NON-RANDOM USE OF THREE-DIMENSIONAL STRUCTURES BY THREE CARIBBEAN CORAL REEF FISHES

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Abstract. Two major hypotheses focus on the coexistence of coral reef fish under spatial limitations: habitat specialization and niche partitioning, and habitat generalization and lottery recruitment. To investigate potential niche partitioning in the back reef of Little Cayman Research Centre, we compared the use of different types of three-dimensional structures to their availability in the environment, for three diurnally territorial fish: squirrelfish (*Holocentrus spp.)*, French grunt (*Haemulon flavolineatum*), and beaugregory (*Stegastes leucostictus*). Individual fish of these species were censused in a 100 m section of the back reef, recording structure use for each fish. We used 30 one-m^2 quadrats to determine the availability of each type of structure. Except for juvenile beaugregories, fish species used different habitat structures non-randomly, i.e., in significantly different proportions from what was available. Patterns of use of habitat structures differed significantly across species. Our results suggest the importance of heterogeneity in three-dimensional structure and niche partitioning in maintaining reef fish diversity.

Key Words: niche partitioning, lottery theory, space limitation

INTRODUCTION

Despite many years of investigation, the mechanisms allowing coexistence of so many fish species on coral reefs are still somewhat unclear. Major hypotheses have focused on two distinct processes maintaining coral reef fish diversity: habitat specialization and niche partitioning (equilibrial dynamics), and habitat generalization and lottery recruitment (non-equilibrial dynamics) (Sale 1977, Gladfelter and Johnson 1983, Gratwicke and Speight 2005). However, there has been no general agreement on the relative importance of these processes.

Peter Sale, who has extensively researched reef fish dynamics, focuses on generalized habitat use as a key component of fish coexistence, suggesting that the frequent disturbances and changes of structural complexity on coral reefs select (within a species) for individuals who are habitat generalists, as specialization would reduce reef available for colonization (Sale 1977). Other studies of habitat use and fish recruitment to new substrates have supported this hypothesis, showing that the identity of colonizing species may be driven solely by who arrives first on the new substrate (e.g., Sale 1977, Sale and Dybdahl 1978, Sale 1978a, Sale 1978b, Gratwicke and Speight 2005).

This lottery model of colonization states that all fish species are equally likely to colonize a substrate, with none having a competitive advantage at that stage. Despite this, Sale and others (e.g., Gratwicke and Speight 2005) still demonstrate the need for a diversity of three-dimensional structure in reef ecosystems, and focus on space as the major limiting factor in coral reef fish ecosystems.

Others disagree with the lottery model, focusing instead on niche specialization to explain coexistence (Gladfelter et al. 1980, Gladfelter and Johnson 1983). These authors suggest that specialized habitat requirements are important in reef species colonization and survival, and that the small-scale studies suggesting high niche overlap (e.g., Sale and Dybdhal 1978) may have limited applicability to reef-wide community processes (Gladfelter *et al.* 1980).

We believe that Sale overstates habitat generalization in coral reef fish species, using their ability to colonize similar coral structures on a reef as evidence against niche partitioning (Sale and Dybdahl 1978, Sale 1975, Sale 1978a). To better understand space limitation and niche partitioning, we studied substrate use and habitat availability of three different fish species on the back reef of Little Cayman. We hypothesized that spatial resources (in this case three dimensional habitat structures) are partitioned even among species known as habitat generalists. Support for our hypothesis would, in turn, support niche partitioning (at least for these three species) as an important process in fish species coexistence.

We chose three diurnally territorial fish. Squirrelfish (*Holocentrus spp.*) are sedentary and aggressively territorial during the day (Deloach and Humann 1999), but disperse at night to feed on benthic crustaceans (Gladfelter and Johnson 1983). French grunts (*Haemulon flavolineatum*) are noctural feeders on benthic prey, such as polychaetes and crabs (Burke 1995). Both solitary and schooling French grunts defend territory diurnally. Nocturnally, they migrate to and from foraging territories in predetermined pathways that may persist for up to two years (Burke 1995). Beaugregory damselfish (*Stegastes leucostictus*) are carnivores with small territories, feeding primarily on crabs, shrimp, eggs, and worms diurnally (Deloach and Humann 1999). All three fish species are abundant on the back reef directly offshore from the Little Cayman Research Centre. Hereafter, we refer to these species as the "target species".

We focused on two main questions, namely (1) do habitat structures used by the target species differ and (2) does a target species'

use of different habitat structures reflect the abundances of those structures in the reef environment.

We hypothesized that partitioning of spatial resources would occur on the back reef. Therefore, we expected habitat use to differ among species and each species to use structures "preferentially", i.e., disproportionately to their availability. Based on previous literature (Deloach and Humann 1999, Burke 1995, Sale 1978a), we predicted squirrelfish would be found mostly under overhangs, French grunts and juvenile beaugregories would use any three-dimensional structure available, and adult beaugregories would use rough coral.

METHODS

To determine fish substrate use, we observed 219 fish (110 adult beaugregories, 37 juvenile beaugregories, 41 French grunts, and 28 squirrelfish) on 25-26 February 2007, on the back reef behind the Little Cayman Research Centre on Little Cayman Island. Beginning *c.* 100 meters east of the research station, and continuing for 100 m toward the west, we censused all target species within five meters of the back reef. For each fish, we noted the species, whether it was juvenile or adult, and the type of three dimensional habitat structure where we found the fish (i.e., the nearest structure to the fish). No juvenile French grunts or squirrelfish were found during the census.

We separated structures used by fish into the following categories: plant/algae matter, branching coral (e.g., staghorn coral, sea fans), smooth coral (e.g., starlet coral or brain coral), overhang (defined as any coral growth that protruded over another substrate and provided shelter from light), and rough coral (defined as any coral with holes or crevices). Because there was a wide range in the size of the holes within rough coral, we split it into two size categories: "Rough ≤ 5" (with an average hole size of 0-5 cm) and "Rough > 5" (with an average hole size greater than 5 cm). Average hole size was calculated using all hole sizes in the coral under the surveyed fish.

To determine the availability of each of the above categories of habitat structure, we sampled 30 randomly-placed quadrats (1 x 1 m) on 26 February and estimated the proportion of each type of substrate within each quadrat. Quadrats were placed in the same area as the fish census.

We used four chi-square tests to determine if fish were using certain substrates disproportionately to their availability, for all species combined and for each target group (species and adult/juvenile stage). Sand, branching coral, plants, and

smooth coral were excluded from these analyses because very few fish (10 out of 216) were found on these substrates. Excluding them created a more demanding statistical test, because including them would have made a chi-square test highly significant (these substrates comprise a significant proportion of the sampled environment).

RESULTS

Across all target fish individuals, 40.4% used overhangs, 32.3% used Rough>5cm, 23.3 % used Rough≤5cm, 1.6% used smooth coral, 1.3% used branching coral, and 0.2% used plants.

Adult beaugregories, French grunts, and squirrelfish each used coral structure types (Rough ≤ 5 cm, Rough > 5 cm, overhang) disproportionately to their availability (χ^2_2=70.26, P<0.0001; χ^2_2=45.53, P<0.0001; χ^2_2=79.36, P<0.0001, respectively). Beaugregories used Rough > 5cm 268% more than expected if they were using habitat structures randomly. French grunts used Rough > 5cm and overhangs 287% and 150% more than expected, respectively. Squirrelfish used overhangs 438% more than expected by chance. French grunts were the only species for which individuals shared a single structure with other individuals (up to 11 total individuals). Juvenile beaugregories used coral structures in a proportion similar to their availability (χ^2_2=2.70, P>0.25). Their largest deviation from random use of structures was use of overhangs (154% greater than expected by chance). See Fig. 1.

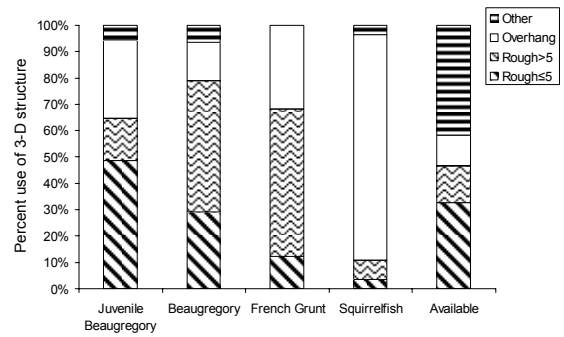

Figure 1. Fish microhabitat use and availability on the back reef of Little Cayman Research Centre on Little Cayman Island. Fish microhabitat use differed significantly from habitat available, for all species categories except juvenile beaugregories. Data were collected 25-26 February 2006. "Rough≤5" represents rough coral with an average hole depth of five centimeters or less; "Rough>5" represents rough coral with an average hole depth greater than five centimeters; "Other" represents sand, plant/algae material, smooth coral, and branching coral. Categories were lumped for "other" because few fish used these substrates.

DISCUSSION

Across target species, most individuals (98.9%) held territories in three-dimensional coral structures, providing support for the importance of shelter and structural complexity as a resource for reef fish (Sale 1972a,b, Shulman 1985, Walker *et al.* 2002, Gratwickel and Speight 2005). Smooth and branching coral were almost never utilized. These

structures have few to no areas (e.g. holes or crevices) where fish can seek refuge and may not be ideal sites for territory establishment.

The results supported our hypothesis that target species would show differential habitat use and generally supported our predictions for age classes within species. Most adult French grunts used large-gap rough coral and overhangs, the only habitat categories that could fully shelter an individual of the species. Our results suggest that shelter may be important in diurnal territory selection. After returning from nocturnal foraging migrations, French grunts may seek protective structures on the back reef, in addition to the protection afforded by their schooling behavior (Burke 1995).

Most squirrelfish used overhangs, large bodies of coral that block light from above. As nocturnal foragers who are sedentary and territorial diurnally (Deloach and Humann 1999, *personal observations*), they may prefer darker areas that isolate them from the water column above.

We observed a shift in microhabitat and structure use from juvenile to adult beaugregories. Although juveniles used rough coral and overhangs in rough proportion to their availability, they were often in overhangs created by coral rubble on the ocean floor. Most adult beaugregories were in large-gap rough coral on the top of coral heads. Because older and larger beaugregories establish territory in more preferred spaces (Ebersole 1985, Deloach and Humann 1999), this shift in habitat use suggests that large-gap rough coral may be a preferred structure for beaugregories within the back reef.

In developing the implications of our findings, we are limited by existing knowledge of space limitation and density dependence in reef fishes at Little Cayman Island. The reef structures of Cayman island are extremely healthy compared to many reefs in the world and therefore space limitation and density dependence may act differently in this community (H. Fourie, *personal communication*). We suggest investigation of space limitation and density dependence in future studies in this community, because of the fundamental importance of these processes. Experimental exclusion of different fish species from various habitat structures would be useful to analyze the partitioning of microhabitats in the back reef system, and elucidate the role of competition, preference, and habitat utility.

In an attempt to disprove the hypothesis that most reef fish are generalists and display high niche overlap (i.e., the lottery hypothesis; Sale 1975, 1977, 1978a), evidence has been provided of resource

partitioning and specialization among taxonomically similar species (e.g., squirrelfish or damselfish) (Gladfelter and Johnson 1983; Ebersole 1985). The debate is complicated by the fact that definitions of generalist and specialist differ among authors and the specificity used when categorizing resources (e.g., habitat structures). We examined microhabitat use by our target species and demonstrated that resource partitioning occurs even among species known as habitat generalists. We found that spatial resources (i.e., habitat structures) are partitioned, supporting the theory that niche partitioning helps maintain fish diversity.

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