DIEL PATTERNS OF CORAL REEF FISH BEHAVIOR IN JACKSON'S BAY, LITTLE CAYMAN ISLAND

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Faculty Editor: David R. Peart

Abstract: Tropical coral reefs harbor a diversity of fish species that may coexist through resource partitioning. This study measured how a reef fish community varied in its species composition and how fish species partitioned their activities from day to night. Nine pairs of snorkelers each observed fish for 40 minutes starting at 0900 and 40 minutes starting at 2000 in Jackson's Bay, Little Cayman Island. We recorded whether we saw fishes'alone' (1-2 fishes) and/or schooling (> 2 fishes) and whether they were active (swimming, feeding, or territory holding) and/or hiding. Since food and predator-free space may be more available during the day, we expected to find greater fish activity and species richness during the day than at night. Out of the 72 fish species we observed, only 23 were found during both the day and night, and the average species richness observed per snorkeler pair was 43% higher during the day than at night. As predicted, we found more species schooling, swimming, feeding, and defending territories during the day than at night. However, contrary to our prediction that fishes would display more predator-avoidance behaviors at night than during the day, the number of fish species alone or hiding did not vary between night and day. These results suggest that fishes increase activity levels during the day but do not increase predator-avoidance behaviors at night. Overall, our study demonstrates that diel resource partitioning may be an important factor in structuring coral reef fish communities.

Key Words: diel fish behavior, coral reef, Little Cayman Island, predator-avoidance, resource partitioning

INTRODUCTION

Resource partitioning may help maintain species coexistence in diverse communities (Diamond 1978). Species may partitioning many different types of resources, including food, shelter, and predator-free space. In diverse fish communities, multiple important resources may vary from day to night, and therefore fish species may partition a suite of resources by partitioning their day and night activities (e.g., deep reefs: Travers et al. 2006, tide-pools: Arakaki and Tokeshi 2006, mangroves: Laroche et al. 1997).

Tropical coral reefs harbor a diversity of fish species that may partition day and night resources. Some reef fish species migrate to different parts of the reef from day to night (e.g., Ruso and Bayle-Sempere 2006). Fishes may also vary their behaviors within habitats from day to night to reduce predation or parasitism risks and/or to maximize foraging efficiencies (e.g., parasitism risk: Sikkel et al. 2006, foraging efficiency: Rickel and Genin 2005, food quality: Zemke-White et al.

2002, predation risk and foraging efficiency: Rickel and Genin 2005). Since many reef fish species appear to use similar food and shelter resources (Sale 1977), dividing these resources between day and night may help facilitate species coexistence. Despite the potential importance of diel resource partitioning in tropical fishes, there are still few studies that document how community assemblages and fish behaviors within habitats change from day to night.

In this study, we compared fish species richness and behaviors from day to night in a Caribbean fringe coral reef in Jackson's Bay, Little Cayman Island. Little Cayman Island is home to an abundance of healthy coral reefs and harbors a large diversity of fish species (H. Fourie, *personal communication*). We hypothesized that patterns in food resource availability and predation risk might drive diel patterns in fish species assemblages and behaviors. During the day, photosynthetic food resources as well as herbivorous fish prey may be more available. Additionally, predators may be easier to see and avoid in the light. Therefore, overall, we predicted fishes to be more active during the day. Alternatively, some species may have adapted to night conditions (e.g., by developing large eyes to spot predators and/or feeding preferences for nocturnal zooplankton). We tested how the fish community as a whole (using species as replicate samples) varied in their propensity to: be 'alone' (1-2 fishes), school (>2 fishes), swim, hide, feed, and defend territories. Specifically, we predicted to see more species being solitary at night and more schooling during the day than at night. We expected species to swim, feed, and defend territories more during the day and hide more at night.

METHODS

We observed diel patterns of fish behavior on 25 February, 2007 in Jackson's Bay on the north side of Little Cayman Island. We snorkeled in pairs (9 pairs total), and each pair recorded all fish species observed in a 4 m x 3 m section of the shoreward side of the fringing coral reef. Each group observed the reef for 40 minutes during two time periods: day (starting at 0900) and night (starting at 2000). Groups were evenly spaced over 100 m of this reef approximately 25 m to the west of the Little Cayman Marine Research Center. For each fish species, we recorded whether or not we observed it in either of two grouping categories: ('alone': 1-2 fishes or 'schooling': >2 fishes) and in any of four activity categories (swimming, hiding, eating, and defending territories). Each group recorded the presence or absence of fishes in each category for each species.

We compared fish species richness during the day and night by comparing the total number of species observed and the mean number of species observed per group in each time period. Using the 23 species that we found in both day and night samples, we tested whether or not each grouping and behavior category was more frequently seen during the day or at night with six separate matched-pairs t-tests (pairing by species, n = 23 species).

RESULTS

We observed 72 total fish species, 23 of which were found both during the day and at night (Table 1). During the day, we observed 51 species, 28 of which were only found during the day. At night, we observed 44 species, 21 of which were only found at night. Average fish species richness per snorkeler pair was 43% higher during the day than at night (t_{16} = 4.64, P = 0.0003; Figure 1). Significantly more groups on average observed fish schooling (t_{22} = -3.4, P = 0.0012), swimming (t_{22} = -2.0, P = 0.027), and feeding (t_{22} = -2.7, P = 0.007) during the day than at night (Table 2). Marginally significantly more groups observed fish defending territories during the day than at night (t_{22} = -1.6, P = 0.057, Table 2). We found no difference in the average number of pairs that observed fish alone (t_{22} = -1.1, P = 0.86) or hiding (t_{22} = 1.1, P = 0.14) between day and night (Table 2).

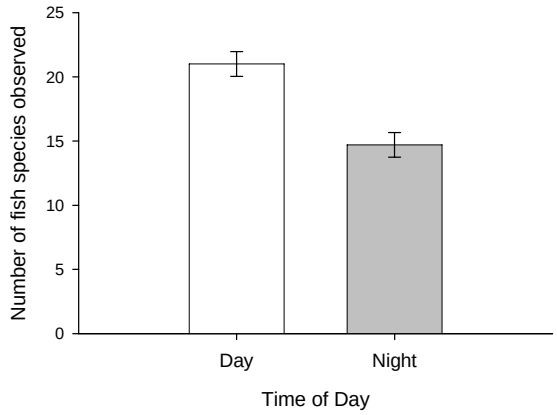

Figure 1. The average number of fish species observed by each group (n = 9) at Jackson's Bay, Little Cayman Island during the day and at night. Error bars represent ± 1 SE.

Table 1. All fish species found by 9 pairs of snorkelers observing fish for 40 minutes during the day and 40 minutes at night in a 100 m stretch of fringing coral reef at Jackson's Bay, Little Cayman Island and the number of snorkeling pairs that observed the species in two grouping categories and four behavioral categories. Bolded species were observed both day and night and used in the paired t-tests.

	Grouping				activities							
species	day alone	night alone	day school	night school	day swim	night swim	day feed	night feed	day territory	night territory	day hide	night hide
Anchovy	0	1	0	3	0	3	0	0	0	0	0	0
Banded Butterflyfish	**8**	**7**	**2**	**1**	**7**	**7**	**4**	**0**	**0**	**0**	**1**	**1**
Bar Jack	**2**	**0**	**0**	**1**	**2**	**1**	**1**	**0**	**0**	**0**	**0**	**0**
Beaugregory	**8**	**4**	**1**	**0**	**4**	**2**	**2**	**0**	**9**	**0**	**4**	**3**
Belted Cardinalfish	0	1	0	0	0	1	0	0	0	0	0	0
Bermuda Chub	1	0	1	0	2	0	0	0	0	0	0	0
Bicolor Damselfish	2	0	0	0	1	0	0	0	2	0	0	0
Big-tooth Cardinalfish	0	1	0	0	0	1	0	0	0	0	0	0
Blue chromis	0	0	0	1	0	1	0	0	0	0	0	0
Blue Headed Wrasse	4	0	8	0	7	0	7	0	1	0	2	0
Blue Striped Grunt	**4**	**5**	**0**	**1**	**1**	**5**	**1**	**0**	**0**	**0**	**2**	**3**
Blue Tang	**8**	**8**	**3**	**0**	**9**	**3**	**3**	**0**	**0**	**0**	**1**	**7**
Bridled Goby	1	0	0	0	1	0	0	0	0	0	1	0
Ceasar Grunt	**2**	**5**	**5**	**1**	**6**	**4**	**0**	**0**	**0**	**0**	**1**	**2**
Clown Wrasse	1	0	0	0	1	0	0	0	0	0	1	0
Cocoa Damselfish	2	0	0	0	2	0	0	0	0	0	1	0
Dash Goby	1	0	0	0	1	0	1	0	0	0	1	0
Doctorfish	**2**	**4**	**0**	**0**	**1**	**2**	**1**	**0**	**0**	**0**	**2**	**3**
Dusky Cardinalfish	0	6	0	4	0	8	0	1	0	0	0	2
Dusky Damselfish	3	0	0	0	2	0	1	0	1	0	0	0
Dusky Squirrelfish	0	0	0	1	0	1	0	0	0	0	0	1
Flamefish	0	3	0	0	0	2	0	1	0	0	0	2
Foureye Butterflyfish	1	0	0	0	1	0	0	0	0	0	0	0
French Angelfish	**8**	**1**	**0**	**0**	**6**	**0**	**1**	**0**	**0**	**0**	**3**	**1**
French Grunt	**6**	**5**	**2**	**1**	**8**	**4**	**0**	**0**	**0**	**0**	**4**	**3**
Glasseye Snapper	0	1	0	0	0	1	0	0	0	0	0	1
Greater Soapfish	0	2	0	0	0	2	0	0	0	0	0	0
Houndfish	0	1	0	0	0	1	0	0	0	0	0	0
Longjaw Squirrelfish	**6**	**6**	**0**	**0**	**2**	**5**	**0**	**0**	**1**	**0**	**5**	**4**
Longspined Squirrelfish	0	2	0	0	0	2	0	0	0	0	0	0
Mahogany Snapper	**4**	**2**	**3**	**0**	**5**	**2**	**2**	**0**	**1**	**0**	**0**	**1**

species	Grouping				activities							
	day alone	night alone	day school	night school	day swim	night swim	day feed	night feed	day territory	night territory	day hide	night hide
Molly miller	0	1	0	0	0	0	0	0	0	0	0	1
Mutton Snapper	**1**	**1**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**0**	**1**
Neon Goby	1	0	1	0	1	0	0	0	0	0	0	0
Ocean Surgeonfish	**7**	**5**	**2**	**1**	**6**	**2**	**6**	**0**	**0**	**0**	**1**	**5**
Peacock Flounder	1	0	0	0	1	0	0	0	0	0	1	0
Porcupine Fish	**1**	**1**	**0**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**1**	**0**
Princess Parrotfish	2	0	1	0	2	0	3	0	0	0	0	0
Puddingwife Wrasse	1	0	0	0	1	0	0	0	0	0	0	0
Rainbow Parrotfish	0	1	0	0	0	1	0	0	0	0	0	1
Red Hind	0	1	0	0	0	0	0	0	0	0	0	1
Redband Parrotfish	2	0	0	0	1	0	1	0	0	0	0	0
Redtail Parrotfish	0	1	0	0	0	1	0	0	0	0	0	1
Reef Squirrelfish	0	4	0	0	0	3	0	2	0	0	0	2
Rock Beauty	2	0	0	0	1	0	2	0	0	0	0	0
Rockhind	1	0	0	0	0	0	0	0	0	0	1	0
Rosy Razorfish	0	1	0	0	0	1	0	0	0	0	0	0
Saddled Blenny	**2**	**2**	**0**	**0**	**1**	**1**	**0**	**0**	**0**	**0**	**1**	**1**
Sandtile	1	0	0	0	0	0	1	0	0	0	0	0
Schoolmaster Snapper	**4**	**3**	**7**	**2**	**7**	**3**	**0**	**0**	**0**	**0**	**2**	**2**
Scorpionfish	2	0	0	0	0	0	0	0	0	0	2	0
Sergeant Major	**7**	**8**	**4**	**1**	**9**	**3**	**1**	**0**	**1**	**0**	**4**	**6**
Sharpnose Pufferfish	1	0	0	0	1	0	0	0	0	0	0	0
Sheapshead	1	0	0	0	0	0	0	0	0	0	1	0
Slippery Dick	2	0	3	0	4	0	3	0	0	0	1	0
Soapfish	2	0	0	0	2	0	0	0	0	0	1	0
Spotted Goatfish	3	0	1	0	2	0	1	0	0	0	0	0
Spotted Moray	0	3	0	0	0	1	0	2	0	0	0	2
Spotted Scorpionfish	0	4	0	0	0	0	0	2	0	0	0	3
Squirrelfish	**9**	**9**	**0**	**0**	**1**	**7**	**0**	**4**	**2**	**1**	**8**	**5**
Stoplight Parrotfish	**5**	**7**	**3**	**0**	**6**	**5**	**5**	**0**	**0**	**0**	**1**	**7**
Striped Parrotfish	0	0	3	0	1	0	2	0	0	0	1	0
Surgeonfish	0	2	0	0	0	2	0	0	0	0	0	1
Three Spotted Damselfish	1	0	0	0	1	0	0	0	1	0	0	0
Tiger Grouper	1	0	0	0	0	0	0	0	0	0	1	0

species	Grouping				activities							
	day alone	night alone	day school	night school	day swim	night swim	day feed	night feed	day territory	night territory	day hide	night hide
Trunkfish	**1**	**1**	**0**	**0**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**1**
Two-spot Cardinalfish	0	4	0	0	0	4	0	0	0	0	0	1
Yellowfin Mojarra	2	0	0	0	2	0	0	0	0	0	0	0
Yellowtail Damselfish	**8**	**4**	**0**	**0**	**6**	**1**	**2**	**0**	**2**	**0**	**6**	**4**
Yellowtail Goatfish	**2**	**4**	**2**	**0**	**4**	**4**	**0**	**0**	**0**	**0**	**0**	**0**
Yellowtail Parrotfish	3	0	2	0	3	0	1	0	0	0	1	0
Yellowtail Snapper	**1**	**2**	**2**	**0**	**3**	**2**	**1**	**0**	**0**	**0**	**1**	**0**

Table 2. The average (± SE) number of observer pairs (out of 9 total pairs) that observed fish alone, schooling, swimming, hiding, feeding, and territory holding during the day and at night for the 23 fish species seen at both these time periods at Jackson's Bay, Little Cayman Island.

Fish Behavior	Day	Night
Alone	4.6 ± 0.60	4.1 ± 0.54
Schooling	1.6 ± 0.40	0.39 ± 0.12
Swimming	4.2 ± 0.60	2.8 ± 0.42
Feeding	1.3 ± 0.36	0.17 ± 0.17
Defending territory	0.70 ± 0.40	0.043 ± 0.043
Hiding	2.1 ± 0.45	2.6 ± 0.47

DISCUSSION

Our results suggest that coral reef fishes in Jackson's Bay, Little Cayman Island, change in composition and species richness from day to night. The greater number of species present during the day versus the night may be a result of greater food or predator-free space availability during the day. To determine if food availability is an important factor driving diel fish community and behavioral patterns, future studies on Little Cayman Island could measure the relative availability of fish food and predation pressures during the day versus the night. Studies could also experimentally augment food availability and/or exclude fish predators during the night to test the degree to which species respond to food and/or predator-free space availability. If day fishes do not become more night active as a result of augmented night food resources or decreased predation risk, this would suggest that either these resources are unimportant for diel fish community patterns or that their diel behaviors are fixed. Understanding the flexibility of fish behaviors may help us understand

natural selection on fish behaviors and on plasticity in fish behaviors.

While our data suggest that overall activity levels drop at night, we did not find evidence for increased predator-avoidance behaviors at night (i.e., being alone or hiding). This lack of apparent predator-avoidance behaviors may be because we did not analyze species separately, and while some species may decrease hiding behaviors at night, other species may increase hiding at night (as in Nagelkerken et al. 2000). Future studies should analyze how particular species alter predator-avoidance behaviors along with their overall abundance from day to night.

Finally, while our study quantified diel patterns of reef fish community assemblages and species richness, future studies are needed to test the relative importance of diel resource partitioning in promoting coral reef fish species coexistence. Multiple mechanisms are likely involved in facilitating reef fish species resource partitioning (Sale 1977). Grouping resources available during the day and night helps to incorporate many different resources simultaneously, but does not identify which of these resources is most important in driving community patterns. Additionally, resource partitioning may only be part of why many species can coexist in the same spatial area. Periodic disturbances in the reef may also promote species coexistence, allowing for random recruitment of different reef species at different points in time (Munday 2004). Future studies that explore the mechanisms promoting reef fish species coexistence will contribute to our overall understanding of species coexistence. The rapidly increasing human-mediated deterioration of coral reef habitats adds to the urgency of understanding the coral reef fish community structure.

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