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

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*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.

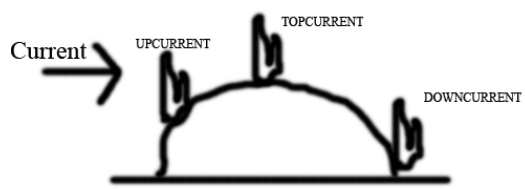


Figure 1. Upcurrent, topcurrent, and downcurrent locations of corky sea finger colonies on a coral head, relative to prevailing longshore (east to west) current, in Grapetree Bay, Little Cayman Island. Upcurrent colonies are directly influenced by the current, while downcurrent colonies are sheltered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

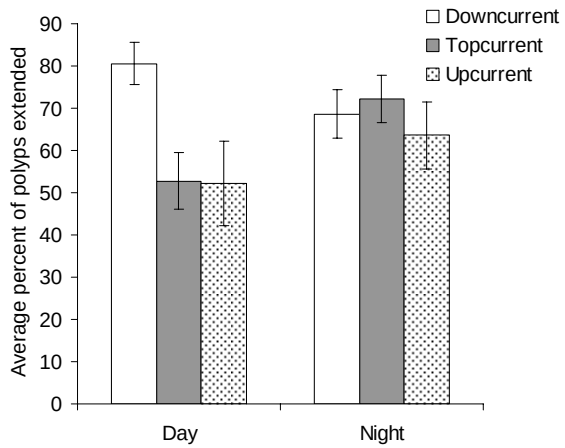


Figure 2. Average percent of polyps extended on 24 corky sea finger colonies at three locations on coral heads (differing in exposure to current), between the day and night. During the day there is a significant difference in the downcurrent colonies vs. topcurrent and upcurrent colonies; however, this 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).

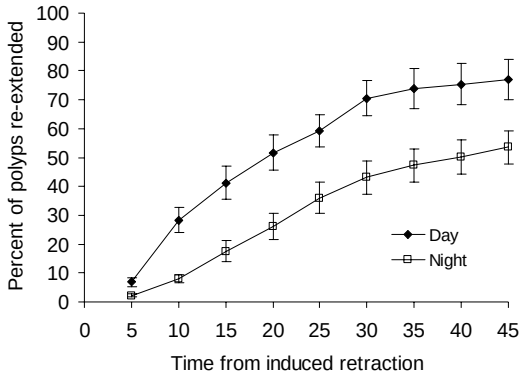


Figure 3. Poly re-extension over time for 24 sea finger colonies that were rubbed until colonies were fully retracted. "a" denotes a statistically significant difference at ∝=.05, "b" for ∝=.01, "c" for ∝=.001, and "d" for ∝=.0001.

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).

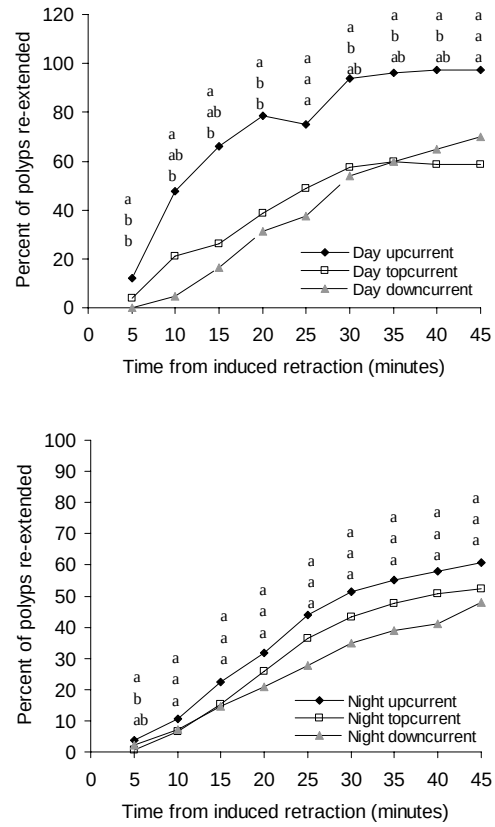


Figure 4. After induced retraction by rubbing, upcurrent daytime colonies re-extended much faster that topcurrent or downcurrent colonies. However, there was no such difference during the night, except at 5 minutes. Letters denote statistically significant differences at ∝=.10 using a students t test.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

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