Journal of Fish Biology (2006) **69,** 883–891
doi:10.1111/j.1095-8649.2006.01166.x, available online at http://www.blackwell-synergy.com

The goatfish *Pseudupeneus maculatus* and its follower fishes at an oceanic island in the tropical west Atlantic

C. Sazima*†‡, J. P. Krajewski*, R. M. Bonaldo* and P. R. Guimarães Jr§

**Museu de História Natural, Caixa Postal 6109, Universidade Estadual de Campinas, 13083-970 Campinas, São Paulo, Brasil, †Departamento de Zoologia, Caixa Postal 199, Universidade Estadual Paulista, 13506-900 Rio Claro, São Paulo, Brasil and §Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain*

(Received 8 September 2005, Accepted 15 April 2006)

The influence of a substratum-disturbing forager, the spotted goatfish *Pseudupeneus maculatus* on the assemblage of its escorting, opportunistic-feeding fishes was examined at Fernando de Noronha Archipelago (tropical west Atlantic). Followers attracted to spotted goatfish foraging singly differed from followers of spotted goatfish foraging in groups in several characteristics. The larger the nuclear fish group, the greater the species richness and number of individuals of followers. Moreover, groups of foraging spotted goatfish attracted herbivores, not recorded for spotted goatfish foraging singly. The size of follower individuals increased with the size and the number of foraging spotted goatfish. The zoobenthivorous habits of the spotted goatfish and its ability to disturb a variety of soft substrata render it an important nuclear fish for several follower species of the reef fish assemblage at Fernando de Noronha.

Key words: equatorial west Atlantic; foraging associations; Mullidae; nuclear and follower fishes; *Pseudupeneus maculatus*; reef fishes.

INTRODUCTION

Following behaviour is a foraging mode commonly recorded for reef fishes during heterospecific feeding associations (Ormond, 1980; Strand, 1988; Lukoschek & McCormick, 2000; Sazima *et al.*, 2005). The followers escort foraging so called nuclear fishes and other animals to capitalize on food items exposed or produced by the activity of the nuclears, including stirred organic particles and algae, uncovered or flushed small invertebrates and fishes and even faeces (Fricke, 1975; Ormond, 1980; Silvano, 2001; Sazima *et al.*, 2005). Such foraging associations are widespread and recorded for several fishes and other marine

‡Author to whom correspondence should be addressed. Tel.: +55 19 32844197; fax: +55 19 32893124; email: csazima@gmail.com

animal taxa and geographic sites (Diamant & Shpigel, 1985; Lukoschek & McCormick, 2000; Gibran, 2002; Sazima *et al.*, 2005).

Following behaviour, as other types of social foraging habits, may enhance the fitness of individuals within the group and provide increased protection from predators (Aronson & Sanderson, 1987; Baird, 1993; Lukoschek & McCormick, 2000; Auster & Lindholm, 2002). Relationships of costs and benefits for both nuclear and follower species, however, are not clearly defined and following behaviour is sometimes regarded as a type of commensalism (Lukoschek & McCormick, 2000) although Baird (1993) considers both nuclear and follower species to profit. Nevertheless, several fish species of many families and trophic levels engage in following behaviour and spend up to 25% of their time in this association type (Strand, 1988; Lukoschek & McCormick, 2000).

Goatfish species (Mullidae) are noted as either nuclear or follower fishes (Aronson & Sanderson, 1987; Sikkel & Hardison, 1992; Lukoschek & McCormick, 2000). The spotted goatfish *Pseudupeneus maculatus* (Bloch) dwells on sandy and rocky bottoms in reef areas in the west Atlantic (Starck & Davis, 1966). This goatfish is a zoobenthivore (benthic carnivore) and uses its chin barbels to search for food over substrata types as diverse as sand, rubble and rocks covered with sand and algae (Randall, 1967; Carvalho-Filho, 1999). The spotted goatfish is diurnally active and may be very abundant locally, foraging either solitary or in groups, small to large (Starck & Davis, 1966; Munro, 1976; Carvalho-Filho, 1999). Thus, the overall habits of the ubiquitous *P. maculatus* would render it a nuclear fish attractive for a variety of opportunistic follower fishes.

At Fernando de Noronha Archipelago, tropical west Atlantic, the spotted goatfish is a common species, which uses variable feeding modes over several habitat types (pers. obs.). To assess how the foraging nuclear spotted goatfish influence the behaviour of potential follower fishes, four main questions were addressed in the present study: 1) How many and which species follow the spotted goatfish? 2) Is the followers' species richness or number of individuals related to the number of foraging goatfish? 3) Are there differences in the trophic categories of followers associated with spotted goatfish foraging singly or in groups? 4) Does the size or the number of foraging spotted goatfish influence the size of associated follower individuals? The answers to these questions bring new insights about the organization of heterospecific associations (Lukoschek & McCormick, 2000). Additionally, the present study is the first attempt to relate the characteristics and habits of the nuclear fish to the followers' species richness and their distribution in heterospecific associations.

MATERIALS AND METHODS

The foraging activity and associations between *P. maculatus* and its follower fishes were recorded at Fernando de Noronha Archipelago (03°50′ S; 32°25′ W), *c.* 345 km off the coast of north-east Brazil, tropical west Atlantic (Sazima *et al.*, 2005). Preliminary data were gathered in June 2001, the core of the study being carried out in June 2002, May to July 2003, November 2003 and October 2004. Records on the foraging associations were made at seven sites around the archipelago, all of these with similar features: bottom composed of rocky reefs covered mostly with green, brown and red algae, stony corals and fine sand sediment, with adjacent sand flats. The substrata over which the spotted goatfish foraged consisted of mixed sand, gravel and rock.

Foraging activities and associations of spotted goatfish with followers were recorded while snorkelling and scuba diving in observation sessions of 30–120 min, totalling 2534 min over 34 non-consecutive days. Behavioural data were recorded directly on slates, photographed and video-recorded. A voucher DVD with selected video-recordings is on file at the Museu de História Natural of the Universidade Estadual de Campinas (ZUEC # 01). Associations between foraging spotted goatfish and their followers were assessed with the use of instantaneous samplings (Altmann, 1974), in which the fish species, number of individuals and their estimated sizes were recorded on plastic slates with standardized sketches, for each studied association. Total length (L_T, cm) was visually estimated both for the nuclear and follower fishes. For a better assessment, followers were grouped in four size classes: 'very small' (*c.* 4–11 cm), 'small' (*c.* 12–22 cm), 'medium' (*c.* 23–35 cm) and 'large' (*c.* 36–50 cm).

The following pair-wise relationships were analysed by least squares regression with a randomization test, and significance levels were estimated with $n = 10\ 000$ resamplings (Manly, 1997): 1) species richness of followers and the number of foraging goatfish; 2) number of follower individuals and the number of foraging goatfish; 3) size of the largest follower individual and the size of the largest nuclear goatfish individual; 4) size of the largest follower individual and the number of foraging goatfish. The relationship between gregarious behaviour ('singly' or 'groups') and the size ratio between nuclear and follower individuals ('the nuclear is larger than the follower' and 'the follower is larger than the nuclear') was tested using the χ^2 test (Zar, 1999).

RESULTS

A total of 223 foraging associations were recorded for *P. maculatus* (10–30 cm L_T, mean ± S.E. = 19·29 ± 0·13 cm; $n = 495$). Of these, 120 associations (*c.* 54%) contained a spotted goatfish foraging singly and 103 (*c.* 46%) contained groups of two to 36 spotted goatfish (mean ± S.E. = 10·87 ± 0·66). Seventeen reef fish species were recorded associated with the spotted goatfish (Table I). Zoobenthivore fish species dominated among the followers, with the exception of five mainly herbivorous species and one omnivorous wrasse (Table I).

Species richness of followers increased ($r^2 = 0{\cdot}35$, $n = 223$, $P < 0{\cdot}001$) with the number of foraging spotted goatfish [Fig. 1(a)]. Spotted goatfish foraging singly attracted one to three follower species (1·12 ± 0·03; $n = 120$) at a time, but one species was the commonest situation (88%). On the other hand, spotted goatfish foraging in groups attracted one to six follower species at a time (1·79 ± 0·10; $n = 103$), two or more species being a common situation (51%). The number of follower individuals increased ($r^2 = 0{\cdot}37$, $n = 223$, $P < 0{\cdot}001$) with the number of foraging spotted goatfish [Fig. (1b)]. Spotted goatfish foraging singly attracted one to five follower individuals at a time (1·33 ± 0·07; $n = 120$), whereas spotted goatfish foraging in groups attracted one to 13 follower individuals at a time (2·94 ± 0·25; $n = 103$).

Besides zoobenthivores and piscivores, spotted goatfish groups attracted five herbivores: *Sparisoma axillare* (Steindachner), *Sparisoma amplum* (Ranzani), *Sparisoma frondosum* (Agassiz), *Acanthurus chirurgus* (Bloch) and *Acanthurus coeruleus* Bloch & Schneider, none of which was recorded following spotted goatfish foraging singly (Table I). Whereas zoobenthivores were recorded in 100% of the associations, herbivores were recorded in only 7·6% of these, always following large spotted goatfish groups (eight to 36 individuals;

TABLE I. Reef fish species recorded as followers of *Pseudupeneus maculatus* at Fernando de Noronha Archipelago. Trophic category and minimum and maximum total length of the followers, the condition of the foraging spotted goatfish (single or grouped) and number of observations. Taxonomic arrangement of families follows Nelson (1994), genera and species in alphabetical order

Families and specific names of followers	Trophic category	L_T (cm)	Spotted goatfish condition (*n*)
Aulostomidae (trumpetfishes) *Aulostomus strigosus* Wheeler	Zoobenthivore/piscivore	35–48	Grouped (3)
Serranidae (groupers and sea basses) *Cephalopholis fulva* (L.)	Zoobenthivore	10–25	Grouped (42)/single (22)
Malacanthidae (tilefishes) *Malacanthus plumieri* (Bloch)	Zoobenthivore/piscivore	17	Grouped (2)
Carangidae (jacks) *Caranx bartholomaei* (Cuvier)	Zoobenthivore/piscivore	25–40	Grouped (30)/single (1)
Caranx latus (Agassiz)	Zoobenth./piscivore/planktivore	15–20	Grouped (10)/single (6)
Haemulidae (grunts) *Anisotremus surinamensis* (Bloch)	Zoobenthivore	23–38	Grouped (3)
Haemulon chrysargyreum (Günther)	Zoobenthivore	15	Single (1)
Haemulon parra (Desmarest)	Zoobenthivore	12–20	Grouped (5)
Mullidae (goatfishes) *Mulloidichthys martinicus* (Cuvier)	Zoobenthivore	19	Single (1)
Labridae (wrasses) *Halichoeres dimidiatus* (Agassiz)	Zoobenthivore	11–20	Single (5)/grouped (3)
Halichoeres radiatus (L.)	Zoobenthivore	06–28	Single (89)/grouped (64)
Thalassoma noronhanum (Boulenger)	Zoobenth./planktivore/cleaner	04–12	Single (10)/grouped (3)
Scaridae (parrotfishes) *Sparisoma amplum* (Ranzani)	Herbivore	23	Grouped (1)
Sparisoma axillare (Steindachner)	Herbivore	16–38	Grouped (12)
Sparisoma frondosum (Agassiz)	Herbivore	20–32	Grouped (2)
Acanthuridae (surgeonfishes) *Acanthurus chirurgus* (Bloch)	Herbivore	18–22	Grouped (3)
Acanthurus coeruleus (Bloch & Schneider)	Herbivore	17–25	Grouped (2)

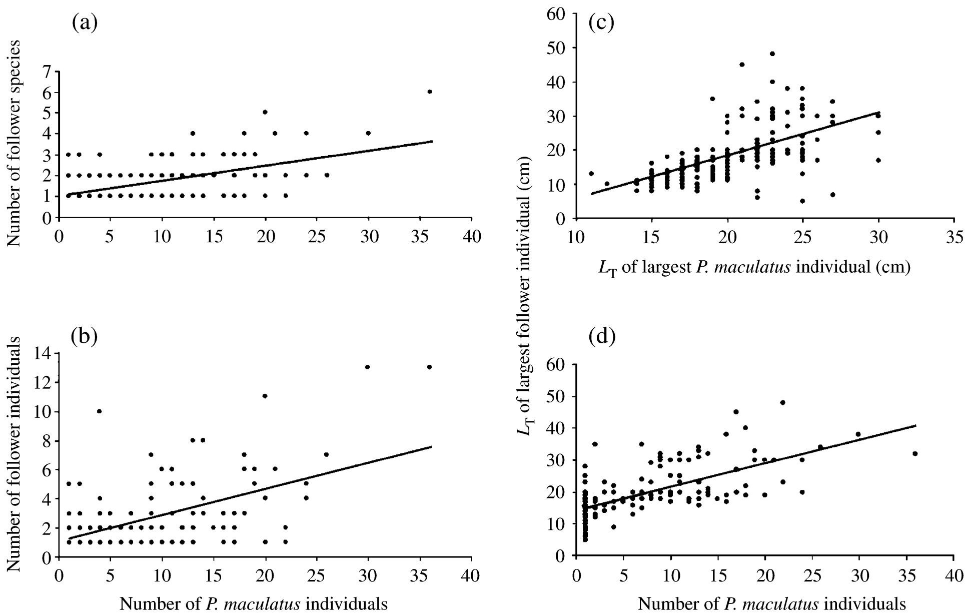

FIG. 1. Quantitative relationships between follower fishes and *Pseudupeneus maculatus* at Fernando de Noronha Archipelago: (a) follower fish species richness increased with the number of foraging spotted goatfish, (b) number of follower individuals increased with the number of foraging spotted goatfish, (c) size (total length, L_T) of the largest follower individual increased with size of the largest foraging spotted goatfish individuals and (d) size (L_T) of the largest follower individual increased with the number of foraging spotted goatfish. The curves are fitted by: (a) $y = 1{\cdot}04x + 0{\cdot}07$, (b) $y = 0{\cdot}18x + 1{\cdot}09$, (c) $y = 1{\cdot}25x - 6{\cdot}67$ and (d) $y = 0{\cdot}74x + 14{\cdot}2$.

18·18 ± 1·70; $n = 17$). To investigate if followers' assemblages with herbivores were non-randomly associated to large groups, an *a posteriori* randomization test (Manly, 1997) was performed. The group sizes of the spotted goatfish were randomized among records of associations and the average number of goatfishes was computed for followers' assemblages containing herbivores (10 000 resamplings). No randomization achieved a group size equal or higher than that observed for herbivores, which indicates that the herbivores follow only larger groups of spotted goatfish (Fig. 2).

The size of the largest follower increased with the size of the largest nuclear spotted goatfish ($r^2 = 0{\cdot}37$, $n = 223$, $P < 0{\cdot}001$) [Fig. 1(c)]. The size of the largest follower individual also increased with the number of foraging spotted goatfish ($r^2 = 0{\cdot}46$, $n = 223$, $P < 0{\cdot}001$) [Fig. 1(d)]. Spotted goatfish foraging singly (12–30 cm L_T) were mostly (92·5%, 111 records) larger than their followers (4–28 cm L_T). On the other hand, for spotted goatfish foraging in groups (10–30 cm L_T), in about a half of the associations (57 records, 55·3%), the largest spotted goatfish within the group was larger than the largest follower (6–48 cm L_T, χ^2, d.f. = 1, $P < 0{\cdot}001$). Disregarding the species, in a total of 463 follower fishes, 69 individuals were very small (8·42 ± 0·26 cm), 308 were small (16·95 ± 0·15 cm), 78 individuals were medium (28·68 ± 0·40 cm) and only eight were large (40·00 ± 1·50 cm).

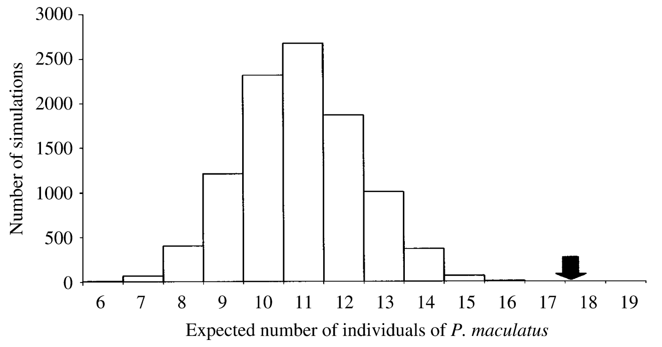

FIG. 2. The distribution of the average number of *Pseudupeneus maculatus* individuals expected for follower assemblages containing herbivores under the assumption of randomness (10 000 resamplings). ⬇, the observed value for real data.

DISCUSSION

In heterospecific associations, the nuclear species attract mostly opportunistic carnivore predators (Fricke, 1975; Ormond, 1980; Lukoschek & McCormick, 2000). At Fernando de Noronha, the spotted goatfish seems to exert a pervasive influence on the assemblage of opportunistically foraging reef fishes that feed near the bottom. Zoobenthivorous and piscivorous species dominated among the followers of *P. maculatus* in the present study. An entirely different follower type, the herbivorous parrotfishes and surgeonfishes, however, was recorded here associated with the spotted goatfish. Most records on feeding associations involving these herbivores characterize them as nuclear fishes or do not describe their role at all (Ormond, 1980; Strand, 1988; Sazima *et al.*, 2005) although others (Lukoschek & McCormick, 2000; Dias *et al.*, 2001) suggest that herbivores may feed on items made available by other nuclear fishes, thus acting as followers. The suggestion is made that the herbivores join foraging groups to feed upon suspended items and pieces of algae loosened or unearthed by the nuclear and follower fishes. At Fernando de Noronha, parrotfishes and surgeonfishes have been reported to feed on floating particles including dolphin faeces (Sazima *et al.*, 2003; pers. obs.).

As herbivores were only recorded following groups of eight or more spotted goatfish, it is probable that their presence in the associations is related to larger numbers of nuclear fish. A group of spotted goatfish is likely to produce a considerable bottom disturbance and would thus provide herbivorous fishes with drifting bits of food (algae). Thus, herbivorous species would associate with nuclear species that form larger aggregations while foraging, an idea to be tested with additional records of heterospecific associations.

The number of nuclear foraging individuals influenced the followers' species richness and the number of follower individuals in the present study, the main reason probably being the amount of disturbance produced. Strand (1988) noted that the mean number of followers and their preferences for a particular nuclear species are related to the amount of disturbance created. Visual signals elicit following behaviour by opportunistic fish species (Fricke, 1975; Fishelson, 1977; Diamant & Shpigel, 1985), and both the sand clouds produced by the disturbance and specific features of the nuclear fishes (shape, behaviour and colouration) influence the followers' behaviour (Fricke, 1975; Fishelson, 1977). Thus, a spotted goatfish foraging singly may go unnoticed or be uninteresting to some fish species, whereas a foraging group would attract more attention. Notwithstanding the conspicuous and diverse consequences produced by variable numbers of foraging nuclear fishes (both to the habitat and the follower fishes), no published comparative approach such as that presented here has been found, which prevents additional considerations.

Several fish species may join foraging groups both for feeding and antipredatory advantages that may occur simultaneously (Morse, 1977; Diamant & Shpigel, 1985; Strand, 1988; Auster & Lindholm, 2002). Feeding advantages would include minimizing effort duplication, food-finding facilitation, and catching uncovered and otherwise unavailable food (Morse, 1977). Antipredatory advantages include vigilance, confusion effect, discouraging predators, cover-seeking and dilution effect (Morse, 1977). Evidence of feeding advantages for nuclear and follower association is supported by several studies (Diamant & Shpigel, 1985; Aronson & Sanderson, 1987; Strand, 1988; Baird, 1993). Antipredatory advantages of this association, however, still need to be verified (Auster & Lindholm, 2002; Lukoschek & McCormick, 2000). It is suggested here that feeding and other advantages may be found even when a follower associates with a single nuclear fish, but most likely a larger number of foraging nuclear fishes increases some of these advantages.

The number and diversity of species engaged in following the spotted goatfish, recorded in the present study, indicate that the benefits are higher than the costs to the followers. The nuclear fish may also benefit from the association, since social stimuli from the follower fishes may increase foraging opportunities for the nuclear ones (Baird, 1993; Lukoschek & McCormick, 2000). Food pilfering by followers, however, may represent a high cost to the nuclear fish (Strand, 1988; Baird, 1993; Lukoschek & McCormick, 2000). Despite the dietary overlap between most followers and the spotted goatfish, no food pilfering or aggressive behaviour between them was here recorded, which indicates little if any cost to *P. maculatus*.

In the present study, minimum and maximum sizes of spotted goatfish foraging singly or in groups were similar. Spotted goatfish foraging singly, however, were mostly larger than their followers, whereas grouped spotted goatfish commonly attracted followers larger than themselves. The analysis of several pictures available in the literature (Diamant & Shpigel, 1985; Aronson & Sanderson, 1987; Auster & Lindholm, 2002) indicates a trend: followers are mostly smaller than the nuclear fish, especially when the latter is foraging singly. Although data on sizes of both nuclear and follower fishes are rarely available, some studies comment on the size relationships between associated foraging fishes (Sikkel & Hardison, 1992; Silvano, 2001; Gibran, 2002), and a few of them relate size classes of the followers to ontogenetic factors (Strand, 1988; Lukoschek & McCormick, 2000). Another factor that may influence size classes of followers, however, would again be the amount of disturbance created by the foraging nuclear fish. If this is the case, larger followers would be more prone to join large foraging groups due to the greater amount of disturbance they cause, which may dislodge greater amount of prey, as well as possibly more types and even larger sizes of prey. Thus, the maximum size of follower fishes in a foraging association seems to be mostly related to the number of nuclear individuals within the group rather than only to the size of the latter.

Sixteen follower species correspond to the largest list of fishes reported as associated with a nuclear species at a given locality, namely the goatfish *Parupeneus barberinus* (Lacepède) at Lizard Island in the south-west Pacific (Lukoschek & McCormick, 2000), a region with greater reef fish species richness than the west Atlantic (Carvalho-Filho, 1999; Allen & Adrim, 2003). The richness notwithstanding, the number of follower species recorded for *P. maculatus* at Fernando de Noronha (present study) exceeds the above-mentioned record, and thus renders it the largest list of followers recorded to date. It is suggested here that the spotted goatfish has a pervasive influence on several opportunistically feeding species in the reef fish community of Fernando de Noronha, and that the number of follower species is an indication of the importance of its role. Other goatfish species, especially those that form aggregations while foraging, are worth study in other areas to examine the view that nuclear fishes that produce substantial bottom disturbance are targeted by a varied assemblage of followers, as seems to be the case of *P. barberinus* at Lizard Island (Lukoschek & McCormick, 2000) and *P. maculatus* at Noronha (present study).

We thank the Ibama (M. A. Silva) for the study permits at Fernando de Noronha Archipelago and for logistic support; the Centro Golfinho Rotador (J. M. Silva Jr) and the Projeto Tamar (C. Bellini and A. Grossman) for logistic support; K. S. Brown Jr for improving our English; the Águas Claras and the Atlantis diving centres for allowing free use of their facilities; and CAPES, CNPq and FAPESP for essential financial support. C. S. is recipient of scholarships from the CNPq— Brasil. We dedicate this paper to I. Sazima, whose charming, skilful and open mind showed us the windows for the study of reef fishes and their ways.

References

Allen, G. R. & Adrim, M. (2003). Coral reef fishes of Indonesia. *Zoological Studies* **42,** 1–72.

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

Aronson, R. B. & Sanderson, S. L. (1987). Benefits of heterospecific foraging by the Caribbean wrasse, *Halichoeres garnoti* (Pisces: Labridae). *Environmental Biology of Fishes* **18,** 303–308.

Auster, P. J. & Lindholm, J. (2002). Pattern in the local diversity of coral reef fishes versus rates of social foraging. *Caribbean Journal of Science* **38,** 263–266.

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

Carvalho-Filho, A. (1999). *Peixes: costa brasileira.* São Paulo: Melro.

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

Dias, T. L. P., Rosa, I. L. & Feitoza, B. M. (2001). Food resource and habitat sharing by the three Western South Atlantic surgeonfishes (Teleostei: Acanthuridae: *Acanthurus*) off Paraíba Coast, North-eastern Brazil. *Aqua*, *Journal of Ichthyology and Aquatic Biology* **5,** 1–10.

Fishelson, L. (1977). Sociobiology of feeding behavior of coral fish along the coral reef of the Gulf of Elat (=Gulf of 'Aqaba), Red Sea. *Israel Journal of Zoology* **26,** 114–134.

Fricke, H. W. (1975). The role of behaviour in marine symbiotic animals. In *Symbiosis, Symposia of the Society for Experimental Biology 29* (Jennings, D. H. & Lee, D. L., eds), pp. 581–594. Cambridge: Cambridge University Press.

Gibran, F. Z. (2002). The sea basses *Diplectrum formosum* and *D. radiale* (Serranidae) as followers of the sea star *Luidia senegalensis* (Asteroidea) in southeastern Brazil. *Brazilian Journal of Biology* **62,** 591–594.

Lukoschek, V. & McCormick, M. I. (2000). A review of multi-species foraging associations in fishes and their ecological significance. *Proceedings of the 9th International Coral Reef Symposium* **1,** 467–474.

Manly, B. F. J. (1997). *Randomization, Bootstrap and Monte Carlo Methods in Biology*. London: Chapman & Hall.

Morse, D. H. (1977). Feeding behavior and predator avoidance in heterospecific groups. *BioScience* **27,** 332–339.

Munro, J. L. (1976). Aspects of the biology and ecology of Caribbean reef fishes: Mullidae (goat-fishes). *Journal of Fish Biology* **9,** 79–97.

Nelson, J. S. (1994). *Fishes of the World*. New York: John Wiley & Sons.

Ormond, R. F. G. (1980). Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. *Journal of Zoology, London* **191,** 247–262.

Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Studies on Tropical Oceanography* **5,** 665–847.

Sazima, I., Sazima, C. & Silva, J. M. Jr (2003). The cetacean offal connection: feces and vomits of spinner dolphins as a food source for reef fishes. *Bulletin of Marine Science* **72,** 151–160.

Sazima, C., Bonaldo, R. M., Krajewski, J. P. & Sazima, I. (2005). The Noronha wrasse: a jack-of-all-trades follower. *Aqua*, *Journal of Ichthyology and Aquatic Biology* **9,** 97–108.

Sikkel, P. C. & Hardison, P. D. (1992). Interspecific feeding association between the goatfish *Mulloides martinicus* (Mullidae) and a possible aggressive mimic, the snapper *Ocyurus chrysurus* (Lutjanidae). *Copeia* **1992,** 914–917.

Silvano, R. A. M. (2001). Feeding habits and interspecific feeding associations of *Caranx latus* (Carangidae) in a subtropical reef. *Environmental Biology of Fishes* **60,** 465–470.

Starck, W. A. & Davis, W. P. (1966). Night habits of fishes of Alligator Reef, Florida. *Ichthyologica* **38,** 313–356.

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

Zar, J. H. (1999). *Biostatistical Analysis*. New Jersey: Prentice-Hall.

