A COMPARISON OF HERBIVORY RATES ON TURTLEGRASS, *THALASSIA TESTUDINUM*, AT TWO CARIBBEAN SITES

MAYDA H. NATHAN

Faculty Editor: David R. Peart

Abstract: Herbivory is believed to be a factor controlling seagrass distribution and abundance, but the type of herbivory, identity of the herbivores, and the consequent pattern of herbivory may vary among seagrass beds. The marine angiosperm *Thalassia testudinum*, or turtlegrass, is ubiquitous in the Caribbean, and is consumed primarily by fish and sea urchins. I predicted that *Thalassia* would experience higher herbivory in beds at Little Cayman Island than in beds at Discovery Bay, Jamaica, where fish and sea urchin populations are depressed. Instead, I found almost no evidence of herbivory on experimentally-placed *Thalassia* blades in beds at Little Cayman Island. I explore several mechanisms behind this unexpected result, including altered food webs, differences in bed configuration, and idiosyncratic characteristics of *Thalassia* subpopulations.

Key Words: Little Cayman Island, Discovery Bay, Jamaica, Scaridae, Diadema

INTRODUCTION

Tropical coral reef plants may experience the highest herbivory rates of any plant community on earth (Bolser and Hay 1996), and herbivory is thought to influence the productivity, abundance, spatial distribution, and chemical composition of algae and seagrasses (Randall 1965, Ogden *et al.* 1973, Ogden 1976, Hay *et al.* 1983, Bolser and Hay 1996, Valentine and Heck 1999). The angiosperm turtlegrass, *Thalassia testudinum*, dominates shallow-water seagrass beds throughout the Caribbean and feeds a number of marine species (Randall 1965, Ogden 1976). Chief among these herbivores are the sea urchin *Diadema antillarum*, a nocturnal feeder, and fishes of the Scaridae (parrotfish) family, which feed diurnally (Ogden *et al.* 1973, Ogden 1976, Hay *et al.* 1983). *Diadema* and most of the Scarids make regular forays from the reef to inshore seagrass beds, *Diadema* traveling up to 10 m (Ogden 1976) and Scarids traveling up to 500 m to feed (Valentine and Heck 1999). These forays may result in *Thalassia*-free "halos" surrounding coral outcrops, although which type of herbivore is responsible for the halo appears to be site-specific (Randall 1965, Ogden 1976, Valentine and Heck 1999).

Extensive herbivory has been reported on the *Thalassia* beds in Discovery Bay, Jamaica. For example, Berry *et al.* (1994) observed bite marks on 39% of

experimentally-placed *Thalassia* blades after just three hours, and Calvi *et al.* (2000) reported instances of 100% area loss of experimental blades over a 24-hour period. In Discovery Bay, Scarids appear to be the primary herbivores, followed by *Diadema* (Dums *et al.* 1997, Rutar *et al.* 1997, Berg *et al.* 1998). The reefs surrounding Little Cayman Island are undisturbed relative to those of Jamaica, where hurricane damage, overfishing, and disease have depleted fish, *Diadema*, and coral populations (Hughes 1994). Because herbivore habitat and populations are more intact at Little Cayman, I predicted that rates of herbivory on *Thalassia* blades at Little Cayman Island would be higher than those found previously at Discovery Bay. Furthermore, since herbivorous fish may be more abundant near coral head shelters, I predicted that there would be higher herbivory on *Thalassia* near the coral than on *Thalassia* near the shore.

METHODS

On the afternoon of 25 February, 2007 I collected undamaged *Thalassia* blades from the back reef and lagoon (landward of the reef crest) outside the Little Cayman Research Center, Little Cayman Island. I collected the blades haphazardly from two 120-m transects paralleling the shore – one in the *Thalassia* bed, approximately 20 m seaward, and the other within 6 m of the coral, where *Thalassia* appeared less dense. I selected 36 blades from each transect, choosing blades of similar width and with similar epibiont communities, and trimmed all to 8.25 cm long. I randomly grouped the *Thalassia* from each transect into 12 clusters of three blades each, and secured them together using clothespins weighted with steel bolts and flagged with buoys. On the evening of 25 February, 2007 I placed these blades in the fore-reef in a nested design. I chose six sites along the original two transects: three sites 20 m from shore in the *Thalassia* bed paired with three sites 4-6 m from the coral. Each site received four clusters of *Thalassia*, two clusters from the bed and two clusters from the region near the coral, placed approximately 80 cm from one another on the sandy substrate.

I checked the sites on the morning of 26 February, 2007, and noted the loss of one cluster and the entanglement of the buoys and clusters at three sites. Because the tangled string and buoys might deter herbivores, I untangled them and moved them slightly farther apart.

On 27 February, 2007 I collected all clusters 39 hours after placing them on the fore-reef.

RESULTS

Apart from a single Scarid bite mark, no leaf showed any sign of herbivory.

DISCUSSION

Despite extensive herbivore damage to *Thalassia* on the fore-reef of Little Cayman Island (personal observation), I found no evidence of short-term herbivory anywhere on the reef. My field methods differed only in minor details from those of previous short-term studies at Discovery Bay, Jamaica (Berry *et al.* 1994, Dums *et al.* 1997 Berg *et al.* 1998, Calvi *et al.* 2000). Contrary to my predictions, grazing pressure both near shore and near coral in the seagrass beds surrounding Little Cayman Island may be much lower than in Discovery Bay.

Differences in the populations of fish and sea urchins between Little Cayman Island and Discovery Bay may account for my finding. While *Diadema* density at Discovery Bay may be quite high (approximately one individual per square meter) (Dallison *et al.* 1999), I saw very few *Diadema* over the three days of the study. A lower level of fish herbivory at Little Cayman Island is more difficult to explain, but could be attributable to the nature of the overfishing afflicting Jamaica. Fishermen in Jamaica probably target larger fish, releasing small species (such as *Sparisoma radians*, the smallest Scarid and a species that uniquely lives in and mostly eats *Thalassia*) (Ogden 1976) from predation pressure, thus allowing them to expand their ranges and/or population sizes. However, in 1992, *Scarus taeniopterus* and *Sparisoma viride*, larger Scarid species, were the most abundant Scarids in the fore-reef of Discovery Bay (Bizzarro *et al.* 1992). Taking the prevalence of these large species into account, an alternative explanation for my finding could be that the depletion of living coral in Discovery Bay may have forced the Scarids there to graze in seagrass beds more frequently than they would otherwise. Future studies that document which Scarid species consume *Thalassia* at Discovery Bay would reveal which of these scenarios is correct.

The orientation of a seagrass bed in relation to the reef may also determine the extent to which the seagrass is consumed. While the beds at Little Cayman Island are in swaths that parallel the beach and reef crest, the bed studied at Discovery Bay is roughly square, bordered on one side by mangroves and on another by coral (Calvi *et al.* 2000). Fish and sea urchins may be more likely to enter the Discovery Bay seagrass bed because of the protection afforded by nearby mangrove roots and coral. *Thalassia* beds more similar to those at Little

Cayman do apparently occur in Jamaica, outside Discovery Bay (Macia and Robinson 2005); by comparing these beds to those at Little Cayman, researchers could start to disentangle the effects of seagrass bed layout and fish and urchin communities on herbivory.

Other features of seagrass beds that could influence herbivory include *Thalassia* density, the epibiont load of *Thalassia*, and *Thalassia* palatability. If *Thalassia* density were much higher in the beds at Little Cayman Island, an equivalent amount of total daily herbivory would be dispersed among more blades and would therefore be more difficult to observe. If epibiont density were lower in the Little Cayman *Thalassia* beds, they may be less nutritious for Scarid herbivores who prefer epibionts on the *Thalassia* they eat (Berry *et al.* 1994). Finally, future studies could test for differences in *Thalassia* toughness, chemical defenses, and other factors that may render it less palatable on Little Cayman Island than at Discovery Bay.

In contrast to my results, recent observational studies of the seagrass beds at Little Cayman Island suggest that patterns of herbivory may be similar to those of Discovery Bay. At Little Cayman, the number of bite marks on *Thalassia* leaves per unit area does not change with distance from the reef (Marlow *et al.* 2007); similarly, there is no distance effect on the amount of leaf material removed from experimental blades at Discovery Bay (Berg *et al.* 1998). It is possible that the tangled *Thalassia* clusters in this study frightened herbivores away, but given the consistent lack of herbivory across sites, it seems unlikely that the deterred herbivores would have eaten enough leaf material to equal the rates of herbivory at Discovery Bay. Further studies within *Thalassia* beds at Little Cayman Island may help explain the striking difference in levels of short-term herbivory between these two Caribbean locations.

LITERATURE CITED

Berg, E.S., S.C. Braman, and B.W. Wright. 1998. How fah is fah? Changes in herbivory on Thalassia testudinum with distance from the reef. Dartmouth Studies in Tropical Ecology.

Berry, M.E., D.J. Gardella, and A.N. Swanson. 1994. The importance of visual cues in Scaridae selection of Thalassia testudinum blades. Dartmouth Studies in Tropical Ecology.

Bizzarro, J.J., J.L Dudycha, and A.B. Shabel. 1992. Coral reef fish community structure as a function of substrate complexity. Dartmouth Studies in Tropical Ecology.

Bolser, R.C. and M.E. Hay. 1996. Are tropical plants better defended?

Palatability and defenses of temperate vs. tropical seaweeds. *Ecology* 77(8): 2269-2286.

Calvi, M.S., M.K. Jennings, and K.W. Manaras. 2000. A comparison of herbivory rates in an algae and seagrass bed in the west back reef of Discovery Bay, Jamaica. Dartmouth Studies in Tropical Ecology.

Dallison, C.R.E., B.J. Garcia, A.M. Kim, and M.S. Kim. 1999. Distribution and density of two urchin species and their effects on coral reef community structure. Dartmouth Studies in Tropical Ecology.

Dums, C.I., J.W. Gilbertson, A.J. Siegel, and A. Tolonen. 1997. Herbivory and epiphyte load on turtle grass, Thalassia testudinum, as a function of distance from the reef crest. Dartmouth Studies in Tropical Ecology.

Hay, M.E., T. Colburn, and D. Downing. 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* 58: 299-308.

Hughes, T.P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.

Macia, S. and M.P. Robinson. 2005. Effects of habitat heterogeneity in seagrass beds on grazing patterns of parrotfishes. *Marine Ecology Progress Series* 303: 113-121.

Marlow, J., J. Post, and H.L. Vu. 2007. Patterns of *Thalassia testudinum* density and herbivory as a function of distance from coral heads. Dartmouth Studies in Tropical Ecology.

Ogden, J.C., R.A. Brown, and N. Salesky. 1973. Grazing by the echinoid Diadema antillarum Philippi: formation of halos around West Indian patch reefs. *Science* 182(4113): 715-717.

Ogden, J.C. 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquatic Botany* 2: 103-116.

Randall, J.E. 1965. Grazing effect on sea grasses by herbivorous reef fishes in the West Indies. *Ecology* 46(3): 255-260.

Rutar, T., J. Shandro, E. Sohn, and A. Williams. 1997. Density dependent herbivory on Thalassia testudinum. Dartmouth Studies in Tropical Ecology.

Valentine, J.F. and K.L Heck, Jr. 1999. Seagrass herbivory: evidence for the continued grazing of marine grasses. *Marine Ecology Progress Series* 176: 291-302.

POPULATION STRUCTURE AND SIZE DISTRIBUTION OF QUEEN CONCH IN GRAPE TREE BAY, LITTLE CAYMAN ISLAND

PAMELA M. COLLINS AND TINA HARRISON

Faculty Editor: David R. Peart

Abstract: Queen conch have been over fished throughout the Caribbean, making population studies important for informing management decisions. We surveyed the conch in a back reef lagoon and found most adult conch were dead from human fishing. Dead conch were larger than live conch. The live conch were concentrated on sandy algal turf and also found in areas of sandy mixed greens (algae and seagrass) and backreef rubble. Our information on shell size, population density, and habitat use by conch wintering at Grape Tree Bay forms the foundation for a more extensive survey currently in progress.

Key Words: fisheries, conservation, Strombus gigas

INTRODUCTION

The queen conch (*Strombus gigas*) is a large herbivorous gastropod found in coastal waters throughout the Caribbean. Though once abundant, conch have been heavily exploited by humans for decades. Local populations have declined, and conch are now protected under Appendix II of CITES (FAO 2004). Conch fisheries are important to the cultures and economies of many Caribbean nations. Since the goal of effective management is to maintain sustainable harvest levels, it is essential to understand the links between conch population structure, distribution, and patterns of human exploitation.

In summer 2006 at Grape Tree Bay, Little Cayman Island, Manfrino and Brown (2006) found low densities of conch (0.25/m^2 alive, 0.36/m^2 dead) and more dead than living individuals. They inferred a declining population, although conch fishing in the Cayman Islands has been regulated by increasingly stringent laws since 1978 (DOE 2004; Timothy Austin, *personal communication*). The study area in Grape Tree Bay falls on the border between a marine park established in 1986 and unprotected waters where harvesting is allowed from May 1 to October 31 (DOE 2004). In 2003, the Cayman Islands Department of the Environment responded to a long-term decline in conch populations by dropping daily harvest limits from 20 conch per person per day to 5 conch per person or 10 conch per boat per day, whichever is lower (Timothy Austin, *personal communication*). Poaching has been an issue around the island because

the position of marine conservation officer on Little Cayman has only recently been filled (John Bothwell, *personal communication*).

As the first part of a larger study examining conch size and distribution around Little Cayman Island (Collins 2007), we expanded on previous work done in Grape Tree Bay by measuring the sizes and age classes of dead as well as live conch and recording occurrences of conch killed by humans. Because conch are subject to size-selective fishing pressure, we predicted that dead conch would be larger and older than live conch.

We also characterized the available benthic habitats within the lagoon and the distribution of conch across those habitats. In the Bahamas, juvenile conch form large aggregations in shallow seagrass beds, while conch older than two years tend to disperse and seek deeper waters, especially in winter when seas are rough (Stoner and Sandt 1992). We therefore expected to find juvenile conch concentrated in shallow seagrass habitat and larger mature conch in deeper sandy habitat closer to the reef.

METHODS

Study organism

Juvenile conch grow by shell accretion until sexual maturity is achieved, between 3.5 and 4 years of age (Stoner and Sandt 1992). Conch then develop a broad flare on the shell lip, known as a flange. Shell length remains constant after sexual maturity, but the flange thickens (Martín-Mora, et al 1995). A combination of length and flange thickness can thus be used as a proxy for age; however, this proxy is not perfect since shell erosion offsets nacre deposition (Stoner and Sandt 1992).

Because conch are generally taken by individual fishermen with minimal technology, conch in shallow water can be heavily exploited compared to conch in deep water, which are accessible only by SCUBA. Therefore, deep water conch may provide larval recruits to heavily fished shallow habitats (Stoner and Sandt 1992).

Sampling

We surveyed the conch population of Grape Tree Bay on 25 – 27 February, 2007, in seven 4-m wide belt transects perpendicular to the shoreline, from the water's edge to the back of the fringing reef (an average distance of 104 m). The study area was a continuous 360 m-long section of shoreline, and transects were separated by 60 m. Maximum water depth was *c.* 3 m.

We counted all conch shells visible within each belt. For each shell found, we recorded distance from shore, shell length (Figure 1), lip thickness, if it was alive or dead, whether there was a chisel opening

in the apical spiral (evidence of human predation), and the habitat in which the conch was found. We observed 7 distinct habitat types distributed in bands across the study area, which we categorized qualitatively by physical substrate and by the type and abundance of vegetative growth (macroalgae and seagrasses) (Table 1). We recorded which habitats were present within each belt transect and the distance from shore where each habitat boundary occurred.

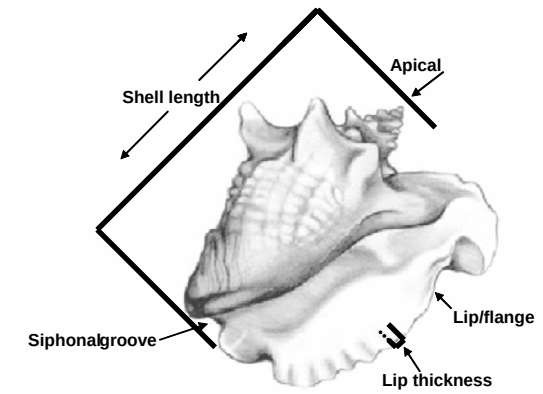

Figure 1. The shell of a mature queen conch (*Strombus gigas*), with measured dimensions and significant features labeled. (Ferren, www.sherpaguides.com).

Table 1. Habitats available to the queen conch, *Strombus gigas*, in a back reef lagoon near Little Cayman Research Center, Little Cayman Island.

Habitat	Substrate	Benthic growth	Est. depth (m)	% of total area
Turtle grass bed	Sand	Turtle grass (*Thalassia testudinum*) and some interspersed manatee grass (Cymodoceaceae) dominate (about 75% or greater cover of angiosperms)	< 1	35.9
Sandy mixed greens and calcareous algae	Sand	Similar to sandy mixed greens, but with high abundance (about 50%) of calcareous algae	< 1	6.6
Crumbly limestone	Limestone	Some calcareous macroalgae; frequent sea urchin colonies	< 1	3.6
Limestone algal turf	Limestone	Similar to sandy algal turf, but on hardpan substrate; calcareous algae often dominant	1.5 - 2	2.0
Sandy mixed greens	Sand	Sparser seagrasses mixed with macroalgae	1.5 - 3	36.3
Sandy algal turf	Sand	Open sand covered with a thin layer of algae; sparse macroalgae present.	1.5 - 3	4.0
Back reef rubble	Broken coral, shells, limestone	Some macroalgae present.	1 – 2	11.6

Statistical analysis

We tested for differences in shell size (i.e., shell length and log-transformed lip thickness) between dead and live conch, first with a MANOVA and then with two one-way ANOVAS. We used a chi-squared analysis to test if conch were randomly distributed with respect to habitat across the habitat types inhabited by conch.

RESULTS

We surveyed a total area of 2907 m^2 and found 59 conch shells, 29 of which contained live conch. Of these 59, 40 were juveniles (flange absent) and 19 were adults (flange present). Roughly two thirds of the juveniles were alive, while only one adult was alive (Table 2). Of the 18 dead adults, 14 had the chisel hole in the apical spiral indicating harvest by humans. Shell size was greater for dead than for living conch (MANOVA, $F_{2,55}$=29.27, P<0.0001) for both shell length (ANOVA, $F_{1,59}$=27.36, P<0.0001) and lip thickness (ANOVA, $F_{1,57}$=59.34, P<0.0001) (Figure 2, Table 2).

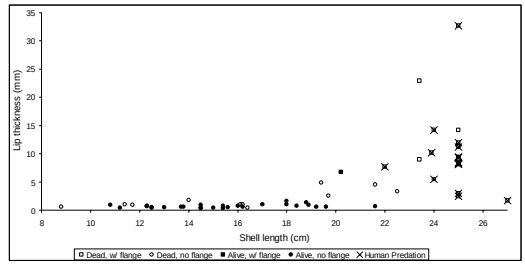

Figure 2. Shell lengths and lip thicknesses of living and dead queen conch (*Strombus gigas*) from Grape Tree Bay, Little Cayman Island. An X overlies each point representing a conch killed by human predation (bearing a chisel hole in its apical spiral).

We found live conch in only three of the seven available habitat types (sandy mixed greens, back reef rubble, and sandy algal turf; Table 1), which comprised 52% of the benthic area surveyed. Conch were distributed non-randomly across these three habitats (χ^2_2 = 171, P < 0.001), showing strong preference for sandy algal turf (Figure 3).

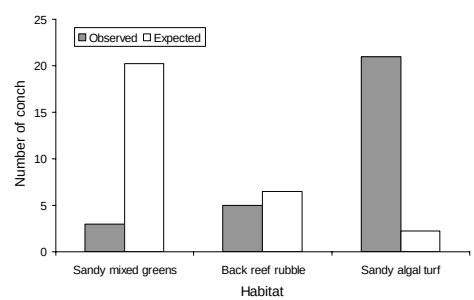

Figure 3. Queen conch were non-randomly distributed with respect to habitat across three of the seven available habitat types (Table 2) surveyed along seven shore-to-reef belt transects in Grape Tree Bay, Little Cayman Island. The three preferred habitats comprised 51.9% of the 2907 m^2 surveyed. "Expected" refers to numbers of conch expected in each habitat if conch were randomly distributed across habitats based on relative area of each habitat.

Table 2. Characteristics of 59 live and dead queen conch (*Strombus gigas*) in seven 4-m wide shore-to-reef belt transects 60 m apart in Grape Tree Bay, Little Cayman Island.

Alive	Juveniles (no flange)	Reproductive adults (with flange)
N	28	1
Mean length ± SE (cm)	15.8 ± 0.6	20
Length range (cm)	11 – 23	N/A
Mean lip thickness ± SE (mm)	0.7 ± 0.06	6.8
Lip thickness range (mm)	0.3 – 1.6	N/A

Dead	Juveniles (no flange)	Reproductive adults (with flange)
N	12	18
Mean length ± SE (cm)	16.8 ± 1.4	24.7 ± 0.4
Length range (cm)	9 - 24	18 - 27
Mean lip thickness ± SE (mm)	2.3 ± 0.5	10.9 ± 1.7
Lip thickness range (mm)	0.4 – 5.5	1.7 – 32.7

All	Juveniles (no flange)	Reproductive adults (with flange)
N	40	19
Mean length ± SE (cm)	16.1 ± 0.6	24.4 ± 0.9
Length range (cm)	10.8 – 24.0	20.2 – 27.0
Mean lip thickness ± SE (mm)	1.2 ± 0.2	10.8 ± 1.1
Lip thickness range (mm)	0.3 – 5.5	1.7 – 32.7

DISCUSSION

We characterized the size structure, habitat use, and population density of the conch at Grape Tree Bay in winter. From the high proportions of dead conch with chisel holes, we infer that fishing was the main cause of adult mortality. Further inferences are limited by our inability to determine how long ago the conch died or to account for harvested conch whose shells have been removed from the site.

We may have failed to find more living adult conch because older conch may migrate to deeper, calmer waters during the winter (Hesse 1979). All the live conch that we recorded were between the back reef wall and 60 m from shore, in the deepest part of the lagoon (2-3 m); this may be the most protected habitat for conch that do not migrate to deeper waters beyond the reef. All but one of the live conch were juveniles, but none of these juveniles was found in seagrass habitat, contradicting our prediction for habitat preference. It is possible that rough waves render the shallow seagrass beds inhospitable to young conch during winter. We found sandy algal turf mainly in the deepest part of the lagoon (*c.* 3 m); thus, conch may be selecting this habitat for its depth rather than for its benthic substrate.

If the conch in this study area were patchily distributed and we

failed to sample local aggregations, it is possible that our data may be biased to low estimates of adult conch density. We observed one such aggregation outside our belt transects, with 17 conch in a *c.* 20 m^2 area; all were alive and large, and five appeared to be adults. Future studies should account for the possibility of patchy distributions when designing sampling methods.

Collins (2007) expands on these findings by sampling additional areas around the island, including the shallow lagoon waters of the Jackson's Bay no-take zone to the west and the deeper waters beyond the fringing reef.

LITERATURE CITED

Austin, Timothy. E-mail, Feb 22, 2007.

Bothwell, John. Research Officer, Department of Environment, Cayman Islands. E-mail, March 8, 2007.

Brown, A. and C. Manfrino. 2006. First Report on the Tropical Habitats of Little Cayman Island, Data Collection, Review, and Analysis, CCMI Special Report No.1:0306 (Lamp Third Quarter Report).

Clamp, Jonathan. Manager, Little Cayman Research Center. Personal communications, March 2007.

Collins, P. 2007. Age-specific habitat preference by the queen conch, *Strombus gigas*, at Little Cayman Island. In press.

DOE (Department of Environment), Cayman Islands. 2004. Marine Park Regulations & Marine Conservation Laws.

FAO. 2004. World markets and industry of selected commercially-exploited aquatic species with an international conservation profile: Caribbean queen conch (Strombus gigas). FAO Fisheries Circulars. http://www.fao.org/docrep/006/Y5261E/y5261e07.htm, accessed 3/1/07.

Ferren, Ro. Longstreet Highroad Guide to the Florida Keys & Everglades. http://www.sherpaguides.com/florida/upper_keys/upper_keys.html, accessed 3/1/07.

Martín-Mora, E., F. C. James, and A. W. Stoner. 1995. Developmental plasticity in the shell of the Queen Conch *Strombus gigas*. Ecology 76(3), pp. 981-994.

Ray, M, and A. W. Stoner. 1995. Growth, survivorship, and habitat choice in a newly settled seagrass gastropod, *Strombus gigas*. Marine Ecology Progress Series 123:83-94.

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

SARAH C. ISBEY AND CHAD S. GORBATKIN

Faculty Editor: David R. Peart

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.

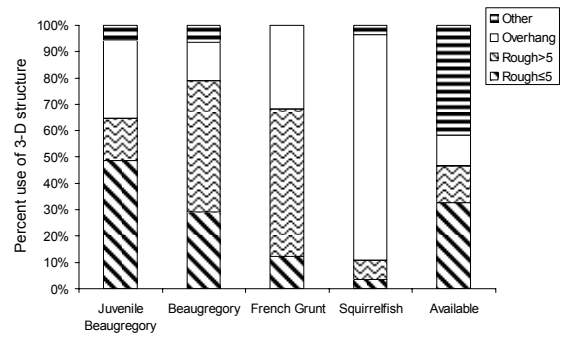

Figure 1. Fish microhabitat use and availability on the back reef of Little Cayman Research Centre on Little Cayman Island. Fish microhabitat use differed significantly from habitat available, for all species categories except juvenile beaugregories. Data were collected 25-26 February 2006. "Rough≤5" 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.

LITERATURE CITED

Burke, N.C. 1995. Nocturnal foraging habitats of French and bluestripe grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. Environmental Biology of Fishes 42: 365-374.

Deloach, N. and P. Humann. 1999. Reef Fish Behavior. New World Publications, Inc.: Jacksonville, Florida, USA.

Ebersole, J.P. 1985. Niche separation of two damselfish species by aggression and differential microhabitat utilization. Ecology 66.1: 14-20.

Gladfelter, W.B. and W.S. Johnson. 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). Ecology 64.3: 552-563.

Gladfelter, W.B., J.C. Ogden, and E.H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical Western Atlantic (Virgin Islands) and tropical Central Pacific (Marshall Islands) patch reefs. Ecology 61.5: 1156-1168.

Gratwickel, B. and M.R. Speight. 2005. Effects of habitat complexity on Caribbean marine fish assemblages. Marine Ecology 292: 301-310.

Kendall, M.S., J.D. Christensen and Z. Hillis-Starr. 2003. Multi-scale data used to analyze the spatial distribution of French grunts, Haemulon flavolineatum, relative to hard and soft bottom in a benthic landscape. Environmental Biology of Fishes 66: 19-26.

Sale, P.F. 1972a. Influence of corals in the dispersion of the Pomacentrid fish, Dascyllus Aruanus. Ecology 53.4: 741-744.

Sale, P.F. 1972b. Effect of cover on agnostic behavior of a reef fish: a possible spacing mechanism. Ecology 53.4: 753-758.

Sale, P.F. 1975. Patterns of use of space in a guild of territorial reef fishes. Marine biology 29: 89-97.

Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. The American Naturalist 111: 337-359.

Sale, P.F. 1978a. Coexistence of coral reef fishes—a lottery for living space. Environmental Biology of Fishes 3: 85-102.

Sale, P.F. 1978b. Chance patterns of demographic change in populations of territorial fish in coral rubble patches at heron reef. Journal of Experimental Marine Biology and Ecology 34: 233-243.

Sale, P.F. and R. Dybdahl. 1978. Determinants of community structure for coral fishes in isolated coral heads at lagoonal and reef slope sites. Oecologia 34.1: 57-74.

Shulman, M.J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66.3: 1056-1066.

Walker, B.K., B.H. Henderson and R.E. Spieler. 2002. Fish assemblages associated with artificial reefs of concrete aggregates or quarry stone offshore Miami Beach, Florida, USA. Aquatic Living Resources 15: 95-105.

DIEL PATTERNS IN ZOOPLANKTON ASSEMBLAGES OVER A LITTLE CAYMAN ISLAND CORAL REEF

BRIGETTE A. JONES, SONIA LEI, AND JENNIFER N. CECH

Faculty Editor: David R. Peart

Abstract. Zooplankton are heavily preyed upon by diurnal planktivorous fish, and hide in the benthos during the day, emerging into the water column at night to feed. Small zooplankton often forage during the day because they are below the visual threshold of many predators, whereas large zooplankton forage only at night. We compared the day and night zooplankton communities on the back reef of Grape Tree Bay, Little Cayman Island and found a higher density of zooplankton at night than during the day. Zooplankton ≥ 1 mm length were abundant only at night. Zooplankton < 1 mm comprised 96% of day samples and were abundant both day and night. However, the density of copepod nauplii < 0.5 mm decreased slightly at night. This decrease is unusual; previous studies show increased abundances of all sizes of zooplankton at night.

Keywords: copepods, decapods, polychaete larvae, mysids

INTRODUCTION

On coral reefs such as those at Little Cayman Island, many organisms are completely planktonic, and others have planktonic larval stages. To avoid predation by diurnal predators, many zooplankton feed in the water column after dusk, when the foraging efficiency of planktivorous fishes is much reduced (Koski et al. 2003, Rickel and Genin 2005, Ohlhorst 1982).

Small zooplankton (< 1 mm) are less likely to be consumed during the day when high light allows predators to be more size selective (Brooks and Dodson 1965, Koski et al. 2003, Ohlhorst 1982). Small zooplankton are below the visual threshold of many planktivores and are thus subject to consistently lower predation risk than large zooplankton.

Based on previous studies in Discovery Bay, Jamaica (Sullan et al. 2006, Calvi et al. 2000, Chiavelli 1998, Dartmouth FSP 1995, Ohlhorst 1982), we predicted that total zooplankton abundance and density would be higher at night. We also predicted that large zooplankton (≥ 1 mm) would show the greatest difference in abundance and density between day and night, with greatest abundances at night because of the risk of size selective predation. Lastly, we predicted that small zooplankton would be found in greater or equal abundances and densities during the day than at

night, because of their low predation risk.

METHODS

We sampled zooplankton in the water column along the coral reef of Grape Tree Bay, Little Cayman Island, on 25 February 2007. We used three contiguous 10 m transects running parallel to the reef, 93 m from the shore. We towed a plankton net 0.3 m in diameter, once back and forth along each transect, sampling a total of 1.41 m^3 of water per transect. Each transect was sampled twice: at 1400 (day) and at 2200 (night). Sample sizes were 3 for day and 2 for night; one night sample was lost due to sampling error.

We preserved zooplankton samples immediately in 5% formalin solution. Under a microscope, we placed organisms into nine taxonomic groups: Copepoda, Amphipoda, Isopoda, Decapoda, Polychaete larvae, Mysidacea, Cumacea, Cnidaria, and Actinoptergii larvae. Zooplankton sizes ranged from <0.5 mm to >8 mm. We grouped them into four size classes: 0-1 mm, 1-2 mm, 2-4 mm, 4+ mm. This allowed us to compare the densities of zooplankton below the visual threshold of planktivores with the densities of larger zooplankton.

For analyses, we lumped zooplankton into two size classes: small (< 1 mm) and large (≥ 1 mm). We used a MANOVA to determine whether there were significant differences in abundances of size classes between day and night. We used t-tests assuming unequal variance to determine differences in total density, in density within the two size classes of zooplankton, and in abundance within taxa between day and night. We used power analysis to determine the sample sizes necessary for significant differences. The differences between the abundances of copepods in different size classes between day and night were determined using t-tests.

RESULTS

There was a significant difference in zooplankton abundance of the two size classes between day and night (MANOVA $F_{2,2} = 18.88$, $P = 0.050$). We found a much greater mean sample density of zooplankton at night (mean ± SE = 386 ± 112 individuals per m^3) than during the day (98 ± 12); however we found no significant difference with our high variance and low sample size ($t_{1.02} = 2.55$, $P = 0.12$) Power analysis showed a sample size of 5 would yield a significant difference at $\alpha = 0.05$. We found two other marginally significant trends: a higher density of large zooplankton at night than during the day ($t_{1.00} = 3.28$, $P = 0.094$) and a higher density of small zooplankton during the day than at night ($t_3 = 1.34$, $P = 0.14$; Figure 1).

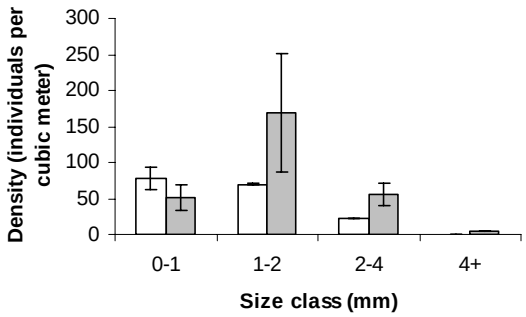

Figure 1. Density ± SE of zooplankton by size class found during day (light bars) and night (dark bars) sampling at Jackson's Bay reef, Little Cayman Island. Light and dark bars represent day and night samples, respectively.

We recorded a total of seven taxa during the day and nine at night (Table 1). The three most common taxa overall were Copepoda, Decapoda, and Polychaete larvae (Figure 2). There were no significant differences between day and night abundances for the six least abundant taxa: Amphipoda (t_1 = -1, P = 0.25), Isopoda ($t_{1.1}$ = 2.49, P = 0.11), Mysidacea (t_1 = 3.89, P = 0.08), Actinoptergii larvae ($t_{1.01}$ = 2.92, P = 0.10), Cnidaria ($t_{2.43}$ = 0.5, P = 0.66) and Cumacea ($t_{1.02}$ = 1.25, P = 0.21), though all had higher sample densities at night than during the day (Figure 3). During the day, most copepods were nauplii < 0.5 mm (t_3 = 4.53, P = 0.010) and at night were mostly larger copepods ≥ 0.5 mm (t-test assuming unequal variances $t_{1.02}$ = -2.18, P = 0.13, Table 2).

Table 1. Mean abundances of common zooplankton taxonomic groups per sample (1.41 m^3) found during day and night sampling at Jackson's Bay reef, Little Cayman Island.

Taxa	Description	Mean Abundance ± SE	
		Day n=3	Night n=2
Copepoda	Small crustaceans	126 ±13.61	86.5 ± 28.5
Amphipoda	Small crustaceans	0	1 ± 1
Isopoda	Small crustaceans	0.67 ± 0.33	0.45 ± 1.5
Decapoda	Crustacean larvae	2.33 ± 0.88	274.5 ± 80.5
Mysidacea	Mysid shrimp	0	17.5 ± 4.5
Polychaeta	Worm larvae	6 ± 2.08	11 ± 3
Actinopterygii	Fish larvae	0.33 ± 0.33	13.5 ± 4.5
Cnidaria	Jellyfish larvae	1.67 ± 0.88	1 ± 1
Cumac	Cumacean shrimp	1.33 ± 0.66	9.5 ± 6.5
Total Zooplankton		98 ± 12	386 ± 112

Table 2. Density (individuals/m^3) of copepods by size class found during day and night sampling at Jackson's Bay reef, Little Cayman Island.

Size class (mm)	*<0.5*	*0.5-1*	*>1*
Day n=3	75.18 ± 11.66	13.48 ± 2.05	0.71 ± 0
Night n=2	6.74 ± 1.77	42.91 ± 13.12	11.70 ± 5.32

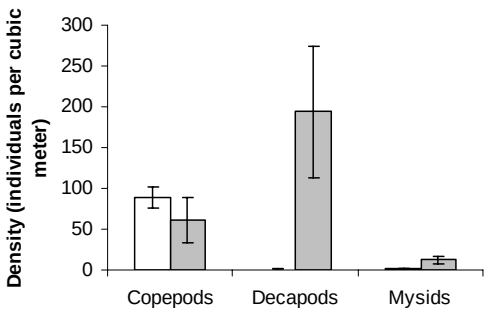

Figure 2. Density ± SE of the three most common zooplankton taxonomic groups found during day (light bars) and night (dark bars) sampling at Jackson's Bay reef, Little Cayman Island.

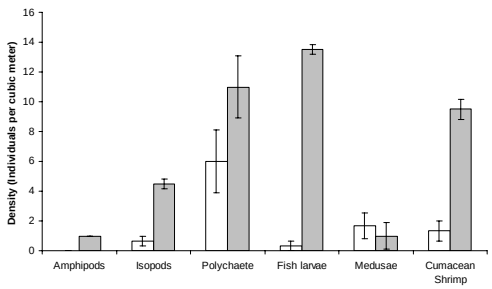

Figure 3. Density ± SE of less common zooplankton taxonomic groups found during day (light bars) and night (dark bars) sampling at Jackson's Bay reef, Little Cayman Island.

DISCUSSION

Our finding that the average total zooplankton abundance is four times greater at night demonstrates the diel movement of zooplankton and supports our first prediction. While this pattern has been documented at other reefs, such as Discovery Bay, Jamaica (Sullan et al. 2006, Calvi et al. 2000, Chiavelli 1998, Dartmouth FSP 1995, Ohlhorst 1982), the Great Barrier Reef (Roman et al. 1990), and the Florida Keys (Walters 1988), it has not previously been studied at Little Cayman Island.

Large zooplankton comprised only 4% of individuals in the day sample, compared to 81% at night. The density of large zooplankton also increased 60 fold from an average of 3.8 individuals per m^3 during the day to 241.2 individuals per m^3 at night, supporting our second prediction that large zooplankton would be found in higher densities at night.

While 84% of daytime individuals were small zooplankton (< 1mm), they made up only 11% of the nighttime individuals. Their densities decreased only slightly, from an average of 94.2 day individuals per m^3 during the day to 55.2 night individuals per m^3 at night. Our data support previous work showing that small zooplankton forage in the water column during the day when they are less vulnerable to predation; and large zooplankton emerge only at night when decreased light reduces their vulnerability to predation (Brooks and Dodson 1965, Koski et al. 2003).

Copepods were one of the most dense taxa during both the day and night, and this trend is consistent with previous Jamaican studies (Sullan et al. 2006, Calvi et al. 2000, Chiavelli 1998, Dartmouth FSP 1995, Ohlhorst 1982). The densities of our three most common daytime taxa (copepods, decapods, and polychaete larvae) fell within ranges documented in Jamaica. However, our nighttime copepod density was almost ten times lower than the lowest nighttime copepod densities found in Jamaica. Low nighttime copepod densities may be unique to Little Cayman zooplankton communities, or a result of localized sampling of patchy distributions. Because of high live coral densities at Little Cayman, small zooplankton may be subject to stronger coral predation than at Discovery Bay, resulting in lower copepod densities.

Size selective predation in high visibility conditions has resulted in clear diel patterns of zooplankton abundance in reef communities. From our study off the coast of Little Cayman Island, we conclude that established diel patterns of zooplankton densities can be broadened to apply to the reef communities there. Further investigation of abundances in different habitats will increase the understanding of the zooplankton community structure on Little Cayman Island.

LITERATURE CITED

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size and composition of plankton. Science **150**:28-35.

Calvi, M. S., K. W. Manaras, Z. M. McLaren, W. H. Lowe, and the 2000 Dartmouth FSP class, 2000. Diel changes in the zooplankton assemblage over a Caribbean coral reef. Dartmouth Studies in Tropical Ecology. pp 169-172.

Chiavelli, D. A. and the 1998 Dartmouth FSP class, 1998. Diel changes in the zooplankton assemblage over a Caribbean coral reef. Dartmouth Studies in Tropical Ecology, pp 159-161.

Dartmouth FSP class, 1995. Day and Night comparison of zooplankton density and richness in Discovery Bay, Jamaica. Dartmouth Studies in Tropical Ecology.

Koski, M. L., B. M. Johnson, and T. M. Stecklein. 2003. Effects of light on size-selectivity of kokanee feeding on Daphnia. Journal of Fish Biology **62**:1456-1461.

Ohlhorst, S. L. 1982. Diel migration patterns of demersal reef zooplankton. Journal of Experimental Marine Biology and Ecology **60**:1-15.

Rickel, S., and A. Genin. 2005. Twilight transitions in coral reef fish: the input of light-induced changes in foraging behaviour. Animal Behaviour **70**:133-144.

Roman, M.R., M. J. Furnas, and M.M. Mullin, 1990. Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. Marine Biology **105:**73-82.

Walters, K., 1988. Diel Vertical Migration of sediment-associated meiofauna in sub-tropical sand and sea grass habitats. Journal of Experimental Marine Biology and Ecology **117:**169-186.

THALASSIA TESTUDINUM DENSITY AND HERBIVORY AS A FUNCTION OF DISTANCE FROM CORAL HEADS

JAMES A. MARLOW, JENNIFER R. POST, AND HA LINH VU

Faculty Editor: David R. Peart

Abstract. Turtlegrass (*Thalassia testudinum)* provides food and shelter for many organisms in marine coastal ecosystems. In the West Indies, where turtlegrass grows near coral reefs, there is a band of nearly bare sand separating these two communities. This band has been attributed to herbivory by parrotfish, surgeonfish, and the sea urchin *Diadema antillarum*, which find refuge in the coral heads. We studied the density and distribution of *T. testudinum* on Little Cayman Island and the patterns of sea urchin and fish herbivory on *T. testudinum,* as a function of distance from coral heads. We found that density of *T. testudinum* increased and total herbivory decreased with distance away from the coral head. These findings are consistent with the hypothesis that herbivory causes or reinforces this pattern of *T. testudinum* density.

Keywords: Diadema antillarum, *parrotfish, surgeonfish, Little Cayman Island, herbivory, plant density*

INTRODUCTION

Thalassia testudinum (turtlegrass) provides food and shelter for many organisms in marine coastal ecosystems (Valentine and Heck 1999). Parrotfish, surgeonfish and sea urchins consume *T. testudinum* (Dineen 2001, Kirsh et al. 2002), potentially limiting its abundance and distribution. Nearby patch reefs provide refuge for these herbivores (Ogden et al. 1973).

A band of nearly bare sand between the base of the reef and the beds of seagrass, often referred to as a halo, occurs on patch reefs in the West Indies (Randall 1965). These bands occur independent of the physical factors around the base of coral reefs, including wave surge and turbidity (Ogden et al. 1973). These halos may be created by parrotfish (*Scarus* spp. and *Sparisoma* spp.) and surgeonfish (*Acanthurus* spp.) herbivory (Randall 1965), or by sea urchin (*Diadema antillarum)* herbivory (Ogden et al. 1973).

We measured the density and distribution of *T. testudinum* on Little Cayman Island and the patterns of sea urchin and fish herbivory, and their relationships to distance from coral heads. Since the coral heads may provide refuges for *T. testudinum* herbivores, we predicted that herbivory would be highest, and density of *T. testudinum* lowest, close to the coral head.

METHODS

We studied *T. testudinum* in the lagoon along a 200 m stretch of northern Little Cayman Island in front of the Little Cayman Research Center, from 25-26 February 2007. A strip of patch reef lies parallel to and 50 m from the shore. From this patch reef, we selected 10 isolated coral heads of approximately equal size. We ran 20-m transects from the coral heads towards the shore; these transects did not pass over other coral heads. Along each transect, we placed 0.5 m X 0.5 m quadrats every 2 m starting at 0 m. In each quadrat, we counted the number of *T. testudinum* shoots, and, in one haphazardly chosen quarter of the quadrat, we counted the number of leaves. We then counted the number of leaves with fish bite marks and *D. antillarum* bite marks in each quarter-quadrat. Herbivorous fish leave scallop-shaped marks on the *T. testudinum* blades, while *D. antillarum* leave jagged marks (Ogden et al. 1973). We also counted leaves with bite marks that were neither obviously scallop-shaped, nor jagged.

We used correlation analyses to determine the relationship between *T. testudinum* density (leaves per 0.25 m^2, square-root transformed for normality) and distance from the coral head, and between *T. testudinum* herbivory and distance from the coral head. Herbivory was quantified as the total number of leaves with bite marks. Percent herbivory was calculated for each quarter-quadrat as the number of leaves with bite marks divided by the total number of leaves. There was an effect of transect on density, absolute herbivory and percent herbivory (MANOVA, Wilks' Lambda=0.47, $F_{27,269.3}$=2.98, P<0.0001). However, a nested ANOVA ($F_{19,103}$=2.10, P=0.01) showed that the transect effect on percent herbivory (F_{10}=2.07, P=0.04) did not overwhelm the effect of distance from coral head, nested within transect (F_9=2.01, P=0.04). Therefore, in the rest of our analyses, we tested the effect of distance from coral head on density and different herbivory metrics, with data from all transects combined.

RESULTS

Thalassia testudinum density increased with distance from coral head (r = 0.45, df= 109, P< 0.0001, Figure 1). But the total number of leaves with signs of herbivory did not vary with distance from coral head (r = 0.07, df= 109, P= 0.46, Figure 2). Nor did leaves with fish herbivory (r = 0.02, df= 109, P< 0.0001) or leaves with *D. antillarum* herbivory (r = -0.06, df= 109, P< 0.0001) vary with distance from coral head. The percent of leaves with herbivory decreased with distance from the coral head (r = -0.33, df= 109, P< 0.0001, Figure 3), as did the

percent of leaves with fish herbivory (r = -0.21, df= 103, P= 0.03) and with *D. antillarum* herbivory (r = -0.25, df= 103, P= 0.01).

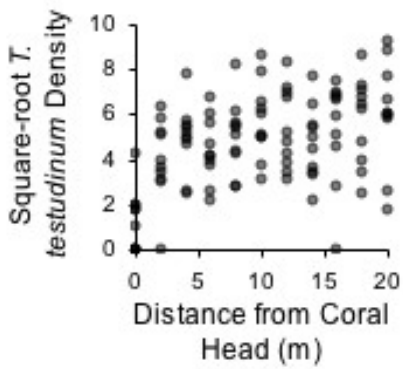

Figure 1. The number of *T. testudinum* leaves (square-root transformed) per 0.25 m^2 along 20 m transects running from coral heads perpendicular towards the northern shore of Little Cayman Island (n = 110 quadrats along 10 transects). Some dots appear darker due to overlap.

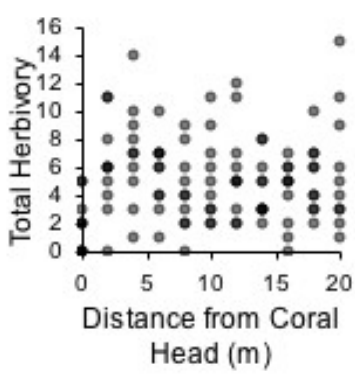

Figure 2. Total herbivory on *T. testudinum* (number of leaves with either fish bites, *D. antillarum* bites or unidentified bites) in 0.0625 m^2 subquadrats along 20 m transects running from coral heads perpendicular towards the northern shore of Little Cayman Island (n = 110 quadrats along 10 transects). Some dots appear darker due to overlap.

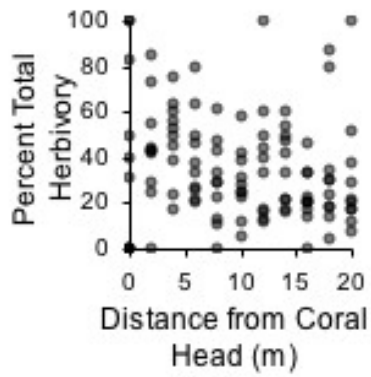

Figure 3. Percent total herbivory in *T. testudinum* (number of leaves with either fish, *D. antillarum* bites, or unidentified bites divided by the total number of leaves) in 0.0625 m^2 subquadrats along 20 m transects running from coral heads perpendicular towards the northern shore of Little Cayman Island (n = 110 quadrats along 10 transects). Some dots appear darker due to overlap.

DISCUSSION

The density of *T. testudinum* shoots increased and percent of leaves attacked by herbivores decreased with distance away from coral heads, suggesting that density is affected by and/or influences rates of herbivory. Since our transects ran perpendicular to the shore, the relationship between density and herbivory could be confounded by other gradients. *Thalassia testudinum* grows optimally in a temperature range of 20-30^{0}C (Dineen 2001) and temperature varies with water depth. While the density trend is consistent with our hypothesis and with our data on herbivore damage, a more controlled experimental design would be necessary to establish rigorously the mechanisms

responsible for the pattern in *T. testudinum* shoot density.

Since absolute herbivory, measured as the total number of leaves with herbivore damage, did not vary with distance from the coral head, our data suggest that herbivores may not seek out dense *T. testudinum* patches. Instead, they may consume whatever leaves they encounter, regardless of density. If total herbivore foraging effort were positively related to the density of *T. testudinum*, herbivory may have acted in the past to reduce the density gradient with distance from the coral head.

We calculated herbivory as the number of leaves with bite marks regardless of the number or size of marks; it might be possible to explain more of the variation in herbivory by measuring the total amount of biomass lost per leaf.

For a given patch of *T. testudinum*, the percent of leaves consumed by herbivores (which we called percent herbivory) may be more important to individual plants than the number of leaves consumed per-unit area, because the percent herbivory represents the risk of herbivory to each individual leaf. The higher percent herbivory closer to the coral head could be stunting the growth of individual *T. testudinum*, thereby decreasing its density. Alternatively, abiotic factors could be limiting *T. testudinum* density close to the coral head and herbivory may reinforce these trends.

Our study suggests that fish and urchin herbivory could be driving and/or reinforcing the pattern of increased *T. testudinum* density with distance away from the coral head. Further studies are needed to clarify causal relations between *T. testudinum* density and absolute and percent herbivory.

LITERATURE CITED

Buesa, R. J. 1975. Populations biomass and metabolic rates of marine angiosperms on the northwestern Cuban shelf. Aquatic Botany. 1:11-23.

Dineen. J. 2001. *Thalassia testudinum*. Smithsonian Marine Station at Fort Pierce. <http://www.sms.si.edu/IRLSpec/Thalas_testud.htm>

Kirsch, K. D., J. F. Valentine, and K. L. Heck Jr. 2002. Parrotfish grazing on turtlegrass *Thalassia testudinum*: evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. Marine Ecology Progress Series. 227:71-85.

Ogden, J.C., R.A. Brown, and N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science 182:715-717

Randall, J.E. 1965. Grazing effect on sea grasses by herbivorous reef fishes in

the West Indies. Ecology. 46:255-260.

Valentine, J.F. and K.L. Heck Jr. 1999. Seagrass herbivory: evidence for the continued grazing of marine grasses. 176:291-302.

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

SUSAN E. ELLIOTT, LAURA A. BURKLE, AND ALLISON M. CITRO

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).

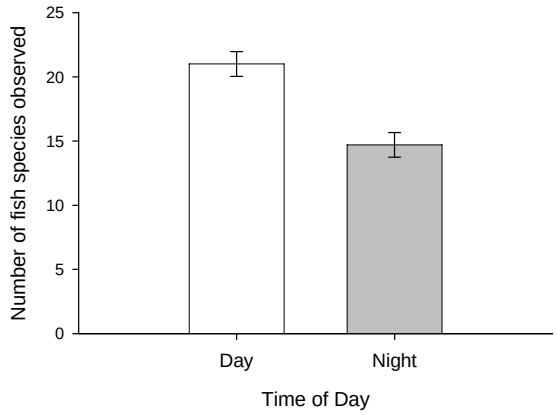

Figure 1. The average number of fish species observed by each group (n = 9) at Jackson's Bay, Little Cayman Island during the day and at night. Error bars represent ± 1 SE.

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.

LITERATURE CITED

Arakaki, S. and M. Tokeshi. 2006. Short-term dynamics of tidepool fish community: Diel and seasonal variation. *Environmental Biology of Fishes* 76: 221-235.

Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. *American Scientist* 66(3): 322-331.

Nagelkerken, I. et al. 2000. Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Marine Ecology-Progress Series* 194: 55-64.

Laroche, J., E. Baran, and N. B. Rasoanandrasana. 1997. Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. *Journal of Fish Biology* 51: 3-20.

Munday, P. L. 2004. Competitive coexistence of coral-dwelling fishes:

The lottery hypothesis revisited. *Ecology* 85(3): 623-628.

Rickel, S. and A. Genin. Twilight transitions in coral reef fish: the input of light-induced changes in foraging behaviour. *Animal Behaviour* 70: 133-144.

Ruso, Y. D. and J. T. Bayle-Sempere. 2006. Diel and vertical movements of preflexion fish larvae assemblages associated with Posidonia oceanica beds. *Scientia Marina* 70(3): 399-406.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* 111: 337-358.

Sikkel, P. C., C. S. Schaumburg, and J. K. Mathenia. 2006. Diel infestation dynamics of gnathiid isopod larvae parasitic on Caribbean reef fish. *Coral Reefs* 25(4): 683-689.

Travers, M. J., S. J. Newman, and I. C. Potter. 2006. Influence of latitude, water depth, day v. night and wet v. dry periods on the species composition of reef fish communities in tropical Western Australia. *Journal of Fish Biology* 69(4): 987-1017.

Zemke-White, W. L., J. H. Choat, and K. D. Clements. 2002. A re-evaluation of the diel feeding hypothesis for marine herbivorous fishes. *Marine Biology* 141(3): 571-579.

AGE-SPECIFIC HABITAT PREFERENCE BY THE QUEEN CONCH, *STROMBUS GIGAS*, AT LITTLE CAYMAN ISLAND

PAMELA M. COLLINS

Faculty Editor: David R. Peart

Abstract: Many Caribbean nations regulate harvesting of the queen conch, *Strombus gigas*, but not all regulations are based on reliable local data. It is not known if the conch of Little Cayman Island exhibit the same habitat preferences as do conch on other Caribbean islands. I measured live conch at four sites with depths from < 1m to *c.* 17 m. Shallow sites had a high percentage of juveniles, while deep sites lacked juveniles. At sites in deeper water, adult conch had thicker shell lips (and were thus older), but there was no increase in adult age beyond 3m depth. Since the conch of Little Cayman Island exhibit the same age-specific habitat preferences as do conch studied elsewhere in the Caribbean, conch research throughout this region may be relevant to management decisions about the conch of Little Cayman.

Key Words: fisheries management, spillover effect

INTRODUCTION

The Queen Conch, *Strombus gigas*, supports locally important commercial fisheries throughout the Caribbean. While the science of conch fisheries management is imperfect, some conch populations have been so depleted by over-harvesting that Caribbean governments are taking action to regulate the industry (Aiken et al 1999). Along with many other Caribbean nations, the Cayman Islands have designated areas of conch habitat where harvesting is either seasonally regulated or forbidden entirely (Collins and Harrison 2007). This approach to fisheries management utilizes the "spillover principle," whereby protected areas may act as sources for supplying new recruits to fished areas, protecting local populations from collapse caused by over-fishing (Tewfik 2003).

Determining which habitats are most important for population maintenance and growth is difficult because benthic conch are highly mobile, and different ages may prefer different habitats. Three factors complicate how to maximize reproduction via habitat protection: 1) reproducing adult conch occupy deeper waters, while larvae metamorphose into young conch in the shallows (Ray and Stoner 1995); 2) conch fecundity increases with age (Gascoigne and Lipcius 2004); and 3) since conch larvae are pelagic, the conch population of any one island may derive varying proportions of recruits from local conch or from

breeding conch of islands upstream (Roberts 1997).

Since no data have been published describing age-specific habitat use by conch on Little Cayman, I wished to determine if the same patterns of age distribution with depth observed at other sites in the Caribbean occurred here as well. I predicted that 1) proportionally more juvenile conch would be found in shallower waters than in deeper waters, and that 2) lip thickness (and thus age) of adult conch would progressively increase with water depth across habitats. My findings may help determine whether management strategies developed elsewhere are applicable locally.

METHODS

Study organism

Juvenile conch grow by shell elongation. Once sexual maturity is reached at 3.5 to 4 years, a flange grows on the leading edge (lip) of the shell, and elongation ceases. Further growth occurs via thickening of the shell, which continues throughout the lifespan of the conch (6 to 7 years) (Ray and Stoner 1995).

Study sites

I sampled four study sites, two on the north side of Little Cayman Island and two on the south side. All were in areas where conch harvesting is illegal year-round, with the possible exception of the Grape Tree Bay site. This site straddles the actual legal boundary between protected and unprotected waters; however, the onshore signs that mark park boundaries indicate that this site lies completely within protected waters. Thus, we assume that no conch fishing legally occurs in any of the sample areas (though some poaching may occur). See Table 1 for descriptions of each site.

Table 1: Live conch shells were measured at four sites around Little Cayman Island. All sites were contained within no-take zones, with the possible exception of Grape Tree Bay.

Site	Proximity to protected areas	Habitat Description
South Hole Sound	Within South Hole Sound Replenishment Zone	Max depth 1 m, back reef lagoon, substrate sand & reef rubble, some T. testudinum and algal turf
Grape Tree Bay	Eastern boundary of Bloody Bay Marine Park, abuts Little Cayman Research Centre, park signage inaccurate	Max depth 2 m, back reef lagoon, substrate rubble, algal turf, Thalassia testudinum beds
Jackson Bay	Within Bloody Bay Marine Park	Max depth 3 m, no barrier reef, flat uneven hardpan pocked with sinkholes, substrate sandy/rocky algal turf
Preston Wreck	Within Preston Bay Marine Park	Max depth 17 m (bare sand), min depth 8 m (reef top), seaward of barrier reef

Sampling

At Jackson Bay and Grape Tree Bay, conch were sampled along belt transects 4 m wide, perpendicular to the shoreline. Four transects were done at Jackson Bay and 7 at Grape Tree Bay. Each transect was between 90 and 120 m long, extending from the shore to the barrier reef (if present). No transects were laid out in South Hole Sound or near the Preston Bay wreck; due to time constraints, conch were sampled haphazardly and opportunistically at these sites. The following data were recorded for each live conch found: shell length from apical spiral to siphonal groove to the nearest cm, lip thickness to the nearest mm, and whether the conch was an adult or a juvenile, indicated by presence or absence of a flange (Collins and Harrison 2007).

Statistical Analyses

Percentages of juveniles and adults found at each site were compared, and mean lip thicknesses of adults were compared for all sites with >1 adults, both using ANOVA.

RESULTS

In South Hole Sound and Grape Tree Bay, the two shallowest sites, 38.1% and 96.5% of the conch sampled were juveniles, respectively (only one adult was found in Grape Tree Bay). In Jackson Bay, the site of intermediate depth, 96.9% of the conch sampled were adults (only 1 juvenile was found), and at the deepest site, around Preston Wreck, all conch sampled were adults (Figure 1).

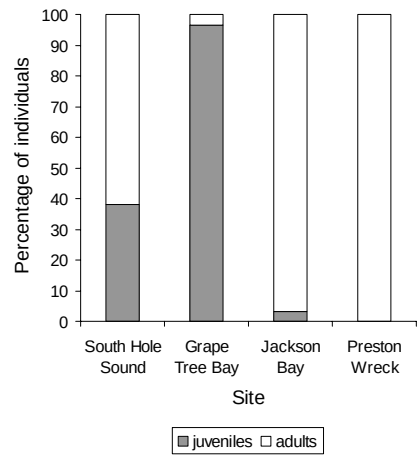

Figure 1: Percentages of juvenile v. adult conch found differed among four different habitats around Little Cayman Island, with higher percentages of juveniles occurring at shallow sites and few to no juveniles found in the deeper sites. See Table 1 for site descriptions. South Hole Sound: 16 juveniles, 26 adults; Grape Tree Bay: 28 juveniles, 1 adult; Jackson Bay: 1 juvenile, 31 adults; Preston Wreck: 0 juveniles, 20 adults.

Mean lip thickness of adults was lowest (12.2 mm) at South Hole Sound (the shallowest site), greatest (26.2 mm) at Jackson Bay, and intermediate (20.7 mm) around Preston Wreck. All differences in adult lip thickness among sites were statistically significant (Figure 2, ANOVA, $F_2 = 55.31$, $P < 0.0001$).

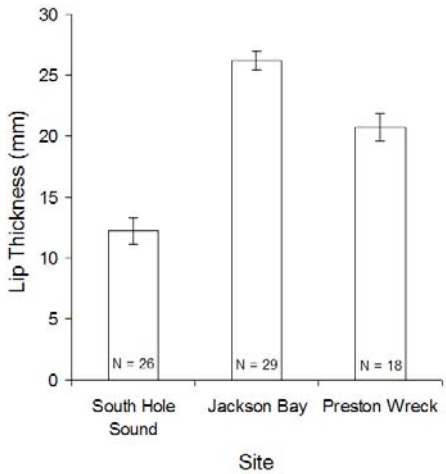

Figure 2: Mean lip thicknesses (± 1 SE) for adult conch in three different habitats around Little Cayman Island were significantly different. Mean thickness was lowest for the shallowest site (South Hole Sound), intermediate for the deepest site (Preston Wreck), and highest for the site of intermediate depth (Jackson Bay). See Table 1 for site descriptions.

DISCUSSION

A higher proportion of the conch found in the shallow sites were juveniles (Figure 1), as has been found elsewhere in the Caribbean. However, the higher percentage of adult conch at South Hole Sound compared to Grape Tree Bay was surprising since both sites are of comparable depth. These results may be due to differences in benthic substrate type, food availability, water temperature, predation, or water flow regime. Since time constraints caused me to shift from sampling transects to sampling opportunistically part way through the study, it is also unclear which sites contain the highest absolute abundance of conch.

The adult conch of South Hole Sound have the lowest mean lip thickness, so they are younger than the adult conch found in Jackson Bay and near Preston Wreck. This supports my hypothesis that as the conch of Little Cayman Island mature, they leave the shallows for deeper waters. However, I cannot rule out the possibility that large adults are absent from the shallow waters of South Hole Sound because they are illegally harvested. If large numbers of juvenile conch were tagged in the shallows, a multi-year study could observe their movements and determine exactly where the conch go as they age.

The greater mean lip thickness (and thus age) of the conch at Jackson Bay (the site of intermediate depth) compared to Preston Wreck (the deepest site) suggests that there may be a threshold beyond which conch age does not increase with depth. While the large conch of Preston Wreck would only be accessible to harvesting by SCUBA, the larger conch of Jackson Bay would be easily harvestable by free diving. Conch fecundity increases with age (Gascoigne and Lipcius 2004), so the fertile adults near Preston Wreck would be protected from harvesting by depth, but the larger (and presumably more fecund) conch of Jackson Bay would not be. Thus, management decisions for the conch of Little Cayman Island must

account for the fact that reproductive adults can be found in water as shallow as 3 m or as deep as 17 m, remembering that juvenile conch require shallow water habitats as well.

LITERATURE CITED

Aiken, K., G. Kong, S. Smikle, R. Mahon, and R. Appeldoorn. 1999. The queen conch fishery on Pedro Bank, Jamaica: discovery, development, management. Ocean & Coastal Management 42: 1069-1081.

Collins, P. and T. Harrison. 2007. Population structure and size distribution of queen conch in Grape Tree Bay, Little Cayman Island. In press.

Gascoigne, J. and R. Lipcius. 2004. Conserving populations at low abundance: delayed functional maturity and Allee effects in reproductive behavior of the queen conch *Strombus gigas*. Marien Ecology Progress Series 284: 185-194.

Ray, M, and A. W. Stoner. 1995. Growth, survivorship, and habitat choice in a newly settled seagrass gastropod, *Strombus gigas*. Marine Ecology Progress Series 123:83-94.

Roberts, C. 1997. Connectivity and Management of Caribbean Coral Reefs. Science 278: 1454-1457.

Tewfik, A. and C. Béné. 2003. Effects of natural barriers on the spillover of a marine mollucs: implicatiosn for fisheries reserves. Aquatic Conservation: Marine and Freshwater Ecosystems 13: 473-488.

APPENDIX I

Table 2: Descriptive statistics for all live conch measured at four sample areas around Little Cayman Island, encompassing shallow and deep habitats (Table 1).

Site	Age class	N	Mean Lip Thickness (mm)	Range (mm)	± 1 SE	Mean Shell Length (cm)	Range (mm)	± 1 SE
Grape Tree Bay	**All**	29	0.9	0.3 – 6.8	0.22	15.9	11 – 23	0.59
	Juveniles	28	0.7	0.3 – 1.6	0.057	15.8	11 – 23	0.59
	Adults	1	6.8	N/A	N/A	30	N/A	N/A
Jackson Bay	**All**	32*	25.4	2 – 32	1.1	23.1	12 – 25	0.41
	Juveniles	1	1.5	N/A	N/A	12.0	N/A	N/A
	Adults	31*	26.2	15 – 32	0.80	23.5	20 – 25	0.22
Preston Wreck	**All**	20*	20.7	16 – 31	1.1	21.0	18 – 25	0.37
	Juveniles	0	N/A	N/A	N/A	N/A	N/A	N/A
	Adults	20*	20.7	16 – 31	1.1	21.0	18 – 25	0.37
South Hole Sound	**All**	42	8.7	2 – 23	0.98	18.2	9 – 22	0.62
	Juveniles	16	2.9	2 – 5	0.27	15.5	9 – 21	1.0
	Adults	26	12.2	4 – 23	1.1	19.9	11 – 22	0.58

*A pair of conch were found mating at Jackson Bay, and another pair were found mating near Preston Wreck. To avoid disturbing them, the lip thicknesses of these conch were not measured. Thus, the N values used for mean lip thickness at these sites are as follows: Jackson Bay (All 30, Juveniles 1, Adults 29), Preston Wreck (All 18, Juveniles 0, Adults 18).

FISH COMMUNITIES IN CONTINUOUS AND PATCH MANGROVE HABITATS ON LITTLE CAYMAN ISLAND

JAMES A. MARLOW, TINA HARRISON, ANKIT RASTOGI,
HA LINH VU, AND JENNIFER R. POST

Faculty Editor: David R. Peart

Abstract. Mangroves, highly productive ecosystems that provide habitat for fish, are being fragmented by coastal development in the South Hole Sound, Little Cayman Island. We evaluated fish communities between continuous mangrove habitats and mangrove patches, by comparing total abundance, species richness, and community composition, and found that the two communities did not differ. Because docks and other man-made structures have replaced mangrove habitats, we also observed fish communities under the docks to see if they were comparable to those in mangrove habitats. The fish communities under the docks had lower abundance and lower species richness than continuous and patch mangrove habitats.

Keywords. Habitat fragmentation, docks, fish species richness, fish abundance

INTRODUCTION

Mangroves are highly productive ecosystems that provide habitat for fish (Laegdsgaard and Johnson 2001). The complex root structures and high turbidity of mangrove habitats provide protection from predators (Robertson and Blabber 1992). In recent years, mangroves have been heavily fragmented by coastal development. Mangrove fragmentation increases light penetration, visibility and proximity to open water, reducing protection from predators (Clynick and Chapman 2002). Thus, mangrove fragmentation is responsible for decreases in abundance and diversity of fish (Pittman et al. 2004).

The coastal development on South Hole Sound of Little Cayman Island has fragmented the formerly continuous stretches of mangroves (T. Collins, *personal communication*). We compared fish communities between the two habitats in terms of total abundance, species richness, and community composition. We predicted that the continuous mangrove habitat would have higher abundance and higher species richness than patch habitats. We also observed sandy shore habitats between mangrove patches to compare areas with and without mangroves. We predicted that sandy shore habitats would have different community structure than mangrove habitats. Because docks and other man-made structures have replaced mangrove habitats, we also observed

fish communities under the docks to see if they were comparable to those in mangrove habitats.

METHODS

We studied fish communities in red mangrove (*Rhizophora mangle*) stands along the coast of South Hole Sound on Little Cayman Island from 3-6 March 2007. We observed fish in three habitat types: continuous mangrove (coastline with > 100 m stretches of unbroken mangroves), fragmented mangrove (coastline with mangrove patches *c.* 5-35 m long), and stretches of sandy shore (*c.* 5-20 m long) between mangrove patches. In each habitat type, we haphazardly chose 1 m x 2 m quadrats and counted the abundances of all fish species in each quadrat during 15 minute observations (n=18 quadrats for continuous, n=14 for patches, n=14 for sandy shore). We used the same methods to observe fish communities under boat docks at a distance from shore and depth comparable to that around mangrove roots (n=14).

Statistical Analyses. To test if both fish abundance (square-root transformed) and species richness differed among habitat types, we used a MANOVA. To test if mean fish abundance (square-root transformed) and species richness differed among habitat types, we used two one-way ANOVAs. Because we had different numbers of samples across habitats, we generated species-sample accumulation curves using EcoSim 7.0 (iterations = 5000, random seed = 10) (Gotelli and Entsminger 2001) for all four habitat types (Figure 2). Using the fish species that we observed in both continuous and patch mangrove habitats, we performed a matched pairs t-test to determine whether there was a difference in fish abundance between continuous and patch mangrove habitats.

RESULTS

Abundance and species richness differed among the four habitats (MANOVA, Wilks' Lambda =0.38, $F_{6,100}$=11.27, P<0.0001). Total fish abundances were similar for continuous mangroves, patch mangroves, and sandy shore habitats, but lower for dock habitats (ANOVA, $F_{3,54}$=12.62, P<0.0001) (Figure 1a). Species richness was higher for continuous and patch mangrove habitats than for open water and dock habitats (ANOVA, $F_{3,54}$=16.08, P<0.0001) (Figure 1b). The 95% confidence intervals on the species accumulation curves are more informative: species richness of continuous habitats was higher than that of sandy shore and dock habitats, and species richness of patch habitats was similar to that of the other three habitats (Figure 2).

Continuous and patch mangrove habitats shared 14 species in common, 10 of which were the most abundant species in all habitats (Table 1, Figure 3). We observed more schoolmaster, French grunts, and Caesar grunts in patch than continuous mangroves and more striped parrotfish in continuous than patch mangroves (Table 1). Abundances of those species occurring in both continuous and patch mangrove habitats did not differ significantly between the two habitats (matched paired t-test, t_{13}=1.01, P=0.16**).**

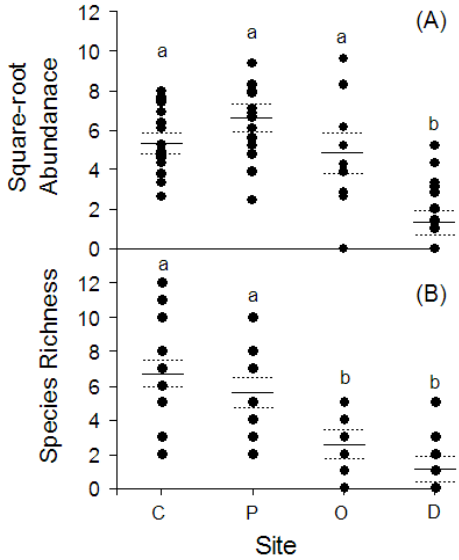

Figure 1. Number of fish (square-root transformed) (A) and species richness of fish (B) that were present in or passed through 1 m x 2 m quadrats during 15 minute observations at continuous mangrove (C, n=18), patch mangrove (P, n=14), sandy shore habitats (S, n=14) and dock habitats (D, n=14) along South Hole Sound, Little Cayman Island. Bars represent mean ± SE.

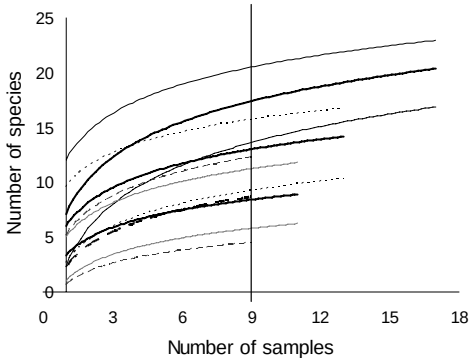

Figure 2. Species-sample accumulation curves for fish present in 1 m x 2 m quadrats over 15 minutes observation periods in South Sound, Little Cayman Island. The four bold lines represent four habitats: continuous mangrove (C), patch mangrove (P), sandy shore habitat (S), and docks habitat (D; dashed line). Thin grey lines are 95% confidence intervals: solid dark lines for C, dark dotted lines for P, solid light lines for S, and dark dashed lines for D. The vertical line aids comparison of the four habitats at the highest common number of samples (9).

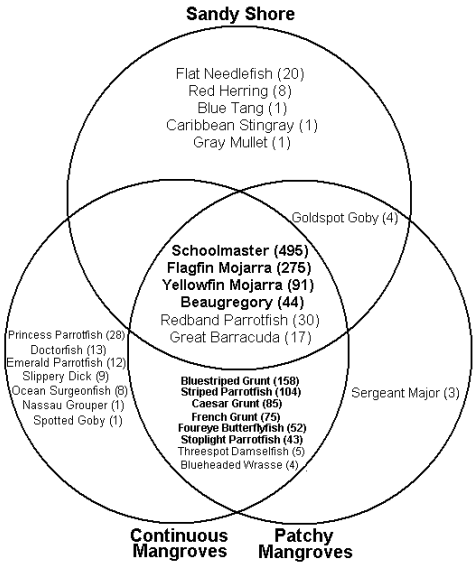

Figure 3. Venn diagram of fish species that were present in or passed through 1 m x 2 m quadrats during 15 minute observations in three habitats in South Hole Sound, Little Cayman Island. The total abundances (counts) are in parentheses; the 10 most abundant species are in bold.

Table 1. Abundance and percent abundance of fish species that were present in or passed through 1 m x 2 m quadrats during 15 minute observations in continuous and patchy mangrove habitats in South Hole Sound, Little Cayman Island. Abundance of species in bold are significantly different between the two habitats (matched pairs t-test).

Fish Species	Continuous		Patch	
	Abundance	% Abundance	Abundance	% Abundance
Beaugregory	18	3.23	17	2.94
Blueheaded Wrasse	2	0.36	2	0.35
Bluestriped Grunt	91	16.31	64	11.07
Caesar Grunt	**13**	**2.33**	**71**	**12.28**
Doctorfish	2	0.36	0	0.00
Emerald Parrotfish	12	2.15	0	0.00
Flagfin Mojarra	5	0.90	14	2.42
Foureye Butterflyfish	39	6.99	11	1.90
French Grunt	**9**	**1.61**	**66**	**11.42**
Goldspot Goby	0	0.00	1	0.17
Great Barracuda	6	1.08	6	1.04
Nassau Grouper	1	0.18	0	0.00
Ocean Surgeonfish	8	1.43	0	0.00
Princess Parrotfish	25	4.48	0	0.00
Redband Parrotfish	12	2.15	6	1.04
Red Herring	0	0.00	0	0.00
Sargeant Major	0	0.00	1	0.17
Schoolmaster	**154**	**27.60**	**269**	**46.54**
Slippery Dick	9	1.61	0	0.00
Spotted Goby	1	0.18	0	0.00
Stoplight Parrotfish	33	5.91	10	1.73
Striped Parrotfish	**93**	**16.67**	**11**	**1.90**
Threespot Damselfish	3	0.54	2	0.35
Yellowfin Mojarra	22	3.94	3	4.67

DISCUSSION

Although continuous and patch mangrove habitats differed in the spatial scale of their mangrove root coverage (*personal observation*), we found no difference in fish abundance and species richness between these two habitats. However, species richness was lower in sandy shore habitats than in both mangrove habitats, suggesting that fish communities in mangrove habitats have more in common with each other than those in sandy shore habitats (see Figure 3). The degree of fragmentation in our study area did not alter fish communities in mangrove patches.

Fish community composition also did not differ greatly between continuous and patch mangrove habitats. However, there were strong differences associated with fragmentation when we considered particular fish species. Because some species were more common in one habitat than the other, there may be species-specific responses to

mangrove fragmentation. Anecdotally, we also observed large fish individuals in continuous mangroves, but not in patch mangroves.

Fish abundance and species richness of both dock and sandy shore habitats were lower than in mangrove habitats. While docks provide structure for fish communities, they are inadequate substitutes for mangroves. Fish communities were apparently not affected by the current degree of fragmentation of mangrove habitats, but they were strongly and negatively affected by mangrove removal.

LITERATURE CITED

Clynick, B. and M.G. Chapman. 2002. Assemblages of fish in patchy mangrove forests in Sydney Harbour. Marine and Freshwater Research. 53:669-677.

Collins, T. Personal Communications: 8 March 2007.

Gotelli, N. J. and G. L. Entsminger. 2001. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm.

Gotelli, N. J. and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, DC.

Laegdsgaard, P. and C. Johnson. 2001. Why do juvenile fish utilize mangrove habitats? Journal of Experimental Marine Biology and Ecology. 257:229-253.

Pittman, S.J., C.A. McAlpine, and K.M. Pittman. 2004. Linking fish and prawns to their environment: a hierarchical landscape approach. Marine Ecology Progress Series. 283:233-254.

Robertson, A.I. and S.J.M. Blaber. 1992. Plankton, epibenthos and fish communities. Pp. 173-224 *in* A.I. Roberston and D.M. Alongi, editors. Tropical Mangrove Ecosystems. American Geophysical Union: New York, New York.

TRADEOFFS BETWEEN PREDATOR AVOIDANCE STRATEGIES IN TWO SABELLID FAN WORMS

BRIGETTE A. JONES AND ALLISON M. CITRO

Faculty Editor: David R. Peart

Abstract: Organisms avoid predation in many ways. Sabellid fan worms exhibit four methods for avoiding predation: cryptic habitat, cryptic coloration, unpalatability, and behavioral predator avoidance (escape). We examined the tradeoffs between cryptic habitat and predator avoidance in two species of fan worms (Order Sabellidae), the yellow fan worm, *Notualax occidentalis,* and the split-crown feather duster, *Anamobaea orstedii*. We made four predictions. (P1) We predicted that yellow fan worm individuals in more cryptic habitats would be less sensitive to disturbances because they are more protected from predation. (P2) We predicted that there would be no relationship between fan worm diameter (which should be positively related to growth and survival) and crevice depth, because of a potential tradeoff between exposure to predators in the water column and increased food availability and growth rate in an exposed position. (P3) Between species, we predicted that the split-crown feather dusters would be more sensitive to disturbances than the yellow fan worms because the feather dusters are more exposed and therefore more vulnerable to predation. (P4) Across both species, we predicted that fan worms that retracted at a greater distance from the disturbance would take longer to re-emerge, and that larger fan worms would be more sensitive to disturbance because they would be at higher risk for predation.

Our first prediction about the yellow fan worm was not supported, indicating that the advantages of living in a more cryptic habitat are not associated with response to perceived predation risks. Our remaining three predictions were supported by our results. We feel that *N. occidentalis* and *A. orstedii* are characteristic of the order sabellidae because they span a large portion of the size range of the sabellids and represent two of the largest families in the order. Therefore, our results indicate that sabellid worms as a whole may experience strong tradeoffs between habitat crypticity and behavioral predator avoidance.

Key Words: Notualax occidentalis, Anamobaea orstedii, Sabellidae, *fan worms, polychaetes, cryptic habitat*

INTRODUCTION

Sessile organisms have many strategies for minimizing predation, including camouflage and unpalatability. However, behavioral mechanisms for avoiding predation in sessile organisms are not as well understood, because these strategies typically involve significant movement. Sabellid fan worms are unusual in this respect; though sessile, they are not completely immobile. The bodies of sabellid fan worms remain in protective tubes in the substrate while the fan worm's radioles extend out for feeding and respiration; the crown of radioles retracts inside the tube when the

worm is threatened (Fauchaud 1977, Fauchaud and Jumars 1979.

Sabellid fan worms have four strategies for deterring predation: cryptic habitat, cryptic coloration, unpalatability, and behavioral avoidance (escape), and any combination is possible. The tradeoff between palatability and escape has been demonstrated by Kicklighter and Hay (2007), who found that there is a negative relationship between palatability and sensitivity to disturbance for all of the species they studied.

We examined the relationship between habitat crypticity and escape (measured as crown retraction) in two species of fan worm. One species, the yellow fan worm *Notualax occidentalis* (Sabellidae), has a bright yellow radiole fan that ranges from 1 – 4.5 cm in diameter (Table 2) and is found in crevices of varying sizes in the coral rock of tropical reefs. We predicted that worms in deeper crevices would be less sensitive to disturbance (P1), because they are less vulnerable to predators than those in shallower crevices. However, we predicted that there would be no relationship between fan worm diameter and crevice depth (P2), because although worms in deeper crevices should have higher survivorship, they may receive less food from the water column, and thus have slower growth rates.

We also compared *N. occidentalis* to the split-crown feather duster, *Anamobaea orstedii* (Sabellidae). Split-crown feather duster worms have white and either maroon or brown bands on the fans, which range from 2 – 7 cm in diameter (Table 2). They live directly in the sand and hard pan substrate and are typically found on the edges of depressions in the sea floor. Although they are usually more exposed than the yellow fan worms, their coloring is more cryptic. We predicted that the feather dusters would retract when the potential predator was farther away (P3a) and take longer to re-emerge (P3b) than the yellow fan worms, because the feather dusters are larger (and potentially more valuable prey for fish) and their habitats are less cryptic.

Across both species, we expected that the time until the worm re-emerged would increase with the distance at which it retracted (P4a). We reasoned that worms that are at high risk of predation would retract from fish predators at greater distances, and would also remain retracted longer, to minimize the probability of consumption by a fish that had recently disturbed them. We also predicted that the larger fan worms would be more sensitive to disturbance than the smaller fan worms (P4b), because they would be

more susceptible to predation because of their larger size.

METHODS

Study System: We collected data between 0800 and 1800 on 3 and 4 March, 2007 on Little Cayman Island. We studied *N. occidentalis* in Grape Tree Bay behind the Little Cayman Research Center, and *A. orstedii* in Jackson's Bay Marine Park.

Field Methods: We haphazardly selected 67 yellow fan worms (*N. occidentalis)* on 3 March and 69 split-crown feather dusters (*A. orstedii)* on 4 March. As one measure of sensitivity to disturbance we simulated an approaching fish predator by swimming at the fan worm while waving a ruler in front, until the crown retracted. We recorded the distance from the edge of the ruler to the fan worm at the time of retraction. When it was necessary to touch the fan worm to induce retraction, a distance of 0 cm was recorded. Our second measure of sensitivity to disturbance was the time between retraction and the complete re-emergence of the crown. We measured the diameter of yellow fan worm crowns and width of split-crown feather duster crowns to the nearest 0.5 cm. For the yellow fan worms, the length and width of the crevice opening was measured, as well as the depth to the fan worm in the crevice.

Statistical Analyses: We used a total of three MANOVAs within and combining species to test the effect of diameter as the independent variable on the two dependent variables, re-emergence time and response distance. We used pair-wise correlations within species and combining species to analyze the relationships between crevice size, depth, response distance, response time, and crown diameter. We tested the differences in re-emergence time, response distance, and diameter between the two species with three t-tests assuming unequal variances.

RESULTS

Within N. occidentalis: A MANOVA of the effect of diameter on re-emergence time and response distance was marginally significant ($F_{2,64} = 2.60$, $P = 0.082$). The strongest correlation for the yellow fan worm was between worm diameter and response distance (Table 1). There were no other significant correlations between depth inside crevice, response distance, re-emergence time, and diameter for *N. occidentalis* (Table 1).

Table 1. Correlation coefficients and associated p-values for each pair of variables for the yellow fan worm *Notualax occidentalis*. "Distance" refers to the distance between the edge of the ruler (simulated fish disturbance) and the fan worm crown at the time of retraction. "Diameter" is the approximated diameter of the extended fan worm crown. "Time" refers to the total time from full retraction until the fan worm was fully re-extended. "Depth" is the depth to the fan worm inside a crevice. n = 67 worms.

Variable Pair	r	P
Distance (cm) by Diameter (cm)	-0.2309	0.0602
Distance (cm) by Time (s)	0.1088	0.3806
Time (s) by Diameter (cm)	0.1216	0.3271
Diameter (cm) by Depth (cm)	-0.0487	0.6958

Within A. orstedii: A MANOVA of the effect of crown diameter on re-emergence time and response distance was not significant ($F_{2,66}$ = 0.012, P = 0.67). For the 69 feather duster worms, response distance and re-emergence time were correlated (r = 0.52, P < 0.0001). Crown diameter was not correlated with either distance (r = 0.11, P = 0.39) or re-emergence time (r = 0.031, P = 0.80).

Between species: The split-crown feather dusters had a significantly greater re-emergence time ($t_{75.87}$ = 7.59, P < 0.0001) and response distance ($t_{98.99}$ = 8.93, P <0.0001) than the yellow fan worm. The split-crown feather dusters were also 47% larger than the yellow fan worms ($t_{123.50}$ = 7.57, P <0.0001; Table 2).

Table 2. Means and ranges of the diameter, response distance, and re-emergence time for the yellow fan worm *Notualax occidentalis* (n=67) and the split-crown feather duster *Anamobaea orstedii* (n=69). "Diameter" is the approximated diameter of the extended fan worm crown. "Distance" refers to the distance between the edge of the ruler (simulated fish disturbance) and the fan worm crown at the time of retraction. "Time" refers to the total time from full retraction until the fan worm was fully re-extended.

	N. occidentalis			***A. orstedii***		
	Mean ± 1 SE	**Min**	**Max**	**Mean ± 1 SE**	**Min**	**Max**
Diameter (cm)	2.58 ± 0.093	2	7	3.79 ± 0.13	1	4.5
Distance (cm)	1.42 ± 0.26	0	10	9.94 ± 1.1	1	40
Time (sec)	22.70 ± 2.65	3	114	76.32 ± 5.39	15	225

Combined species: Combining both species (N = 136 worms), strengthened the correlation between re-emergence time and response distance (r = 0.64, P < 0.0001; Fig. 1). A MANOVA of the effect of worm diameter on re-emergence time and response distance was highly significant ($F_{2,133}$ = 0.18, P < 0.0001; Fig. 1). With both species, diameter was also positively correlated with both re-emergence time (r = 0.37, P < 0.0001) and response distance (r = 0.33, P < 0.0001; Fig. 2).

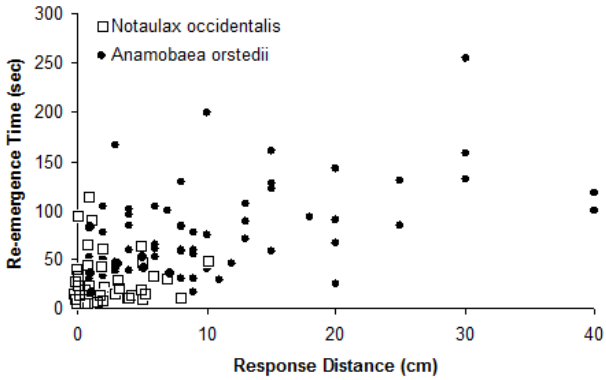

Figure 1. Relationship between two measures of sensitivity to disturbance: time until re-emergence after disturbance and distance between the crown and disturbance at retraction ($r = 0.64$, $P < 0.0001$) for two representative sabellid species: the yellow fan worm *Notualax occidentalis* (n=67) and the split-crown feather duster *Anamobaea orstedii* (n=69). "Re-emergence Time" refers to the total time from full retraction until the fan worm was fully re-extended. "Response Distance" refers to the distance between the edge of the ruler (simulated fish disturbance) and the fan worm crown at the time of retraction.

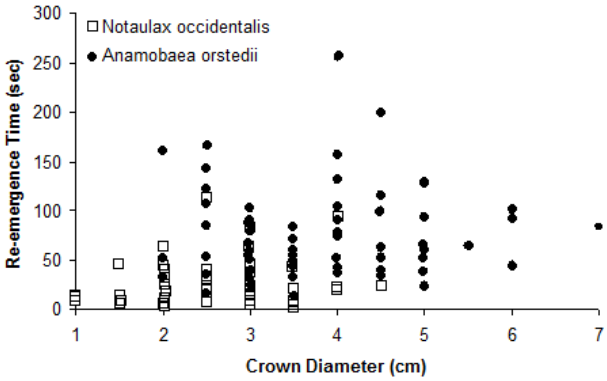

Figure 2. Relationship between crown diameter of the yellow fan worm *Notualax occidentalis* (n=67) and the split-crown feather duster *Anamobaea orstedii* (n=69) and re-emergence time ($r = 0.37$, $P < 0.0001$). "Diameter" is the approximated diameter of the extended fan worm crown. "Re-emergence Time" refers to the total time from full retraction until the fan worm was fully re-extended.

DISCUSSION

Within species: N. occidentalis: Contrary to our first prediction, yellow fan worms were not differentially sensitive to disturbance based on their level of habitat crypticity as measured by depth within substrate crevices. This suggests that having a more cryptic habitat may directly decrease predation risk, rather than causing a change in the behavioral response to perceived predation risks. We found no relationship between worm diameter and habitat crypticity, supporting our second prediction that there would be a tradeoff between protection from predation and growth rate. *Between species:* The larger, less cryptically located, split crown feather duster *A. orstedii* was more sensitive to disturbance, supporting our predictions that there should be a positive relationship between size and sensitivity, and a negative relationship between habitat crypticity and sensitivity.

Both species combined: Our measures of sensitivity to disturbance, re-emergence time and response distance were strongly correlated, suggesting that both may be useful measures of sensitivity. Larger fan worms were also more sensitive to disturbance across species, supporting our prediction and suggesting that they may indeed be favored food resources for fish. The more cryptic yellow fan worm

N. occidentalis was less sensitive than *A. orstedii*; this negative relationship suggests that there is a tradeoff between cryptic habitat and behavioral predator avoidance strategies.

N. occidentalis and *A. orstedii* span a large portion of the known size range of sabellids (the species overlap in size) and are present in habitats of varied crypticity. We suggest that the positive relationship between sensitivity to disturbance and crown diameter that we observed may apply more generally in the order Sabellidae.

Our findings are consistent with the existence of tradeoffs between escape and habitat crypticity, in addition to the known tradeoffs between escape and deterrence.

Alternatively, this relationship could result from larger fan worms detecting predators sooner, rather than being more vulnerable to predation. Both could result in a greater response distance. Furthermore, the alternative hypothesis that retraction would have greater energetic costs for larger worms would show a negative relationship between fan worm diameter and sensitivity, generating a trend opposite to our results.

Though it has been demonstrated that fan worms have structural and chemical defenses to decrease the palatability of their radioles (Kicklighter and Hay 2007), we were unable to address the interaction of palatability and crypticity in our study species. The split-crown feather duster has chemically defended radioles (Kicklighter and Hay 2007), but the palatability of the yellow fan worm is unknown. Physical and behavioral methods of decreasing predation appear to be combined by sabellid fan worms to create an effective defense.

LITERATURE CITED

Fauchald, K. 1977. The Polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angelos County Science Ser* 28: 1-190.

Fauchald, K. and P. A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17: 193-284.

Kicklighter, C. E., and M. E. Hay. 2007. To avoid or deter: interactions among defensive and escape strategies in sabellid worms. *Oecologia* 151**:** 161-173.

REDUCING THE SPACE LIMITATIONS ON JUVENILE FISH IN REEF SYSTEMS

CHAD S. GORBATKIN AND SARAH C. ISBEY

Faculty Editor: David R. Peart

Abstract: Spatial resources, especially three-dimensional structures, are generally considered the most limiting resources to fish abundance and diversity on coral reefs. Therefore, this space limitation should be considered in the design of artificial reefs. Despite extensive studies of the use of artificial reefs by adult fish, few studies have determined how juveniles use artificial reefs. To understand how artificial reefs may create new recruitment locations in space-limited fish communities, we need to also examine how juveniles use artificial reef structures. We monitored juvenile fish colonization of different types of artificial reef structures. We placed 18 structures, of three three-dimensional configurations, varying in complexity, around each of two coral heads on Little Cayman Island, one coral head on the north side and one on the south side. We installed the structures on 2 March 2007 and monitored juvenile fish colonization through 7 March 2007. We predicted that more fish would colonize the most three-dimensionally complex structures. Overall, we expected rapid colonization followed by a plateau, for all structure types. We recorded fish species composition and abundance on each structure during both day and night observation periods. Our data supported our prediction, with significantly more fish on more complex structures and fish abundance and species richness reaching a plateau after three days. Our results demonstrate that small-scale artificial reef structures may be important for reducing space limitations in diverse groups of juveniles and may form an integral part of artificial reef systems.

Key Words: artificial reef, microhabitat preference, spatial limitation

INTRODUCTION

Spatial limitation, especially of three-dimensional structure, is arguably the most important limitation on fish diversity and abundance in coral reefs (Sale 1977, Sale 1978, Gladfelter 1983, Holbrook 2000). There has been extensive research on the processes that lead to spatial limitations, including the limitations of structural habitat and the density-dependence of fish populations. Habitat availability is one of the best predictors of fish densities and abundance (Sale 1977; Holbrook et al. 2000). Where space is limiting, recruitment and survivorship of juveniles can be reduced, decreasing population carrying capacity and growth rate. Fish populations also show different degrees of vulnerability to density dependent mortality at varying levels of habitat availability, food resources, and predation risks (Anderson 2001; Holbrook and Schmitt 1988a, b, 2000; Schmitt and Holbrook 1999a, b). Because even taxonomically and functionally

similar fish can have different responses to prey and predator densities (Forrester and Steele 2000; Leis et al. 2002), understanding fish responses to different levels of these factors is complicated, but critical to understanding reef fish community dynamics.

Understanding the processes driving spatial limitation can help in designing the most effective artificial reefs. Artificial reefs increase fish abundance and species richness in areas that also have natural reefs by reducing spatial limitations on fish (Walker et al. 2002; U.S. Coral Reef Task Force 2005). Artificial reefs may help maintain species richness in reef fish communities where habitat degradation occurs (Rilav and Benayahu 1997; Golani and Diamant 1999; Strelcheck et al. 2005). In light of global climate changes and degradation of existing coral reefs, artificial reef research is increasingly important for the future of coral reef ecology (Bellwood et al. 2004; Hughes et al. 2003).

To create functional artificial reefs, many design factors must be considered, including structural complexity (Gratwickel and Speight 2005, Charbonnel et al. 2002), spatial orientation (Rivlov and Benayahu 1997), and location of the artificial reef with respect to surrounding structures and substrates (Strelcheck et al. 2005; Moreno 2002). Past studies highlight the importance of creating heterogeneous artificial reefs using different rugosities, orientations, and substrates. There is no single artificial reef structure equally suited for all fish or all age classes. Use of artificial reefs by coral and other reef species also needs to be considered (Eggleston and Lipcius 1992; Oren and Benayahu 1997).

The role of artificial reefs as habitat for juveniles has been examined in few published studies (e.g. Schmitt and Holbrook 1999a). The lack of research on use of artificial reefs by juvenile fish is surprising, given that juveniles have different habitat requirements from adults, including smaller-scale structural requirements. In addition, they may experience different degrees and types of space limitation, and display different territoriality behaviors than adult conspecifics (Holbrook et al. 2000). The lack of information on juvenile response to artificial reefs represents a substantial gap in our knowledge of artificial reef ecology (Bohnsack and Sutherland 1985).

Here we contribute to addressing this need by studying juvenile colonization of small-scale, three-dimensional structures at two patch reef locations on Little Cayman Island. We tested the potential for these structures to increase available space for juveniles, which might in turn reduce juvenile mortality in natural or artificial reef systems. We addressed three main

questions: (1) Do juvenile fish prefer certain artificial reef structure types?; (2) Does fish colonization in artificial reefs change over a period of several days; and (3) Do artificial structures support fish at night during periods of rest? Based on previous studies that found rapid adult fish colonization on large-scale artificial reefs (Golani and Diamant 1999; Gratwickel and Speight 2005; Santos et al. 2002), we also expected to see rapid colonization by juveniles, followed by a plateau in fish and species abundance. We also predicted that fish would prefer structures with more overhang (as found by Isbey and Gorbatkin 2007), and fewer fish would use the artificial reef structures at night than during the day.

METHODS

Study Site:

We monitored juvenile fish colonization of experimental reef structures on 2-7 March, 2007, at two locations on Little Cayman Island. Each study site contained 18 experimental structures, including six replicates of each of three structure types described below. One study site, on the north side of the island, was directly behind the Little Cayman Research Centre. The second, on the south side, was in Preston Bay, *c.* 300 m west of Pirate's Point. At both sites, we placed all 18 structures around a single coral head that was *c.* 4 m in diameter and separated by at least 5 m on all sides from other large coral structures (e.g., other coral heads and the back reef). This allowed 18 structures to be placed around the perimeter of the coral head, approximately 1.5 m from the head edge, with approximately 1 m between structures.

Experimental Methods:

At both sites, we created three-dimensional structures from dead coral heads found on the beach. Each structure consisted of five dead coral heads, arranged in one of three configurations that varied in the amount of space between heads (Fig.1). The first structure, henceforth referred to as "large overhang", had one large hole. The second structure ("double overhang"), had two holes (both smaller than the single hole in the large overhang structure). The third structure ('flat"), was a single line of five contiguous coral heads.

Each structure was placed in the water in the morning of 2 March, 2007. We collected data on fish colonization of each structure on 2 March (day 0) through 7 March (day 5). Due to rough weather, we could not collect data from the north site on 6-7 March. Each day, we observed each structure for two three-minute periods, recording the number and species of fish on the structure and noting interesting behaviors. All

structures were observed once before the second three-minute observation period began. Observation periods were summed for a daily total number of fish individuals and species per structure. For fish abundance, daily totals were averaged for each structure to calculate the mean number of fish individuals per structure over the 5 observation days. For fish species richness, we calculated the total number of species observed on a structure through the entire experimental period. To examine nocturnal structure use, we observed the structures at night, on 3 and 4 March (days 1 and 2).

Because the central coral heads chosen were at least 5 m from other corals, our coral heads were assumed to be the only source of juvenile fish. We censused the central coral heads once on 4 March to determine the species richness of the source populations of juvenile fish.

Statistical Methods:

We tested the effect of structure type on total number of fish species observed and mean fish per day with two one-way ANOVAs, and we used Tukey-Kramer multiple comparisons tests to compare fish abundance and species richness among structure types at alpha = 0.05. Since north and south sites (N = 6 replicates per structure type per site) had equal colonization, (Mean number of individual fishes per structure: north = 2.6 ± 0.3 (mean ± 1 SE) and south = 2.8 ± 0.3, t_{34}=0.48, P=0.63; Number of species per structure: north = 4.3 ± 0.5 and south = 5.1 ± 0.5, t_{34}=1.20, P=0.24), we combined the sites for analyses.

RESULTS

Both fish species richness and abundance increased rapidly from days 0-3 and then remained relatively constant through day 5 (Fig. 2). We saw no fish in the structure areas before placement and we saw fish entering the structure areas only from the central coral head, not from surrounding patch reef.

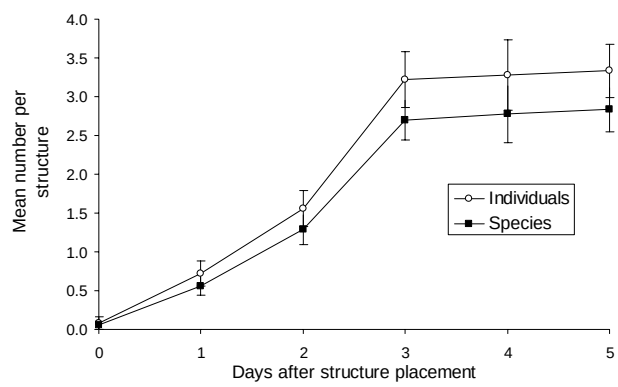

Figure 2: Mean number of individuals and species of fish (± 1 SE) colonizing 36 artificial reef structures over five days on Little Cayman Island. Data were collected 2-7 March 2007 at two locations on the island for three types of artificial reef structures (see Fig. 1 for details). Here we combine all data (overhang and no overhang, north and south locations) to show overall colonization patterns.

Structure type affected the average fish species richness and abundance ($F_{2,33}$=5.46, P=0.0089; $F_{2,33}$=9.44, P=0.0006, respectively). The average number of species per structure and mean fish abundance per day per structure for large overhang and double overhang structures were higher than flat structures, but there was no significant difference between large and double structure types (total species: Fig. 3). Fish abundance on large overhang structures (3.44 ± 0.25 individuals/day/structure) and double overhang structures (3.09 ± 0.47 individuals/day/structure) were 232% and 209% greater, respectively, than on flat structures (1.48 ± 0.24 individuals/day/structure). The mean total species observed per large overhang structure and per double overhang structure were 172% and 162% greater, respectively, than mean total species observed per flat structure (Fig. 3).

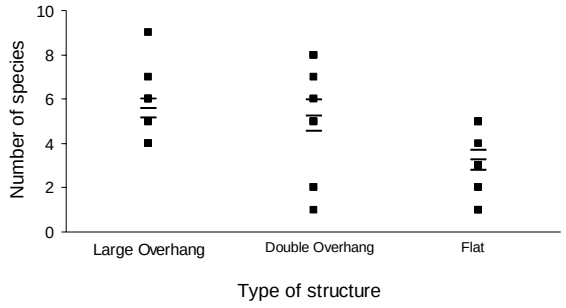

Figure 3: Numbers of fish (mean ± 1 SE) colonizing artificial reef structures with different amounts of overhang. See Fig. 1 for description of the three structure types (N=12 structures per type). Data were collected 2-7 March 2007 on Little Cayman Island.

Approximately 88% of the total juvenile species present in our census of the patch reefs were observed using the structures (22 of 25 species). Fish commonly observed using the structures diurnally included the ocean surgeonfish (*Acanthurus bahianus*), slippery dick (*Halichoeres bivittatus*), bluehead wrasse (*Thalassoma bifasciatum*), bridled goby (*Coryphopterus glaucofraenum*), dashed goby (*Ctenogobius saepepallens*), and rosy blenny (*Malacoctenus macropus*). Juvenile fish that colonized a single structure or two neighboring structures for the duration of the study included the ocean surgeonfish and beaugregory (*Stegastes leucostictus*). The beaugregory was the only individual fish that attempted to monopolize a structure.

An average of only 3.7% of the fish using the structures diurnally spent the night (days 1-2). This included one juvenile ocean surgeonfish, one post-larval ocean surgeonfish, one stoplight parrotfish (*Sparisoma viride*), and two bridled gobies. Post-larval stage fish of two nocturnally active species, the two-spot cardinalfish (*Apogon townsendi*) and the belted cardinalfish (*Apogon pseudomaculatus*), were observed using the structures at night. No nocturnally active fish were observed using the structures during the day.

DISCUSSION

Colonization over time:

The rapid colonization of the 36 artificial structures by juveniles of both common species (e.g. slippery dicks) and rarer species (e.g. the whitespotted filefish) supports the assumption that complex structures are valuable and often limiting resources in coral reef systems (Sale 1977; Holbrook et al. 2000; Anderson 2001). The structures were colonized by most (88%) of the juvenile species present on the two patch reefs and a single structure was rarely monopolized by a single individual, suggesting that these small-scale structural resources are accessible to most juveniles within the community.

After a period of rapid colonization, both the number of fish per structure and number of species per structure appeared to plateau after three days (Fig. 1). Golani and Diamant (1999) observed a similar saturation curve for large-scale artificial reefs, though over a much longer period. The saturation in our study may be attributed to two factors: (1) the structures have a fixed carrying capacity for fish; and (2) all individuals on the nearby patch reef able to colonize new structural resources had already done so after three days.

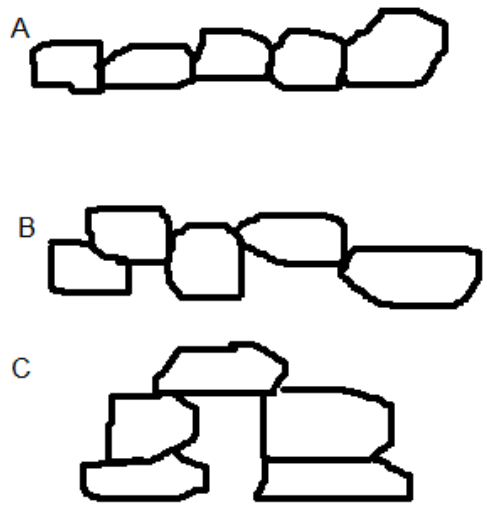

Figure 1: Three structure types used in artificial reef colonization experiment on Little Cayman Island. We refer to structure A as "large overhang," B as "double overhang," and C as "flat." Each structure contained five naturally occurring dead coral blocks of irregular shapes, c. 20-30 cm in mean linear dimensions. Structures were placed in the back reef at two sites: behind Little Cayman Research Centre on the north side, and in Preston Bay on the south side. After placement on 2 March they were observed for colonization until 7 March. . N=6 for each of the three structure types at each site.

Structure type preference:

Results supported our prediction that juveniles would prefer structures with overhangs more than they would prefer flat structures (Fig. 3). We observed no differences between large-overhang and double-overhang structures (for numbers of fish per structure per day, or for total number of species observed on a structure over five days). Overhang space in each of these structure types increases vertical habitat complexity and interstitial space, both of which increase biomass and diversity in fish communities on large-scale

artificial reefs (Rilav and Benayahu 1997; Gratwickel and Speight 2005). Presence or absence of overhang space may be more important than number or volume of overhangs. Structures with overhangs can support both fish who find refuge in overhang spaces (e.g. ocean surgeonfish) and fish that find refuge in crevices between the structure and the ocean floor (e.g. gobies).

Diel patterns:

Although many juvenile fish in the local community used the 36 structures, nearly 100% were diurnally active species, and only 4% of those used the structure to sleep (days 1-2). Our structures were positioned in foraging areas (e.g. sea grass and algae beds) and may have functioned mostly to provide shelter during foraging periods. The 4% that did sleep in the structures used crevices between the dead coral blocks or between the blocks and the ocean bottom. It is possible that a longer time period is necessary for diurnally active fish to begin using a structure at night. Increasing the number and size ranges of these crevices might increase the number of juvenile resting sites. Maximizing the suitable habitat for juveniles to use as resting space may be critical in increasing the overall carrying capacity for juveniles within a patch reef area (Sale 1977; Leis et al. 2002; Gratwickel and Speight 2005).

Significance for use in natural or artificial reefs:

Our results suggest that small-scale three-dimensional structures can be quickly colonized by a diverse group of juvenile fish. With further efforts to optimize sleeping space (e.g. crevices) within these small-scale structures, they could be useful for increasing juvenile survival rates, by reducing predation and increasing the carrying capacity of the habitat (Connell 1997; Forrester and Steele 2000; Anderson 2001). Small-scale structures may create habitat space that supports high fish abundance and diversity in both natural coral reef systems and artificial reef systems.

LITERATURE CITED

Anderson, T.W. 2001. Predator Responses, Prey Refuges, and Density-Dependent Mortality of a Marine Fish. Ecology 82.1: 245-257.

Bellwood, D.R., T.P. Hughes, C. Folke and M. Nystrom. 2004. Confronting the coral reef crisis. Nature 429: 827-833.

Bohnsack, J.A. and D.L. Sutherland. 1985. Artificial reef research: a review with recommendations for future priorities. Bulletin of Marine Science 37: 11-39.

Charbonnel, E., C. Serre, S. Ruitton, J.G. Harmelin and A. Jensen. 2002. Effects of increased habitat

complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). ICES Journal of Marine Science 59: S208-S213.

Connell, S.D. 1997. The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. Journal of Experimental Marine Biology and Ecology 209: 261-278.

Eggleston, D.B. and R.N. Lipcius. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. Ecology 73.3: 992-1011.

Forrester, G.E. and M.A. Steele. 2000. Variation in the presence and cause of density-dependent mortality in three species of reef fishes. Ecology 81.9: 2416-2427.

Gladfelter, W.B. and W.S. Johnson. 1983. Feeding niche separation in a guild of tropical reef fishes (Holocentridae). Ecology 64.3: 552-563.

Golani, D., and A. Diamant. 1999. Fish Colonization of an Artificial Reef in the Gulf of Elat, Northern Red Sea. Environmental Biology of Fishes 54: 275-282.

Gratwickel, B. and M.R. Speight. 2005. Effects of habitat complexity on Caribbean marine fish assemblages. Marine Ecology 292: 301-310.

Holbrook, S.J. and R.J. Schmitt. 1988a. The combined effects of predation risk and food reward on patch selection. Ecology 69: 125-134.

Holbrook, S.J. and R.J. Schmitt. 1988b. Effects of predation risk on foraging behavior: Mechanisms altering patch choice. Journal of Experimental Marine Biology and Ecology 121: 151-163.

Holbrook, S.J., G.E. Forrester, and R.J. Schmitt. 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. Oecologia 122: 109-120.

Hughes, T.P. et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301: 929-933.

Isbey, S.C. and C.S. Gorbatkin. Non-random use of three-dimensional structures by three Caribbean coral reef fishes. Dartmouth Studies in Tropical Ecology, in press.

Leis, J.M., B.M. Carson-Ewart and J. Webley. 2002. Settlement behaviour of coral-reef fish larvae at subsurface artificial-reef moorings. Marine and Freshwater Research 53: 319-327.

Moreno, I. 2002. Effects of substrate on the artificial reef fish assemblage in Santa Eulalia Bay (Ibiza, western Mediterranean). ICES Journal of Marine Science 59: S144-S149.

Oren, U., and Y. Benayahu. 1997. Transplantation of juvenile corals: a new approach for enhancing colonization of artificial reefs. Marine Biology 127: 499-505.

Rilov, G. and Y. Benayahu. 1997. Rehabilitation of coral reef-fish communities: The importance of artificial-reef relief to recruitment

rates. Bulletin of marine science 70: 185-197.

Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. The American Naturalist 111: 337-359.

Sale, P.F. 1978. Coexistence of coral reef fishes—a lottery for living space. Environmental Biology of Fishes 3: 85-102.

Santos M.N., C.C. Monteiro and M.B. Gaspar. 2002. Diurnal variations in the fish assemblage at an artificial reef. ICES Journal of Marine Science 59: S32-S35.

Schmitt, R.J. and S.J. Holbrook. 1999a. Mortality of juvenile damselfish: implications for assessing processes that determine abundance. Ecology 80: 35-50.

Schmitt, R.J. and S.J Holbrook. 1999b. Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. Oecologia 118: 76-86.

Schmitt, R.J. and S.J. Holbrook. 2000. Habitat-limited recruitment of coral reef damselfish. Ecology 81.12: 3479-3494.

Strelcheck, A.J., J.H. Cowan and A. Shah. 2005. Influence of reef location on artificial-reef fish assemblages in the northcentral Gulf of Mexico. Bulletin of Marine Science 77: 425-440.

U.S. Coral Reef Task Force Working Group on Ecosystem Science and Conservation. 2005. Implementation of the National Coral Reef Action Strategy: Report to Congress. U.S. Coral Reef Task Force, Department of the Interior: Washington D.C.

Walker, B.K., B.H. Henderson and R.E. Spieler. 2002. Fish assemblages associated with artificial reefs of concrete aggregates or quarry stone offshore Miami Beach, Florida, USA. Aquatic Living Resources 15: 95-105.

THE EFFECTS OF OCEAN VERSUS LAND INFLUENCES ON BARRIER REEFS AROUND A CARIBBEAN ISLAND

JENNIFER N. CECH, SAMUEL J. HAYNOR, ZACHARY A. MAYER, MAYDA H. NATHAN, AND SONIA LEI

Faculty Editor: David R. Peart

Abstract: Coral reef health is rapidly declining worldwide as ocean temperatures increase and negative land influences on these marine systems intensify. It is difficult to observe declines in coral health directly because mortality often occurs immediately after episodic disturbance events. Little Cayman Island offers a special opportunity to evaluate some factors influencing coral health. Overfishing, pollution and sedimentation are minimal or absent, and the geologic structure of the island creates a clear spatial gradient of land vs ocean influences. We predicted that measures of coral health would decrease along a gradient of increasing land influence. We studied three sites across that gradient, sampling each at three scales: 20-m transects for substrate composition (sand vs coral), 1-m^2 quadrats on coral heads for health and diversity of corals, and individual colonies of selected species for more detailed coral health assessment. The gradient of land vs ocean influence strongly affected coral health on all three scales, and the effects differed among species. Coral cover, healthy tissue on coral heads, and species richness were all lower at sites with greater land influence. The effects of land influences on coral health were greater in *Diploria strigosa* and *Siderastrea siderea* than in *Porites porites*.

Key Words: coral reef health, Little Cayman Island, land influences, ocean influences

INTRODUCTION

Coral reef health is declining rapidly worldwide as ocean temperatures increase and terrestrial influences on coastal systems intensify. Many studies have focused on declines of coral reef health after episodic disturbances such as hurricanes (Woodley et al. 1981; Harmelin-Vivien and Laboute 1986), extreme water temperatures (Goreau 1992; Marshall and Baird 2000), outbreaks of coral disease (Bruckner and Bruckner 1997; Porter et al. 2001), and oil spills (Guzman et al. 1994). These disturbances can lead to reef coral mortality rates as high as 90% in one week (Glynn 1990). Some authors have argued that even natural disturbances, which have previously maintained high coral reef diversity via intermediate disturbance, have increased in severity and can now cause irreversible declines in coral reef health (Williams and Bunkley-Williams 1990; Rogers and Miller 2006). Others maintain that these disturbance regimes will lead instead to a shift in coral community structure, as a few species have already shown resilience to extreme episodic disturbances (Wilkinson

1999; Hughes et al. 2003). However, many of these studies are limited, in that they only look at single disturbance events without taking into account how future coral reef degradation may magnify the effects of episodic disturbance.

Few studies have examined the effects of chronic disturbance on coral reefs. These effects, classified here as "land influences," include a suite of factors that have negative impacts on coral growth: nutrient-loading from runoff, increased sedimentation, and higher surface temperatures (Nystrom et al. 2000). "Ocean influences," in contrast, positively affect coral health through upwellings of cooler pelagic water to shallow barrier reefs, which buffers against coral bleaching (West and Salm 2003). Chronic, land-based disturbance can strongly influence the future health of coral reefs (Pastorok and Bilyard 1985, Gates 1990). There is increasing awareness that humans can alter the frequency and intensity of these subtler disturbance regimes (Wilkinson 1999). Global warming amplifies the negative effects of land influences.

The Marine Conservation Law of 1979 established marine parks and other protected areas around Little Cayman Island in an attempt to slow the coral degradation that was apparent around the Caribbean. However, Little Cayman's barrier reefs lost 40% of their coral cover from 1997 to 2005 (Brown et al. 2006) and in 2003 a research group found that there was no difference in coral health between protected and unprotected sites on Little Cayman (Manfrino et al. 2003). The group postulated that coral health was correlated with large-scale ocean (positive) and land (negative) influences rather than localized human impact.

To test this hypothesis, we compared coral health between sites likely to have different levels of land and ocean influence. We predicted that in sites with a greater predominance of ocean influences, there would be higher coral cover, more healthy corals among living colonies, and higher coral species richness. We also predicted that the impact of land influences on coral health would differ among coral species.

METHODS

We studied reefs and corals at three sites on Little Cayman Island, along the island's southern coast, from 3 - 7 March, 2007. Our sites were located on the back barrier reef along Owen Island, South Sound (west of the beach resorts), and in Preston Bay (Fig. 1). Based on our knowledge of reef geology and prevailing currents, we assumed these sites would provide a gradient of ocean and land influences. Preston Bay, the closest to the outer reef wall and farthest from developed areas,

was our least land-influenced site, with a reef exposed to pelagic water. Owen Island lies in a shallow sound with several resorts and docks; we assumed it would have the most land influence and lowest ocean influence. We assumed the South Sound site, which was outside the main sound and was close to the channel leading to the ocean, would be intermediate between the two others. We reasoned that South Sound, being closer to the ocean than Owen Island, would receive a mix of land and ocean influences, while receiving more land-based run-off and higher temperatures than Preston Bay.

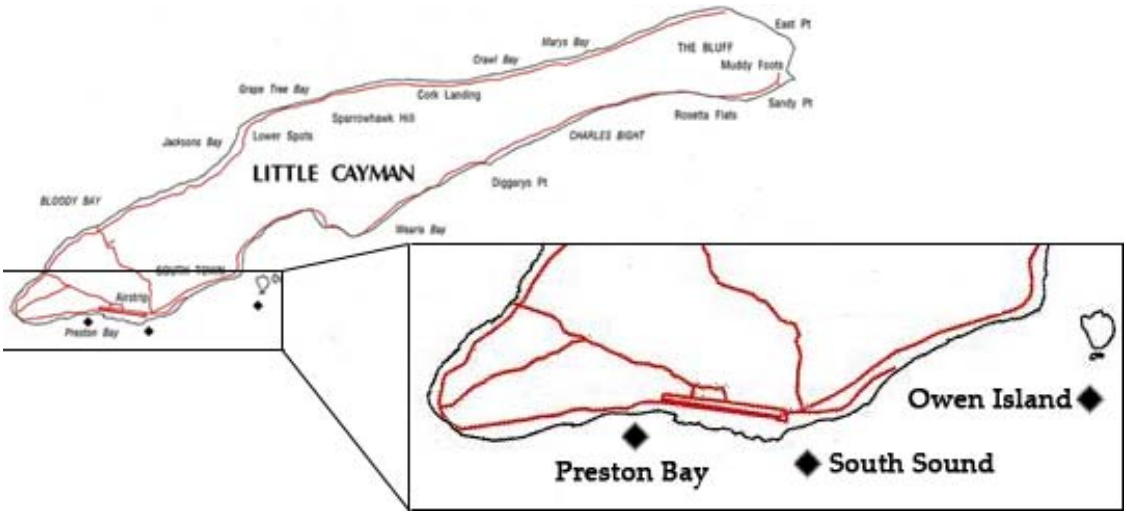

Figure 1: Our three sample sites were on the southern back barrier reef of Little Cayman Island. We expected a gradient of increasing ocean influences and decreasing land influences on the back reef from east to west. Land influences include warm water from the shallows around Owen Island and runoff from resorts around Owen Island and South Sound. Ocean influences include cold, nutrient-poor upwellings from the steep, 1,000-meter wall associated with Little Cayman Island. Preston Bay is closest to the edge of this wall, while South Sound is more removed, and a shallow, warm bay separates Owen Island from the wall.

We sampled at three spatial scales, focusing on four metrics of coral community health - total coral cover, percent live coral, percent healthy coral, and coral species richness. At each site, we first sampled five 20-m transects parallel to the back reef and recorded the substrate type or coral species (single point assessment) at 1 m intervals. If a point fell over coral, we noted species and condition (healthy or unhealthy). We also sampled 40 1 m x 1 m quadrats haphazardly placed on coral heads along the back reef at each site. Within each quadrat, we recorded the percentage cover of healthy coral (normal coloration), unhealthy coral (discolored or bleached), dead coral, and sand, as well as the species of stony and fire corals encountered.

To assess coral health at the species level, we took measurements of individual colonies of the three most abundant stony coral species in our sites: massive starlet coral (*Siderastrea siderea*), symmetrical brain coral (*Diploria strigosa*), and finger coral (*Porites porites*). We sampled 10 colonies of each species per site, using colonies that fell within our quadrats and haphazardly selecting additional colonies as needed. We calculated surface area by noting the geometric shape that most accurately matched the colony (sphere, hemisphere, cube or cylinder) and taking diameter, length, width, and height as needed. We reported the health of each colony using six descriptive categories: healthy, bare coral skeleton (BCS), BCS with low algal turf, BCS with dense algae, discolored, and bleached.

Statistical analysis: In back reef transects, we compared the percent sand and percent coral (alive and dead combined) between sites using a chi-squared test. To test for difference in percent healthy coral and percent dead coral among the three sites in our coral head quadrats, we used ANOVA tests. We compared species richness among sites using an ANOVA and then a Tukey-Kramer HSD test (alpha = 0.05).

RESULTS

Along 20-m transects, Owen Island had significantly more sand and less coral cover (live and dead combined) than South Sound or Preston Bay ($X^2_{df=2,297}$ = 16.752, P=.0002, Fig. 2). Furthermore, we found that the percent of dead coral per quadrat declined from Owen Island to South Sound to Preston Bay (ANOVA, $F_{df = 2,117}$ = 31.97, P = 0.001; Fig. 4), while the percent of healthy coral increased across the same sites (ANOVA, $F_{df = 2,117}$ = 31.97, P = 0.001; Fig. 4).

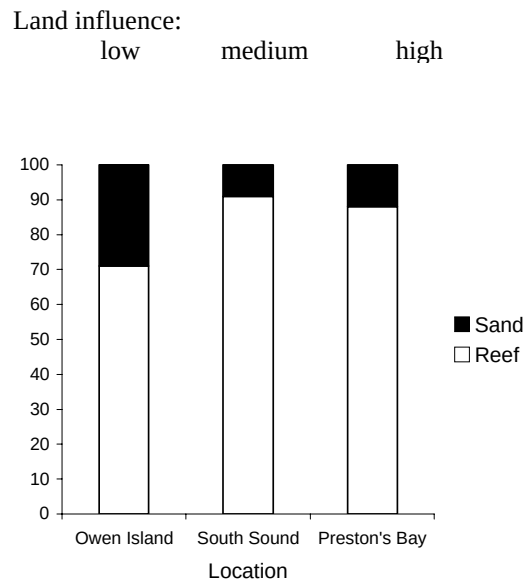

Figure 2: Mean percent cover of sand and coral (live or dead) on five 20-meter transects at three sites along a gradient of land vs ocean influences (gradient from left to right in the figure; see Fig. 1 for details) on Little Cayman Island. South Sound and Preston Bay had significantly more coral cover than Owen Island, but South Sound was not significantly different from Preston Bay.

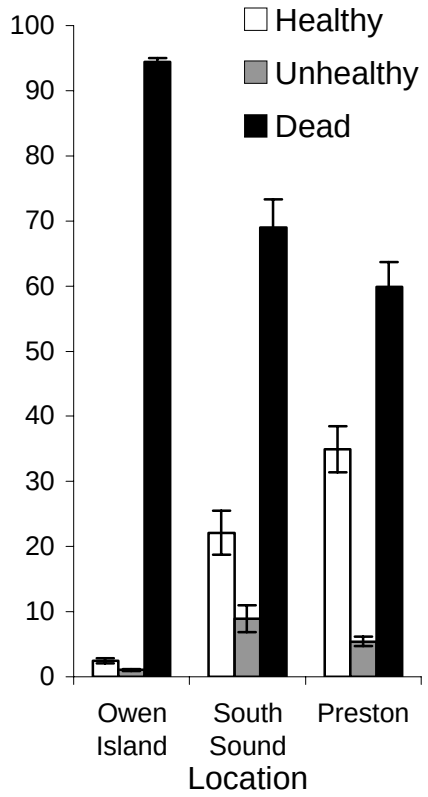

Figure 4: Coral health along a gradient of land vs ocean influence (gradient from left to right in figure; see Fig. 1 for details), on Little Cayman Island. Living coral was classified as unhealthy if it was discolored or bleached. Healthy coral tissue cover increased significantly along this gradient, while percent dead coral decreased. n = 40 quadrats sampled for each site.

In our coral head quadrats, Preston Bay had significantly higher coral species richness per quadrat (3.55 ± 0.24271, mean ± 1 SE), than both South Sound (1.575 ± 0.14272), and Owen Island (1.425 ± 0.10674), but there was no significant difference between South Sound and Owen Island.

Our individual colony samples indicated that the health and abundance of *Siderastrea* and *Diploria* colonies changed with the land-ocean gradient, while *Porites* did not.

For *Siderastrea*, we found the highest percentage of healthy tissue in Preston Bay (67% ± 5.4; ANOVA, $F_{df=2,27}$=17.02, P <0.0001), the highest percentage of unhealthy tissue in South sound (20% ± 3.61; ANOVA, $F_{df=2,27}$=2.32, P =0.12), and the highest percentage of dead tissue in Owen Island (76% ± 8.43 ANOVA, $F_{df=2,27}$=16.90, P <0.001) (Fig. 5). In coral head quadrats, *Siderastrea* was most abundant at South Sound (Fig. 3).

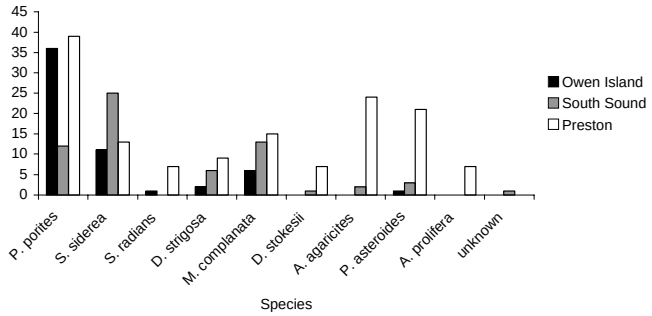

Figure 3: Abundance of ten species of coral in 40 quadrats (each 1 m x 1 m) on three sites over a gradient of land vs ocean influences (gradient from top to bottom in key; see Fig. 1 for details), on Little Cayman Island. For six species, abundance increased along this gradient. *P. porites* and *S. siderea* were the most abundant species across the three sites.

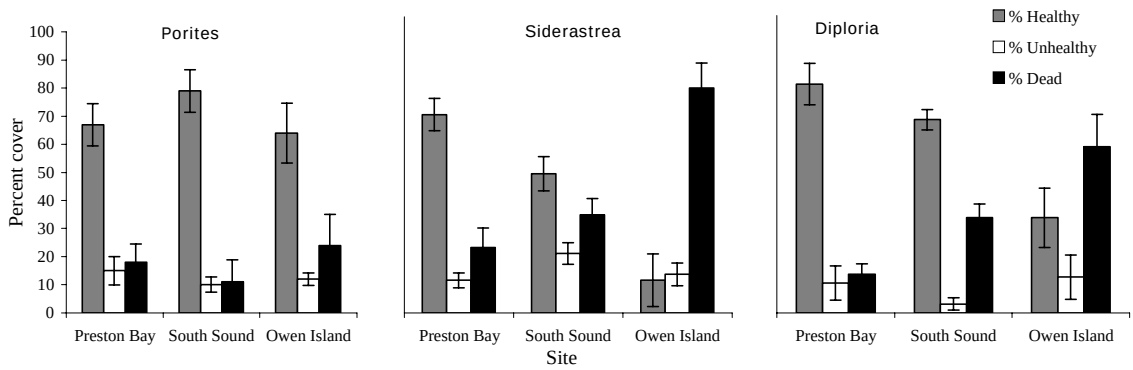

Figure 5. Health of individual coral colonies (percent healthy, unhealthy and dead tissue – 1 S.E.), for the three most abundant species across a gradient of land vs ocean influences (left to right in figure; see Fig. 1 for details) on the barrier reefs of Little Cayman Island. n = 10 colonies for each species for each site. *Porites* health did not differ significantly among sites, while *Siderastrea* and *Diploria* colonies were healthier at Preston Bay.

For *Diploria*, we found the highest percentage of healthy tissue in Preston Bay (77% ± 8.66; ANOVA, $F_{df=2,30}$=8.49, P =0.0012) and the highest percentage of both unhealthy (12 ± 7.46; ANOVA, $F_{df=2,30}$ =0.61, P =0.55) and dead tissue in South Sound (56 ±10.86; ANOVA, $F_{df=2,30}$=8.56, P =0.001) (Fig. 5). In coral head quadrats, *Diploria* was most abundant at Preston Bay (Fig. 3).

For *Porites*, we found no difference among sites for healthy tissue (ANOVA, $F_{df=2,27}$=0.78, P =0.47), unhealthy tissue (ANOVA, $F_{df=2,27}$=0.32, P =0.73), or dead tissue (ANOVA, $F_{df=2,27}$=.60, P =0.56), indicating that the health of this species is less responsive to land and ocean influences (Fig. 5). In coral head quadrats, *Porites* was most abundant at Preston Bay (Fig. 3).

DISCUSSION

Total coral cover, percent live coral, percent healthy coral, and coral species richness – our four metrics of coral community health – were all higher at Preston Bay, the site with the least land influence. These findings are consistent with the hypothesis that coral reefs are healthier at sites where ocean influences are greater than land influences.

Along broad-scale transects, there was significantly more sand and significantly less total coral cover (alive and dead combined) at Owen Island than at either South Sound or Preston Bay. Coral skeletons, whether live or dead, provide the structural living space for many other reef organisms (Clark and Edwards 1999); therefore, total

coral coverage is a measure of the quality of a reef as habitat to other organisms. Live coral has more structural integrity than dead coral, as evidenced by the destruction caused by storms on reefs that experienced previous coral mortality (Manfrino et al. 2003). Therefore, reefs containing more live coral should provide habitat that is superior to reefs with less live coral. As we predicted, Owen Island had significantly less live coral than either South Sound or Preston Bay, although there was no significant difference in percent live coral between South Sound and Preston Bay. Finally, the health of existing live coral can be an indicator of the future health of a reef, allowing for projections of structural and habitat quality on the reef (Manfrino et al. 2003). Preston Bay had the most healthy coral, followed by South Sound, with Owen Island having the least.

Preston Bay's reef supported more coral species than South Sound and Owen Island, upholding our predictions. Coral diversity is critical to the maintenance of suitable habitat for the rest of the reef community; thus, factors affecting coral diversity have indirect effects on the diversity of the entire reef (Connell et al. 1997). Coral species differ in their tolerance to adverse environmental conditions (Meesters et al. 1997). *P. porites* appears to be a resilient species. It was the most frequently encountered species at two of the three sites and had the most healthy coral across all three sites (Fig. 5). *S. siderea* and *D. strigosa* were somewhat less prevalent and less healthy overall than *P. porites*, and *A. palmata* was entirely absent from all sites but Preston Bay, where land-based influences are least.

Based on previous studies of coral reef degradation (Wilkinson 1999) and the logic of our predictions, we expect that monitoring land influences such as pollution, suspended sediment, salinity, temperature, and pH would reveal correlations between these variables and coral health at Little Cayman Island. Future studies of the aquatic abiotic conditions at Little Cayman would be especially valuable given the recent establishment of a long-term coral monitoring program along the island's northern coast (*personal communication, Carrie Manfrino LCRC*), under the direction of the Little Cayman Research Center. In conjunction with seawater data, such knowledge of the temporal change in coral health could reveal important connections between oceanic conditions and the status of the reef. Taken as a whole, such a program would contribute immensely to our understanding of the relative importance of land and ocean influences, a modified ocean environment, and global climate change for coral reef health.

LITERATURE CITED

Brown, A., R. Deo, J. Earp, J. Harvey, and five other authors. 2006. White plague disease and the decline of a Caribbean coral reef. Presented at 2006 Ocean Sciences Meeting.

Bruckner, A. W. and R. J. Bruckner. 1997. Outbreak of coral disease in Puerto Rico. Coral Reefs 16 (4): 260.

Clark, S. and A.J. Edwards. 1999. An evaluation of artificial reef structures as tools for marine habitat rehabilitation in the Maldives. Aquatic Conservation: Marine and Freshwater Ecosystems 9(1): 5-21.

Connell, J.H., T.P. Hughes, and C.C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67(4): 461-488.

Gates, R.D. 1990. Seawater temperature and sublethal coral bleaching in Jamaica. Coral Reefs 8: 193-197.

Glynn, P. W. 1990. Coral mortality and disturbances to coral reefs in the tropical eastern Pacific. Elsevier oceanography series 52 (9): 55-126.

Goreau, T. J. 1992. Bleaching and reef community change in Jamaica: 1951-1991. American Zoology 32: 683-695.

Guzman, H. M., K. A. Burns, and J. B. C. Jackson. 1994. Injury, regeneration and growth of Caribbean reef corals after a major oil spill in Panama. Marine ecology progress series 105 (3): 231-241.

Harmelin-Vivien, M. and P. Laboute. 1986. Catastrophic impact of hurricanes on atoll outer reef slopes in the Tuamotu (French Polynesia). Coral Reefs 5: 55-62.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, and 13 other authors. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 15: 929-933.

Manfrino, C., B. Riegl, J.L. Hall, and R. Graifman. 2003. Status of coral reefs of Little Cayman, Grand Cayman and Cayman Brac, British West Indies, in 1999 and 2000 (Part 1: Stony corals and algae). Atoll Research Bulletin 46: 204-225.

Marshall, P. A. and A. H. Baird. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19: 155-163.

Meesters, E.H., I. Wesseling, and R.P.M. Bak. 1997. Coral colony tissue damage in six species of reef-building corals: Partial mortality in relation with depth and surface area. Journal of Sea Research 37: 131-144.

Nystrom, M., C. Folke, and F. Moberg. 2000. Coral reef disturbance and resilience in a human-dominated environment. Tree 15 (10): 413-417.

Pastorok, R.A. and G.R. Bilyard. 1985. Effects of sewage pollution on coral-reef communities. Marine Ecology – Progress Series 21: 175-189.

Porter, J. W., P. Dustan, W. C. Jaap, K. L. Patterson, V. Kosmynin, O. Meier, M. E. Patterson, and M. Parsons. 2001. Patterns of spread of coral disease in the Florida Keys. Hydrobiologia 460 (1-3): 1-24.

Rogers, C. S. and J. Miller. 2006. Permanent 'phase shifts' or reversible declines in coral cover? Lack of recovery of two coral reefs in St. John, US Virgin Islands. Marine Ecology Progress Series 306: 103-114.

West, J. M. and R. V. Salm. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. Conservation Biology 17 (4): 956-967.

Williams, E. H. Jr. and L. Bunkley-Williams. 1990. The world-wide coral reef bleaching cycle and related sources of coral mortality. Issued by the Museum of Natural History.

Wilkinson, C. R. 1999. Global and local threats to coral reef functioning and existence: review and predictions. Marine and Freshwater Research 50: 867-878.

Woodley, J. D., E. A. Chornesky, P. A. Clifford, J. B. C. Jackson, and 16 other authors. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214: 749-755.

DIEL POLYP BEHAVIORS AND DISTURBANCE RESPONSE IN A CARIBBEAN GORGONIAN, *BRIAREUM ASBESTINUM*

ZACHARY A. MAYER, ANKIT RASTOGI,
ALLISON M. CITRO, AND SAMUEL J. HAYNOR

Faculty Editor: David R. Peart

Abstract: The feeding behavior of many corals varies on a diel cycle. While most corals extend polyps during the night to capture zooplankton, the gorgonian *Briareum asbestinum* (the corky sea finger) also extends its polyps during the day, and appears to retract its polyps only when disturbed. Most of the corky sea finger's carbon uptake comes from its photosynthetic zooxanthellae symbionts, in the polyps' pseudotentacles. We measured diel variation in the percent of polyps extended, polyp re-extension after experimental physical disturbance, and estimated diel patterns in fish disturbance frequency to sea finger colonies. We measured how feeding behavior may also depend on colony position relative to water currents. We found no overall difference in percent of polyps extended between night and day. During the day, upcurrent and topcurrent colonies had fewer polyps extended than downcurrent colonies, while at night, there was no difference in polyp extension between up-, top-, and downcurrent colonies. We observed greater disturbance rates to colonies during the day than the night and more disturbances to colonies upcurrent than those top- or downcurrent. After experimental physical disturbance, polyps re-extended faster during the day than at night, and upcurrent colonies re-extended faster than downcurrent colonies. Using the diel observations of percent polyps extended and re-extension rates following experimental disturbance, we constructed a mathematical model to estimate disturbance frequencies to corky sea finger colonies during the day and night. The model predicts that corky sea finger colonies experience disturbances four times more frequently during the day than during the night. This study indicates that diel polyp extension is a function of disturbance frequency and polyp re-extension after disturbances, which vary from day to night and with their position on a coral head.

Key Words: corky sea finger, zooxanthellae, soft coral, Little Cayman Island, disturbance

INTRODUCTION

Polyp feeding behavior of most corals fluctuates on a diel cycle. While many corals extend tentacles only at night to feed on zooplankton, some corals that have zooxanthellae symbionts in their pseudotentacles extend their polyps during the day, which allows the zooxanthellae to photosynthesize. Several coral species in the Gorganaceae family have polyps extended during both the day and night for photosynthesis and zooplankton feeding, respectively.

In the gorgonian, *Briareum asbestinum* (the corky sea finger), most of its energy uptake comes from photosynthetic symbionts (Sebens and Miles 1998), with zooplankton providing the

remainder. Corky sea finger polyps may only contract to prevent fish predator damage and collisions with objects (Sebens and Miles 1998). There is no variation in the time it takes for polyps to contract among colonies. Within five minutes of disturbance, corky sea finger colonies begin to re-extend their polyps (personal observation). During the day, polyp re-extension following disturbances allows the zooxanthelle to continue photosynthesizing. However, daytime polyp extension also leaves the corky sea finger more vulnerable to predation because most of their fish predators are diurnal. At night, while the corky sea finger acquires small amounts of carbon from zooplankton feeding, they also experience less predation because fewer of their predators are nocturnally active. Polyp re-extension after disturbances may be affected by the different costs and benfits of polyp extension during the day and at night.

Corky sea finger polyp extension after disturbances may also be related to the colony's position on the coral head, relative to the water current. We initially observed that colonies being hit by the current (upcurrent of the coral head to which they were attached) had more scarring from fish predation. These colonies either experience more disturbances or they do not contract as quickly when preyed upon. However, since we observed no variation in contraction times among colonies, it is likely that the upcurrent colonies experience more fish disturbances. If upcurrent colonies are disturbed more, the benefit of reduced damage by contracting polyps may outweigh the costs of reduced carbon acquisition from photosynthetic zooxanthelle. However, to limit the metabolic costs of polyp contraction, the upcurrent colonies' polyps may re-extend faster.

In this study, we measured differences in polyp extension between night and day, among positions on a coral head, and following simulated disturbances. Because most corky sea finger carbon uptake comes from zooxanthellae photosynthesis, we predicted that corky sea fingers would have a higher percent of polyps extended and would re-extend faster after disturbances during the day than the night. We also predicted that polyps on colonies upcurrent of the coral head to which they are attached would re-extend faster—because up current colonies are probably disturbed more, so they must extend their polyps faster to maintain carbon acquisition.

METHODS

Field Methods: We performed our study on 25 and 26 February,

2007, in the coral reef on Jackson Bay on the flats in front of the Little Cayman Research Center, Little Cayman Island. We observed 100 haphazardly-selected branching corky sea finger colonies during the day at 1600 and another 100 colonies during the night at 2200, on 25 February. We measured colony height in two ways: distance from the tip of the tallest branch to the base of the colony, and the distance from the tip to the sea floor. We also recorded the number of branches, the position of the colony in relation to the current (upcurrent, topcurrent, or downcurrent), the level of damage to the colony (high, low, or none), the colony's exposure (high = fully exposed without any surrounding substrates, medium = partially tucked behind rocks or coral head, or low = almost completely tucked behind rocks or coral head), and the percent of polyps extended. While sampling, we noted any fish or other organisms that were touching the corky sea finger. We also recorded all fish that touched or attacked groups of corky sea finger colonies for two ten-minute periods during both the day and night.

We tested corky sea finger polyp re-extension after disturbance after simulated disturbances, during the day at 1500 and at night at 2200 on 26 February. We sampled 16 colonies at each time, eight colonies on the upcurrent side of coral heads, eight on the topcurrent, and eight on the downcurrent (Fig. 1). We chose colonies that had all polyps fully extended. We measured the same colony characteristics as in the observational study (i.e., height from sea floor to colony base, number of branches, position, damage level, exposure, and percent of polyps extended). We disturbed one branch from each colony by gently stroking the branch from base to the tip repeatedly until all of the polyps contracted. We then checked the branches every five minutes for a total of 45 minutes and recorded the percent of polyps extended at each time.

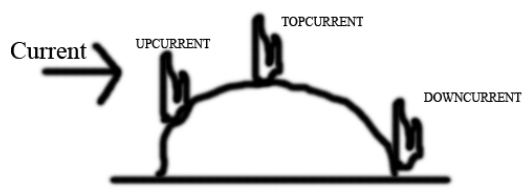

Figure 1. Upcurrent, topcurrent, and downcurrent locations of corky sea finger colonies on a coral head, relative to prevailing longshore (east to west) current, in Grapetree Bay, Little Cayman Island. Upcurrent colonies are directly influenced by the current, while downcurrent colonies are sheltered from the current by the coral head. Topcurrent colonies fall between the two.

Statistical Analyses: In our observational study, we tested the difference in the mean percent of polyps extended per colony between day and night with a t-test, assuming equal variances. We tested the difference in damage and exposure

between colony positions with a chi-square test. We tested the differences in percent of polyps extended among upcurrent, topcurrent, and downcurrent colonies, for the day and then for the night, using two Tukey-Kramer tests.

In our experimental study, we used a t-test to determine the difference in time to 50% re-extension between the day and the night. We used a repeated measures MANOVA to test how polyp re-extension after induced disturbance varied over time, varied between day and night with time, and if the effect of time on percent re-extended was significantly different between day and night.

We also used a repeated measures MANOVA to evaluate how percent of polyps re-extended after experimental rubbing vary over time and vary with time among positions. We used Wilks' lambda to test whether the effect of time on percent of polyps re-extended differed between positions. In these tests, we evaluated day and night samples separately.

Modeling Our sampling of fish attacks on colonies was too limited to draw strong conclusions about day-night differences in disturbance rates. However, our data provided an opportunity to estimate these rates indirectly. We used our observations of the percent of polyps extended in the day and night, along with polyp re-extension after disturbance, to construct a model that predicts the mean frequency of disturbance endured by colonies in the day and night. The model is based on two empirical findings. First, the percent of extended corky sea finger polyps was the same in the day and night (around 67 percent). Second, the re-extension after disturbance was higher during the day. The model uses this information to predict that frequency of disturbance, which, when combined with data on polyp re-extension after disturbance, would lead to 67 percent polyp extension in both day and night.

We assumed for simplicity that disturbances occur at regular intervals in both the day and night. Although this assumption may not be strictly valid, we felt that it would allow us to make a useful comparison of relative disturbance rates in the day compared to the night. We first fitted a logarithmic curve to the percent polyp re-extension vs. time data, separately for the day and night. We then used these fitted curves to estimate the average time between disturbances, calculated as T_{67} = time at which 67% of polyps on a single colony are extended, following artificial disturbance. The day and night T_{67} values are approximately equivalent to the time intervals between disturbances, averaged over individual colonies, that would produce the observed 67 percent

extension of polyps (across all colonies) in the day and at night. The logarithmic fits to the percent extension versus time for day and night were y = 33.70ln(x) – 48.31 and y = 25.64 ln(x) – 46.18, respectively. We did not apply this model to frequencies of disturbance separately by position on coral head, because no curves accurately fitted re-extension after disturbance by coral head.

RESULTS

We found no difference in the percent of extended polyps on a given colony between day and night ($t_{df=198}$= -0.57, P=0.57). However, percent polyp extension varied with position; 67% of downcurrent colonies were undamaged, compared to 32% of topcurrent colonies and 29% of upcurrent colonies (both time periods combined: X^2_4 = 36.593, P<.0001). A greater percent of downcurrent colonies had low exposure (45%) than topcurrent and upcurrent colonies (7% and 19%, respectively) (X^2_4 = 35.40, P<.0001). Finally, a lower percent of downcurrent colonies were highly exposed, as compared to topcurrent and upcurrent colonies (26.97%, 61.76 and 46.51%, respectively; $X^2_{df=4}$ = 35.397, P<.0001).

During the day, a greater percent of polyps on downcurrent colonies was extended compared to topcurrent and upcurrent colonies (ANOVA, $F_{2,97}$=6.8517, P=.0016; Fig. 2). During the night, however, there was no significant difference between the percent of polyps extended among positions relative to coral heads (ANOVA, $F_{2,97}$=.3880, P=.6795; Fig. 2).

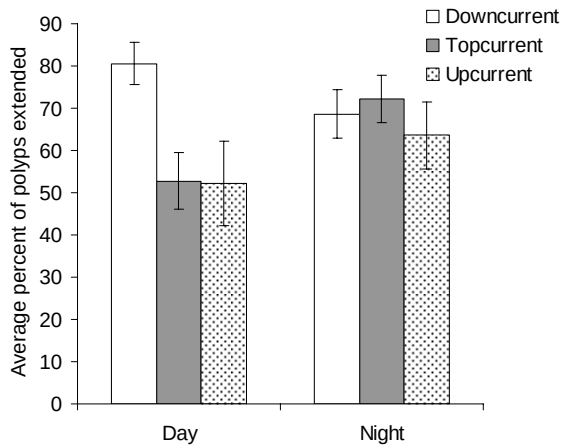

Figure 2. Average percent of polyps extended on 24 corky sea finger colonies at three locations on coral heads (differing in exposure to current), between the day and night. During the day there is a significant difference in the downcurrent colonies vs. topcurrent and upcurrent colonies; however, this difference does not hold during the night. (Observational data)

Polyps re-extended faster after artificial disturbance in the day, reaching 50% re-extension after 19.4 minutes, compared to 32 minutes at night (ANOVA $F_{1,28}$=15.08, P=.0006; Fig. 3).

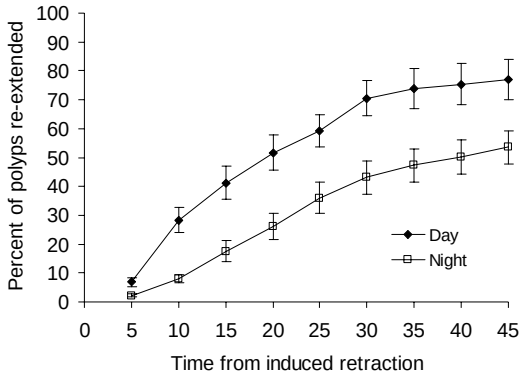

Figure 3. Poly re-extension over time for 24 sea finger colonies that were rubbed until colonies were fully retracted. "a" denotes a statistically significant difference at ∝=.05, "b" for ∝=.01, "c" for ∝=.001, and "d" for ∝=.0001.

We found that day vs. night had a significant effect on the percent of polyps re-extended with time (MANOVA, $F_{df=1,34}$=0.29, P=0.004; Fig. 3), while percent of polyps re-extended also varied significantly over time (MANOVA, $F_{df=8,27}$=20.05, P<0.0001; Fig. 3). Finally, the effect of time on polyp percent of polyps re-extended did not differ between day and night treatments (MANOVA, $F_{df=8,27}$=1.62, P=0.17.; Fig. 3).

During the day alone, we found that position had a marginally significant effect on the percent of polyps re-extended with time (MANOVA, $F_{df=2,9}$=4.10, P=0.054; Fig. 4) and that the percent of polyps re-extended also varied significantly over time (MANOVA, $F_{df=8,2}$=73.5, P=0.014; Fig. 4). Finally, the effect of time on percent of polyps re-extended differed significantly between positions (MANOVA, $F_{df=16,4}$=6.78, P=0.039; Fig. 4).

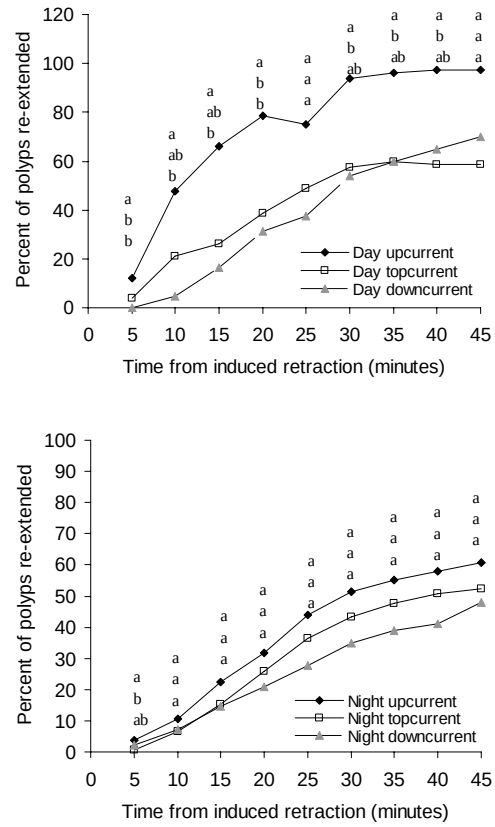

Figure 4. After induced retraction by rubbing, upcurrent daytime colonies re-extended much faster that topcurrent or downcurrent colonies. However, there was no such difference during the night, except at 5 minutes. Letters denote statistically significant differences at ∝=.10 using a students t test. (Upcurrent is the top letter, then topcurrent, and then downcurrent is on bottom.)

During the night alone, we found that position had no effect on the percent of polyps re-extended with time (MANOVA, $F_{df=2,21}$=0.66, P=0.53; Fig. 4), while the percent of polyps re-extended varied significantly over time (MANOVA, $F_{df=8,14}$=9.37, P=0.0002; Fig. 4). The effect of time on percent of polyps re-extended did not differ

significantly between positions (MANOVA, $F_{df=16,28}$=0.65, P=0.82.; Fig. 4).

In our fish observations, we observed an average of 33 fish bumping into or eating corky sea fingers during the day during 20 minutes of observation, and only 5 at night during 20 minutes of observation. While these scant data may not be representative of the disturbances experienced by an average colony, it is indicative of a large difference in disturbance rate between day and night.

When we modeled the natural frequency of disturbance based on diel observations of percent polyps extended and re-extension after disturbance, we found that the mean frequency of disturbances to a colony was four times higher during the day (once every 58 minutes) than during the night (once every 234 minutes).

DISCUSSION

Corky sea finger diel foraging appears to be due in part to exposure to predators. While many coral species retract all foraging polyps during the day, corky sea fingers forage constantly, but polyps are contracted part of the time on individual colonies, depending on frequency of disturbance (presumably by fish).

We found that the frequency of disturbances varied with the positions relative to coral heads, during the day and night. Fish predators disturbed and damaged upcurrent colonies (which were more exposed) more often than topcurrent or downcurrent colonies. In experimental trials, Kaandorp et al. (1996) found that stony corals grew upcurrent when nutrients were present. If corky sea finger colonies follow this pattern, upcurrent colonies should grow away from their host coral head and therefore become more exposed to predation than topcurrent or downcurrent colonies.

Although we found no difference in the percent of polyps extended between day and night for each position on a coral head, upcurrent and topcurrent colonies had fewer polyps extended than downcurrent colonies in the day. In the day, upcurrent colonies experience disproportionately more disturbance from diurnal fish predators, causing a greater proportion of the polyps to contract; however, at night, when most of these fish are inactive, there was no significant variation in polyp extension between positions on coral heads. With a lower risk of disturbance at night, corky sea finger colonies may be able to remain extended evenly across positions on coral heads relative to current.

During the day, corky sea fingers, while having a high risk of predation from fish, may also receive

high nutritional rewards from photosynthesis, compensating for the energy associated with frequent polyp contraction and re-extension. Nocturnal polyp foraging on zooplankton accounts for the remainder of their metabolic requirements. Higher nutrient availability may encourage coral polyps to extend faster (Lehman and Porter 1973; Lewis and Price 1975). The high polyp extension after disturbance that we found in the day may be proximally caused by the greater carbon uptake during the day.

Experimental manipulations have shown that polyp re-extension after disturbance in corals is greater at high flow rates (Levy et al. 2001), which the researchers attributed (i.e. the ultimate cause) to a higher likelihood of encountering prey in high flow environments. The more exposed upcurrent corky sea finger colonies are probably in higher water flow than downcurrent colonies.

The increase in polyp extension after disturbance during diurnal foraging may explain why we find an equal percent of polyps extended between day and night. Using the data on average percent of polyps extended along with the day and night polyp extension after disturbance, our model predicted that corky sea fingers are approximately four times more likely to be disturbed in the day than at night. The validity of this model in the field may be tested by observing diel variation in disturbance frequencies over longer periods and more colonies than we were able to do.

While most coral species extend polyps exclusively either during the day or at night, the corky sea finger can extend polyps during both day and night. The costs of disturbances to corky sea fingers, such as fish predation, may determine the percent of polyps extended. In contrast, time of day may drive re-extension after disturbance, since the benefit of re-extending should depend on the potential benefits gained from carbon acquisition from photosynthetic zooxanthellae.

LITERATURE CITED

Kaandorp, J. A., C. P. Lowe, D. Frenkel, and P. M. A. Sloot. 1996. Effect of nutrient diffusion and flow on coral morphology. *Physical Review Letters.* 77 (11): 23-28.

Levy, O., L. Mizrahi, N. E. Chadwick-Furman, and Y. Achituv. 2001. Factors controlling the expansion behavior of *Favia favus* (Cnidaria: Scleractinia): Effects of light, flow, and planktonic prey. *Biol. Bull.* 200: 118-126.

Lewis, J. B. and W. S. Price. 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. *Journal of Zoology*. 176: 527-544.

Muscatine, L., L. R. McCloskey, and R. E. Marian. 1981. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnology and Oceanography* 26: 601-611.

Sebens, K. P. and J. S. Miles. 1998. Sweeper tentacles in a gorgonian octocoral: morphological modifications for interference competition. *Biol. Bull.* 175: 378-387.

Sorokin, Y. U. I. 1990. Plankton in the reef ecosystems. Pp. 291-327 in Ecosystems of the World: Coral Reefs, Z. Dubinsky and, editor. Elsevier, Amsterdam.

THE EFFECTS OF GEOTHERMAL AND ANTHROPOGENIC PHOSPHORUS INPUTS ON TROPICAL MACROINVERTEBRATE COMMUNITIES

ANKIT RASTOGI, SAMUEL J. HAYNOR, BRIGETTE A. JONES,
JAMES A. MARLOW, AND PAMELA M. COLLINS

Faculty Editor: David R. Peart

Abstract: At La Selva Biological Station in Costa Rica, some streams receive geothermal groundwater enriched with phosphorus from the Barva Volcano. Others receive anthropogenic inputs from pastures. We sought to understand how macroinvertebrate abundance and diversity varies with non-geothermal, geothermal, and anthropogenic phosphorus inputs. We collected and morphotyped macroinvertebrates from each stream. There was no difference in average abundance or diversity per sample among the streams. We were unable to detect differences among streams because patchiness in macroinvertebrate distributions resulted in high variance among samples. Our results suggest that macroinvertebrate abundance and diversity in streams at La Selva may be strongly influenced by factors other than P inputs.

Key Words: La Selva Biological Station, nutrient inputs, soluble reactive phosphorus, detrital food web

INTRODUCTION

Phosphorus (P) is frequently a limiting nutrient in stream systems (Ramirez et al. 2003). Phosphorus is also a major component of industrial and agricultural runoff, as well as of natural inputs from geothermal groundwater (Pringle 1991). Phosphorus inputs can increase the abundance and diversity of macroinvertebrates by increasing detrital decomposition rates and autochthonous primary production, both of which provide carbon to macroinvertebrates (Ramirez et al. 2003, Hedin et al. 1995).

At La Selva Biological Station, several streams differ in soluble reactive phosphorus concentrations (SRP) and geomorphology (Ramirez and Pringle 2004; Triska et al. 2004). Despite the differences in SRP and geomorphology among streams, invertebrate communities do not differ among streams when all substrates are included in sampling protocols (Ramirez et al. 2006). However, since invertebrates have patchy distributions over different substrates, sampling all substrates may mask important substrate-specific differences in P responses of invertebrate communities. By focusing on cobble, we controlled for differences in substrate.

Because human disturbances are common in aquatic systems, we sought to compare the relative effects of anthropogenic and natural nutrient inputs on biotic communities. Specifically, we

wanted to know how P inputs from a cattle pasture and geothermal groundwater might affect the macroinvertebrate communities in streams. Ramirez et al. (2002) hypothesized that greater SRP would support higher macroinvertebrate abundances, resulting in more trophic levels and higher diversity. We predicted that since P is often limiting in stream ecosystems, streams with higher SRP would have both higher abundances and diversity of invertebrates.

METHODS

Study System: Our study was conducted at La Selva Biological Station, which includes 1536-ha of lowland tropical rainforest on the Caribbean slope of Costa Rica (10° 26′ N, 84° 01′ W). Depending on their location, some streams at La Selva receive groundwater inputs from the Barva Volcano that are rich in SRP from newly weathered rock (Pringle 1991). Additionally, there are pastures near the margins of La Selva, which provide anthropogenic P inputs into the adjacent streams.

Sampling Sites: We chose three streams based on their different P inputs. Two of them, Piper and Surá, have been extensively studied by Catherine Pringle and collaborators on the University of Georgia STREAMS Project. Piper (SRP = 12 μg/L[1]) is a non-geothermal stream in secondary forest on the west side of La Selva (Fig. 1). Surá (SRP = 227 μg/L[1]) is on the east side of La Selva (Fig. 1), surrounded by old growth forest. Thirty-three percent of the water in Surá comes from geothermal inputs (Genereux and Pringle 1997). The third stream, the Sábalo-Esquina (SRP = 26 μg/L[1]), runs through a cattle pasture that borders La Selva to the east (Fig. 1). The Sábalo-Esquina riparian zone contains some large trees and moderate undergrowth along both sides, but pasture is within 5 m of the eastern stream edge.

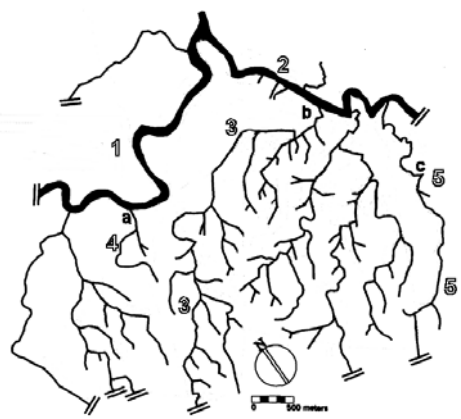

Figure 1. Streams at La Selva Biological Station. 1 = Río Sarapiquí, 2 = Río Puerto Viejo, 3 = Surá, 4 = Piper, 5 = Sábalo-Esquina. Chemical and macroinvertebrate samples were taken from Surá, Piper, and Sábalo-Esquina streams at the points indicated by letters a-c. Piper is a natural, non-geothermal stream in secondary growth forest. The Surá is a geothermal stream located surrounded by old growth forest. The Sábalo-

[1] SRP values for the Piper and Surá streams were taken from Ramirez and Pringle (2004). The SRP values for the Sábalo-Esquina stream was taken from Triska et al. (2004).

Esquina is adjacent to a large pastured area that borders La Selva. Figure is adapted from Genereaux and Pringle (1997).

Sampling methods: We sampled macroinvertebrates in two 10 m sections of predominantly cobble substrate in each stream. Within each sampling area, we collected invertebrates at approximately 2 m increments at haphazard points. For each sample, we agitated the substrate and washed all rocks in a 30 cm x 30 cm square immediately upstream of a D-frame net. We morphotyped all macroinvertebrates in each sample under a microscope.

Statistical Analysis: To test how mean invertebrate abundance and diversity per sample differed among streams, we used two one-way ANOVAs. We calculated diversity using the Shannon-Weiner diversity index[2]. We also examined patterns of overall invertebrate diversity on cobble substrate in the streams.

RESULTS

We found 78 distinct macroinvertebrate morphotypes in 12 orders. Streams did not differ in average invertebrate abundance ($F_{2,27}$ =0.725, P=0.49, Fig. 2A) or diversity ($F_{2,26}$ = 0.985 P=0.39, Fig. 2B), per sample. The lack of difference among streams may be a result of macroinvertebrate patchiness and subsequently high variance among samples. Therefore, we also

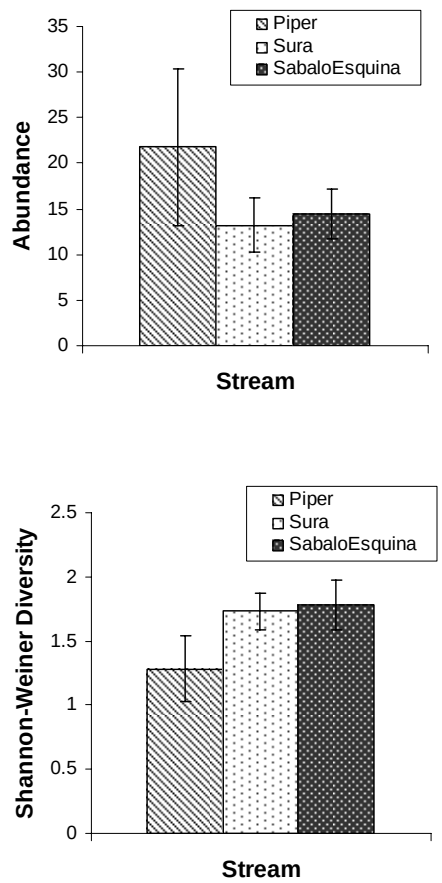

Figure 2. Average abundance (number per sample, all taxa combined) and diversity (Shannon-Weiner index) of macroinvertebrates in 0.30 x 0.30 m samples in three tropical streams at La Selva Research Station, Costa Rica. Samples were collected haphazardly at 2 m intervals on cobble substrate. Error bars represent ± 1 SE, n = 10 samples per stream.

examined overall diversity and abundance in each stream. Overall diversity was greater in the

[2] $H = \sum_{i=1}^{S} p_i \ln p_i$, where "H" is Shannon-Weiner diversity, "S" is species richness, and "p_i" is the proportion of species "i" in the total number of macroinvertebrates.

agricultural stream, Sábalo-Esquina, than in the geothermal stream, Surá, and both had higher overall diversity than the non-geothermal stream, Piper (Table 1).

Table 1. Soluble reactive phosphorus concentrations (SRP) and macroinvertebrate abundance and diversity for three streams at La Selva Biological Research Station, Costa Rica. Diversity (H) was calculated using the Shannon-Weiner index[2].

	Sábalo-Esquina	Surá	Piper
SRP (µg/L)	26	227	12
Abundance	146	132	219
Diversity (H)	3.40	3.35	2.13

DISCUSSION

Contrary to our predictions, we found a higher abundance of macroinvertebrates in the non-geothermal stream. This may be because factors other than P are affecting macroinvertebrate communities. For example, in La Selva streams, invertebrate abundance has been shown to be strongly correlated with the number of days since the last large storm (Ramirez and Pringle 2004).

The geothermal and non-geothermal streams both have detritus-based food webs (Rosemond et al. 2002); however, in the pasture stream, energy input to the food web may be partly from primary production, because of high light conditions and low detritus inputs. Although SRP should increase carbon availability in both detritus-based and primary production-based food webs, SRP may influence each food web differently.

We found that macroinvertebrate diversity was higher in streams with higher SRP (as predicted), but these streams had lower overall macroinvertebrate abundances, contradictory to our prediction. Ramirez et al. (2002) hypothesized that higher SRP increases carbon availability, which can maintain more macroinvertebrate trophic levels and higher diversity. However this argument is apparently based on a positive relationship between P inputs and invertebrate abundances. The argument does not hold for our results, because macroinvertebrate abundance and diversity exhibit opposite trends with higher SRP; according to the logic of Ramirez et al. (2002) they would exhibit the same pattern.

Studies of stream invertebrate communities have demonstrated how single nutrients such as P alter the biotic communities of stream systems (Ramirez et al. 2003; Ramirez and Pringle 2004; Ramirez et al. 2006). However, our results suggest that macroinvertebrate abundances and diversity in streams at La Selva Biological Station may be strongly influenced by factors other than P inputs. For example, high

discharge rates during floods can alter invertebrate communities. Thus, invertebrate abundances and diversity may depend strongly on the time since flooding, which may differ among streams with different catchment areas (Ramirez and Pringle 2004). Unfortunately, time series data on discharge rates for the three streams in our study were not available to explore these relationships.

LITERATURE CITED

Genereux, D., and C. M. Pringle. 1997. Chemical mixing model of stream flow generation at La Selva Biological Station, Costa Rica. Journal of Hydrology 199: 319-330.

Hedin, L. O., J. J. Armesto, and A. H. Johnson. Patterns of nutrient loss from unpolluted, old-growth temperate forests: evaluation of biogeochemical theory. Ecology 76(2): 493-509.

Landsberg, J. H. 2002. The effects of harmful algal blooms on aquatic organisms. Review in Fisheries Science 10(2): 113-390.

Pringle, C. M. 1991. Geothermally modified waters surface at La Selva Biological Station, Costa Rica: volcanic processes introduce chemical discontinuities into lowland tropical streams. Biotropica 23: 523-529.

Ramírez, A., C. M. Pringle, and L. Molina. 2003. Effects of stream phosphorus levels on microbial respiration. Freshwater Biology 48(1): 88-97.

Ramírez, A. L., and C. M. Pringle. 2004. Do macroconsumers affect insect responses to a natural stream phosphorus gradient? Hydrobiologia 515: 235-246.

Ramírez, A. L., C. M. Pringle, and M. Douglas. 2006. Temporal and spatial patterns in stream physicochemistry and insect assemblages in tropical lowland streams. Journal of the North American Benthological Society 25(1): 108-125.

Rosemond, A. D., C. M. Pringle, A. Ramírez, M. J. Paul, J. L. Meyer. 2002. Landscape variation phosphorus concentration and effects on detritus-based tropical streams. Limnology and Oceanography 47(1): 278-289.

Triska, F.J., C.M. Pringle, A.P. Jackman, J.H. Duff, A. Ramirez, and M. Ardón, 2004. SRP transport in the Salto River and nearby streams draining a volcanic landscape in Costa Rica. Presented at the meeting of the Ecological Society of America. Portland, OR 2004.