

Effects of Positional Overlap on Interactions and Co-occurrence of Follower Fishes in Benthic Foraging Associations

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Abstract: Opportunistic predatory reef fishes commonly follow foraging benthivores to feed on prey disturbed by the benthivores. This study examined factors that may restrict the number and the species composition of follower fishes. Association groups common on the reefs around Bonaire were followed and videotaped. The follower compositions and interactions were quantified. Time spent by the followers in different positions around the nuclear benthivore was calculated. Follower species occupied some positions more often than others, and the preferred positions were species-specific. A high degree of overlap in these positions corresponded to repelling interactions between followers and to the absence of their co-occurrence in the associations. A low degree of the positional overlap corresponded to the absence of repelling interactions and to co-occurrence of the followers in the same association.

Keywords: Follower relations, nuclear benthivore, repelling interactions, species composition, behaviour.

INTRODUCTION

Many opportunistic predatory reef fishes spend significant time following benthic carnivores and feeding on prey disturbed by the foraging activities of these species [1, 2]. Such benthic foraging associations are a common phenomenon and are considered an important factor in reef ecology [1-5]. Previous studies of these associations focused mainly on description and investigation of nuclear-follower relations [1-28]. Interactions between followers were noted [4, 6-11, 29], but relations between followers and their effect on the followers' individual and species composition in the associations were not specifically studied.

It was noted in the literature and also observed by the author (GF) that followers of some species repel each other and apparently prevent con-specific and some hetero-specific assemblages while other followers appear mutually indifferent and commonly co-occur in the associations. This study aimed to find factors that may explain these differences. Previous studies [9, 10] suggested that followers seek to maintain an advantageous position near the nuclear benthivore and repel others from this location. During observations of reef fish, species following a benthivore appeared to be non-random. Thus, we hypothesized that followers in benthic foraging associations occupy species-specific positions relative to the nuclear benthivore, and that followers repel each other if their preferential positions overlap but are indifferent otherwise.

MATERIALS AND METHODS

To test the hypothesis that followers in a benthic foraging association occupy different positions, data were collected during 30 SCUBA dives lasting approximately 35 hours

made by GF between May 2007 and October 2009 on the leeward reefs of Bonaire and around Klein Bonaire, Lesser Antilles (12° N, 68° W). The area of study was a shallow reef-flat (4 - 10 m depth) covered with sand, coral rubble, and patches of live corals and gorgonians. The dives were made at various daytime hours, at various sites separated by 0.1 - 5.0 km.

The common nuclear benthivores in the study area were spotted goatfish *Pseudupeneus maculatus* (Bloch) and yellow goatfish *Mulloidichthys martinicus* (Cuvier) [29]. Their common followers were bar jack *Caranx ruber* (Bloch), yellowhead wrasse *Halichoeres garnoti* (Valenciennes), and Spanish hogfish *Bodianus rufus* (Linnaeus) [29]. Nuclear *P. maculatus* were observed mostly foraging singly while nuclear *M. martinicus* foraged both singly and in groups of up to dozens individuals. For consistency, only foraging associations with a single nuclear *P. maculatus* or *M. martinicus* and with the followers being *H. garnoti*, *B. rufus*, or *C. ruber*, were used in this study.

Observed associations were followed at a distance of 2-3 m and video recorded using a Sony DCR-HC20 digital video camera in Ewa-Marine aqua-housing. For analysis, snapshots were taken every 10 seconds from the video recordings and then used to calculate the followers' time spent in different positions in the associations. To determine significant interactions, benthic follower associations were analyzed using Chi-squared Goodness of Fit tests ($P < 0.05$) for single followers and followers observed in pairs.

RESULTS

A total of 70 benthic follower associations were observed. In 28 of them a nuclear benthivore was followed by a single *H. garnoti*, in 19 - by a single *B. rufus*, and in 14 - by a single *C. ruber*. An individual *C. ruber* with an individual *B. rufus* were observed in six of the associations, and an individual *C. ruber* with an individual *H. garnoti* were observed three times. No con-specific followers were

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Fig. (1). Repelling interactions between followers. **(A)** A smaller *C. ruber* waits to replace a larger *C. ruber* in an association of *C. ruber* and *B. rufus* following a nuclear *P. maculatus*. **(B)** A larger *B. rufus* chases away and replaces a smaller *B. rufus* in the association with a nuclear *M. martinicus*. **(C)** A smaller *H. garnoti* replaces a larger *H. garnoti* after the latter leaves the association with a nuclear *M. martinicus*. **(D)** *B. rufus* chases away and replaces *H. garnoti* in the association with a nuclear *M. martinicus*.

observed in an association, nor were *B. rufus* observed with *H. garnoti* in the same association.

While observing associations where *C. ruber* were followers, other individuals of *C. ruber* were seen to approach the associations. These approaches always led to repelling interactions in which an established following *C. ruber* either chased away an approaching one, a newcomer replaced the resident individual, or an individual *C. ruber* followed the association at a distance and replaced the resident individual as soon as the latter left (Fig. 1A). Such interactions occurred during all 23 observed associations with *C. ruber*.

While observing 6 of 25 associations where *B. rufus* were followers, other individuals of *B. rufus* were seen to approach the associations. In all these cases either the resident individual *B. rufus* repelled the newcomer or the resident was replaced by the newcomer (Fig. 1B). Individuals of *H. garnoti* were observed approaching and having the same repelling interactions with the resident individual *H. garnoti* during 6 of 31 associations in which *H. garnoti* were followers (Fig. 1C). In 9 associations, *B. rufus* and *H. garnoti* individuals were observed to approach a

nuclear benthivore and have repelling interactions between themselves. These interactions involved a newcomer individual *B. rufus* chasing away and replacing the resident individual *H. garnoti* (Fig. 1D), a resident *B. rufus* chasing away an approaching individual *H. garnoti*, and individual *H. garnoti* following an association at a distance and replacing the resident *B. rufus* as soon as it left. No repelling interactions were observed between *C. ruber* and *B. rufus* or between *C. ruber* and *H. garnoti*.

The followers *C. ruber* were recorded for a total of 10.3 hours in 17 dives, *H. garnoti* - for a total of 3.8 hours in 18 dives, and *B. rufus* - for a total of 2.1 hours in 19 dives. Positions of the followers were categorized as front, behind, right, left, and above according to the position of their head relative to the nuclear benthivore (Fig. 2, Table 1). Analysis of the times spent in different positions showed significant differences for each follower (Table 2). The distribution of the position usage also significantly differed between the followers (Table 3). The follower *C. ruber* strongly preferred the position above the nuclear benthivore, while both *H. garnoti* and *B. rufus* preferred positions behind it (Fig. 3).

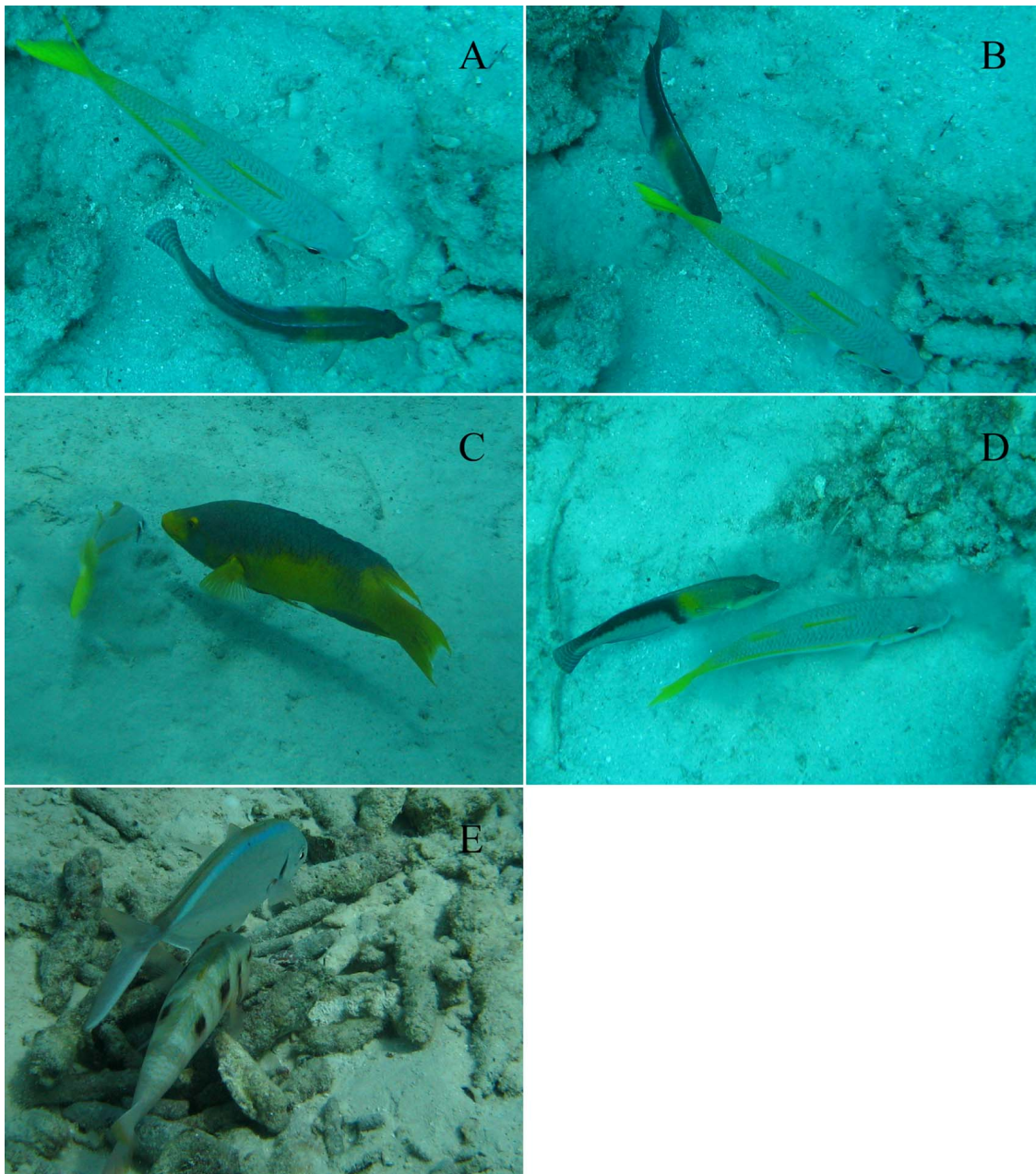


Fig. (2). Follower positions in the associations (A) in front, (B) behind, (C) right, (D) left, and (E) above a nuclear benthivore.

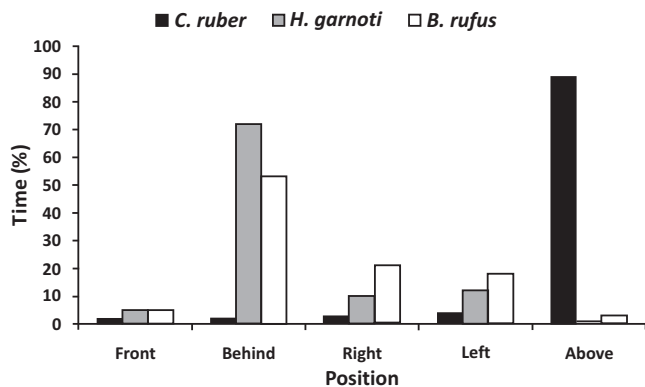


Fig. (3). Percentage time spent by the follower species in different positions relative to the nuclear benthivore.

Table 1. Number of Snap-Shots of Follower Species in Different Positions Relative to the Nuclear Benthivore
HG = *H. garnoti*, BR = *B. rufus*, CR = *C. ruber*

Followers	Observed association numbers	Observation time (hrs)	Position of followers in snap-shot numbers					
			Front	Behind	Right	Left	Above	
1 HG	28	3.7	62	981	134	165	7	
1 BR	19	1.9	25	388	135	112	3	
1 CR	14	10.0	87	74	118	123	3,194	
1 CR + 1 BR	6	0.2	CR	2	2	7	5	69
			BR	12	22	22	25	4
1 CR + 1 HG	3	0.1	CR	1	1	4	3	26
			HG	6	16	7	6	0
Total	70	15.9	195	1,484	427	439	3,303	

Table 2. Test of Preferential Positions by a Follower
HG = *H. garnoti*, BR = *B. rufus*, CR = *C. ruber*

Follower	Number of snap-shots	Chi-square	P
CR alone	3596	10,647	<0.001
CR in CR+BR pair	85	200	<0.001
CR in CR+HG pair	35	65	<0.001
BR alone	663	709	<0.001
BR in CR+BR pair	85	18	<0.005
HG alone	1,349	2,400	<0.001
HG in CR+HG pair	35	19	<0.001

Table 3. Pairwise Comparisons of Position Distributions between Followers
HG = *H. garnoti*, BR = *B. rufus*, CR = *C. ruber*

Follower combination	Chi-square	P
CR alone/ BR alone	2,691	<0.001
CR alone/ BR in CR+BR pairs	542	<0.001
CR in CR+BR pairs/ BR alone	568	<0.001
CR in CR+Br pairs/ BR in CR+BR pairs	103	<0.001
CR alone/ HG alone	3,709	<0.001
CR alone/ HG in CR+HG pairs	373	<0.001
CR in CR+HG pairs/ HG alone	803	<0.001
CR in CR+HG pairs/ HG in CR+HG pairs	45	<0.001
BR alone/ HG alone	57	<0.001
BR alone/ HG in CR+HG pairs	14	<0.01
BR in CR+BR pairs/ HG alone	94	<0.001
BR in CR+BR pairs/ HG in CR+HG pairs	n/a	cannot be tested

The positional overlaps in the three con-specific follower pairs and that of *B. rufus* with *H. garnoti* were high, while positional overlap of *C. ruber* with *B. rufus* and that of *C.*

Table 4. Overlap of the Preferential Positions, Observation of Repelling Interactions and of Co-Occurrences of the Follower Pairs in Benthic Foraging Associations

Follower pair	Positional preferences	Repelling interactions	Co-occurrences
<i>C. ruber</i> / <i>C. ruber</i>	Above / Above	Yes	No
<i>H. garnoti</i> / <i>H. garnoti</i>	Behind / Behind	Yes	No
<i>B. rufus</i> / <i>B. rufus</i>	Behind / Behind	Yes	No
<i>B. rufus</i> / <i>H. garnoti</i>	Behind / Behind	Yes	No
<i>B. rufus</i> / <i>C. ruber</i>	Behind / Above	No	Yes
<i>H. garnoti</i> / <i>C. ruber</i>	Behind / Above	No	Yes

ruber with *H. garnoti* were low (Table 4). The co-occurrence of followers in the associations and the repelling interactions between them corresponded to the preference of their positions. Individuals of four species-pairs with highly overlapping positions displayed repelling interactions every time two of them were observed near the nuclear benthivore, and they were not observed to co-occur in associations (Table 4). The followers of two species-pairs with low positional overlap did not display repelling interactions and were observed in the same associations (Table 4).

DISCUSSION

A high degree of overlap in preferred positions in benthic followers is likely to lead to conflict because two followers cannot occupy the same position at the same time. This conflict may cause repelling interactions between the followers and act as a restricting factor on individual followers' number and species composition. Thus, a high degree of positional overlap can be used to predict followers that repel each other and that do not or only rarely co-occur in foraging associations.

Any follower with a strong positional preference has a high degree of positional overlap with its con-specifics. Consequently, frequent repelling interactions between con-specific followers are predicted and were supported by the observed repelling interactions between con-specific followers in this study. Previously, con-specific repulsion of followers has been observed with *Bodianus diplotaenia* (Gill) in the Gulf of California [4], *Ocyurus chrysurus* (Bloch) on the Atlantic coast of Panama [6], *C. ruber* in Belize [7], *Pseudolabrus eoethinus* (Richardson) and *P. sieboldi* (Mabuchi and Nakabo) near the southern coast of Japan [8], *Thalassoma pavo* (Linnaeus) and *Diplodus sargus cadenati* (de la Paz, Bauchot & Daget) in the Azores [9], and *Epinephelus marginatus* (Lowe) off the coast of Southern Brazil [10]. For the same reason, it can be predicted that associations with multiple species of followers will show repulsion when the following species have the same positional preferences, as was documented in this study.

Positional preferences may result from a multitude of factors including the follower's diet, morphology, predatory behavior, and foraging tactics. In this paper we documented assemblages of two nuclear benthivorous predators with three common followers and found that mutual exclusion occurred most often between con-specifics and between species of the same family, Labridae. Of the follower species, *C. ruber* spent the majority of its time above the nuclear individual, while *H. garnoti* and *B. rufus* spent most of their time in the position behind the nuclear individual. Based on these observations, multi-species assemblages can frequently occur between *C. ruber* and the other species, but will be limited between *H. garnoti* and *B. rufus*. Additional research in areas where these species occur singly and in mixed populations is warranted to better elucidate competition and co-existence.

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CONFLICT OF INTEREST

None declared.

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