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ORIGINAL PAPER

Nuclear-follower foraging associations of reef fishes and other animals at an oceanic archipelago

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Synopsis Fish species in many families and different trophic levels forage by following fishes and other animals. This interspecific foraging association was examined at an oceanic archipelago in the tropical West Atlantic. We recorded 27 reef fish species, two invertebrate species, and one turtle species playing the nuclear role, and 26 reef fish species acting as followers. The puddingwife wrasse following the spotted goatfish was the commonest foraging association recorded. The spotted goatfish was the nuclear fish that attracted the largest number of follower species (68% of the total number of follower species). The coney and the Noronha wrasse were the follower species that associated with the largest number of nuclear species (63 and 55% of the total number). About 20% of the reef fish species recorded in the archipelago engages in interspecific foraging associations. Substratum disturbance is a strong predictor for a fish displaying the nuclear role in the association, whereas the follower role may be predicted by carnivory. Nuclear species are diverse both in morphology and behaviour, and the nuclear role may be played either by fishes or other marine animals from invertebrates to turtles. Followers, on the other hand, comprise fishes only, which tend to display a more uniform feeding behaviour.

Keywords Feeding assemblages · Following behaviour · Mullidae · Labridae · Serranidae · Tropical West Atlantic

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Introduction

One type of temporary feeding association is formed when reef fishes follow other animals (Hobson 1968; Strand 1988; Lukoschek and McCormick 2000). So called following association comprises a nuclear species disturbing the bottom while foraging, and opportunistic follower species that feed on the exposed items (Fricke 1975; Lukoschek and McCormick 2000; Sazima et al. in press). The nuclear role is mostly displayed by fishes, but octopuses, sea stars, and turtles are recorded in such activity as well (Diamant and Shpigel 1985; Gibran 2002; Sazima et al. 2004). Following behaviour is widespread and recorded for many reef fish species of most trophic groups (e.g. Lukoschek and McCormick 2000; Auster and Lindholm 2002; Sazima et al. in press).

Among reef fishes, nuclear species are mainly carnivores and occasionally herbivores from the

Acanthuridae and Scaridae (Ormond 1980; Lukoschek and McCormick 2000; Sazima et al. 2005a). Followers are usually carnivores and other opportunistic feeding species, but this role also includes some herbivores (Strand 1988; Lukoschek and McCormick 2000; Sazima et al. in press). Opportunistic feeding seems to be a common trait for species recorded in the follower role. Since most fishes tend to be opportunistic and generalists in their feeding habits (Gerking 1994; Bellwood et al. 2006) the follower assemblages likely are composed of greater number of species than the nuclear ones.

Varied foraging tactics are employed by carnivorous fishes, including disguise, ambush, stalking, and roving (e.g., Sazima 1986; Gerking 1994; Krajewski et al. in press). Some species habitually use one or two tactics, whereas others may employ several tactics that vary considerably according to circumstances (Hobson 1968; Sazima 1986; Gerking 1994). In heterospecific foraging associations, feeding behaviour plasticity seems related to a high tendency of some species joining the nuclear species (Strand 1988). Thus, carnivores with variable foraging tactics likely associate with large number of nuclear species.

Most studies on interspecific foraging associations and following behaviour in reef fishes focus on one or a few nuclear and/or follower species or a particular kind of association (e.g., Diamant and Shpigel 1985; Baird 1993; Sazima et al. in press, but see Ormond 1980; Strand 1988; Auster and Lindholm 2002). The number of species within a local assemblage that engage in such type of association has been largely ignored (but see Auster and Lindholm 2002).

One aim of the present study is to assess the composition, richness, and relative number of species that engage in nuclear and follower feeding roles within a reef fish assemblage in an oceanic archipelago. We examine interspecific foraging associations of reef fishes following nuclear species (especially other fishes) at the oceanic archipelago of Fernando de Noronha in the tropical West Atlantic. We sought answers for the following main questions: (1) How many and which species act in the nuclear role? (2) How many and which species act in the follower role? (3) Which species act most frequently as nuclear or follower in the associations? (4) Which is the commonest interspecific foraging association? (5) Do follower species with variable foraging tactics associate with large numbers of nuclear species? (6) What is the proportion of species in the studied reef fish assemblage that engage in interspecific foraging associations? Answers to these questions may contribute towards a more comprehensive framework of interspecific foraging associations in reef fishes. Studies like the present one, with data about species composition and the contribution of each species in heterospecific associations, form the basis for comparisons between nuclear and follower species in different areas to assess whether there are common traits in this type of social foraging. Additionally, the present study attempts to assess whether disturbing the substratum is an important predictor for a species to play the nuclear role, and whether there are any features able to predict the follower role.

Material and methods

We recorded interspecific nuclear-follower associations at the oceanic archipelago of Fernando de Noronha (03°50′S, 32°25′W), about 345 km off the coast of northeast Brazil, tropical West Atlantic (Fig. 1). Study sites were mostly composed of irregular rocky reefs sparsely to thickly cover with green, brown and red algae, hydrocorals, stony corals, colonial zoanthids and fine sand

Fig. 1 Fernando de Noronha Archipelago (03°50′S, 32°25′W) off the coast of Brazil, Western South Atlantic. Modified from Maida and Ferreira (1997)

sediment, and adjacent sand flats. The seafloor habitats may affect the species composition within the foraging groups, as different species may forage over different types of substrata (Bonaldo et al. 2005; Krajewski et al. in press). However, the substrata over which nuclear species foraged consisted of mixed sand, gravel and rocks covered with algae and sessile invertebrates. Thus, no stratification by habitat appears in our data. Our field observations were conducted in June 2001 and 2002, May-July and November 2003, October 2004 and October–November 2005.

The foraging associations were recorded while snorkelling and scuba diving in observation sessions of 30–120 min, totalling 4308 min over 56 non-consecutive days. During the diving sessions we searched haphazardly for interspecific foraging associations and recorded every association observed with use of instantaneous sampling (Altmann 1974). A given foraging group was not followed over successive periods of time to avoid the risk of collecting non-independent data, and thus all individual data likely came from different foraging groups (Zar 1996). Records on plastic slates or photographs were used throughout the observation sessions. Foraging associations were recorded in the daytime from morning (09:00 h) to afternoon (18:00 h). We also conducted a few observations (300 min) from 18:30 to 20:30 h searching for night time foraging associations.

A nuclear species is habitually characterized as a predator that disturbs or explores the bottom while foraging (e.g., Diamant and Shpigel 1985; Strand 1988; Gibran 2002; Sazima and Grossman 2005). Additionally, an herbivore that disturbs the substratum and stirs particles while foraging falls within the nuclear category (Sazima et al. 2005a). A follower species is any fish that perceives the feeding conditions created by a nuclear species and forages in its close proximity, and, thus, a follower is usually treated as an opportunistic forager (e.g., Strand 1988; Lukoschek and McCormick 2000; Sazima and Grossman 2005).

For the reef fish assemblage of Fernando de Noronha two logistic regression analyses (Tabachnick and Fidell 2001) were performed on the role of a fish species in the feeding association. We considered the nuclear (coded as ''nuclear'' or ''non-nuclear'') and follower (coded as ''follower'' or ''non-follower'') roles as outcomes and five behavioural ''predictors'': (1) substratum disturbance, (2) group foraging, (3) bottom foraging, (4) carnivory and (5) herbivory. Substratum disturbance was categorized in increasing levels ranging from 0 (species that forage in the water column) to 3 (species that cause great substratum disturbance while foraging). The other behavioural predictors were classified as ''0'' for absence and ''1'' for presence. In the analyses we considered fish species recorded in heterospecific associations and also fish species that we assumed not to engage in heterospecific associations, haphazardly chosen from the community. Data from 56 species were used in each analysis: 26 nuclear species and 28 non-nuclear ones, and 26 follower species and 28 non-follower ones.

Results

We recorded 27 reef fish species, two invertebrate species and one turtle species (totalling 30 species) in the nuclear role, and 26 reef fish species in the follower role (Tables 1 and 2) at Fernando de Noronha. Among the foraging associations recorded between fishes, bottom-disturbing carnivores accounted for 74% of the species in the nuclear role, whereas roving or sedentary carnivores accounted for 72% of the species in the follower role (Table 1). Followers of species other than fishes also were mostly (75%) roving or sedentary carnivores (Table 2).

A total of 531 interspecific foraging associations of reef fishes following nuclear species were recorded in the archipelago. From these, 508 associations (95%) had fishes as the nuclear species, the spotted goatfish *Pseudupeneus maculatus* being the most frequent nuclear species (50%, $N = 258$) (Table 1). In 23 associations (5%) octopuses, turtles, or brittle stars were the nuclear species, the octopus *Octopus* sp. being the most frequent nuclear species (82%, $N = 19$) (Table 2). The puddingwife wrasse *Halichoeres radiatus* was the most frequent follower of fishes (37%, $N = 187$) (Table 1), whereas the coney *Cephalopholis fulva* was the most frequent follower of invertebrates (65%, $N = 15$) (Table 2).

Table 1 Nuclear fish species, their social behaviour while followed, and their follower fish species at Fernando de Noronha Archipelago, tropical West Atlantic. Numbers are absolute and relative frequencies (%) of associated fish species, where $N = 508$ recorded associations. Each nuclear species and its follower species in decreasing order of relative frequency of occurrence in the associations. Where social behaviour is double, the prevalent one is placed first

Nuclear species	*N* (%)	Social behaviour	Follower species	*N* (%)
Pseudupeneus maculatus	258 (50.78)	Single, grouped	*Halichoeres radiatus*	149 (29.33)
			Cephalopholis fulva	88 (17.32)
			Caranx bartholomaei	44 (8.66)
			Caranx latus	35 (6.88)
			Sparisoma axillare	15 (2.95)
			Thalassoma noronhanum	9 (1.77)
			Halichoeres dimidiatus	7 (1.38)
			Acanthurus coeruleus	7 (1.38)
			Acanthurus chirurgus	6 (1.18)
			Haemulon parra	5 (0.98)
			Aulostomus strigosus	5 (0.98)
			Anisotremus surinamensis	4 (0.78)
			Sparisoma frondosum	4 (0.78)
			Haemulon chrysargyreum	2 (0.39)
			Malacanthus plumieri	2 (0.39)
			Mulloidichthys martinicus	1 (0.19)
			Sparisoma amplum	1 (0.19)
Sparisoma frondosum	52 (10.23)	Single	*Thalassoma noronhanum*	50 (9.84)
			Anisotremus surinamensis	1 (0.19)
			Halichoeres dimidiatus	1 (0.19)
Dasyatis americana	26 (5.11)	Single	*Caranx bartholomaei*	20 (3.93)
			Caranx latus	2 (0.39)
			Cephalopholis fulva	2 (0.39)
			Halichoeres radiatus	2 (0.39)
			Halichoeres dimidiatus	1 (0.19)
			Dactylopterus volitans	1 (0.19)
			Lactophrys trigonus	1 (0.19)
Sparisoma axillare	25 (4.92)	Single	*Thalassoma noronhanum*	25 (4.92)
Haemulon parra	24 (4.72)	Single, grouped	*Thalassoma noronhanum*	20 (3.93)
			Halichoeres radiatus	7 (1.38)
			Halichoeres dimidiatus	2 (0.39)
			Caranx latus	1 (0.19)
			Cephalopholis fulva	1 (0.19)
Mulloidichthys martinicus	23 (4.52)	Single, grouped	*Halichoeres radiatus*	20 (3.93)
			Cephalopholis fulva	3 (0.59)
			Halichoeres dimidiatus	2 (0.39)
			Thalassoma noronhanum	2 (0.39)
Sparisoma amplum	15 (2.95)	Single	*Thalassoma noronhanum*	15 (2.95)
Anisotremus surinamensis	11 (2.16)	Single, grouped	*Thalassoma noronhanum*	5 (0.98)
			Caranx latus	4 (0.78)
			Caranx bartholomaei	1 (0.19)
			Halichoeres radiatus	1 (0.19)
Acanthurus chirurgus	10 (1.97)	Grouped	*Pseudupeneus maculatus*	5 (0.98)
			Caranx bartholomaei	3 (0.59)
			Haemulon parra	3 (0.59)
			Haemulon chrysargyreum	2 (0.39)
			Aulostomus strigosus	2 (0.39)
			Cephalopholis fulva	1 (0.19)
			Anisotremus surinamensis	1 (0.19)
			Sparisoma amplum	1 (0.19)

Table 1 continued

Nuclear species	*N* (%)	Social behaviour	Follower species	*N* (%)
Gymnothorax vicinus	9 (1.77)	Single	*Caranx bartholomaei*	7 (1.38)
			Cephalopholis fulva	6 (1.18)
			Pseudupeneus maculatus	1 (0.19)
			Haemulon parra	1 (0.19)
			Halichoeres radiatus	1 (0.19)
			Acanthurus coeruleus	1 (0.19)
Lactophrys trigonus	9 (1.77)	Single	*Thalassoma noronhanum*	8 (1.57)
			Halichoeres radiatus	3 (0.59)
			Malacoctenus sp.	1 (0.19)
Acanthurus coeruleus	6 (1.18)	Grouped	*Caranx bartholomaei*	2 (0.39)
			Thalassoma noronhanum	2 (0.39)
			Aulostomus strigosus	1 (0.19)
			Cephalopholis fulva	1 (0.19)
			Pseudupeneus maculatus	1 (0.19)
			Abudefduf saxatilis	1 (0.19)
			Anisotremus surinamensis	1 (0.19)
			Haemulon parra	1 (0.19)
			Sparisoma amplum	1 (0.19)
Acanthostracion polygonius	6 (1.18)	Single	*Thalassoma noronhanum*	6 (1.18)
Muraena pavonina	5 (0.98)	Single	*Cephalopholis fulva*	3 (0.59)
			Labrisomus cf. *nuchipinnis*	2 (0.39)
			Caranx latus	1 (0.19)
Halichoeres radiatus	5 (0.98)	Single	*Cephalopholis fulva*	2 (0.39)
			Pseudupeneus maculatus	2 (0.39)
			Thalassoma noronhanum	2 (0.39)
Malacanthus plumieri	4 (0.78)	Single	*Halichoeres radiatus*	2 (0.39)
			Halichoeres dimidiatus	1 (0.19)
			Thalassoma noronhanum	1 (0.19)
Caranx bartholomaei	3 (0.59)	Single, grouped	*Cephalopholis fulva*	3 (0.59)
Haemulon chrysargyreum	3 (0.59)	Grouped, single	*Caranx latus*	1 (0.19)
			Mulloidichthys martinicus	1 (0.19)
			Halichoeres radiatus	1 (0.19)
			Thalassoma noronhanum	1 (0.19)
Ginglymostoma cirratum	2 (0.39)	Single	*Caranx bartholomaei*	2 (0.39)
			Cephalopholis fulva	1 (0.19)
			Lutjanus jocu	1 (0.19)
Albula cf. *vulpes*	2 (0.39)	Grouped	*Caranx crysos*	1 (0.19)
			Abudefduf saxatilis	1 (0.19)
Gymnothorax funebris	2 (0.39)	Single	*Cephalopholis fulva*	1 (0.19)
			Caranx bartholomaei	1 (0.19)
Myrichthys ocellatus	2 (0.39)	Single	*Cephalopholis fulva*	1 (0.19)
			Halichoeres radiatus	1 (0.19)
			Thalassoma noronhanum	1 (0.19)
Halichoeres dimidiatus	2 (0.39)	Single	*Cephalopholis fulva*	1 (0.19)
			Thalassoma noronhanum	1 (0.19)
Dactylopterus volitans	1 (0.19)	Single	*Cephalopholis fulva*	1 (0.19)
Cephalopholis fulva	1 (0.19)	Single	*Aulostomus strigosus*	1 (0.19)
Rypticus saponaceus	1 (0.19)	Single	*Cephalopholis fulva*	1 (0.19)
Aluterus scriptus	1 (0.19)	Single	*Cephalopholis fulva*	1 (0.19)

Pseudupeneus maculatus followed by *H. radiatus* was the most frequently recorded association, accounting for about 29% of all associations between fishes (Table 1). The same goatfish species followed by the coney *Cephalopholis fulva* was another common association (about 17%) (Table 1). The Noronha wrasse *Thalassoma noronhanum* as a follower of an herbivore, the parrotfish *Sparisoma frondosum*, ranked third in frequency (about 10%) (Table 1). Other

Table 2 Nuclear species other than reef fishes and their follower fish species at Fernando de Noronha Archipelago, tropical West Atlantic. Numbers are absolute and relative frequencies (%) of associated fish species, where $N = 23$ recorded associations. Each nuclear species and its follower species in decreasing order of relative frequency of occurrence in the associations

Nuclear species	*N* (%)	Follower species	*N* (%)
Octopus	19 (82.6)	*Cephalopholis fulva*	14 (60.87)
Octopus sp.n.		*Halichoeres radiatus*	4 (17.39)
		Pseudupeneus maculatus	3 (13.04)
		Caranx bartholomaei	2 (8.7)
		Caranx latus	1 (4.34)
Sea turtle	2 (8.7)	*Pomacanthus paru*	1 (4.34)
Eretmochelys imbricata		*Halichoeres radiatus*	1 (4.34)
		Thalassoma noronhanum	1 (4.34)
Brittle star	2 (8.7)	*Cephalopholis fulva*	1 (4.34)
Ophioderma appressum		*Malacoctenus* sp.	1 (4.34)

associations had an occurrence of less than 10% each (Table 1).

Pseudupeneus maculatus was the nuclear fish that attracted the largest number of follower species, a total of 17 (about 68% of the total number of followers of fishes only) (Table 1). The coney *C. fulva* was the follower fish that associated with the largest number of nuclear fish species (17, about 63% of the total number of nuclear fish species). Two wrasse species, *T. noronhanum* and *H. radiatus*, associated with a large number of nuclear fish species (15, about 55% and 10, about 37% respectively) as well. The remainder follower species were recorded associated with less than 30% of the total number of nuclear fish species.

From the about 170 reef fish species recorded in the archipelago (Soto 2001; A. Carvalho-Filho, personal communication), nearly 20% of these engage in interspecific foraging associations, playing the nuclear or the follower roles. About 50% of the bottom-disturbing carnivores and/or herbivores recorded for the archipelago play the role of nuclear fishes in the interspecific foraging associations. On the other hand, about 25% of the roving or sedentary carnivores play the role of followers.

For the nuclear role logistic regression analyses, a test of the full model with all five predictors against a constant-only model was statistically reliable ($X^2 = 53.75$; $df = 5$; $p < 0.001$), which indicates that the predictors, as a set, distinguish between nuclear and non-nuclear species. The variance accounted by the model is high ($\rho^2 = 0.72$) and overall prediction success was also high (87%). However, only substratum disturbance (t-ratio = 38.46, $p < 0.001$; odds ratio = 8604055.68; regression coefficient = B = 15.96) and carnivory (t-ratio = 14.41, $p < 0.001$; odds ratio = 3387.4; $B = 8.12$) reliably predicted the nuclear role in the association. This indicates that the substratum disturbance is the strongest reliable predictor of the nuclear role in a foraging association.

For the follower role logistic regression analyses, a test of the full model with all five predictors against a constant-only model was statistically reliable ($X^2 = 15.82$, $df = 5$; $p < 0.01$), which indicates that the predictors, as a set, distinguish between follower and non-follower species. The variance accounted by the model is small ($\rho^2 = 0.21$) and overall prediction success was 62%. Only carnivory (t-ratio = 18.18, $p < 0.001$; odds ratio = 2239.93, $B = 7.71$) predicted the follower role in the association. Thus, although carnivory apparently predicts the follower role in the association, no behavioural predictors here examined can compose a model that strongly predicts the follower role in a foraging association.

During our night dives we observed the stingray *Dasyatis americana* in foraging activity ($N = 5$). This ray is an important nuclear species for many followers at daytime (Table 1), and its night time foraging behaviour is similar to the observed during the day, excavating portions of the sand flat while searching for small invertebrates and fishes. This stingray was the only nuclear species we recorded foraging at night, but we observed no followers at night time.

As for interspecific associations between fishes only, half of the species was recorded in both roles, i.e., as nuclear and follower ones. However, this switch was mostly recorded in different foraging bouts (i.e., rarely a nuclear species switched to the follower role in the same occasion). The most important nuclear species, *P. maculatus*, was also recorded as follower of four nuclear species, including herbivores (Table 1). Species of Haemulidae and Labridae commonly switched between the two roles. Highly opportunistic carnivores such as the coney *C. fulva* and the yellow jack *Caranx bartholomaei*, mainly recorded as followers, were recorded in the nuclear role as well.

Four families (Carangidae, Haemulidae, Labridae, and Scaridae) accounted for 48% of the follower species (Fig. 2a). The remaining 52% were spread over 10 families (Fig. 2a). The proportion of species in each family that played the follower role was mostly high, 25% or more (Fig. 2a). Three families (Muraenidae, Haemulidae and Scaridae) accounted for about 30% of the species recorded in the nuclear role, but several families also were well represented as the remaining 70% was spread over only 13 ones (Fig. 2b). The proportion of species that played the nuclear role in each family was usually high, 25% or more (Fig. 2b).

We chose four types of nuclear fishes as representative of our study (Fig. 3). The spotted goatfish *P. maculatus* (Fig. 3a) represents the commonest nuclear species in foraging associations (Table 1). This goatfish may forage single or in small to large groups of up to 36 individuals and is a very active substratum-disturbing ubiquitous fish, which attracts a large and diverse array of follower species (Table 1). Moray eels (Fig. 3b) and snake eels played the nuclear role infrequently (Table 1), and were recorded mostly wandering on the reef unescorted. However, as these fishes habitually explore crevices and poke in holes, their hunting behaviour expose prey that other carnivore would not reach otherwise. Grazers, mainly *Sparisoma* species (Fig. 3c), were conspicuous in the reef fish assemblage and foraged throughout the day, scraping algae and other encrusting organisms from the bottom, and acted as important nuclear fishes for some followers (Table 1). The stingray *D. americana* was recorded to forage single in our study, but nevertheless it disturbed large portions of the sandy bottom while foraging and thus raised large and well visible clouds of stirred sediment, thus attracting several follower species (Fig. 3d). Among nuclear species other than fishes, the octopus *Octopus* sp. was regularly followed by opportunistic carnivores (Table 2). The octopus foraged by entering holes and crevices in the rocks or poking its arms into interstices of the reef. Additionally, it frequently wrapped a rock with its mantle and thus prevented potential prey to evade.

Discussion

Our study has the broadest coverage of nuclear-follower foraging associations at a tropical reef assemblage to date. This coverage accounts for the variety (brittle-stars to turtles) and the number of species involved in such interspecific foraging association. A study on interspecific foraging associations in a temperate rocky reef in the Gulf of California, with a similarly broad coverage (Strand 1988), records 21 nuclear species and 17 followers. The ratio between follower and nuclear species is 0.80 in the Gulf of California and 0.86 in Fernando de Noronha (present study). Additional studies on interspecific foraging associations in both tropical and temperate sites would clarify whether this similar ratio is coincidental or may be a trend for this association type.

The goatfish *Pseudupeneus maculatus* was the most prominent nuclear species at Fernando de Noronha, both in frequency of associations and number of follower species. Goatfishes are habitual as nuclear or follower species in heterospecific foraging associations (Fricke 1975; Fishelson 1977; Lukoschek and McCormick 2000), and *P. maculatus* is already recorded as a ubiquitous nuclear species at our study site (Sazima et al in press). Moray eels generally are prominent nuclear species that are followed regardless of their foraging or not, being even considered as

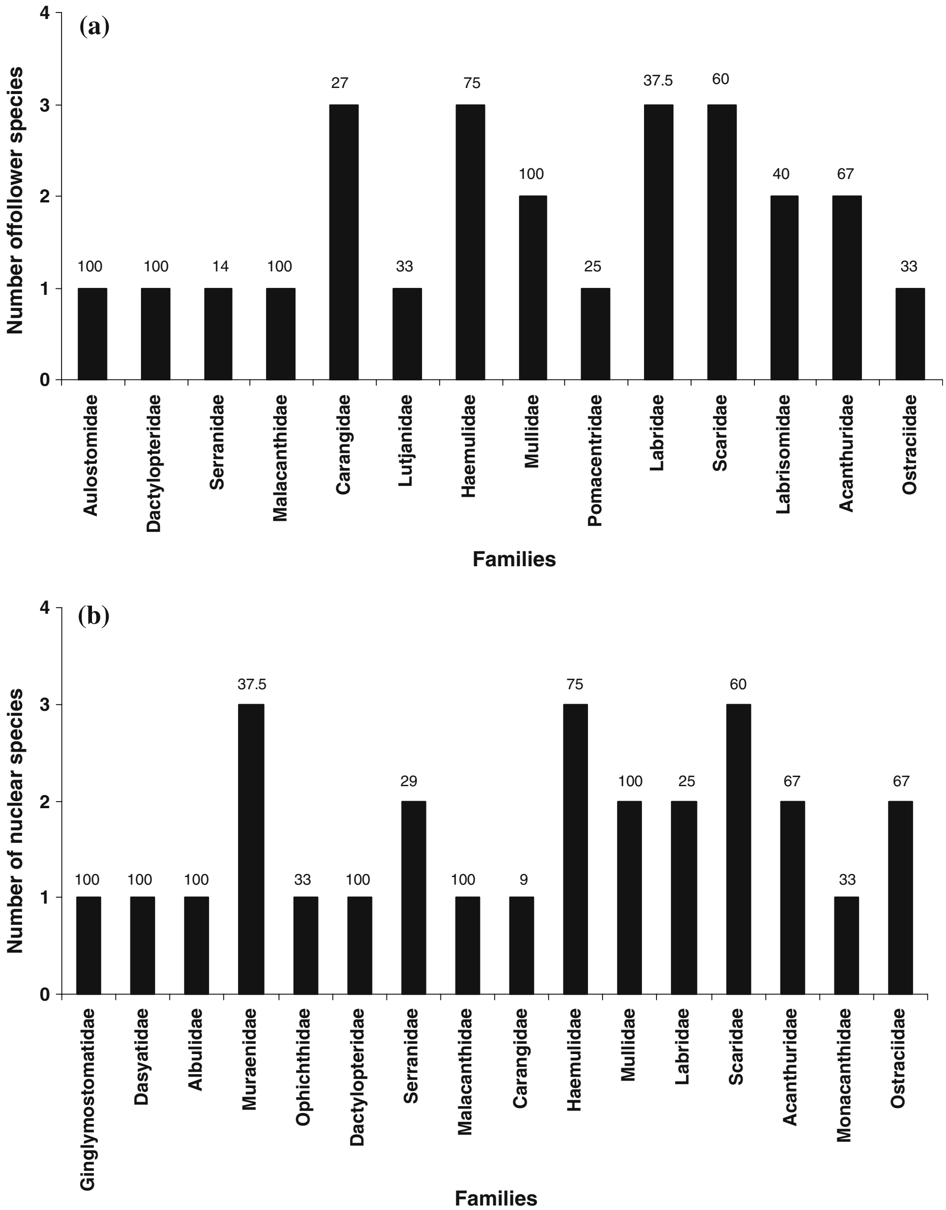

Fig. 2 (**a**) Number of reef fish species recorded as followers of nuclear fishes at Fernando de Noronha Archipelago. Numbers above each column is the proportion (%) of follower species recorded for each fish family in the archipelago. Proportions calculated from data on fish species richness from the archipelago (Soto 2001; A. Carvalho-Filho, personal communication). Arrangement of families follows Nelson (1994). (**b**) Number of reef fish species recorded in the nuclear role in foraging associations at Fernando de Noronha Archipelago. Numbers above each column is the proportion (%) of nuclear species recorded for each fish family in the archipelago. Proportions calculated from data on fish species richness from the archipelago (Soto 2001; A. Carvalho-Filho, personal communication). Arrangement of families follows Nelson (1994)

more rewarding to the followers than any other nuclear species (Diamant and Shpigel 1985; Strand 1988). However, during our study at Fernando de Noronha moray eels were not favoured nuclear species. Aside the chained moray (*Echidna catenata*), which has few or no followers due to its peculiar hunting behaviour (Sazima and Sazima 2004), nine additional moray and snake

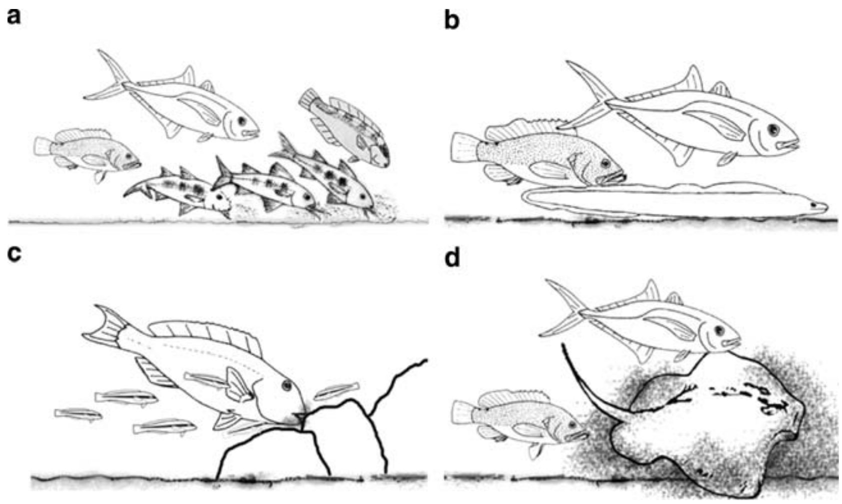

Fig. 3 Nuclear fishes representative of the present study at Fernando de Noronha Archipelago, tropical West Atlantic. (**a**) The spotted goatfish *Pseudupeneus maculatus* foraging as a small group followed by the puddingwife wrasse *Halichoeres radiatus*, the yellow jack *Caranx bartholomaei*, and the coney *Cephalopholis fulva*. (**b**) The purplemouth moray *Gymnothorax vicinus* closely followed by the yellow jack *Caranx bartholomaei* and the coney *Cephalopholis fulva*. (**c**) A foraging Agassiz's parrotfish *Sparisoma frondosum* surrounded by a small group of the Noronha wrasse *Thalassoma noronhanum*. (**d**) A foraging southern stingray *Dasyatis americana* escorted by a yellow jack *Caranx bartholomaei* and a coney *Cephalopholis fulva* while stirring sand and other particles

eel species at our study site could act as nuclear fishes and nonetheless only four of them were recorded in this role. We surmise that this apparent lack of interest of followers in eels may be related to the ubiquity of *P. maculatus*, a very active and versatile forager at the archipelago (Krajewski et al. in press, Sazima et al. in press).

The puddingwife *H. radiatus* (Labridae) and the coney *C. fulva* (Serranidae) stand out among the followers due both to their high frequency in the associations and by following a large number of nuclear species. Wrasses are a fish group well-known for its foraging versatility, which range from planktivory to durophagy and includes cleaning other fishes and anvil use to break large preys into smaller pieces (Itzkowitz 1979; Coyer 1995; Sazima et al. 2005a). Several serranids, particularly epinepheline groupers, are inquisitive fishes and display variable foraging behaviour, aggressive mimicry and illness-feigning being the most notable tactics (Hobson 1968; Diamant and Shpigel 1985; Shpigel and Fishelson 1989; Gibran 2004, Sazima et al. 2005b). Both *H. radiatus* and *C. fulva* are highly opportunistic hunters and their ubiquity in interspecific foraging associations is likely related to their versatile behaviour.

We found that a high proportion (~20%) of species in the reef fish assemblage of Fernando de Noronha engage in foraging associations as a nuclear and/or a follower species. No other study is available with such an estimative, and it would be rewarding to count with additional studies to clarify whether this proportion holds true for other tropical or temperate reef fish assemblages. Half of the bottom-disturbing carnivores and/or herbivores within the studied assemblage play the role of nuclear fishes in agreement with our finding that substratum disturbance is a strong predictor of the nuclear role in the association. Thus, it seems acceptable to suggest that any fish that causes such disturbance has a high potential to act as a nuclear species. Moreover, the proportion of roving or sedentary carnivores that act as followers agrees with our finding that carnivory may predict the follower role in an interspecific foraging association. Therefore, carnivorous species have a higher potential to act as followers than the species in other trophic categories.

The zoobenthivore guild, especially the species that forage over soft bottoms, seems to be the only trophic group that may be consistently characterized as playing the nuclear role. Thus, we surmise that most, if not all, species that have zoobenthivorous habits will eventually be recorded in the nuclear role. Moreover, the diverse array of escorts of each nuclear species may be related to some characteristics of this latter, such as degree of substratum disturbance, foraging versatility, and relative abundance (see a similar view in Sazima et al. in press). Accordingly, Mullidae seems to be the only taxonomic group that may be consistently characterized as composed entirely by actual or potential nuclear species. Several mullid species are already recorded as nuclear fishes worldwide (e.g., Fishelson 1977; Strand 1988; Lukoschek and McCormick 2000; Sazima et al. in press) and this probably is a trend within the family.

In conclusion, the nuclear-follower interspecific association is likely an important, even if understudied component of the reef assemblages, both tropical and temperate. Nuclear species are diverse both in morphology and behaviour, foraging with the use of a wide array of bottom-disturbing tactics. Moreover, the nuclear role may be played either by fishes or other marine animals from invertebrates to turtles. Followers, on the other hand, comprise fishes only, which tend to display a more uniform feeding behaviour by exploiting food disclosed or made available by the variable foraging of the nuclear species.

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References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–265

Auster PJ, Lindholm J (2002) Pattern in the local diversity of coral reef fishes versus rates of social foraging. Caribb J Sci 38:263–266

Baird TA (1993) A new heterospecific foraging association between the puddingwife wrasse, *Halichoeres radiatus*, and the bar jack, *Caranx ruber*: evaluation of the foraging consequences. Environ Biol Fishes 38:393–397

Bellwood DR, Wainwright PC, Fulton CJ, Hoey S (2006) Functional versatility supports coral reef biodiversity. Proc Roy Soc 273:101–107

Bonaldo RM, Krajewski JP, Sazima C, Sazima I (2005) Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. Mar Biol DOI 10.1007/s00227-005-0233-9

Coyer JA (1995) Use of a rock as an anvil for breaking scallops by the yellowhead wrasse, *Halichoeres garnoti* (Labridae). Bull Mar Sci 57:548–549

Diamant A, Shpigel M (1985) Interspecific feeding association of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). Environ Biol Fishes 13:153–159

Fishelson L (1977) Sociobiology of feeding behavior of coral fish along the coral reef of the Gulf of Elat (=Gulf of ‘Aqaba), Red Sea. Isr J Zool 26:114–134

Fricke HW (1975) The role of behaviour in marine symbiotic animals. In: Jennings DH, Lee DL (eds) Symbiosis, Symposia of the Society for Experimental Biology 29. Cambridge University Press, Cambridge, pp. 581–594

Gerking SD (1994) Feeding ecology of fish. Academic Press, California

Gibran FZ (2002) The sea basses *Diplectrum formosum* and *D. radiale* (Serranidae) as followers of the sea star *Luidia senegalensis* (Asteroidea) in southeastern Brazil. Braz J Biol 62:591–594

Gibran FZ (2004) Dying or illness feigning: an unreported feeding tactic of the comb grouper *Mycteroperca acutirostris* (Serranidae) from the Southwest Atlantic. Copeia 2004:403–405

Hobson ES (1968) Predatory behavior of some shore fishes in the Gulf of California. US Fish Wildl Serv 73:1–92

Itzkowitz M (1979) The feeding strategies of a facultative cleanerfish, *Thalassoma bifasciatum* (Pisces: Labridae). J Zool (Lond) 187:403–413

Krajewski JP, Bonaldo RM, Sazima C, Sazima I (in press) Foraging activity and behaviour of two goatfish species (Perciformes: Mullidae) at Fernando de Noronha Archipelago, tropical West Atlantic. Environ Biol Fish 00:000–000

Lukoschek V, McCormick MI (2000) A review of multispecies foraging associations in fishes and their ecological significance. In: Proceedings of the 9th International Coral Reef Symposium, Bali, Indonesia, 23–27 October 2000

Maida M, Ferreira BP (1997) Coral reefs of Brazil: an overview. In: Proceedings of the 8th International Coral Reef Symposium, Panama, 1996

Nelson JS (1994) Fishes of the world. John Wiley & Sons, New York

Ormond RFG (1980) Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. J Zool (Lond) 191:247–262

Sazima C, Bonaldo RM, Krajewski JP, Sazima I (2005a) The Noronha wrasse: a jack-of-all-trades follower. Aqua J Ichthyol Aq Biol 9:97–108

Sazima C, Grossman A, Bellini C, Sazima I (2004) The moving gardens: reef fishes grazing, cleaning, and following green turtles in SW Atlantic. Cybium 28:47–53

Sazima C, Grossman A (2005) A non-digging zoobenthivorous fish attracts two opportunistic predatory fish associates. Neotrop Ichthyol 3:445–448

Sazima C, Krajewski JP, Bonaldo RM, Sazima I (in press) The goatfish *Pseudupeneus maculatus* and its follower fishes at an oceanic island in the tropical West Atlantic. J Fish Biol 00:000–000

Sazima I (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. J Fish Biol 29:53–65

Sazima I, Krajewski JP, Bonaldo RM, Sazima C (2005b) Wolf in a sheep's clothes: juvenile coney (*Cephalopholis fulva*) as an aggressive mimic of the brown chromis (*Chromis multilineata*). Neotrop Ichthyol 3:315–318

Sazima I, Sazima C (2004) Daytime hunting behaviour of *Echidna catenata* (Muraenidae): why chain morays foraging at ebb tide have no followers. Aqua J Ichthyol Aq Biol 8:1–8

Shpigel M, Fishelson L (1989) Food habits and prey selection of three species of groupers from the genus *Cephalopholis* (Serranidae: Teleostei). Environ Biol Fishes 24:67–73

Soto JMR (2001) Peixes do arquipélago Fernando de Noronha. Mare Magnum 1:147–169

Strand S (1988) Following behavior: interspecific foraging associations among Gulf of California reef fishes. Copeia 1988:351–357

Tabachnick BG, Fidel LS (2001) Using multivariate statistics. Allyn & Bacon, Boston

Zar JH (1996) Biostatistical analysis. Prentice Hall, New Jersey