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ORIGINAL PAPER

Foraging activity and behaviour of two goatfish species (Perciformes: Mullidae) at Fernando de Noronha Archipelago, tropical West Atlantic

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Abstract The goatfishes (Mullidae) include about 50 bottom-foraging fish species. The foraging activity of the yellow goatfish, *Mulloidichthys martinicus*, and the spotted goatfish, *Pseudupeneus maculatus*, was studied comparatively at Fernando de Noronha Archipelago, off coast of Northeast Brazil tropical West Atlantic. *Pseudupeneus maculatus* fed over a larger variety of substrate types, had lower feeding rate, roamed more per given time, spent less time in a feeding event, and displayed a more diverse repertoire of feeding modes than *M. martinicus*. The differences in the foraging activity and behaviour between the two species possibly minimize a potential resource overlap, as already recorded for other sympatric mullids. *Pseudupeneus maculatus* had lower feeding rate most likely because it feeds on larger items, and roamed over greater distance per time. Possibly this is because it foraged over a greater variety of substrate distributed over a larger area than that used by *M. martinicus*. Notwithstanding the overall morphological and behavioural similarity of goatfishes in general, they do differ in their substrate preferences and foraging activity, which indicates that these fishes should not be simply considered generalized bottom foragers.

Keywords *Mulloidichthys martinicus* · *Pseudupeneus maculatus* · Foraging behaviour · Oceanic island

Introduction

Goatfishes (Perciformes: Mullidae) include about 50 species distributed in tropical and subtropical seas (Munro 1976; Gosline 1984). All goatfishes are zoobenthivores and forage mainly over soft sediments (sand and mud) around reefs, oriented mostly by their tactile and chemosensory barbels (Gosline 1984; McCormick 1993, 1995; Platell et al. 1998; Lukoschek and McCormick 2001). During their foraging, the goatfishes disturb the substratum and, thus, change the bottom topography and the distribution of invertebrates associated with soft sediments (McCormick 1995). Additionally, goatfishes act as nuclear species and

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are frequently followed by other carnivorous reef fishes that catch small preys flushed during their substratum disturbance (Gosline 1984; Aronson and Sanderson 1987; Lukoschek and McCormick 2002).

The goatfishes are common and abundant in tropical and sub-tropical shallow reefs (Platell et al. 1998) and two or more goatfish species may occur on a same location (Gosline 1984; Golani 1994; McCormick 1995). Despite their overall morphological similarity and their almost exclusively bottom foraging, sympatric goatfish species usually differ in their depth distribution or foraging substratum selection and feeding modes (Gosline 1984; Golani 1994; McCormick 1995; Platell et al. 1998). Such differences are believed to minimize food overlap between co-occurring species (Labropoulou and Eleftheriou 1997).

Two mullid species, the yellow goatfish, *Mulloidichthys martinicus*, and the spotted goatfish, *Pseudupeneus maculatus*, co-occur at Fernando de Noronha Archipelago, off coast of Northeast Brazil, tropical West Atlantic (author personal observation). *Mulloidichthys martinicus* is a common reef species in the Western Atlantic and ranges from Florida to South-eastern Brazil (Carvalho-Filho 1999; Humann and DeLoach 2002). It feeds both at daytime and night (Randall 1967; Munro 1976; Aronson and Sanderson 1987) and forages solitarily or in groups (Carvalho-Filho 1999). *Pseudupeneus maculatus* is also a common reef fish species in the Western Atlantic and ranges from New Jersey to South Brazil (Carvalho-Filho 1999; Humann and DeLoach 2002). It feeds only at daytime, solitarily or in groups (Starck and Davis 1966; Munro 1976).

Mulloidichthys martinicus and *Pseudupeneus maculatus* feed on similar items (see Randall 1967; Sierra et al. 1994; for food items), but *P. maculatus* generally has a higher volumetric stomach content of mobile preys, such as crabs and shrimps, and also feeds on small fishes (Randal 1967; Sierra et al. 1994).

As recorded for other sympatric goatfish species (e.g. Golani 1994), *M. martinicus* and *P. maculatus* are known to have a degree of separation by depth in the Caribbean, *P. maculatus* being more abundant in deeper shelf areas (Munro 1976). Moreover, these two species appear to differ in their period of activity in the Caribbean, *M. martinicus* feeding mostly at night, whereas *P. maculatus* feeds only during the day (Munro 1976). The differences in depth range and activity period are believed to minimize food competition between these two goatfish (Munro 1976). However, contrasting with studies in the Caribbean, at Fernando de Noronha Archipelago *M. martinicus* and *P. maculatus* are abundant in shallow reefs (1–10 m) where they are both active during the day (author personal observation). Thus, studying the foraging activity of these two species at Fernando de Noronha would bring further insight on a presumed instance of resource partitioning between the two most abundant goatfish species in the reefs of Tropical West Atlantic (Munro 1976; Carvalho-Filho 1999; Humann and DeLoach 2002).

There is no a detailed study on the feeding activity and behaviour of *M. martinicus* and *P. maculatus*. Information about foraging behaviour of similar and abundant species of goatfishes are fundamental to assess the impact of bottom-foraging reef fishes on benthic fauna, both by their direct action as predators and their indirect action as substratum disturbers, as well as acting as nuclear species in heterospecific foraging associations (e.g. Gosline 1984; Aronson and Sanderson 1987; Lukoschek and McCormick 2002). Moreover, a study on *M. martinicus* and *P. maculatus* at sites where the two species are abundant, co-occur at same depth and have similar period of activity may bring new information on their feeding behaviour, which probably differs as a result of a presumable competition for food (Munro 1976).

The foraging activity of *M. martinicus* and *P. maculatus* was studied comparatively at Fernando de Noronha Archipelago. Our main purpose was to investigate whether these two species differ or not in their overall feeding activity and behaviour. The present study addressed five specific questions: (1) Do the two species use the same foraging substratum? (2) Do their feeding rates differ? (3) Are there specific differences in the distance travelled per given period while foraging? (4) Does the time spent in a feeding event differ between the two species? (5) Do their feeding modes differ?

Materials and methods

Procedure

The study was conducted at Fernando de Noronha Archipelago (03º50′ S; 32º25′ W), 345 km off north-eastern Brazil, from June to July 2002 and June 2003. The quantitative data on substratum selection, feeding rate and distance roamed per given time were gathered in an area of about 4000 m^2 at the Praia da Conceição, on the west side of Fernando de Noronha main island (Maida and Ferreira 1997; Sazima et al. 2005; for maps). The bottom of the study site is composed of rocky reefs covered mostly by brown algae (*Dictyota* sp., *Dictyopteris* sp., and *Sargassum* sp.), mixed substratum (composed mostly of sand and an assemblage of filamentous red algae, corallinaceous red algae and *Dictyota* sp.) and adjacent sandy areas (Fig. 1). Depth ranged 1–8 m, visibility ranged 8–30 m and water temperature was 27–28°C.

The foraging activity of the two goatfish species was recorded over 55 non-consecutive days while snorkelling and scuba-diving. During observational sessions of 60–150 min, ‘‘focal animal’’ and ‘‘all occurrences’’ samplings (Lehner 1979) were used in a total of 640 min of direct observation. All observations were conducted at daytime from 09:30 to 17:30.

Selection of foraging substratum and feeding rates for the two species were quantified by following individuals during foraging bouts of 3–5 min and counting the number of feeding events on four substratum types: (1) brown algae; (2) mixed (algae and sand); (3) sandy, and (4) hard substratum (rocks and stony corals). Each feeding event started when the goatfish’s mouth or snout touched the substratum and ended when it left the substratum. A given individual was not followed over successive periods to avoid the risk of collecting non independent data, thus all individual data likely came from different individuals (Zar 1996). The frequency of use of foraging substratum was calculated for each individual, and then the total mean between all individuals was calculated for each species. This procedure was adopted to avoid biased data (Zar 1996). The distance travelled per given time was assessed by following foraging individuals for 3–5 min and measuring the distance the fish moved within this period. Data on feeding rates and distance travelled per time were not collected for the same individual at the same time.

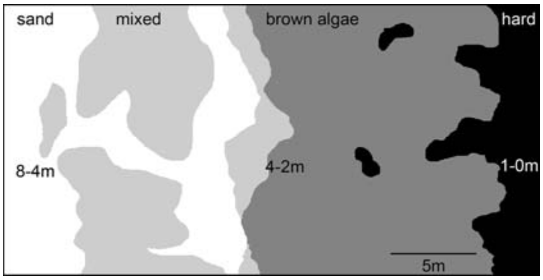

Fig. 1 A schematic map of the distribution of the four substratum types at the study site at the Praia da Conceição, Fernando de Noronha Archipelago. Each shade type corresponds to a substrate type (top); average depths are indicated for each type (centre). As the relative distribution and proportion of the four substrata are similar at the whole study site, only a part of the area is shown

Data used for comparisons of substratum selection was collected in June 2003 at the Praia da Conceição, thus the substratum availability was the same for all individuals studied. Data on feeding rates and distance travelled per time were collected in June and July 2002, and June 2003 at the Praia da Conceição and each species was followed a similar number of foraging bouts in each year. The relative abundance of the four foraging substratum types was quantified by video recording eight 30 × 2 m transects (modified from Birkeland and Neudecker 1981). Transects started on the rocky shore and ended on the sandy area where the two goatfishes were still recorded feeding (Fig. 1). Frames were taken from video-recordings and the percentage of the cover of the four substratum types was thus measured.

Data about feeding modes and time spent in each feeding event of the two species were recorded in four different sites at Fernando de Noronha main island: the Baía do Sueste, Buraco da Raquel, Porto de Santo Antonio and Praia da Conceição (see location on maps in Maida and Ferreira 1997; Sazima et al. 2005). A total of about 120 min of foraging activity of the two goatfish species was video-recorded at these sites.

In all sites the substratum was similar to that of the Praia da Conceição. To measure the time spent in each feeding event of the two species, 58 feeding events of 17 *M. martinicus* individuals and 27 feeding events of 16 *P. maculatus* individuals were analyzed. Time spent during each feeding event was calculated by analyzing the video-records and counting the number of still frames each feeding event lasted, and then the total time the frames lasted. The average of time spent in each feeding event was calculated for each individual recorded, and then the total means between all individuals was calculated for each species. This procedure was adopted to avoid biased data (Zar 1996). The feeding modes of the two goatfish species were described and quantified by analyzing video-records and photographs. For the feeding modes quantification, 50 feeding events of *M. martinicus* and 57 feeding events of *P. maculatus* were analyzed. To avoid no-independent data, only the first displayed feeding event was recorded per individual, thus all feeding events likely came from different individuals. Names of foraging modes are modified from McCormick (1995) and Lukoschek and McCormick (2001).

Statistical analysis

The independent Student *t* test was used to compare variables that presented normal distribution (feeding rates and distance roamed per time) and the non parametric Mann-Whitney test was used when data presented non normal distribution (time spent in each feeding event) (Zar 1996).

We used the Ivlev's electivity index (Krebs 1989) to verify the preference or rejection of each foraging substratum by the two species. The electivity index was calculated as follows:

$$E_i = (r_i - n_i)/(r_i + n_i),$$

in which E_i is the electivity measure for the i food type; r_i is the percentage of bites of each goatfish species on i food type and n_i is the percentage of i food type in the studied site. Electivity index varies from –1 to 1, in which values close to +1 indicate higher preferences and values close to –1 indicate lesser preference or avoidance (Krebs 1989).

The G test for the 2 × 6 contingency table was used to compare the frequency of the six feeding modes displayed by the two species (Zar 1996).

Results

Mulloidichthys martinicus and *Pseudupeneus maculatus* differed in all features examined (Fig. 2 and 3, and Table 1). *M. martinicus* preferred sandy ($E = 0.61$) over mixed substratum ($E = 0.003$), whereas *P. maculatus* preferred mixed substratum ($E = 0.36$) over sandy ($E = 0.09$) and brown algae ($E = -0.53$) substrata (Fig. 2). The three substrata *P maculatus* foraged over span about 93% of the total area of the study site, whereas the substrata used by *M martinicus* span about 47% of the same site (Fig. 1). Both species were also recorded to feed on rubble substratum (composed of pieces of dead calcified algae of about 2–20 mm, and sand) at study sites other than our main study site at the Praia da Conceição. Additionally, *M. martinicus* had higher feeding rate, roamed less per given time, and spent more time during each feeding event than *P. maculatus* (Table 1).

Mulloidichthys martinicus usually ingested part of the mouthed substratum while foraging, apparently swallowing only small and sedentary benthic and interstitial preys. On the other hand,

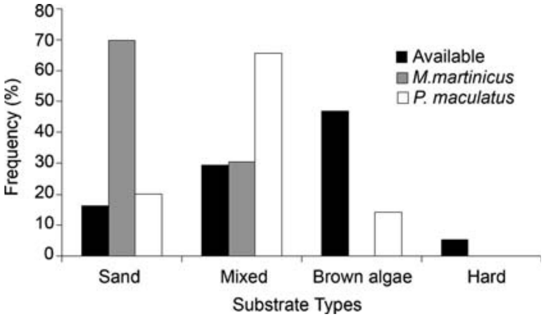

Fig. 2 Frequency of feeding events of *Mulloidichthys martinicus* (n = 20 individuals) and *Pseudupeneus maculatus* (n = 41 individuals) on each substratum type, and the actual relative abundances of these substrata at the Praia da Conceição, Fernando de Noronha Archipelago

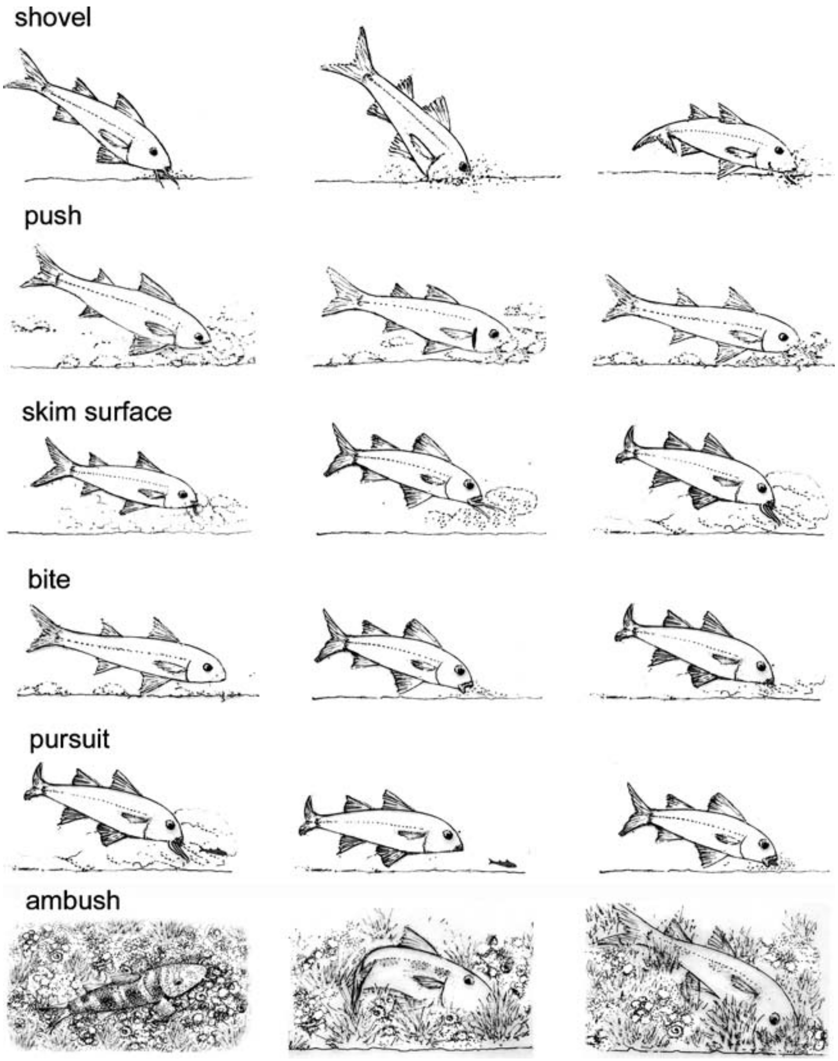

Fig. 3 A hypothetic goatfish displaying the six feeding modes (from the left to the right) recorded for *Mulloidichthys martinicus* and *Pseudupeneus maculatus* at Fernando de Noronha Archipelago. The former species displayed shovel, push, skim surface, and bite, whereas the latter displayed all modes. Based on video frames and photographs

P. maculatus occasionally mouthed and swallowed large preys (up to 4 cm total length) such as fishes and crustaceans.

The feeding modes displayed by the two species were classified into six categories (Fig. 2): 1—**shovel**: burrowing with snout, the body axis

Table 1 Comparisons of feeding rate, distance roamed per time, and time spent in feeding events for *Mulloidichthys martinicus* and *Pseudupeneus maculatus* at Fernando de Noronha Archipelago, given as mean ± standard errors. The parentheses indicate the total number of bouts for feeding rate and distance roamed per time, and number of individuals for time spent in each feeding event; ‘‘*P*’’ was calculated by student *t*-test for feeding rates and distance roamed per time and Mann-Whitney was used to test for time spent during each feeding event

	M. martinicus	*P. maculatus*	*P*
Feeding rate (feeding events min^{-1})	3.42 ± 0.17 ($n = 30$)	1.99 ± 0.16 ($n = 53$)	<0.0001
Distance roamed per time (m min^{-1})	2.99 ± 0.28 ($n = 26$)	5.39 ± 0.39 ($n = 33$)	<0.0001
Time spent in each feeding event (s)	1.56 ± 0.15 ($n = 17$)	0.61 ± 0.10 ($n = 16$)	<0.0001

usually more than 30° relative to substratum; 2—**push**: moving the snout against the substratum, dislodging the top layer (about 2 cm deep) of it horizontally, the body axis usually less than 20° relative to substratum; 3—**skim surface**: barbels actively pushing the top layer of the sediment; 4—**bite**: capture of prey using jaws' movement only; 5—**pursuit**: short distance chase (about 5–30 cm) after a mobile prey flushed during the substratum disturbance; 6—**ambush**: striking a prey after remaining stationary for 1–5 sec camouflaged on the brown algae substratum. *P. maculatus* displayed all six feeding modes, whereas *M. martinicus* displayed four: shovel, push, skim surface and bite. The two species also differed in the frequency that they displayed each feeding mode ($G_5 = 64$; $P < 0.001$), as *M. martinicus* displayed mostly push, shovel and skim surface, whereas *P. maculatus* mostly bite and skim surface (Fig. 4).

Discussion

Differences in foraging activity (this study) and depth distribution (Munro 1976) may minimize food resource overlap and, thus, competition for similar food items where *M. martinicus* and *P. maculatus* live in sympatry. Additionally, the two species are also known to differ in their activity period, as *M. martinicus* is known to feed at night as well (Randall 1967; Munro 1976). However, differences in activity period may not be important to avoid competition for food because the consumption of one food resource at night at a given site also reduces its availability during the day at the same site (Schoener 1974). To have a more complete view about resource partitioning between the two species here studied, it would be of interest to check in what sites and on what substratum type *M. martinicus* forages at night.

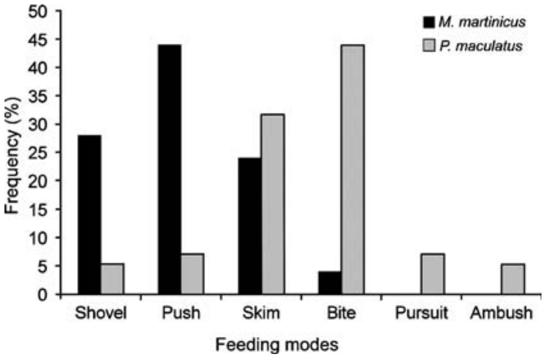

Fig. 4 Frequency of each feeding modes displayed by *Mulloidichthys martinicus* (*n* = 50 individuals) and *Pseudupeneus maculatus* (*n* = 57 individuals) at Fernando de Noronha Archipelago

Although goatfish species usually differ in their feeding activity, which is usually regarded as a mechanism to avoid resource overlap and competition, data from our study do not necessarily indicates that the differences in foraging behaviour of *M. martinicus* and *P. maculatus* may be a result of present competition for food (Connell 1980). To assess present competition between species, experimental studies are better suited than observational ones (see Connell 1980).

Even though there is no study that examines foraging substratum use by *M. martinicus* or *P. maculatus*, in the Caribbean these two species seem to feed almost exclusively over sandy bottoms (Itzkowitz 1977; Aronson and Sanderson 1987; JPK & RMB personal observations). Our findings for *M. martinicus* at Fernando de Noronha are similar to those obtained in the Caribbean (Aronson and Sanderson 1987), as it foraged only over non-consolidate substrata. On the other hand, in our study *P. maculatus* foraged over a wider range of substratum types than those recorded in the Caribbean (Itzkowitz 1977; Aronson and Sanderson 1987; JPK & RMB personal observation), especially in Jamaica, where this goatfish was recorded to forage exclusively on sandy substratum (Itzkowitz 1977). Perhaps *P. maculatus* forages almost exclusively on soft substrata in some areas of the Caribbean because algal cover is not as conspicuous and abundant as it is at Fernando de Noronha (JPK & RMB personal observation). Similar questions related to habitat differences in the Caribbean and in Brazil's coast were raised about the cleaning role of the french angelfish, *Pomacanthus paru* (Sazima et al. 1999).

Differences in substratum preferences between *M. martinicus* and *P. maculatus* are also likely related to their travelling while foraging. We believe that *M. martinicus* roamed for lesser distances because the substratum it used was concentrated on the sand flat, while the substrata on which *P. maculatus* foraged span over 93% of the study site.

As *P. maculatus* was occasionally recorded ingesting large preys, it is possible that its lower feeding rate, when compared to that of *M. martinicus*, is due to its feeding on large food items (which have a higher volumetric contribution) in a higher proportion. Our suggestion is strengthened by the fact that species of the genera *Pseudupeneus* and *Parupeneus* are believed to feed on larger and more mobile preys when compared to other goatfish species (Randall 1967; Gosline 1984). The present study indicates that *M. martinicus* feeds continuously on small preys, whereas the *P. maculatus* feeds on larger preys, thus in lesser amount.

The lesser time spent in each feeding event by *P. maculatus* is possibly related to the ability of species of the genera *Pseudupeneus* and *Parupeneus* to quickly immobilise and ingest preys using their strong jaw teeth (Gosline 1984). On the other hand, *M. martinicus* appears to immobilise its preys pushing them against the substratum and, thus, spending more time in its feeding events, even if preying on different prey types than *P. maculatus* does. This suggestion seems supported by the differences in the frequency and type of feeding modes displayed by the two goatfishes studied here.

In our study *M. martinicus* displayed feeding modes similar to that commonly used by other soft-sediment specialists, such as several *Mulloidichthys* species from the Pacific (Gosline 1984; McCormick 1995; Randall et al. 1997). On the other hand, *P. maculatus* displayed a variable feeding repertoire, including two feeding modes (pursuit and ambush), which are not recorded for any other goatfish species (Gosline 1984; McCormick 1995; Lukoschek and McCormick 2001). While ambushing, the colour of *P. maculatus* matched that of the substratum it hunted over and probably functioned to disguise the predator. The colours most often displayed by *P. maculatus* (light brown with yellow and dark brown spots) are similar to those of the brown algae substratum, abundant in all study sites, which may facilitate its camouflaging during ambush and increasing its hunting success on visually guided and quickly fleeing prey.

Overall, *P. maculatus* may be characterized as a versatile bottom predator that forages both on soft and hard substrata. Additionally, it is known to feed on drifting crustaceans while foraging in groups (Krajewski and Bonaldo 2006), which supports its characterization as a versatile predator. On the other hand, *M. martinicus* seems to be a soft bottom specialist, even if recorded to feed on zooplankton in the Caribbean (Sierra et al. 1994).

The present study and other recent findings indicate that goatfishes should not be simply characterized as soft bottom-specialists (Gosline 1984; McCormick 1995; Lukoschek and McCormick 2001; Krajewski and Bonaldo 2006). Different species of goatfishes may have different impacts on soft, algae, and hard bottom types and the associated organisms, due to their differential consumption and/or disturbance.

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