TEMPORAL ASSOCIATIONS OF CORAL AND ZOOPLANKTON ACTIVITY ON A CARIBBEAN REEF

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Abstract: Coral prey on zooplankton for nutrients not provided by their symbiotic zooxanthellae. Zooplankton stay in the benthos during the day and emerge into the water column to feed at night. We examined zooplankton densities and their relationship to feeding by the coral *Montastrea annularis* at Grape Tree Bay, Little Cayman Island. We predicted coral polyps would open when density of small zooplankton (< 1mm) was highest, which we expected at night and in calm weather. These predictions were supported by the data, with percent open polyps responding sharply to increasing small zooplankton density over a "threshold range" of 5-10 m^{-3}. The trends are also consistent with the hypothesis that polyps are genetically programmed to open at night, but respond plastically to zooplankton density during the day.

Key words: Montastrea annularis*, Little Cayman, zooplankton assemblage, copepod*

INTRODUCTION

Corals acquire most of their energy from symbiotic zooxanthellae, but are also carnivorous, using nematocysts to capture zooplankton suspended in passing currents. Zooplankton contribute a small percentage of the coral's diet but provide critical nutrients such as nitrogen and phosphorus that zooxanthellae cannot supply (Ohlhorst 1982). Fish also prey on zooplankton, which causes many zooplankton, especially large ones, to hide in the benthos during the day when foraging ability of visual planktivores is greatly reduced. Smaller zooplankton can feed in the water column during the day with lower risk, as their size is below the visual threshold of most predatory fish (Ohlhorst, 1982).

A diel vertical migration of zooplankton into the water column at night occurs on the back reef at Grape Tree Bay, Little Cayman Island (Jones et al. 2007). We studied this pattern and its association with feeding activity of the boulder star coral *Montastrea annularis* in a period of high wind and a period of relative calm. Since corals open their polyps to feed, we predicted an increase in coral polyp openness with greater density of accessible prey (zooplankton < 1 mm). We also predicted that high wind would decrease zooplankton density and reduce coral activity.

Zooplankton densities in windy conditions may be influenced by increased water turbulence, which could mix spatially patchy zooplankton distributions, potentially increasing or decreasing densities near the back reef. Zooplankton may also respond to increased water turbulence by staying in the benthos.

Finally, we predicted that lower zooplankton density and increased risk of damage by sedimentation would decrease overall coral polyp openness during periods of high wind.

METHODS

We measured coral and zooplankton activity on February 29 and March 3, 2008, on the back reef at Grape Tree Bay, Little Cayman Island. These dates corresponded with a period of high wind (20-25 knots) and of relative calm (10-15 knots), respectively. We sampled zooplankton density during the day (1400) and at night (2200) using 4 contiguous 26 m straight line transects 0.5 m from the back reef parallel to shore.

At each sample time, we towed a plankton net (diameter = 0.3 m, mesh size 153 μm) twice through each transect, in opposite directions, 0.5 m below the surface for a total sample volume of 3.67 m^3. We preserved zooplankton samples in 50% ethanol and a 5% formalin solution and sorted them under a dissecting microscope. We separated zooplankton by taxonomic group (Copepoda, Decapoda, Mysida, Amphipoda, Isopoda, Polychaeta, Chordata (Fish larvae), and Bivalvia. We also grouped by size (> 1 mm or ≤ 1 mm) to estimate zooplankton densities in a size range available to corals (≤ 1 mm). We examined the association of small zooplankton with changing wind conditions and time of day using a full factorial, two-way ANOVA. We tested for equal variances and used pooled-variance one-tailed t-test to compare temporal differences in small and large zooplankton abundance.

We located every coral species *M. annularis* within 1m of the straight line zooplankton transect at least 0.25 m diameter and at least 0.5 m from the bottom. We visually estimated the percent of open coral polyps on each coral head in 10% interval classes. We used a full factorial, two-way ANOVA to compare the effects of time of day and wind on the percent open coral polyps per coral head, We performed piecewise linear regressions to examine possible correlations between zooplankton (<1mm) density and coral openness, fitting separate models for day and night.

RESULTS

Consistent with our predictions, we found more total zooplankton in the water column at night than during the day (Table 1;

Table 2). Overall nighttime density was 33 times daytime density. Small zooplankton (≤ 1 mm) made up 87.4% percent of total density in the day, while large zooplankton (> 1 mm) comprised 86% of total density at night (one-tailed $t = 23.3$, $df = 6$, $P < 0.0001$). Large zooplankton density was 250 times greater at night than during the day (890 versus 3.54 individuals per $m^{3,}$ respectively). Copepods were the most abundant zooplankton < 1 mm both day and night, making up 67% and 63% of total, respectively. In high winds, zooplankton density decreased, in both night and day, and for both size classes (Table 1).

Polyp openness corresponded to the diel vertical migration of small zooplankton, with more open polyps at night than in the day (Table 1). Coral openness increased with small zooplankton density during the day ($F = 20.4$, $df = 1, 6$, $P = 0.004$; Figure 1) but not at night ($F = 0.97$, $df = 1, 6$, $P = 0.36$).

During the day, polyps were more open in calm than in windy conditions. However, at night, polyps were open, irrespective of wind conditions (Figure 1).

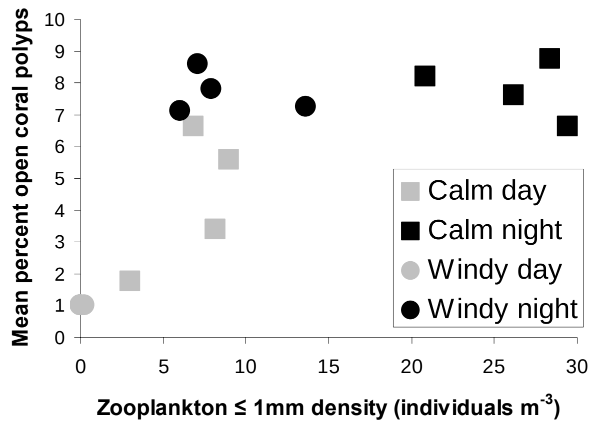

Figure 1. Relationship between mean percent open coral polyps per coral head and zooplankton density on the back reef at Grape Tree Bay, Little Cayman Island.

TABLE 1. Effects of wind, time of day, and their interaction on percent open coral polyps per coral head and small zooplankton abundance at Grape Tree Bay, Little Cayman Island. We collected zooplankton in four 26 m tows at 0.5 m depth, 0.5 m from the back reef.

	Source		df	F	P		df	F	P
Main Effects	Wind	Coral	1	3.40	0.0053	Zooplankton ≤ 1 mm	1	8.4	<0.0001
	Time of Day	Coral	1	9.04	<0.0001	Zooplankton ≤ 1 mm	1	9.73	<0.0001
Interaction	Wind x Time of Day	Coral	1	2.23	0.05	Zooplankton ≤ 1 mm	1	3.77	0.003
Error		Coral	13			Zooplankton ≤ 1 mm	13		

TABLE 2. Mean densities m^{-3} of common zooplankton taxonomic groups during day and night during periods of high wind (ca. 20-25 knots NNE) and relative calm (ca 10-15 knots SE) on the back reef at Grape Tree Bay, Little Cayman Island. See Table 1 for details. Densities of zooplankton >1mm are in regular type; those ≤ 1mm in bold.

Taxa	Mean Density ± SE			
	Calm		High Wind	
	Day	Night	Day	Night
Copepoda	**5.79 ± 1.56**	**17.44 ± 3.78**	**0.07 ± 0.07**	**4.63 ± 1.56**
	0.07 ± 0.07	12.26 ± 5.58	0	1.84 ± 0.23
Decapoda	**0.48 ± 0.23**	**3.27 ± 2.31**	**0**	**1.02 ± 0.23**
	0.20 ± 0.13	110.63 ± 29.18	0	2.52 ± 0.53
Mysidacea	**0.07 ± 0.07**	**0**	**0**	**0.67 ± 0.28**
	0.07 ± 0.07	39.24 ± 15.99	0.27 ± 0.16	4.50 ± 0.65
Amphipoda	**0**	**4.36 ± 2.13**	**0**	**0.95 ± 0.14**
	0.07 ± 0.07	27.52 ± 12.49	0	1.16 ± 0.49
Polychaeta	**0.14 ± 0.14**	**0.27 ± 0.27**	**0**	**0.34 ± 0.07**
	0.20 ± 0.07	2.45 ± 0.69	0.07 ± 0.07	0.75 ± 0.30
Isopoda	**0**	**0.27 ± 0.27**	**0**	**0.27 ± 0.27**
	0	0.27 ± 0.27	0	0.20 ± 0.13
Bivalia	**0.27 ± 0.27**	**0**	**0**	**0.75 ± 0.30**
	0	5.45 ± 2.71	0	1.43 ± 0.46
Fish Larvae	**0**	**0.58 ± 0.30**	**0**	**0**
	0	10.29 ± 5.64	0	0.61 ± 0.26

DISCUSSION

Consistent with diel vertical migration patterns, zooplankton of > 1 mm length were more abundant in the water column at night when risk of predation by visual planktivores is reduced. Most zooplankton in the water column during the day were ≤ 1 mm, possibly because their small size decreases risk of predation by visual predators. Our daytime zooplankton densities were similar to those of a recent Dartmouth study (Jones et al. 2007) at Little Cayman and Dartmouth studies of a Jamaican reef (Dartmouth FSP 2005, Sullan et al. 2006, Calvi et al. 2000). Our night zooplankton densities were slightly lower than those documented in Jamaica, but over 3.5 fold higher than those at Little Cayman in 2007. This may reflect patchy distribution of zooplankton at Little Cayman, or lower densities at Little Cayman than at Discovery Bay, Jamaica.

Total zooplankton density increased at night, but varied in magnitude with weather conditions. Zooplankton density was lower during periods of high wind, perhaps because water turbulence decreases foraging ability, mixes localized zooplankton concentrations away from the reef, or zooplankton take refuge in the benthos to escape physical damage from collisions with the reef. It is unlikely that predation decreased zooplankton abundance during windy days. Control of zooplankton in marine systems is primarily bottom-up (Fredericksen et al. 2006), and total fish abundance decreased during our period of high winds, including juvenile fish that tend to be planktivorous (Lappas et al. 2008).

Coral polyps opened more at night when zooplankton density was highest, regardless of winds. During windy days, however, all corals closed their polyps, perhaps because of low zooplankton density and high sedimentation associated with turbulence. During calm days, when physical stress is lower and zooplankton abundance varies, coral polyp openness increased with greater zooplankton densities.

The variation in openness during a clam day but not at night (Figure 1) suggests two possible mechanisms. The most parsimonious interpretation is that polyps respond to zooplankton density, with a threshold range between 5 and 10 zooplankton/m^3, over which all corals open their polyps. Alternatively, corals may be genetically programmed to open at night, but able to respond plastically to zooplankton densities during the day. Controlled manipulations of zooplankton densities, with concomitant observations of polyp opening, would be needed to distinguish between these alternatives.

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