Effects of life phase and schooling patterns on the foraging behaviour of coral-reef fishes from the genus *Haemulon*

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During this study (December 2009 to December 2010), underwater visual surveys using the focal animal method were performed in the coastal reefs of Tamandaré, north-eastern Brazil. The aim was to analyse the effects of the life phase (juvenile and adult) and schooling patterns (school and solitary) on the feeding behaviour (foraging rates and substratum preferences) of four species of the genus *Haemulon* (*Haemulon aurolineatum*, *Haemulon parra*, *Haemulon plumieri* and *Haemulon squamipinna*). PERMANOVA analysis ($P < 0.05$) indicated that ontogenetic changes and schooling patterns directly influence foraging behaviour. Schooling individuals had low foraging rates (mean $\pm$ s.d. $= 2.3 \pm 2.1$ bites 10 min^{-1}) and mobility, usually remaining near the bottom; however, solitary fishes had high foraging rates (mean $\pm$ s.d. $= 12.5 \pm 4.6$ bites 10 min^{-1}). Juveniles preferred feeding in the water column (75% of the total number of bites), whereas adults foraged mainly in sand (80%) and bare rock (20%). All four *Haemulon* species displayed similar patterns of feeding behaviour as well as preferences for foraging sites and display competition for food resources. In contrast, little is known about their habitat use and foraging behaviour over the diel cycle, particularly the newly settled and early juvenile stages. © 2013 The Authors

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INTRODUCTION

Among coral-reef fishes, mobile invertebrate feeders represent the most abundant trophic group in tropical and temperate reef environments, preying preferentially on crustaceans, molluscs and polychaetes associated with consolidated or unconsolidated substrata (Wainwright *et al.*, 2002; Ferreira *et al.*, 2004; Pinheiro *et al.*, 2011). Species that carry on benthic feeding behaviour have an increased predation risk when foraging (Mitchell *et al.*, 2011). The predation risk directly influences the foraging behaviour, habitat use, diet, food selectivity, growth and even reproduction of many species of reef fishes (Magnhagen, 1988; Dahlgren & Eggleston, 2000). Optimal foraging theories demonstrate that predators display a balance between the time exposed for foraging and time spent avoiding predation. Consequently, there

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is a constant equilibrium between the susceptibility to predation and the need for obtaining food resources (Abrams, 1991; Brown *et al*., 2002).

The feeding behaviour and foraging rates of coral-reef fishes (*e.g*. benthic carnivores) vary considerably at different life stages. These changes are directly related to variations in habitat use, morphology and anatomy of species (Schmitt & Holbrook, 1984; Lukoschek & McCormick, 2001). In some instances, changes in feeding during the life of one species may be higher compared to other species with similar feeding habits (Eggold & Motta, 1992; Gillanders, 1995).

Schooling behaviour is usually promoted by coral-reef fishes to gain access to the defended resources of territory holders, decrease search times for patchily distributed resources and provide increased protection from predation (Debrot & Myrberg, 1988; Ward *et al*., 2002). *Haemulon* spp. play an important ecological and social role in schooling associations where they are involved in nuclear-following behaviour, mixed-species schooling behaviour, protective mimicry and foraging facilitation behaviour with several reef fish species (Sazima *et al*., 2007; Pereira *et al*., 2011, 2012), in addition to forming larger schools in the south Atlantic Ocean coastal reefs (Rocha *et al*., 2008).

Fishes of the genus *Haemulon* (family Haemulidae) are abundant on shallow reef communities and typically form schools associated with natural or artificial structures in the Caribbean Sea and eastern Pacific Ocean (Brotto *et al*., 2007; Rocha *et al*., 2008). This genus represents one of the most important reef fishes because of their abundance, fishery value (Lindeman & Toxey, 2002), phylogenetic distinctions (Sanciangco *et al*., 2011), ecological relevance (Pereira *et al*., 2011) and trophic importance as predators and prey (Lindeman & Toxey, 2002; Ferreira *et al*., 2004). Some species live in mid-water and feed on plankton while most live near the bottom and feed on macrobenthic organisms after migrations from the reef to soft bottom and macroalgae and seagrass beds (Parrish, 1989; Nagelkerken *et al*., 2000; Lindeman & Toxey, 2002; Hitt *et al*., 2011*a*, *b*).

Previous studies based on *Haemulon* spp. behaviour have been carried out in seagrass beds, mangroves and coral-reef areas and have evaluated different biological aspects such as patterns of behaviour (Burke, 1995; Verweij *et al*., 2006; J. P. Krajewski, unpubl. data), daily migrations between ecosystems (McFarland & Wahl, 1996) and agonistic interactions (McFarland & Hillis, 1982; Pereira & Ferreira, 2012). Furthermore, recent studies using acoustic telemetry (Hitt *et al*., 2011*a*, *b*) analysed the patterns of migration and activity of bluestriped grunt *Haemulon sciurus* (Shaw 1803), recording diel migrations with diurnal resting areas over reef or other hard structures and nocturnal foraging over soft sediments including seagrass beds.

This work is the first, as far as is known, to test for differences in feeding behaviour (foraging rates and substratum preferences) between life phase (juvenile and adult) and schooling patterns (schools and solitary) of coral-reef fishes. The following hypotheses were tested: (1) do the foraging rates decrease and substratum preferences change over the different life stages of individuals from the genus *Haemulon*? (2) Do individuals associated with schools have lower foraging rates and use different substrata to feed compared to solitary individuals? (3) Is there a difference in substratum feeding specialization among different life phases and different *Haemulon* species? This was accomplished by studying four species of the genus *Haemulon*: tomtate grunt *Haemulon aurolineatum* Cuvier 1830, sailor's grunt *Haemulon parra*

(Desmarest 1823), white grunt *Haemulon plumieri* (Lacépède 1801) and yellow grunt *Haemulon squamipinna* Rocha & Rosa 1999 from the coastal reefs of north-eastern Brazil.

MATERIALS AND METHODS

STUDY AREA

The reef complex studied is within the limits of the Costa dos Corais marine protected area (MPA) that encompasses 135 km of coastline in Pernambuco State of north-eastern Brazil. The Costa dos Corais MPA was the first Brazilian federal conservation area that included coastal reefs and is the largest multiple-use MPA in the country, encompassing an area of *c*. 41 3563 ha (Maida & Ferreira, 1997). The area presents a tropical climate with an intercalary regime of rainy (October to May) and dry (May to September) seasons reaching maximum temperatures of 26 and 30° C, respectively (Maida & Ferreira, 1997).

The tropical coral-reef ecosystem, in the Pernambuco State, municipality of Tamandaré, is composed of three main lines parallel to the coast (Fig. 1); this research was carried out specifically in areas of the first and second reef line, as the reefs on the third line are deeper and not yet well known. The first line is usually exposed to the largest tidal amplitudes presenting undeveloped algae beds composed primarily of macroalgae of the genera *Sargassum*, *Caulerpa*, *Udotea*, *Neomeris*, *Padina*, *Gracilaria*, *Dictyota* and encrusting coralline algae, *Halimeda opuntia*. The second line is more diverse in terms of habitat, comprising small patch reefs, narrow channels and pools with sandy bottoms. This habitat can remain submerged or exposed during low tide. The last reef line represents the characteristic shape of Brazilian coral reefs, which is distinct from other reef systems developing in isolated columns of 1·5–2·0 m (Maida & Ferreira, 1997).

DATA SAMPLING

The foraging behaviour of individuals was observed over 1 year (December 2009 to December 2010); there was no seasonal variation analysis. Underwater visual surveys were conducted using snorkelling and scuba equipment. Recordings were made from early morning (0800
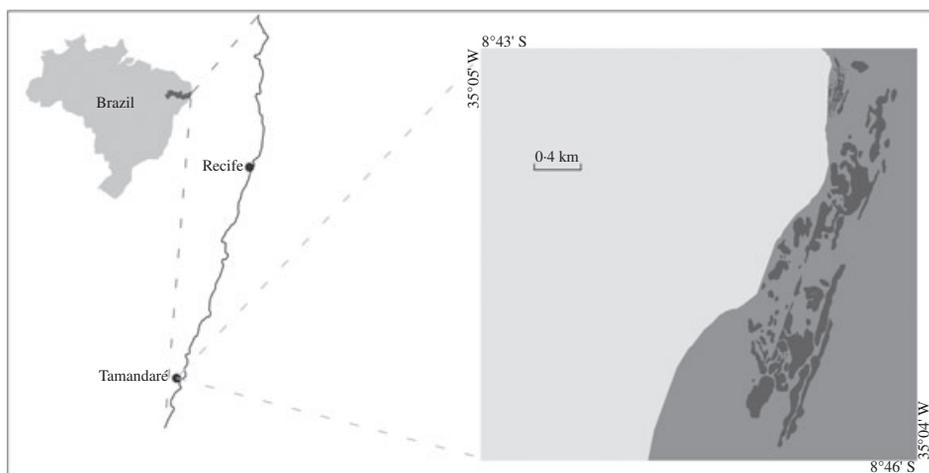

FIG. 1. The study area showing the coral-reef environmental of Tamandaré reef complex, north-eastern Brazil. ■ coral reefs.

hours) until late afternoon (1700 hours) and were standardized in sessions of 10 min, except when the individuals evaded the observer (in these cases, the sample was discarded). The focal animal method was used (Altmann, 1974), recording the behaviours observed on a PVC board.

During each observation session, the feeding rates (total number of bites) of each individual and the substratum type where feeding was observed (sand, water column, algae and bare rock) were recorded. Individuals were visually categorized according to life phase [juvenile: between 5 and 10 cm total (L_T) and adult: ≥ 10 cm L_T] and also based on morphological characteristics (Lindeman, 1986; Humann & Deloach, 2002).

Categories were also established for schooling patterns (schools and solitary) for each species (*H. aurolineatum*, *H. parra*, *H. plumieri* and *H. squamipinna*). Therefore, the observations were grouped into four different categories: adults grouped in schools (ADU-SCH), solitary adults (ADU-SOL), juveniles grouped in schools (JUV-SCH) and solitary juveniles (JUV-SOL).

A total of 12 categories with 20 individuals of each species were observed, totalling 240 observation sessions with duration of 10 min each (a total of 40 h of direct observation). Four specific categories were not observed: *H. aurolineatum* juvenile school, *H. plumieri* solitary adult, *H. squamipinna* solitary adult and *H. squamipinna* solitary juvenile as these species did not exhibit such schooling patterns during these life phases.

STATISTICAL ANALYSIS

PERMANOVA analysis was used to test the hypotheses, comparing the number of bites 10 min^{-1} (*i.e.* foraging rates) on different substrata among the four species (*H. aurolineatum. H. parra*, *H. plumieri* and *H. squamipinna*), life phase (adult and juvenile) and schooling patterns (schools and solitary). In this test, species, life phase and schooling patterns were fixed factors, whereas feeding rates were considered as dependent variables.

Multivariate analyses were also performed with regards to the feeding behaviour of the observed species of the genus *Haemulon*: (1) cluster analysis using the similarity index of Bray−Curtis was used to group categories in relation to foraging rates (bites 10 min^{-1}) and substratum preferences (sand, water column, algae and bare rock); (2) principal component analysis (PCA) independent of species (all species pooled) was used to analyse substratum preference with regard to life phases (juvenile and adult) and schooling patterns (schools and solitary).

Primer-e 6 PERMANOVA+1.0 software (Anderson *et al*., 2008) was used to conduct the PERMANOVA and multivariate analyses.

RESULTS

The foraging rates and substratum preferences for four species of *Haemulon* showed a direct relationship with life phase (juvenile and adult) and schooling patterns (schools and solitary) (Table I and Fig. 2). Adults demonstrated high foraging rates when solitary (mean $\pm$ S.D. $= 12\cdot5 \pm 4\cdot6$ bites 10 min^{-1}) as opposed to low rates when schooling (mean $\pm$ S.D. $= 2\cdot3 \pm 2\cdot1$ bites 10 min^{-1}; Table I). In contrast, juveniles did not have a clear pattern of foraging rates in relation to schooling or solitary individuals (Fig. 2). Moreover, adults exhibited a greater preference for sand (80%) compared with juveniles, which foraged in the water column (75%) (Fig. 2).

Significant differences in the foraging rates were found among the four species (PERMANOVA, $F_{3,228} = 5\cdot62$, $P < 0\cdot001$) (Table II). *Haemulon aurolineatum* showed the highest feeding rates (mean $\pm$ S.D. $= 14\cdot2 \pm 12\cdot8$ bites 10 min^{-1}), whereas *H. plumieri* had the lowest rates (mean $\pm$ S.D. $= 6\cdot1 \pm 4\cdot1$ bites 10 min^{-1}).

TABLE I. Foraging rates (mean $\pm$ s.d. bites 10 min^{-1}) for four species of *Haemulon* with data clustered by categories (life phase and schooling patterns)

	Overall	Adult schools	Solitary adult	Juvenile schools	Solitary juvenile
Haemulon aurolineatum	$14 \cdot 2 \pm 12 \cdot 8$	$2 \cdot 1 \pm 1 \cdot 1$	$16 \cdot 2 \pm 6 \cdot 5$	$24 \cdot 3 \pm 13 \cdot 9$	–
Haemulon parra	$8 \cdot 8 \pm 6 \cdot 4$	$2 \cdot 4 \pm 4 \cdot 6$	$0 \cdot 6 \pm 3 \cdot 4$	$10 \cdot 1 \pm 5 \cdot 6$	$13 \cdot 5 \pm 6 \cdot 0$
Haemulon plumieri	$6 \cdot 1 \pm 4 \cdot 1$	$2 \cdot 6 \pm 2 \cdot 7$	–	$5 \cdot 6 \pm 2 \cdot 6$	$10 \cdot 1 \pm 12 \cdot 4$
Haemulon squamipinna	$10 \cdot 7 \pm 11 \cdot 0$	$2 \cdot 1 \pm 1 \cdot 5$	–	$19 \cdot 3 \pm 9 \cdot 5$	–
Overall	$9 \cdot 95 \pm 8 \cdot 0$	$2 \cdot 3 \pm 2 \cdot 1$	$12 \cdot 5 \pm 4 \cdot 6$	$14 \cdot 75 \pm 7 \cdot 3$	$11 \cdot 05 \pm 8 \cdot 5$

Haemulon squamipinna had the second highest feeding frequency (mean $\pm$ s.d. $= 10 \cdot 7 \pm 11 \cdot 0$ bites 10 min^{-1}) and *H. parra* the second lowest foraging rate (mean $\pm$ s.d. $= 8 \cdot 8 \pm 6 \cdot 4$ bites 10 min^{-1}) (Table I).

With regard to the life phase (juvenile and adult), a significant difference between samples was also observed (PERMANOVA, $F_{1,228} = 4 \cdot 88$, $P < 0 \cdot 001$); foraging rates decreased and substratum preference changed with life phase. Higher foraging rates were observed for juveniles (mean $\pm$ s.d. $= 13 \cdot 8 \pm 6 \cdot 9$ bites 10 min^{-1}) compared with adults (mean $\pm$ s.d. $= 5 \cdot 8 \pm 5 \cdot 9$ bites 10 min^{-1}). There was also a significant effect of schooling pattern (schools and solitary) (PERMANOVA, $F_{1,228} = 53 \cdot 74$, $P < 0 \cdot 001$). Individuals grouped in schools demonstrated low
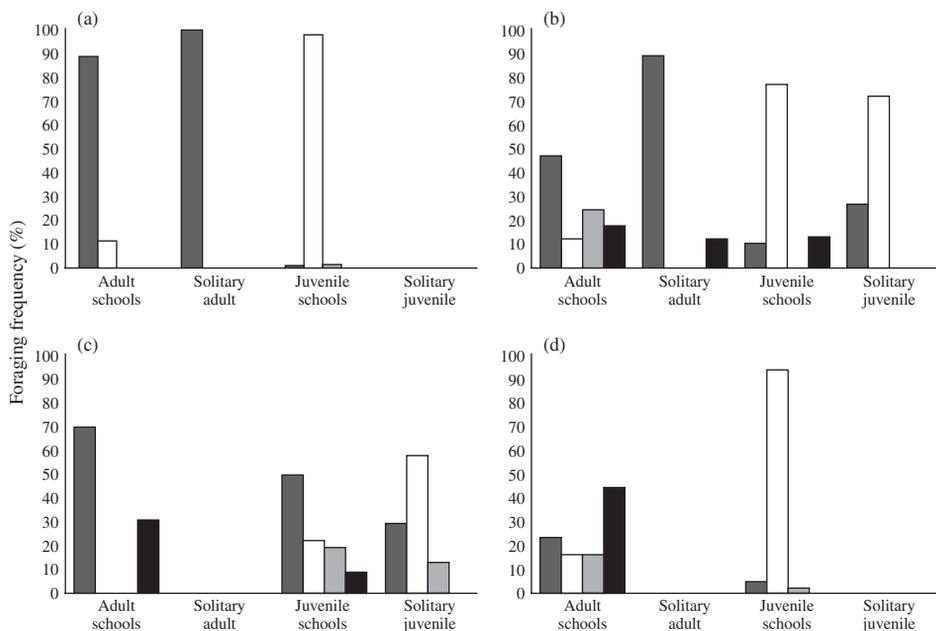

FIG. 2. Foraging frequency for (a) *Haemulon aurolineatum*, (b) *Haemulon parra*, (c) *Haemulon plumieri* and (d) *Haemulon squamipinna*, with data clustered by categories and types of substratum used as a food resource [sand (■), water column (□), algae (▩) and bare rock (■)].

TABLE II. PERMANOVA of the foraging rates (mean ± S.D. bites 10 min^{-1}) of four *Haemulon* species (*Haemulon aurolineatum*, *Haemulon parra*, *Haemulon plumieri* and *Haemulon squamipinna*), life phase (LP; adult and juvenile) and schooling pattern (SP; schools and solitary)

Sources	d.f.	SS	MS	F	P
Species	3	19 998	6666·2	5·62	<0·001
LP	1	5789·5	5789·5	4·88	<0·001
SP	1	63 663	63 663	53·74	<0·05
Species × LP	3	9944·9	4972·5	4·19	<0·001
Species × SP	2	28 402	9467·3	7·99	<0·01
LP × SP	1	1738·3	1738·3	1·46	>0·05
Species × LP × SP	3	65 500	65 500	5·67	>0·05
Residual	228	2·7005E5	1184·4	–	–
Total	239	5·3528E5	–	–	–

feeding frequencies (mean ± S.D. = 9·2 ± 7·8 bites 10 min^{-1}) when compared to the foraging rates of solitary individuals (mean ± S.D. = 12·4 ± 3·1 bites 10 min^{-1}).

The dendrogram generated from the Bray−Curtis similarity index revealed three distinct groups, with close to 55% similarity (Fig. 3). The first group (1) corresponded to the categories that fed in the water column, and had juvenile life stages that grouped in schools (the exception was solitary individuals of *H. parra*). The second group (2) included individuals that foraged in the sand, and were all solitary adults. The third (3) group clustered individuals that did not possess a clear foraging pattern as well as those with low foraging frequencies, *i.e*. schooling adults of the remaining species and *H. plumieri* solitary juveniles.

The PCA explained 89·9% of the total variability; 69·7% PC1 and 20·2% PC2, respectively. The eigenvalue for PC1 was 23·1 and for PC2 was 6·7. The analyses showed that sand substratum was used as a foraging site primarily for adults, both solitary and in schools (Fig. 4), whereas the water column was the site preferred by foraging juveniles, especially in schools (a situation in which they forage almost exclusively in the water column). Nevertheless, no clear pattern existed for use of algae and bare rock, except that schooling adults of *H. squamipinna* showed a preference for rock (and to lesser extent for algae).

Juveniles of all species showed more substratum feeding specialization than adults, feeding preferably in the water column (Table I and Fig. 2). *Haemulon plumieri* was the exception, with juveniles of this species using several substrata as a food resource (40% water column, 35% sand, 15% algae and 10% bare rock). In contrast, among the adults, *H. aurolineatum* was the most specialized, exclusively using one type of substratum (95% sand) compared to *H. squamipinna* which was the most generalist species (Table I and Fig. 2).
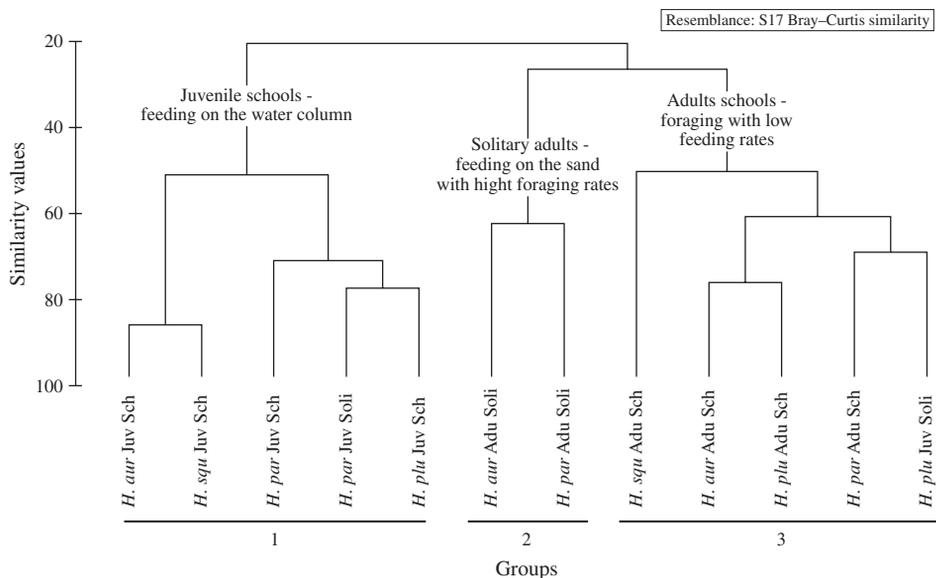
Fig. 3. Similarity analysis with data clustered by foraging rates and types of substrata used as a food resource. Three main groups were formed according to life phase and schooling patterns. *H. aur*, *Haemulon aurolineatum*; *H. squ*, *Haemulon squamipinna*; *H. par*, *Haemulon parra*; *H. plu*, *Haemulon plumieri*; Juv Sch, juvenile schools; Adu Sch, adult schools; Juv Soli, solitary juveniles; Adu Soli, solitary adults.

DISCUSSION

Juvenile coral-reef fishes exhibit greater activity and higher foraging rates than adults, probably because of the need for higher energy levels to supply faster growth rates (Hernaman *et al*., 2009). This fact is also evident for other species of the genus *Haemulon* (Verweij *et al*., 2006), and for other reef-fish families: Labridae (Gillanders, 1995), Lutjanidae (Rooker, 1995; Nanami & Yamada, 2008), Mullidae (Lukoschek & McCormick, 2001) and Scaridae (Van Rooij *et al*., 1996; Bonaldo *et al*., 2006). For the genus *Haemulon*, this difference may also be related to food resources suspended in the water column being more readily available compared to items buried in the substratum. In fact, during the juvenile phase, some species are characterized as zooplanktivorous, using mainly copepods as a food resource, while adults are zoobenthivorous and feed on crabs and polychaetes (Helfman *et al*., 1982; Cocheret de la Morinière *et al*., 2003; Verweij *et al*., 2006; unpubl. data).

Water column foragers, mainly from the families Gobiidae, Apogonidae, Poma-centridae and Haemulidae (Davis & Birdsong, 1973; Coughlin & Strickler, 1990), are planktivorous species that feed on macro- and micro-zooplankton at sites with good water visibility (Ferreira *et al*., 2004). The total percentage of foraging in the water column by the juvenile *Haemulon* spp. observed in this study was nearly 75%. This result, combined with a similar condition observed for juvenile French grunt *Haemulon flavolineatum* (Desmarest 1823) in the Caribbean Sea (Verweij *et al*., 2006), is evidence that grunts can be considered as water-column foragers during their juvenile life phase. Common morphological characteristics are more evident during the juvenile life phase of these species, such as lunate-shaped caudal fins, larger eyes
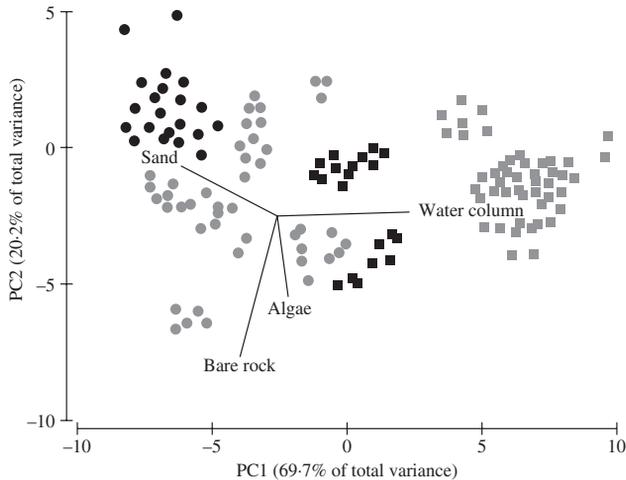
FIG. 4. Principal components analysis with data clustered by types of substrata used as a food resource (sand, water column, algae and bare rock) [adult schools (●), solitary adult (●), juvenile schools (■) and solitary juvenile (■)].

relative to the head, finer teeth in the jaw and powerful protractile jaws (Davis & Birdsong, 1973). In contrast, adult individuals foraged mostly in the sand (80% of feeding frequency), featuring *Haemulon* spp. adults as predators of unconsolidated substratum. Krajewski *et al*. (2011), in their study on the archipelago of Fernando de Noronha, also noted that *H. parra* and smallmouth grunt *Haemulon chrysargyreum* Günther 1859 forage in soft substrata, with 90% of their foraging activities on sand and 95% in algae bottoms, respectively. Among the adults of species examined in this study, *H. aurolineatum* was the most specialized feeder, exclusively using one type of substratum (sand) in contrast with *H*. *squamipinna*, a more versatile species, that fed on all substratum types. Such variations in the feeding behaviour of similar species from the same genus reflect: (1) differences in search processes for specific food items present in each type of substratum, *e.g*. polychaetes in sandy bottoms and mobile invertebrates in algae matrix (Lukoschek & McCormick, 2001); (2) specific characteristics of individual species, such as variety in the perception of sounds made by the movement of invertebrates in unconsolidated substrata (Popper & Hastings, 2009); (3) variations in shape and size of the swimbladder that would provide different movements and consequently different foraging patterns; (4) the use of different types or size of prey as morphological characteristics can drive changes in the use of food resources for coral-reef fishes (Nanami & Shimose, 2012).

The formation of schools for reef fishes has highlighted the protective function and anti-predation mechanism, in a posture adopted by several species called resting schools, in which individuals remain close to the bottom with reduced body activity (Ehrlich & Ehrlich, 1973). Major differences in feeding rates were found between schooling and solitary individuals in this study, always with higher foraging values for solitary *Haemulon* spp. individuals. Verweij *et al*. (2006) observed the feeding behaviour of *H. flavolineatum*, and concluded that when alone, individuals spend more time searching for food resources and have higher feeding rates (bites min^{-1})

than when schooling, where they just fed occasionally. Therefore, the low frequency of foraging rates observed during the formation of schools of *Haemulon* spp. is probably related to decreased predation risk in addition to increased efficiency in foraging. The preference of coral-reef fishes to forage as solitary individuals can be linked to reduced competition for the substratum during feeding (Jones, 1987; Johnsson, 2003), as invertebrates used as food resources are unevenly arranged along the substratum (Ogden & Ehrlich, 1977).

Differences in the feeding pattern between schooling and solitary individuals can also be associated with collaborative hunting tactics such as has been observed for the goatfish *Parupeneus cyclostomus* (Lacépède 1801), a species with feeding habits similar to that of *Haemulon* spp. (Strübin *et al*., 2011). Solitary individuals were associated with searching for hidden immobile prey on sandy areas, whereas schooling patterns were associated with collaborative hunting of mobile prey in corals (Strübin *et al*., 2011).

When comparing the four sympatric species of the genus *Haemulon* analysed in this study, there is clearly competition for resources (*e.g*. food and space); besides having similar patterns of behaviour and foraging sites, they also have similar diets (unpubl. data). A range of ecological differences, however, indicate that resource partitioning could be one of the possible mechanisms for the successful coexistence of these species: (1) feeding changes between daytime and night-time for some grunt species (Burke, 1995), as it was observed that *H. parra* individuals had high activity at night (P. H. C. Pereira, pers. obs.); (2) migration to surrounding ecosystems (*e.g*. mangroves, seagrass beds and muddy bottoms, present in the study area), thereby using different resources with ontogenetic changes (Nagelkerken *et al*., 2000; Verweij & Nagelkerken, 2007; Huijbers *et al*., 2011); (3) displacement of some species to deeper areas, *e.g*. large *H. plumieri* individuals (pers. obs.) that were not observed feeding as solitary adults in the present study area.

Despite the fact that there is not a high diversity of reef fishes in Brazilian waters, the genus *Haemulon* is represented by a relatively large number of species (Rocha *et al*., 2008) for which several theories can be suggested to justify their coexistence on south-west Atlantic Ocean coral reefs. The lottery hypothesis theory (Sale, 1977; Munday, 2004), for instance, proposes that competing species coexist through demographic mechanisms, without the need for resource partitioning. A large number of *Haemulon* larvae species settle at 1 cm or less throughout their ranges and these newly settled cohorts can undergo high mortality before even reaching early juvenile and juvenile life stages (Shulman & Ogden, 1987; Lindeman & Richards, 2005). Furthermore, more recent research, such as the density dependence theory (Stimson, 1990) and the recruitment limitation hypothesis (Doherty, 1998), may also provide information for understanding coexistence of species on reef ecosystems (Chesson, 2000; Hixon, 2011). Expanded research on resource use, recruitment and early demersal demography will shed much more light on the mechanisms underlying species coexistence among the highly endemic Brazilian reef fish fauna.

The groups formed in the cluster analysis showed categories according to similarities in feeding behaviour and activity in each type of substratum. Similarity was large among categories with regards to species (no species had their categories grouped by similarity). Differences in the feeding behaviour and diet of reef fishes can be greater between different life stages of a species owing to large ontogenetic variation than between different species with similar habits (Eggold & Motta, 1992). This can

also explain the coexistence of different species of the genus *Haemulon* in the same area.

The majority of studies on diet and feeding behaviour consider the genus *Haemulon* as nocturnal predators and nocturnal zoobenthivores (Helfman *et al*., 1982; Burke, 1995; McFarland & Wahl, 1996; Nagelkerken *et al*., 2000), owing to the use of significantly larger nocturnal activity spaces, resulting in more extensive searching behaviour associated with foraging during the night (Hitt *et al*., 2011*a*, *b*). Nevertheless, this study carried out observations of feeding behaviour for four species of the genus and showed a high frequency of foraging during the daytime, as observed by Verweij *et al*. (2006) for *H. flavolineatum*. Thus, there may be a difference in the preferred feeding time for each species of the genus or species that can feed both during the day and night.

Haemulon spp. have ecological and social importance in the complex functioning of reef areas and also adjacent ecosystems (*e.g.* seagrass beds and mangroves) (Gillanders *et al*., 2003; Huijbers *et al*., 2011; Pereira *et al*., 2011, 2012). In addition, they display some degree of territoriality and aggression (McFarland & Hillis, 1982; Pereira & Ferreira, 2012). Further work is necessary to better understand their habitat use and foraging behaviour over the diel cycle, particularly the newly settled and early juvenile stages. Little is known about their ecology in artificial reef environments, and where they form large schools that can number several thousand individuals.

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