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How do follower reef fishes find nuclear fishes?

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Abstract Among reef fishes, it is common for "follower" individuals to accompany "nuclear" species and to feed on prey uncovered by their foraging. In this study, I examine the cues used by followers to find nuclear fish. A model of a ubiquitous nuclear fish was maintained immobile or moved to disturb the substratum and the number of fish species and individuals attracted was compared to control treatments. The results showed that: 1) bottom disturbance was the strongest attraction factor for follower reef fishes; 2) visual features of the nuclear also attracted follower reef fishes; 3) there was no evidence of an interaction between bottom disturbance and nuclear fish appearance in the attraction of followers, supporting the idea that both factors independently elicit following behaviour by reef fishes.

Keywords Foraging associations · Following behaviour · Substratum disturbance · *Pseudupeneus maculatus* · Goatfishes · Fernando de Noronha Archipelago

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Introduction

One of the commonest foraging association type in reef fishes is the "following association", in which "nuclear" species, which usually feed disturbing the bottom, are accompanied by "follower" or "attendant" species that feed on prey flushed or uncovered by the nuclear's activity (Lukoschek and McCormick 2002; Sazima et al. 2007). In this association the followers appear to benefit by gaining easier access to prey that would otherwise be unexposed, enhancing prey detection, and increasing protection against predators (Aronson and Sanderson 1987; Lukoschek and McCormick 2002). On the other hand, nuclear species do not appear to benefit from the association or may even be disadvantaged due to competition for food (Lukoschek and McCormick 2002).

Because following associations are relatively common, they are believed to play an important role in the trophic ecology reef fishes (Ormond 1980; Strand 1988; Sazima et al. 2006; Sazima et al. 2007). For example, in the Gulf of California, from a total of 35 reef fish species, 17 are known to be engaged in following associations and some of them spend up to 25% of their time budget following nuclear species (Strand 1988). Also, some single nuclear species appear to play a significant role in multispecies-associations in a given geographic area (Lukoschek and McCormick 2002; Sazima et al. 2007). For example, the goatfish *Pseudupeneus maculatus* (Mullidae) has been recorded to be followed by about 10% of the total number of reef fish species (17 species) of the Fernando de Noronha Archipelago, tropical west Atlantic (Sazima et al. 2006).

The frequency of following associations is directly shaped by the ability of potential follower fishes to detect a nuclear species, since the encounter between follower and nuclear is a prerequisite for the association to occur. Follower fish rely on cues to locate nuclear ones and the type of cue used, as well as the sensorial ability of each follower species, shapes the capacity of followers to detect and associate to a nuclear (Fricke 1975; Sazima et al. 2007). The identification of these cues is, thus, of fundamental importance in predicting the functional role of benthic feeding species on providing feeding opportunities and possibly enhancing the fitness of different potential follower fishes. However, there is no quantitative information on the cues that follower species use to detect nuclear individuals.

Observational studies suggest that follower species are attracted by the disturbance and sediment clouds produced by the nuclear species and by visual features of the nuclear fish itself (Fishelson 1977, Diamant and Shpigel 1985; Strand 1988; Sazima et al 2007). The only experimental study in this context (Fricke 1975) also supports the suggestions above, but lacks quantitative data to determine the relative importance of these two attraction factors (bottom disturbance and nuclear appearance). It has been further suggested that bottom disturbance is the strongest attraction factor and that specific features of the nuclear (e.g. colour, shape, behaviour) may serve, after a closer approach by the follower fish, for recognition of the particular feeding situation and deciding to associate with the nuclear or not (Fricke 1975; Strand 1988). If this latter hypothesis holds true, the effect of nuclear fish appearance would be dependent on the substratum disturbance in the attraction of follower fishes (i.e. there is an interaction between the two factors).

If bottom disturbance is indeed an important attraction factor to follower fishes, then the amount of disturbance created by an organism on the bottom could be positively related to the attractiveness to follower fishes (Sazima et al. 2007). Information on the degree to which a species disturbs the substrate could be use to predict its functional role as nuclear. The same idea could be applied to compare different bottom feeding species, individuals of different sizes of the same species and fish feeding in groups of different sizes, since these entities all vary in the amount of substratum disturbance they cause (Sazima et al. 2006; Sazima et al. 2007). In the same way, the appearance of the nuclear fish, if confirmed as an attraction factor to follower fishes, would also be used to predict the functional role of different potential nuclear fish individuals and species. This information could be particularly important to understand differences in the attractiveness of nuclear fishes with similar bottom disturbing abilities.

In this study I conducted field experiments using models of the goatfish *Pseudupeneus maculatus*, a ubiquitous nuclear species in the Western Atlantic (Aronson and Sanderson 1987; Sazima et al. 2007), to investigate the influence of bottom disturbance and visual features of the nuclear in the attraction of following reef fishes. I investigated the hypotheses that: 1) bottom disturbance is more attractive to follower reef fishes than the nuclear fish appearance per se; 2) nuclear fish visual features also play a role in the attraction of follower fishes; 3) there may be an interaction between the bottom disturbance and nuclear fish's appearance in the attraction of follower fishes. I also investigated whether species differed in their response to the treatments.

Methods

Study site

The experiments were conducted at the Fernando de Noronha Archipelago (03º50′S, 32º25′W), about 345 km off north-east Brazil, tropical West Atlantic (Fig. 1) in October 2005 and June to July 2007. To reduce bias in studying just a single site where fish could behave similarly, replicates were done on snorkelling sessions at five different sites of the archipelago (Fig. 1): Buraco da Raquel, Porto de Santo Antônio, Conceição Beach (sampled in 2005), Meio Beach, and Sancho Beach (sampled in 2007). With the exception of Buraco da Raquel, which is a reef lagoon, all sites are rocky reefs adjacent to sandy beaches. The commonest bottom types are sand, epilithic algal matrix and brown macroalgae, and the fish community is similar in all sites (Krajewski et al. in prep). Depth ranged from 2–5 m, visibility from 4–20 m and the water temperature was 28–29°C during the experiments.

Procedure

For the experiments I used a model of the goatfish *Pseudupeneus maculatus*, a common species along the Brazilian coast. Several goatfishes, including *P. maculatus,* are reported as ubiquitous nuclear species (Aronson and Sanderson 1987; Lukoschek and McCormick 2002; Sazima et al. 2006), and thus, are good targets for studies of following associations. Fish models are also commonly used in behavioural studies and are considered as appropriate tools to quantify fish behavioural response (e.g. Caley and Schluter 2003; Stummer et al. 2004).

The *P. maculatus* model used in the experiments weighed 2 kg, was made of lead painted with acrylic ink and was of a size, shape and colour pattern, specially the three conspicuous black spots on sides, similar to adult *P. maculatus*. As control for nuclear fish appearance I used a lead cube of the same weight (2 kg) and of a uniformly yellowish colour, similar to the background colour of *P. maculatus*. A transparent fishing line tied to the lead cube and the *P. maculatus* model was used to move them up and down.

Four different treatments were used in the experiment: A) immobile piece of lead (control for nuclear fish appearance and substratum disturbance); B) piece of lead moved up and down against the substratum (control for nuclear fish appearance); C) immobile model of *P. maculatus* (control for substratum disturbance); D) *P. maculatus* model moved up and down against the substratum (see Fig. 2 for illustrations of each treatment). Care was taken to produce a similar degree of disturbance of the bottom in all treatments. All treatments were carried out over soft bottoms (sand or epilithic algal matrix with thick sediment cover) and the researcher was at least 2 m above the treatment.

A total of 189 trials were done and samples were distributed over the five study sites proportionally to their reef area (i.e. total area of the reef adjacent to each site). Different treatments were performed a similar number of times. To avoid bias in the samples the order of the treatments and location were haphazardly distributed in the study sites and the minimum distance and time between each treatment was at least 5 m and 3 min respectively. Each single treatment replicate lasted 10 s, and I recorded all fish individuals attracted during this period. Fish were considered attracted when they approached the lead cube or the *P. maculatus* model by at least 30 cm and spent at least 4 s around it. Since only a few fish individuals approached the treatments at each replicate they were memorized and recorded on slates immediately after the trial. The experiments and fish counts were conducted by a single observer. This procedure minimised interference on fish behaviour that an extra diver might cause.

Statistical analysis

The number of species or individuals attracted at each treatment was compared using two distinct one-way ANOVA tests followed by an a-posteriori Tukey test. In both tests, numbers of species or individuals attracted were the response variables and treatment was the fixed factor. The number of species or

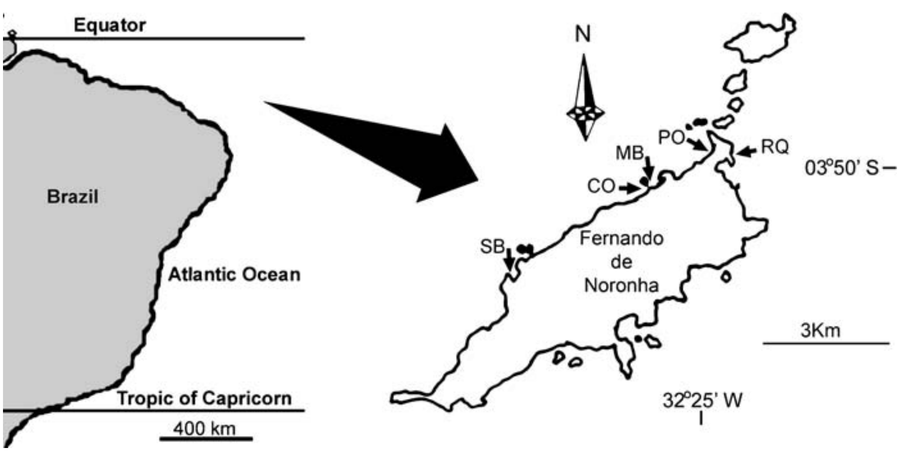

Fig. 1 The studied reefs at the Fernando de Noronha Archipelago: (PO) Porto, (RQ) Buraco da Raquel, (MB) Meio Beach (CO), Conceição Beach and (SB) Sancho Beach

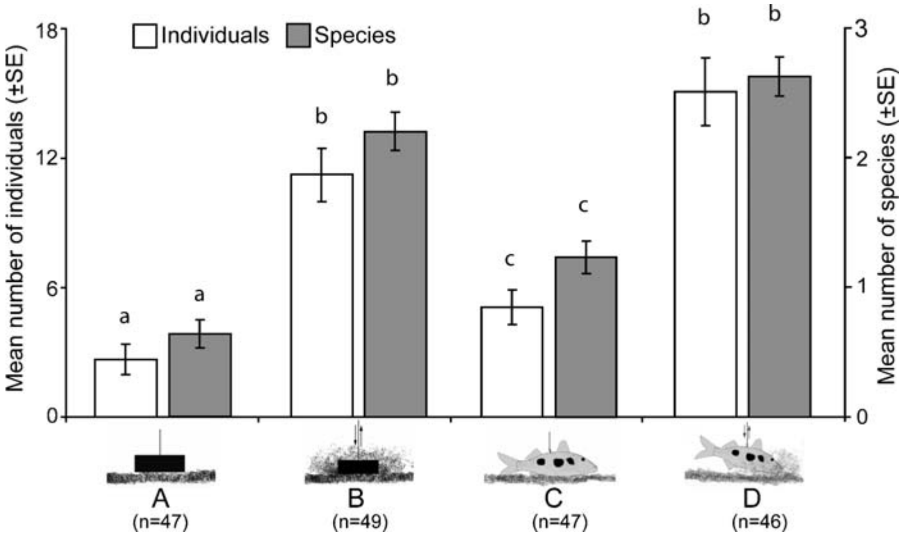

Fig. 2 Number of individuals and species attracted by each treatment (mean±SE). Lower case letters over each bar correspond to statistical groupings resulted from an a-posteriori Tukey test for number of individuals and species respectively, on a level of significance of $p \leq 0.01$

individuals (response variables) attracted were also compared between treatments with and without bottom disturbance and treatments with and without the presence of *P. maculatus* model (factors) in two distinct two-way ANOVA tests. These analyses allowed me to evaluate whether there was or not an interaction between the two factors on the number of individuals or species attracted.

The number of individuals attracted by the experiments were transformed to log (x+1) to meet the assumptions of the parametric tests (Tabachnick and Fidel 2001). Data on number of species attracted required no transformation.

The response of the different species to the treatments was analyzed in a principal component analysis using the covariance matrix extracted from the data on average number of individuals of each species in each treatment. Only species with nine or more individuals attracted by all treatments were considered for this analysis.

Results

A total of 1607 fish individuals from 14 species were attracted in the experiments (Table 1). Most individuals approached the model or lead piece and remained swimming around it, clearly paying attention to the bottom nearby. In treatments with bottom disturbance, some attracted fish, especially *A. saxatilis* and *T. noronhanum*, fed on uncovered prey around the disturbed substratum.

The mean number of individuals differed among treatments ($F_{3,185}$=31.53, P<0.001) and was greater in treatments with bottom disturbance (B + D) than without it (A + C) and in treatments with the *P. maculatus* model (C + D) than with the control lead (A + B) (Table 2, Fig. 2). Treatment D (nuclear model and disturbance) attracted the highest number of individuals, followed by treatment B (control lead and disturbance), C (nuclear model and no disturbance) and A (control lead) (Fig. 2). The number of species attracted also differed among

Table 1 Fish individuals attracted in the experiments (in decreasing order of abundance)

Family	Species	Total abundance
Pomacentridae	*Abudefduf saxatilis*	697
Labridae	*Thalassoma noronhanum*	680
Haemulidae	*Haemulon parra*	111
Labridae	*Halichoeres radiatus*	64
Haemulidae	*Haemulon chrysargyreum*	10
Holocentridae	*Holocentrus adscensionis*	9
Ostraciidae	*Lactophrys trigonus*	9
Chaetodontidae	*Chaetodon ocellatus*	6
Monacanthidae	*Aluterus scriptus*	5
Epinephelidae	*Cephalopholis fulva*	5
Haemulidae	*Anisotremus surinamensis*	4
Lutjanidae	*Lutjanus jocu*	3
Labridae	*Sparisoma frondosum*	2
Mullidae	*Pseudupeneus maculatus*	2

Table 2 Two-way ANOVA for the number of individuals and species attracted by treatments with and without bottom disturbance and presence of nuclear fish model

	Source	SS	df	MS	*F*	*P*
Number of individuals	Disturbance	13.96	1	13.96	81.88	<0.001
	Nuclear model	2.14	1	2.14	12.56	<0.001
	Disturbance × Nuclear model	0.15	1	0.15	0.88	0.349
Number of species	Disturbance	103.59	1	103.59	121.33	<0.001
	Nuclear model	12.33	1	12.33	14.44	<0.001
	Disturbance × Nuclear model	0.33	1	0.33	0.39	0.530

treatments ($F_{3,185}$=45.03, P<0.001) and the overall results were similar to that of number of individuals (Table 2, Fig. 2).

As most of the individuals attracted by the experiments were *A. saxatilis* (N=697) and *T. noronhanum* (N=680), if analysed together the results of the experiment would be biased toward the response of these two species and not necessarily reflect a general response by fishes. To avoid this bias, a one-way ANOVA and an a-posteriori Tukey test was done for the number of individuals attracted (measured variable) by each treatment (factors) for the four more abundant species (i.e. N>64) separately. *A. saxatilis* and *H. radiatus* responded similarly, as they were attracted to disturbance and, to a lesser extent, to nuclear appearance (Fig. 3). *H. parra* and *T. noronhanum* also had the tendency of being more abundant in treatments with disturbance (Table 3) but contrasted with the other species by not differing in their response among treatments B (control lead and disturbance), C (nuclear model and no disturbance) and D (nuclear model and disturbance) (Fig. 3). The principal component analysis also reinforced the same trend with most species more abundant in both treatments with bottom disturbance (Fig. 4).

There was no interaction between bottom disturbance and presence of the *P. maculatus* model on neither the number of species or individuals attracted (Table 1), supporting the idea that there is a consistent difference in the number of species and individuals attracted both in relation to disturbance and to the presence of the nuclear model.

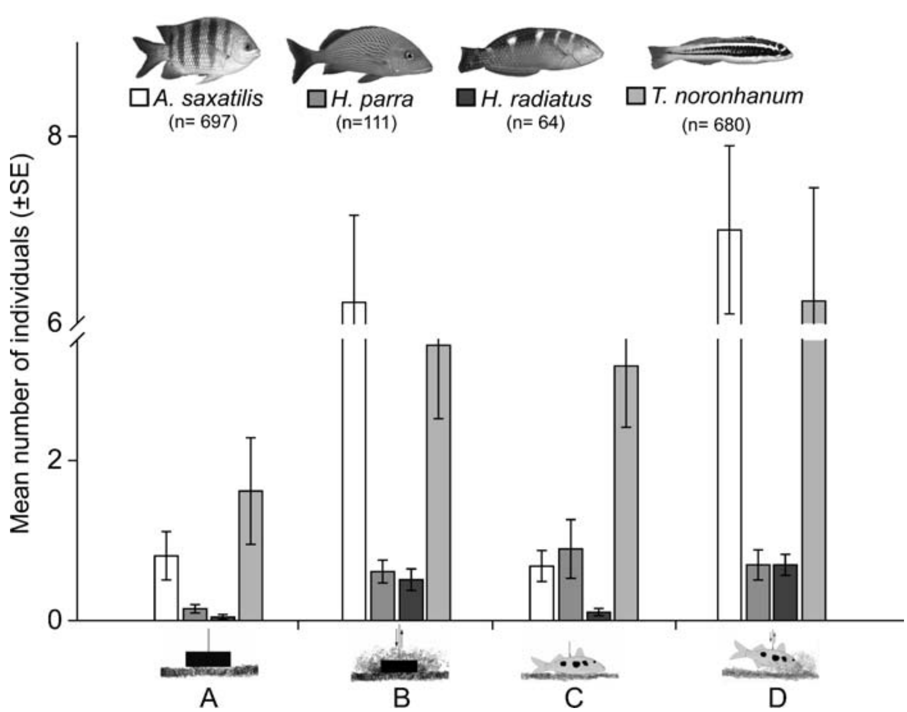

Fig. 3 Number of individuals attracted by each treatment (mean±SE) for the four most abundant 'follower' species in the experiments. Numbers in parenthesis represent sample size

Table 3 One-way ANOVA and a-posteriori Tukey test for the number of individuals attracted by each treatment for *Abudefduf saxatilis*, *Haemulon parra*, *Halichoeres radiatus* and *Thalassoma noronhanum*. Values of $P<0.05$ are marked with asterisks. Capital letters correspond to the treatments as follows: A=lead with no disturbance, B=lead with disturbance, C=nuclear model with no disturbance and D=nuclear model with disturbance

Treatments	*A. saxatilis*	*H. radiatus*	*H. parra*	*T. noronhanum*
General	SS=14.65	SS=0.87	SS=0.38	SS=3.78
	MS=4.88	MS=0.29	MS=0.12	MS=1.26
	$F_{3,185}=36.01$	$F_{3,185}=12.67$	$F_{3,185}=2.72$	$F_{3,185}=5.68$
	$P<0.001$*	$P<0.001$*	$P=0.046$*	$P<0.001$*
A × B	$P<0.001$*	$P=0.001$*	$P=0.080$	$P=0.245$
A × C	$P=1$	$P=0.928$	$P=0.138$	$P=0.193$
A × D	$P<0.001$*	$P<0.001$*	$P=0.071$	$P<0.001$*
B × C	$P<0.001$*	$P=0.011$*	$P=0.996$	$P=0.99$
B × D	$P=1$	$P=0.341$	$P=1$	$P=0.095$
C × D	$P<0.001$*	$P<0.001$*	$P=0.990$	$P=0.138$

Discussion

Bottom disturbance alone explained most of the variance in the response of fishes to the treatments, indicating that this is the main factor eliciting following behaviour in this study. This pattern was strong and similar for most of the follower species attracted in the study. Nuclear visual features alone also seem to play a role in the attraction of some followers, but to a much lesser extent.

The attractiveness of bottom disturbance to opportunistic benthic carnivorous species may be related to its salience as a foraging cue. When the bottom is disturbed, regardless of the cause, potential prey to opportunistic carnivorous fishes are uncovered and can be reached with lower costs for searching and capture. Thus, recognizing bottom disturbance could bring a fast energetic reward to benthic carnivorous fish and also a clue that a potential nuclear is around. Opportunistic carnivorous species may, thus, use

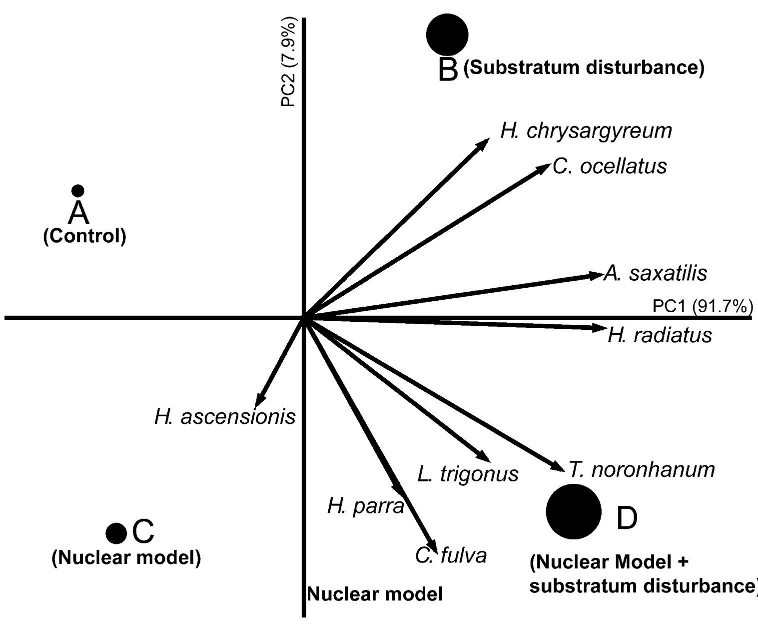

Fig. 4 Principal component analysis for the responses of species (arrows) to treatments (dark circles). The sizes of the circles are proportional to the abundance of all species combined in the treatment

bottom disturbance as a general feeding strategy and consequently find a nuclear bottom disturbing species in this same way.

Any kind of bottom disturbance has the potential to uncover prey (though they may vary in degree) and thus is a universal signal of a feeding opportunity. (i.e. independent of the cause). Substratum disturbance is, thus, both lucrative and easy to memorize (rather than specific colours and shape of the nuclear species for example). The universal significance of bottom disturbance as a foraging opportunity and clue to find a nuclear organism is also supported by the large number of bottom disturbing fish species and other marine animals (e.g. hermit crabs, brittle stars, turtles) recorded as nuclears (Sazima et al. 2004; Sazima et al. 2007; Maia-Nogueira et al. 2008).

Since the bottom is disturbed by benthic carnivorous species when they are feeding and have probably found prey, bottom disturbance may also be interpreted by potential follower fish as a sign of successful foraging. Fishes are known to use behavioural clues of successful foraging to decide to associate to a given individual (Ryer and Olla 1995) and, thus, bottom disturbance by nuclear fishes may also induce following behaviour by this same reason.

The attractiveness of the bottom disturbance to opportunistic carnivorous fishes may be also explained by its mechanical properties since the bottom disturbance also produces mechanic stimuli (e.g. vibrations and sounds) which may be recognized by fishes. Many fishes are known to communicate by sound production (Myrberg and Fuiman 2002), and it is probable that potential follower fish may be attracted by vibrations resulting from bottom disturbance. If this holds true, species primarily oriented by hearing would have an advantage over more visually orientated species in finding nuclear fish in low visibility waters. However, knowledge on the sensorial capabilities of specific fish species is required to give further support to this hypothesis.

Although to a much lesser extent, visual features of nuclear fish also seem to work as an attraction factor to followers. Strand (1988) suggests that some nuclear species, named “primary nuclear species”, elicit following behaviour mainly by their appearance while others, named “secondary nuclear species”, do so mainly by their foraging activity. However, in this study I found that *P. maculatus*, a secondary nuclear species sensu Strand (1988) (Sazima et al. 2006), elicits following behaviour even when immobile on the bottom. These results may be explained by the abundance and frequent feeding activity of *P. maculatus* at Fernando de Noronha, which render it the role of a ubiquitous nuclear species there (Krajewski et al. 2006; Sazima et al. 2006). Potential followers could presumably then learn that such shape and colour pattern belong to a highly valuable” nuclear and decide to associate to it.

Bottom disturbance and nuclear fish visual features were hypothesized to act differently in their attraction of follower fishes. More specifically, it is suggested that followers are initially guided towards the bottom disturbance and after a closer approach recognize the nuclear species (based on its appearance) and decide whether to follow it or not (Fricke 1975; Strand 1988). However, I found no significant interaction between these two factors, indicating that substratum disturbance and nuclear appearance can independently elicit following behaviour by opportunistic fish. However, before drawing any definite conclusions against the interaction hypothesis between these attraction factors it is important to expand on this study by including the duration of the association, and testing if associations last longer in treatments with both bottom disturbance and nuclear appearance.

The differences in species response to the treatments performed found in this study indicate that potential followers may perceive the signals of the nuclear differently. Some would be more visually orientated while others may rely mostly on their hearing. Differences in fish sensorial capabilities would, then, mediate variations on the frequency of feeding association of potential followers with different nuclear species and in different environmental conditions. Further studies on the differences in sensorial capabilities of specific fish species and its interactions with environmental variables are fundamental to evaluating the ability of particular reef fish species to find nuclear ones and benefit from such feeding opportunities.

Species may also differ in their response to the treatments simply because some fishes, even if they are able to perceive the feeding opportunity, decide not to inspect the trial. For example, fishes that are not hungry or do not rely on nuclear fishes for most of its feeding may not interest in the feeding opportunity, while hungry fish would inspect every feeding opportunity available. However, further studies comparing the response of different individuals to nuclear stimulus would be required for corroborating this hypothesis.

The confirmation of bottom disturbance as a strong attraction factor to potential follower fishes supports the hypothesis of substratum disturbing activity as one of the main features that defines a nuclear species (Sazima et al. 2007). Also, previous studies suggest that the amount of substratum disturbance is positively related to the attractiveness to follower fishes, since bigger individuals and larger foraging groups of potential nuclear species cause more disturbance on the bottom and are recorded to attract more follower species and individuals (Sazima et al. 2006; Sazima et al. 2007). Although the present study seems to support this hypothesis as well, experimental studies examining the effects of different amounts of substratum disturbance in the attractiveness of follower fishes would better test it. The field evidence and experimental work conducted so far thus indicates that the amount of bottom disturbance is probably the most important feature to define the functional role of a potential nuclear species.

Foraging associations are widespread and may comprise a high percentage of the time budget of some fish species (Strand 1988; Bellwood et al. 2002; Sazima et al. 2007). Thus, it is possible that several fish species benefit and even depend on foraging associations to obtain of their food. Disturbances on reef habitats, including those influenced by humans, modify physical properties of the environment and consequently change the ability of follower fishes to locate nuclear organisms and benefit from following associations. The deposit of sediments on reefs may be a good example, since it reduces underwater visibility and probably limits the ability of visually oriented fish to find nuclear ones. As substratum disturbance is the main clue used by follower fish to find nuclear ones, understanding specifically how follower reef fishes are able to perceive it is fundamental to estimate the indirect effect of habitat disturbance on the frequency of foraging associations of reef fishes and consequently on reef fish energetic balance.

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