Competition for shelter holes in the coral-reef fish *Acanthemblemaria spinosa* Metzelaar

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Abstract: Spinyhead blennies occupy abandoned worm holes in coral heads on Caribbean reefs. We conducted a series of short-duration field experiments off St. Thomas, US Virgin Islands, which indicated that such holes are a limiting resource and that larger fish competitively dominate smaller fish for access to holes. Few fish that were added to coral heads lacking vacant holes were able to secure holes, and did so only by displacing smaller residents after severe combat. However, when vacant holes were added to coral heads before adding fish, transplanted fish readily occupied the new holes. When holes were added to coral heads without also adding fish, the new holes were colonized by immigrants from the surrounding habitat. Similarly, when resident fish were removed from coral heads, the emptied holes were colonized. Immigrants were smaller than removed residents, and, in cases where resident fish changed holes following removals of neighbors, they moved to sites previously occupied by larger fish. Fish displaced up to 5 m returned to their original holes, consistent with the possibility that spinyhead blennies may occasionally leave their holes and search for sites of better quality. We conclude that intraspecific competition for shelter holes may limit the number of spinyhead blennies occupying a coral head.

Key words: Caribbean; Competition; Reef fish; Shelter

INTRODUCTION

Controversy during the past two decades on the role of competition in determining the distribution and abundance of coral-reef fishes has come full circle (review by Sale, 1991). During the 1970s, competition for space was seen as being the predominant process structuring populations and communities of reef fishes (e.g., Smith & Tyler, 1972). During the 1980s, this paradigm was challenged by the advocates of recruitment limitation, where larval settlement was seen as being so sparse that reef populations seldom reached densities where competition was important (review by Doherty & Williams, 1988). More recently, a pluralistic view has emerged, where multiple processes, including competition, are acknowledged as being important (reviews by Jones, 1991; Sale, 1991).

The chaenopsid fish genus *Acanthemblemaria* is represented by eight species in the western Atlantic Ocean (Smith-Vaniz & Palacio, 1974). These species are inquiline, dwelling in invertebrate worm holes (Stephens, 1963; Thomson et al., 1979; Greenfield & Greenfield, 1982). They consume small benthic and planktonic invertebrates by

darting out of their holes, prompting Kotrschal & Lindquist (1986) to label the genus "hemisessile". There is little sexual dimorphism (Smith-Vaniz & Palacio, 1974), and demersal eggs are laid deep within the male's shelter hole (Stephens et al., 1966). The spinyhead blenny, *Acanthemblemaria spinosa* Metzelaar, occurs commonly in the Caribbean and western Atlantic on coral reefs from the Bahamas and Florida, south to Curacao (Bohlke & Chaplin, 1968).

In Belize, interspecific competition for holes between *A. spinosa* and *A. greenfieldi* was inferred by the field observations of Greenfield & Greenfield (1982). Small-scale microhabitat partitioning between the two species occurred, with *A. greenfieldi* occupying holes in the horizontal surfaces of dead coral and *A. spinosa* occupying holes in the vertical surfaces. *A. greenfieldi* was the larger of the two species, with the males of both species being larger than and outnumbering the females. Although adults exhibited complete habitat separation, larval *Acanthemblemaria* species apparently settled and occupied any available hole or crevice. When they outgrew their holes and searched for larger ones, *A. spinosa* appeared to be excluded from the horizontal habitat by the larger *A. greenfieldi*, possibly because of a size advantage.

In St. Croix, *A. spinosa* occupied higher locations on dead coral heads of *Acropora palmata* than *A. aspera* (Clarke, 1989). Correlative evidence of a substantial increase in their local population sizes after a massive *A. palmata* dieoff, which apparently provided many new shelter holes, suggested that suitable habitat was limiting for these species.

Here we describe an experimental test of the hypothesis that holes are a limiting resource determining the number of *A. spinosa* that can live on a coral head. If this hypothesis is true, then increasing the number of holes on a coral head should allow the local population size to increase, and conversely, increasing only the number of fish on a coral head should not.

To test the hypothesis, we manipulated both the density of spinyhead blennies and the absolute number of holes on isolated coral heads. Specifically, we added blennies to coral heads with and without vacant holes, to determine whether: (1) introduced fish would occupy vacant holes as homesites; and (2) introduced fish could displace residents from their holes. We also monitored the coral heads from which resident blennies were removed, to determine whether: (1) immigration would occur naturally; and (2) remaining resident fish would abandon their holes in favor of the vacated holes. Finally, we displaced blennies various distances from their homesites to determine the homing abilities of this species.

METHODS

STUDY SITE

The study took place on reefs surrounding Saba Island and Flat Cay, located about 2 km off the southwest coast of St. Thomas, US Virgin Islands. The reefs extend

upward from a sand bottom at 10 m depth to a crest 0.5 m deep. The fieldwork was conducted during August and September 1991 in 6–10 m of water while scuba diving.

FISH TAGGING AND CENSUSES

To identify individuals, we marked and measured fish underwater. Fish were captured with a dilute mixture of quinaldine and ethanol, handled in dip nets and plastic bags, and marked in situ immediately after capture to minimize handling stress. Marks were applied by subcutaneous injection of colored acrylic latex paint on the post-anal surface of the fish using a fine-gauge syringe. Each fish received an individual mark by varying paint color and marking position.

While each fish was in captivity, both the fish and the diameter of its hole were measured with a ruler. Hole depth was not measured because: (1) we could not see far into the narrow holes, so we had no way of knowing the internal shape of, and therefore, the depth of natural holes without destroying coral heads; and (2) even though we observed no obvious courtship behavior during the study, we wanted to avoid possibly damaging any clutches of eggs within the holes.

After marking, each fish was returned to its original hole and observed until it was judged to have fully recovered from the anesthetic. A total of 115 fish from 11 coral heads were so marked, and a diagram of each coral head was made to record the location and diameter of all blenny holes, and the identity of the owners.

The inhabited coral heads were censused 2–4 days after fish marking to determine whether the fish were residing in their recorded holes. Censuses were performed by observing a fish's mark when visible, or by squirting a small amount of ethanol into the fish's hole to cause it to temporarily leave its hole. After identification, the fish was watched until it safely returned to its hole. Some of the study fish were used as unmanipulated controls in some experiments, then later as manipulated fish in subsequent independent experiments. However, once a fish was manipulated, it was never used in another experiment.

We estimated the density of fish (number of fish per m^2) on 6 haphazardly chosen coral heads that were roughly cylindrical in shape. In each case, we calculated the surface area of a cylinder of the same height and diameter (minus the basal area), and divided the number of resident fish by the calculated area.

EXPERIMENTAL DESIGN

Controls

As controls for the following experiments, 19 marked and unmanipulated fish occupying three coral heads (6, 6 and 7 fish each) were censused every 3 days before and during the experiments.

Fish and hole additions

We randomly selected and captured 41 marked fish and 39 unmarked fish with identifiable natural markings and transplanted them to five experimental coral heads, each at least 20 m from the site of capture. The experimental coral heads supported average densities of fish (see RESULTS), had their resident fish marked, were separated from each other by 5–100 m, and were assigned one of three hole treatments: (1) no vacant holes, i.e., all holes contained resident fish ($n = 3$ coral heads; 5, 11, and 14 fish added, respectively); (2) 9 vacant holes (0.5 cm diameter, the average of natural holes (see RESULTS), by 5 cm deep) created by drilling directly into a coral head ($n = 1$; 10 fish added); and (3) 68 vacant holes created by adding four blocks of wood ($10 \times 10 \times 25$ cm), each with 16–18 holes (0.5 cm diameter by 5 cm deep) and attached to a rebar stake pounded into a coral head ($n = 1$; 40 fish added). Numbers of fish added and number of replicates in each case were determined solely by logistic constraints (capture success, time limitations, etc.). Each experimental and control coral head was recensused 3 days after these manipulations to determine the number of fish remaining.

Fish removals

The removal experiment ran concurrently with the addition experiment, with some of the fish used for the addition experiment coming from the two coral heads used for the removal experiment. From one of these coral heads, half of the 22 resident fish (randomly chosen) were removed ("50% removal"), and from the other, all 15 resident fish were removed ("100% removal"). Censuses were made every other day for 2 wk to determine immigration levels and movement among the remaining fish.

Hole additions

We tested for immigration to new holes, without concurrent addition of fish, in two ways. First, we drilled eight additional holes into a coral head (as above) and censused this head four times over the next 2 wk. Second, we placed four wooden blocks, each with 16–18 holes (as above), at haphazard locations on the study reef, each separated by at least 10 m. These "blenny condos" were censused five times over the next 2 wk.

Homing

We used a displacement experiment to determine the homing abilities of *A. spinosa*. We transplanted 47 marked fish, 11 fish to coral heads 5 m away, and 36 fish to coral heads 20 m away. The habitat between the home site and the release site for each fish was approximately the same regardless of displacement distance. As a control, 45 marked fish were captured individually and released at their home coral heads. Censuses of the capture and release sites were made 10 min, 24 h, and 48 h after displacement.

RESULTS

Spinyhead blennies on the study reef averaged 2.66 cm in total length (range: 1.1–3.6, SD = 0.42, $n = 98$), occupied abandoned worm holes averaging 0.49 cm in diameter (range: 0.3–0.8, SD = 0.09, $n = 43$), and occurred at densities averaging 9 fish·m^{-2} (range: 4–19, SD = 5.89, $n = 6$ coral heads). Some of the blennies were relatively isolated, whereas others lived as close as 2 cm to each other. The giant brain coral *Colpophyllia natans* and the star coral *Montastrea annularis* had highest densities of both holes and blennies.

Of the 115 marked fish, 109 were located 48 h after marking. Of these 109 fish, 102 were still residing in their previously recorded holes and 7 did not have any obvious hole.

EXPERIMENTAL CONTROLS

The 19 unmanipulated control fish occupying three coral heads remained unchanged throughout the 2 wk covering all experiments.

FISH AND HOLE ADDITIONS

The addition of fish to three populated coral heads lacking vacant holes did not appreciably increase local population sizes after 3 days (Table I, Fig. 1A). Only 4 of the 30 added fish ultimately remained on the coral heads; the remainder disappeared

TABLE I

Summary of fish and hole addition experiments.

| | Number of holes added | | | | |
| | 0 | | | 9 | 68 |
Replicate:	1	2	3	1	1
Beginning of experiment:					
No. of original residents	8	16	17	8	18
No. of transplants added	5	11	14	10	40
Total	13	27	31	18	58
End of experiment:					
No. of original residents	8	15	16	8	17
No. of transplants present	0	2	2	6	26
Total	8	17	18	14	43
Net change in no. of fish[a]	0	+1	+1	+6	+25

[a] Equals the total number of fish present at the end of the experiment minus the original number of residents at the beginning of the experiment.
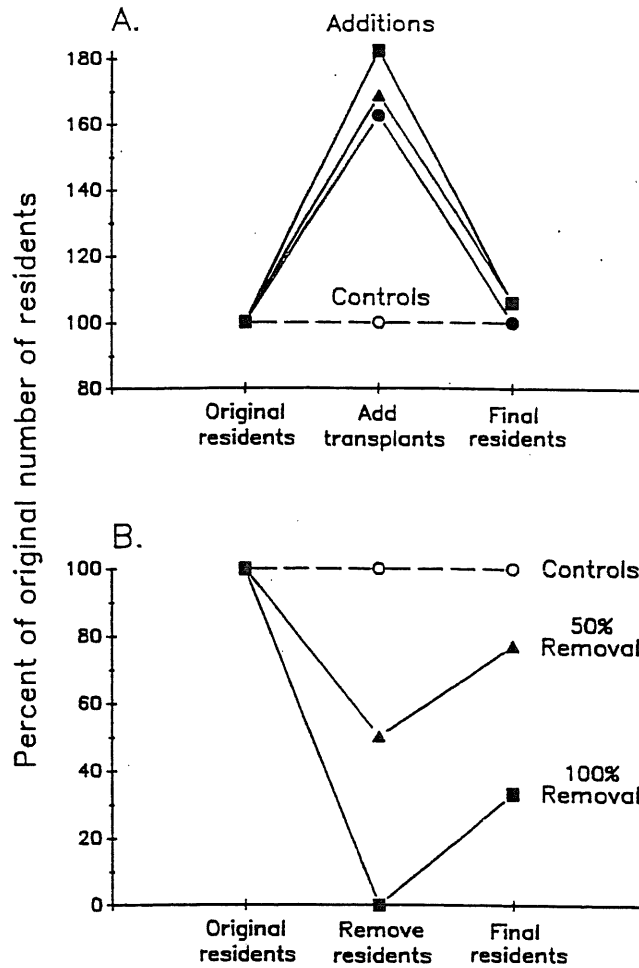
Fig. 1. Results of fish transplants to and from coral heads lacking vacant holes. Each set of solid symbols represents one replicate coral head whose residents were manipulated; the open symbols represent the three unmanipulated control coral heads, whose residents did not change. (A) Fish addition ($n = 3$ coral heads). See Table I for numbers of fish involved in each replicate. (B) Fish removals ($n = 2$ coral heads). The "50% removal" involved 22 original residents, and the "100% removal" involved 15 original residents.

within 3 days. Predation by redspotted hawkfish (*Amblycirrhitus pinos*) and lizardfish (*Synodus* sp.) within an hour after the additions accounted for the disappearance of at least 10 of these fish (pers. obs.). During the experiment, two of the original residents of the coral heads disappeared, so there was a net increase of only two fish despite the addition of 30 fish. Thus, comparing the beginning to the end of the experiment, there was no significant difference in the populations sizes of the three coral heads (Wilcoxon signed ranks test [nonparametric paired comparison], $p \gg 0.05$, $Z = 1.414$).

Casual observation indicated that aggressive interactions between the added fish and the resident fish were common. These interactions were usually initiated by fish that were not in holes. The initiator would invade a hole head first, grab the resident by the head or jaws and spin vigorously. These interactions lasted several minutes, and no initiator was observed removing the resident fish. Resident fish appeared to have the advantage and usually remained in possession of their holes, although the four added fish that secured holes apparently did so by displacing smaller residents. Half of the

four displaced residents remained 3 days after the additions, sheltering in crevices on their home coral heads.

The addition of fish to two populated coral heads with vacant holes added did substantially increase local population sizes (Table I). On the coral head with 9 holes added, 6 of the 10 added fish occupied holes at the end of the experiment (the remainder had disappeared). Five of these fish occupied new holes that had been added, while one displaced an original resident, who in turn moved to one of the new holes. On the coral head with 68 holes added, 26 of the 40 added fish occupied holes at the end of the experiment (the remainder had disappeared). All but 2 of these fish occupied new holes, these 2 having displaced original residents. One of the displaced residents in turn moved to one of the new holes, whereas the other disappeared. Thus, there was a net increase of 31 fish (119% of the original 26 residents) after 50 fish were added to coral heads with newly added vacant holes. We observed 2 of the added fish that had not yet found a hole being eaten by lizardfish within an hour of the additions.

FISH REMOVALS

Fig. 1B combines the results of both removals. Within 2 wk after half of 22 resident fish were removed from one coral head ("50% removal"), 3 of the remaining fish abandoned their original holes and moved into newly vacated holes, which were previously occupied by larger fish (0.3, 0.4, and 0.5 cm larger, respectively). Immigration of fish from the surrounding reef brought the local population size to 17 fish (77% of its original size) within 2 wk.

When all 15 fish were removed from another coral head ("100% removal"), immigration was at a lower rate, reaching 5 fish (33% of the original population size) after 2 wk (Fig. 1B). The average size of the 5 immigrants was 1.86 cm TL, significantly smaller than the 2.46 cm average of the original residents (t-test, $p = 0.001$, df $= 18$).

HOLE ADDITIONS

Five of the 8 holes created by drilling into a coral head were occupied within 3 days, with no subsequent change during the next 2 wk.

Nine fish took up residency in the four empty "blenny condos" within 2 wk of placing them on the reef (0, 2, 3, and 4 fish per condo, respectively). The average size of these immigrants was 1.51 cm TL, significantly smaller than the 2.66 cm average of 98 unmanipulated residents of coral heads (t-test, $p < 0.001$, df $= 105$).

HOMING

When 45 control fish were individually removed from their holes and returned to the same coral head, they rapidly returned to their original holes. Of the 11 fish displaced 5 m, 7 returned to their home corals and holes within 2 days. However, none of the 36 fish displaced 20 m returned to their original coral head within 2 days (Fig. 2).
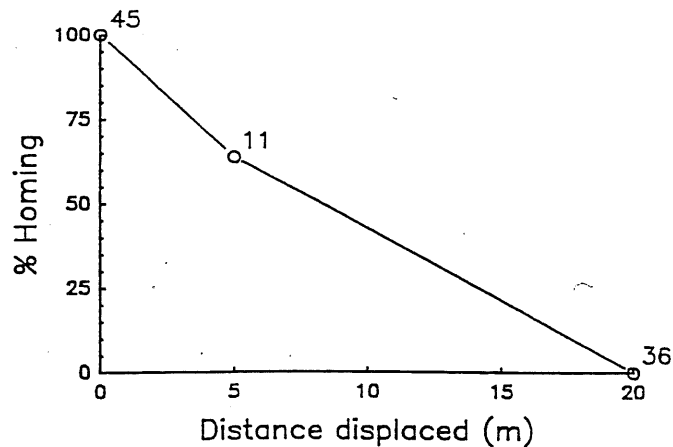
Fig. 2. Results of fish homing experiment, showing the percent of fish homing from three different displacement distances. For each distance, the number of displaced fish is indicated.

DISCUSSION

Our results are consistent with the hypothesis that holes are a limiting resource determining the number of spinyhead blennies that can live on a coral head. By increasing the number of holes on a coral head, we were able to increase the resident population of blennies. In contrast, regardless of the number of fish added to coral heads without vacant holes, the number of resident fish remained relatively constant. These patterns suggest that a coral head could support a larger population of blennies if more suitable shelter holes were available.

A suitable shelter for these fish appears to be a hole deep enough to fully retreat into and slightly larger than the diameter of their body, although internal size and shape may be an important aspect of hole quality. Possession of a hole appears to be critical for survival, since holeless fish were often consumed by predators and fish fiercely defended holes. Prior residency appears to be a major advantage in defending a hole, although larger intruders were sometimes able to displace smaller residents.

Resident fish were observed to redistribute themselves among holes on a coral head after neighbors were removed, suggesting that the holes are of different qualities. In every case, the fish that moved to an emptied hole was smaller than the original resident, which suggests that larger (and presumably aggressively dominant) fish occupied superior holes.

When resident fish were removed from a coral head, the coral head was repopulated by smaller fish from the surrounding reef. This pattern suggests either that there was a population of "floaters", which may occupy crevices or other inferior shelters, or that fish with holes actively searched for higher quality holes. Our homing experiment suggests that spinyhead blennies can leave their holes, move at least 5 m away, and return to their original hole.

Overall, these experimental results suggest that, over the limited spatial and temporal scale of our study, spinyhead blennies compete intraspecifically for shelter holes. These

results bolster conclusions from previous observational studies that interspecific competition for holes occurs in this genus (Greenfield & Greenfield, 1982; Clarke, 1989).

At a broader scale, these studies add to the increasing evidence that competition for shelter is a common occurrence among coral reef fishes (e.g., Shulman, 1985; Hixon & Beets, 1989, 1993; review by Hixon, 1991). This conclusion is complemented by the correlative study of Roberts & Ormond (1987), who found that the density of holes in reefs per se accounted for 77% of the variance in fish abundance on Red Sea reefs. It appears that shelter of the appropriate characteristics is an essential refuge for reef fishes (and/or their demersal eggs) to avoid predation (review by Hixon, 1991). However, it is equally important to note that shelter has also been demonstrated to not be limiting in other studies (e.g., Robertson & Sheldon, 1979; Robertson et al., 1981). Ultimately, the relative importance of competition versus other processes in determining the distribution and abundance of reef fishes depends on a myriad of factors that seems to vary in time and space at many scales.

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