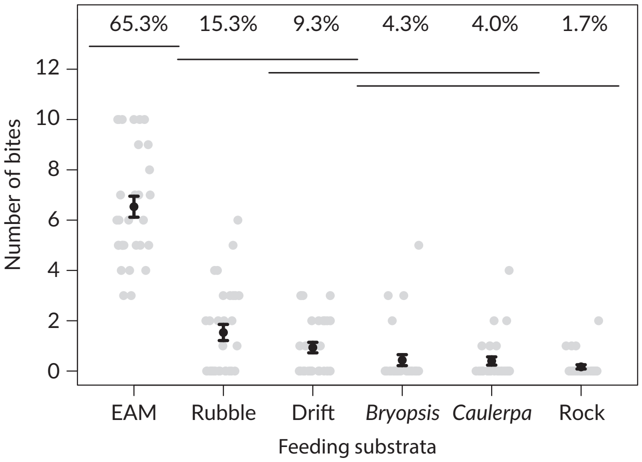

FIGURE 4 Feeding substrates used by *Melichthys niger* at the St Peter and St Paul's Archipelago. ●, Single observation; ●, mean (± SE) bites h^{-1}. Horizontal bars at head of figure indicate homogeneous groups in Tukey HSD *post hoc* test. EAM, epilithic algal matrix

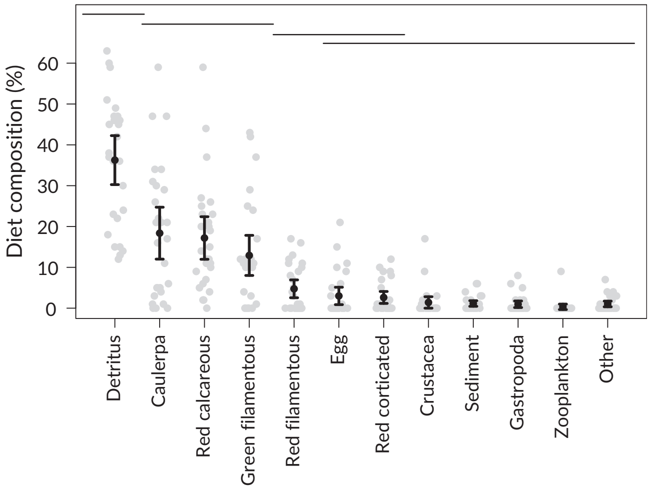

FIGURE 5 Diet composition of *Melichthys niger niger* at the St Peter and St Paul's Archipelago. ●, Single observation; ●, mean (± SE) per food item. Horizontal bars at head of figure indicate homogeneous groups in Tukey HSD *post hoc* test

4 | DISCUSSION

In SPSPA, *M. niger* presented a feeding behaviour that resembles that of a grazing herbivorous fish, including large quantities of algal material and detritus in their diet. SPSPA possess a very depauperate fish fauna characterised by the virtual absence of both surgeonfishes (Acanthuridi) and parrotfishes (Labridae, Scarini), which are conspicuous components of tropical reef-fish fauna worldwide. Only a few parrotfishes (*Sparisoma amplum* (Ranzani 1841), *Sparisoma axillare* (Steindachner 1878) and *Sparisoma frondosum* (Agassiz 1831)) have been recorded in SPSPA, but only as vagrants with limited functional importance (Feitoza *et al.* 2003). Indeed, roving herbivores compose only a minor fraction of both density and total biomass in SPSPA and are represented by the single family Kyphosidae (sea chubs; Luiz *et al.*, 2015). Four species (following Knudsen & Clements, 2013) can be frequently observed solitarily or in small groups in the shallow waters of the SPSPA: *Kyphosus sectatrix* (L. 1758), *Kyphosus vaigiensis* (Quoy & Gaimard 1825), *Kyphosus bigibbus* Lacépède 1801 and *Kyphosus cinerascens* (Forsskål 1775), all of which are known to specifically target brown and red corticated macroalgae as their primary foods (Ferreira & Gonçalves, 2006) and may benefit from the abundant *Dictyota* mats in the area (Magalhães *et al.*, 2015). Besides these roving species, the territorial herbivores *Stegastes sanctipauli* Lubbock & Edwards 1981 and *Ophioblennius trinitatis* Miranda Ribeiro 1919 can reach high densities in shallow areas of the SPSPA but their contribution to total fish biomass is minimal (Luiz *et al.*, 2015). Given the virtual absence of roving herbivores with a similar diet to *M. niger* in SPSPA (Feitoza *et al.*, 2003), their high feeding plasticity (Kavanagh & Olney, 2006) and the contribution of *M. niger* to the total fish biomass in SPSPA (Luiz *et al.*, 2015), we suggest that this single species may dominate the roles of algal turf and detritus removal in this area.

We found that *M. niger* is more abundant in deeper reefs (although the model with interaction between depth and period of the day was the most parsimonious) in comparison to shallower areas. This supports previous findings of Rosa *et al.* (2016), who reported high abundances in the upper mesophotic zone of the SPSPA (30–50 m deep). This pattern is unusual for herbivorous species which are usually more abundant in shallow waters (Brokovich *et al*., 2010; Cordeiro *et al*., 2016), but can be partially explained by *M. niger* swimming capabilities. Balistidae possess one of the most distinctive swimming modes among fishes. They achieve forward thrust by using coupled oscillation and undulation of their paired median fins, in what is known as balistiform swimming (Sfakiotakis *et al*., 1999). The large, low-aspect-ratio fins of *M. niger* are usually associated with increased manoeuvrability and with species that remain in close proximity to reefs. This contrasts with species that possess higher-aspect-ratio fins and commonly use shallower high-energy habitats (Fulton *et al*., 2005). Thus, the swimming capabilities of *M. niger* may prevent them from reaching high densities in shallow, surge-prone areas in the cove. Furthermore, the intermediate depths (11–20 m) contain the maximum richness and density of species, being largely dominated by small species such as *S. sanctipauli*, *O. trinitatis* and juveniles of *Abudefduf saxatilis* (L. 1758) and *Halichoeres radiatus* (L. 1758) (Luiz *et al*., 2015). In this zone, *M. niger* may be exposed to substantial aggressive interactions with its potential territorial competitors, *S. sanctipauli*, and this may also force *M. niger* into more suitable, deeper areas. Considering the above factors, deeper areas (21–30 m) of SPSPA reefs would thus provide an optimum zone for the local *M. niger* population, where the EAM over which they concentrate most of their bites is still abundant (Magalhães *et al*., 2015).

Most herbivorous and omnivorous fishes tend to increase their bite rate at midday or afternoon (Ferreira *et al*. 1998; Mendes *et al*. 2009; Raubenheimer *et al*. 2005), when algal resources attain a higher nutritional value based on digestible starch content (Zemke-White *et al*., 2002). However, this pattern was not observed in *M. niger* which tended to concentrate its feeding in the morning. This may seem counterintuitive for a nominal herbivore, but *M. niger* may not rely heavily on these algal carbohydrates. *M. niger* is likely to adopt a strategy whereby food intake is maximised in the morning and food is then processed continuously throughout the day while food ingestion still takes place.

The EAM is the substrate over which *M. niger* directs 65.3% of its bites and is one of the most important components of the benthic community in both shallow and mesophotic areas in SPSPA, where it can cover up to 60% and 30% of the reefs, respectively (Luiz *et al*., 2015; Magalhães *et al*., 2015). Fishes from various trophic categories use EAM as their primary grazing substrate (Wilson & Bellwood, 1997; Mendes *et al*., 2009; Francini-Filho *et al*., 2010; Kramer *et al*., 2013) in search of algae, detritus, invertebrates or its microbial components. The EAM is therefore considered an important link in the trophodynamics of reef systems (Wilson *et al*., 2003). The EAM is a ubiquitous component of Brazilian reefs (Aued *et al*., 2018) and although no detailed assessment of its components has been carried out in the region, *M. niger* is likely to benefit from the nutrients from algae and detritus from the EAM in the SPSPA. Indeed, the diet of *M. niger* was largely dominated by detritus when feeding upon the EAM. A number of herbivorous fishes ingest detritus (Choat *et al*., 2002; Ferreira & Gonçalves, 2006) using it as their primary nutrition source (Crossman *et al*., 2001; Wilson *et al*., 2001). Organic detritus from the EAM can exhibit higher concentration of protein amino acids than filamentous algae (Crossman *et al*., 2001) and is considered a valuable food source for grazing fish (Wilson *et al*., 2003).

Other feeding substrates used by *M. niger* included rubble (15.3% of bites), which can be colonised by small filamentous algae and used as shelter by mobile invertebrates. Small patches of rubble were seen in the study site and are frequently used by mobile invertebrate feeders such as *H. radiatus* in their search for food (Luiz *et al*., 2015). Drift material accounted for less than 10% of the total bites of *M. niger* and consisted of detached pieces of the alga *C. racemosa* var. *peltata*. However, *Caulerpa* was the second most important food item of *M. niger* and accounted for *c*. 20% of its diet. *Melichthys niger* was never observed ingesting *Caulerpa* while the alga was still attached to the substrate. Instead, in many instances large whitish pieces of *Caulerpa* that were detached and floating in the water column were targeted. It is possible that *Caulerpa* is only edible to *M. niger* after its detachment from the substrate, when its chemical composition may change due to its senescence. This remains to be tested, but given the intense wave action in SPSPA, detached *Caulerpa* may be an important food source to the local population of *M. niger*.

Herbivorous fishes on reef systems exhibit diverse diets and can be broadly classified along a continuum between true herbivores with macroalgal-based diets, dependent of endosymbionts that break down complex macroalgal polysaccharides and protein-scavengers that target cyanobacteria and other algae rich in easily digested nitrogen (Clements *et al*., 2017; Crossman *et al*., 2005). While very few works have evaluated food processing modes or nutritional ecology of omnivores, the strategy of ingesting both animal and algal material is based on complementation rather than substitution in the omnivore *Girella tricuspidata* (Quoy & Gaimard 1824) (Raubenheimer *et al*., 2005). Similarly, in SPSPA *M. niger* may adopt a strategy of maximising their starch intake by eating algae, while being physiologically more adapted to digest protein derived from microorganism-enriched detritus, eggs and small invertebrates. In such a scenario, *M. niger* would modulate the intake of algal and animal-derived material based on a balance between starch and protein requirements. Together with behavioural and dietary data, information about nutritional ecology of *M. niger* including nutrient concentration of its food and its physiological capabilities to digest it, will provide a better picture of the importance of this species to the trophodynamics of SPSPA.

Given that omnivorous fishes have varied diets and habitat use, it is usually assumed that they do not perform any critical roles in reef systems. However, various omnivores have been recognised as important algae consumers in various regions (Mantyka & Bellwood, 2007; Mendes *et al*., 2015) and a number of them include substantial amounts of algae in their diets. This highlights the potential importance of omnivorous fishes as algal consumers in reef systems. Furthermore, a better understanding of the trophic interactions between these species and their food may yield insights into novel physiological strategies.

In summary, we suggest that given the absence of grazing roving herbivorous fishes and the high plasticity and abundance of *M. niger* in the SPSPA, this species can be considered a functional herbivore and an important trophic link between primary productivity and higher levels in the local food chain. While we can suggest that the lack of competitors in the area could favour this feeding behaviour, little information exists to support hypotheses about its nutritional ecology or how *M. niger* modulates its ingestion. By eating detritus and algae in the EAM, *M. niger* would increase the intake of protein and starch respectively, with the additional nutrients derived from senescent detached *Caulerpa*. Given its unique role and high density, *M. niger* should be considered an important link between benthic production and higher trophic levels in the isolated SPSPA. An improved knowledge of the ecological roles of omnivorous species is required, as many of these species experience elevated fishing pressure and the consequences of their potential functional extinction are hard to predict.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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