

An Overview of Symbiont Bleaching in the Epiphytic Foraminiferan *Sorites dominicensis*

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ABSTRACT. Populations of *Sorites dominicensis*, an epiphytic foraminiferan that possesses dinoflagellate endosymbionts (*Symbiodinium*), were sampled from seagrass meadows located in Florida and Belize and surveyed for evidence of bleaching. Symbiont bleaching was first documented in *S. dominicensis* populations in the Indian River Lagoon, Florida, in August 2003. Subsequent surveys indicated high rates of bleaching in August 2004, followed by a near eradication of the epiphytic foraminiferan population as a result of the 2004–2005 hurricane seasons. Two contrasting sites in Belize, seagrass beds on the reef flat at Carrie Bow Cay and in Boston Bay, Twin Cays, were surveyed in 2005 and 2006. High rates of bleaching characterize the *S. dominicensis* populations living on turtle grass on the reef flat off Carrie Bow Cay, although freshwater runoff from summer storms during the rainy season may trigger localized bleaching events. Moderate rates of bleaching were also observed in *S. dominicensis* populations in Florida Bay in July 2007. Symbiont bleaching in *S. dominicensis* appears to be triggered by multiple environmental factors: increased water temperatures, high levels of irradiance, and influx of freshwater during storm events. Seasonal summer bleaching events may leave already compromised *S. dominicensis* populations vulnerable to periodic disturbance by hurricanes.

INTRODUCTION

Sorites dominicensis Ehrenberg, 1839, is one of several living foraminiferan species that are host to algal endosymbionts (Hallock, 1999; Lee et al., 1979). Benthic foraminiferans with algal symbionts occur in several different clades (Soritacea, Alveolinacea, Nummulitacea, Calcarinidae, and Amphisteginidae) and are widely distributed in shallow-water, tropical to subtropical reef-associated marine ecosystems (Langer and Hottinger, 2000). As a group, foraminiferans host a diverse array of endosymbionts, most of which are microbial eukaryotic taxa, including stramenopiles (diatoms and chrysophytes), unicellular rhodophytes, unicellular chlorophytes, and alveolates (dinoflagellates) (Lee, 2006; Hallock, 1999). Cyanobacterial endosymbionts have also been isolated from two different soritid taxa collected from the Red Sea and the Great Barrier Reef (Lee, 2006). Foraminiferans with photosymbionts possess enhanced calcification rates, as well as endogenous sources of nutrition (algal photosynthates) that allow them to allocate more of their energy resources to cell growth and

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maintenance (Lee, 2006; Hallock, 1999; Duguay, 1983; Kremer et al., 1980; Lee and Bock, 1976). The algal endosymbionts presumably benefit from the mutualism as well, gaining access to nutrients that are scarce in oligotrophic environments and to refuge from predation (Lee, 2006; Hallock, 1999).

The mutualistic association of *Sorites* and other taxa in the more inclusive foraminiferal clade Soritida, with dinoflagellate endosymbionts in the *Symbiodinium* clade, is of particular interest to the marine biological community because this clade comprises the zooxanthellae in stony corals, soft corals, gorgonians, anemones, jellyfish, bivalve mollusks, nudibranchs, sponges, and ciliates (Baker, 2003; Douglas, 2003; Glynn, 1996). Originally considered to be a single pandemic species that was symbiotic with a broad range of marine taxa, *Symbiodinium microadriaticum* is now known to be part of a more inclusive and genetically diverse clade composed of eight major subclades, identified by the letters A–H (Pochon and Pawlowski, 2006; Coffroth and Santos, 2005; Baker, 2003; Rowan, 1998; Rowan and Powers, 1991, 1992). *Symbiodinium* symbionts from foraminiferal hosts are found in clades C, D, F, G, and H, with clades F and H being composed almost exclusively of *Symbiodinium* isolated from soritid foraminiferans (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pawlowski et al., 2001; Pochon et al., 2001, 2004, 2006; Rodriguez-Lanetty, 2003). Although there is relatively high specificity between *Symbiodinium* clades F, G, and H and Foraminifera, there appears to be very little congruence between host and symbiont phylogenies, indicating that coevolution has not taken place, at least not at the taxonomic levels sampled to date (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pawlowski et al., 2001; Pochon et al., 2001, 2004, 2006). Although DNA sequences have not yet been obtained from the endosymbionts of either the Belizean or Indian River Lagoon populations of *Sorites dominicensis*, *Symbiodinium* sequences from Florida Keys specimens fall within either clade F (subclade F4) or H (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pochon et al., 2006). In all phylogenies published to date, clade H, the dominant phylotype isolated from the Florida Keys, branches as the sister group to clade C, a clade that is widely distributed in the Indo-Pacific, and exhibits more sensitivity to bleaching than the other *Symbiodinium* clades (Garcia-Cuetos et al., 2005; Pochon and Pawlowski, 2006; Pawlowski et al. 2001; Pochon et al., 2001, 2004, 2006; Rowan, 1998, 2004).

The morphological characteristics of *Symbiodinium* symbionts isolated in culture from specimens of *Sorites dominicensis* collected from the Florida Keys have been

described by Lee et al. (1979, 1997). Symbionts are distributed throughout the foraminiferal cytoplasm, with the highest densities occurring in the intermediate chambers and the lowest densities occurring in the outer chambers where the digestive vacuoles are concentrated (Richardson, 2006; Müller-Merz and Lee, 1976). Similar to other species of foraminiferans, *S. dominicensis* is multinucleate and possesses two different types of nuclei: generative nuclei that participate in reproduction only, and vegetative nuclei that are transcriptionally active and coordinate the day-to-day activities of the cell (Müller-Merz and Lee, 1976). In *S. dominicensis*, the generative nuclei are localized in the central initial chambers of the test (external shell), which are the chambers with the lowest densities of dinoflagellates, whereas the transcriptionally active foraminiferal nuclei are distributed throughout the cytoplasm in regions with the high symbiont densities (Müller-Merz and Lee, 1976).

Estimates of symbiont population size per cell vary depending on the methodology employed (Richardson, 2006; Doyle and Doyle, 1940). Doyle and Doyle (1940) estimated the population of dinoflagellates in a 2-mm sized individual of *S. dominicensis* to be approximately 1.6×10^4 using light microscopy. In contrast, confocal microscopy of a 2-mm sized individual of *S. dominicensis* collected from Jupiter Sound yielded an estimated 4×10^3 dinoflagellates, equivalent to a density of 1.27×10^5 endosymbionts cm^{-2} of cytoplasm (Richardson, 2006) (Figure 1). Hemacytometer estimates of endosymbiont densities in live individuals of *S. dominicensis* collected from Jupiter Sound indicate that symbiont densities range from 6.1×10^2 to 4.8×10^5 dinoflagellates cm^{-2} , with an average of 6.5×10^4 dinoflagellates cm^{-2} ($n = 85$, $\sigma = 7.9 \times 10^4$, $\sigma^2 = 6.2 \times 10^9$) (Ross and Richardson, unpublished data). Endosymbiont populations linearly increase with test size: the average number of symbionts per foraminiferal cell is estimated to be 1,469 ($n = 85$, $s = 2,919$, $s^2 = 8,523,907$) for an individual with a test diameter of 1.42 mm ($n = 85$, $s = 0.62$, $s^2 = 0.39$) (Ross and Richardson, unpublished data).

Live individuals possess a dark yellowish-brown coloration to their cytoplasm as a result of the dense populations of *Symbiodinium* in each cell (Figure 2). In healthy individuals, the coloration is evenly distributed throughout the test, except for the outer chambers, which appear colorless because of the low density or absence of endosymbionts from the zone of cytoplasm where digestion takes place (Figure 2). The distinctive coloration of the foraminiferal cytoplasm makes it easy to recognize bleached or mottled individuals, as described below.

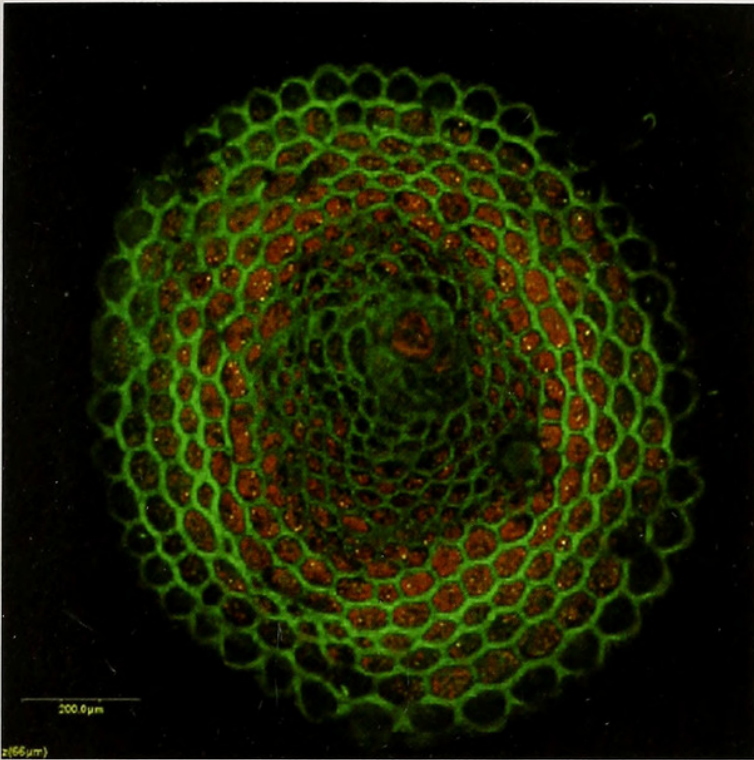


FIGURE 1. Confocal image of live individual of *Sorites dominicensis* from Jupiter Sound, Florida. The foraminiferal test is subdivided into hexagonal chamberlets. The dinoflagellate endosymbionts are most densely packed into the intermediate chambers. Scale bar = 200 μm.

FIELD OBSERVATIONS OF BLEACHING IN *SORITES DOMINICENSIS*

Symbiont bleaching has been observed in field surveys of epiphytic foraminiferal populations from Florida (Indian River Lagoon and Long Key, Florida Keys) and Belize (Carrie Bow Cay and Twin Cays). Bleaching in *Sorites dominicensis* was first documented in epiphytic populations attached to *Thalassia testudinum* (turtle grass) growing in Jupiter Sound in August 2003 and August 2004, followed by field surveys of populations in Belize in July 2005 and July 2006. Bleaching was also observed in epiphytic populations of *S. dominicensis* surveyed from the Florida Keys in July 2007 (Richardson, unpublished data). Although each of the collecting sites studied hosts seagrass meadows dominated by *T. testudinum*, each locality is subject to different physical factors (salinity, temperature, water clarity, and subaerial exposure), as well as differing levels of anthropogenic impact. Detailed descriptions of the field sites in Florida and Belize are given by Richardson (2006). Although experimental studies of bleaching in *S. dominicensis* have yet to be carried out, field observations

indicate that symbiont bleaching may occur in response to a number of environmental stressors, including increased water temperature, freshwater influx, subaerial exposure during extreme low tides, and periodic disturbance by hurricanes.

FIELD METHODS

Only epiphytic specimens of the foraminiferan *Sorites dominicensis* that were attached to blades of the seagrass *Thalassia testudinum* were examined in the studies described below. Blades of *T. testudinum* were harvested by wading or snorkeling. Seagrass leaves were removed at the base of the blade, submerged in seawater in a Ziploc bag, and stored in a cooler until return from the field. Both sides of each seagrass blade were examined for the presence of epiphytic foraminiferans using a binocular dissecting microscope (Leica M5). All specimens of the species *S. dominicensis* were removed from the blade using a fine paintbrush or dental pick, measured, and stored on cardboard microslides for additional study and reference material. The cytoplasmic condition (healthy, pale, mottled, totally bleached) and reproductive state (nonreproductive, presence of brood chambers, presence of embryos in brood chambers, or postreproductive)

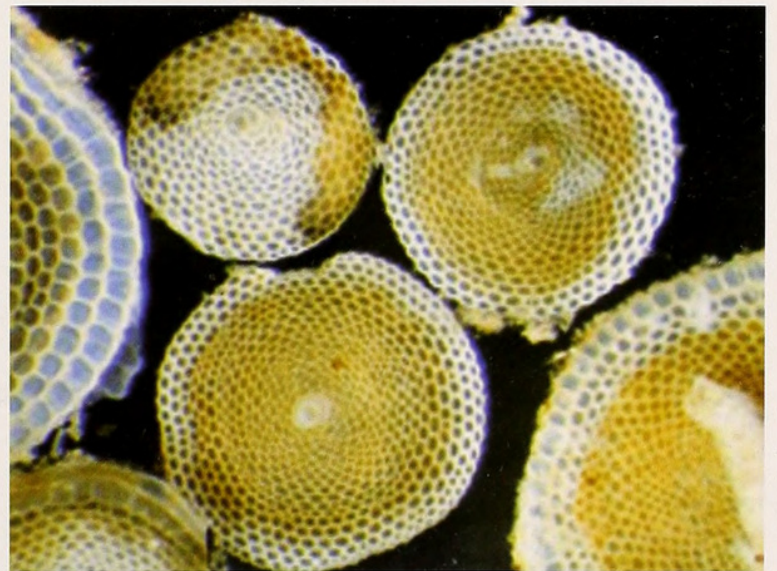


FIGURE 2. Live specimens of *Sorites dominicensis* from Belize, Central America. The two individuals in the upper part of the image show patches of bleached cytoplasm. Note that all specimens, except for the individual in the lower left, possess few, if any, endosymbionts in the outer two or three chambers. The specimen in the lower left is a reproductive individual preparing to undergo multiple fission. The specimen on the upper right is approximately 2 mm in diameter.

of each specimen were noted. Specimens were measured using an optical micrometer calibrated to a stage micrometer. Micrographs of representative individuals (healthy, mottled, and bleached) were taken using a Nikon Coolpix camera with an MCOol (Martin Optics) phototube.

Live individuals were recognized by their distinctive cytoplasmic coloration as described below, and/or by the presence of pseudopodial arrays emanating from around the periphery of the protist's test. Bundles of bifurcating pseudopodia in live individuals are usually covered with a light dusting of fine-grained sediment, giving the specimens a star-shaped appearance. Individuals were recorded as having healthy cytoplasm if the cytoplasm possessed an evenly distributed, yellowish-brown coloration (see Figure 2). Individuals were recorded as having a mottled cytoplasm if the cytoplasm contained white-colored patches, interspersed with yellowish-brown sections of cytoplasm (Figure 2). Mottled individuals contained patches of white cytoplasm that were visible on both sides of the disk-shaped test. Specimens were recorded as being totally bleached if the test was completely white. The tests of postreproductive individuals, that is, individuals that had undergone reproduction by multiple fission, were not included in the tallies of bleached specimens. Postreproductive tests are easily distinguished from bleached tests by the presence of fragmented brood chambers, undisseminated embryos, and clusters of dispersed juveniles in close proximity to the parental test. It is assumed that few, if any, of the totally bleached tests had undergone gametogenesis, as microspheric tests (tests formed by syngamy) have never been observed in any of the populations of this species surveyed by the author.

WATER TEMPERATURE AND BLEACHING

Studies conducted at both the Jupiter Sound and Belize sites indicate that elevated water temperature, or a combination of elevated water temperature and subaerial exposure, can induce symbiont bleaching in *S. dominicensis*. Bleaching was first observed in the Jupiter Sound populations in 2003 during August (Table 1), when water temperatures are typically at their maximum, often reaching extremes as high as 31°C (RiverKeeper Data, Loxahatchee River District). A relatively low abundance of bleached individuals was recorded in late July 2004; however, a resampling of the site a few weeks later in August indicated that the incidence of bleaching had risen 14 fold (Table 2). In July 2004, water temperatures recorded at the Jupiter Sound site ranged from 30° to 31°C between 1:00 PM and 3:30 PM during an extremely low spring tide that resulted in the subaer-

TABLE 1. Relative abundance of bleached individuals of *Sorites dominicensis* from Jupiter Sound, Florida, during August 2003 (n = total number of tests examined).

Test condition	Percent of tests	
	2 Aug 2003 (n = 580)	12 Aug 2003 (n = 147)
Mottled cytoplasm	1.0%	1.0%
White cytoplasm	15%	12%
Total bleached	16%	13%

ial exposure of major portions of the seagrass bed. No water temperature data are available for Jupiter Sound in August 2004, although the water was uncomfortably hot to the touch at the time of collection (Richardson, unpublished). Bleaching was undetectable in surveys of the *S. dominicensis* populations conducted at other times of the year in both 2003 and 2004 (Richardson, unpublished data).

In Belize, water temperatures were recorded using HOBO Tidbit (Onset) submersible temperature loggers deployed for three days in July 2005. One logger was deployed on the reef flat at Carrie Bow Cay and the other in Boston Bay, Twin Cays. The range of water temperatures recorded for both sites are listed in Table 3 and Figure 3. Although the overall mean temperatures were identical for both sites ($s = 32^\circ\text{C}$), the reef flat off Carrie Bow Cay experienced a wider range of temperatures ($29^\circ\text{--}40^\circ\text{C}$), with higher maximum temperatures recorded during the late afternoon and lower minimum temperatures recorded at night (Figure 3; Table 3). Correspondingly, the rate of bleaching recorded from the reef flat at Carrie Bow Cay was almost five times higher than that observed in Bos-

TABLE 2. Relative abundance of bleached individuals of *Sorites dominicensis* from Jupiter Sound, Florida during July and August 2004 (n = total number of tests examined).

Test condition	Percent of tests	
	29 Jul 2004 (n = 446)	19 Aug 2004 (n = 14)
Mottled cytoplasm	2.0%	29%
White cytoplasm	0%	0%
Total bleached	2.0%	29%

TABLE 3. Characteristics of two collecting sites in Belize.

Characteristic	Carrie Bow Cay	Twin Cays
Water depth	<0.5 m	1.0 m
Exposure	Exposed during low tides	Subtidal
Water clarity	Very clear	High tannins and mangrove detritus
Water movement	Swift current	Sheltered with slower current
Temperature range (1–4 July 2005)	30°–35°C	29°–40°C

ton Bay, Twin Cays (Table 4). Although the water temperatures recorded in Boston Bay, Twin Cays, were not as extreme as those recorded off Carrie Bow Cay, they still were higher than the HotSpot (28.9°C) and bleaching (HotSpot + 1°C) thresholds derived by NOAA/NESDIS for Glovers Reef (Opishinski, 2006). The same sites were resurveyed in July 2006, and the incidence of bleaching on the reef flat at Carrie Bow Cay was observed to be 11 times higher than the incidence of bleaching recorded in Boston Bay, Twin Cays, which exhibited almost negligible levels of bleaching (Table 5).

FRESHWATER INFLUX AND BLEACHING

In July and August 2006, continued sampling of the Carrie Bow Cay and Twin Cays field sites in Belize yielded results that indicate that symbiont bleaching in *S. dominicensis* can also be triggered by an influx of freshwater during storm events. In July 2006, field collections were suspended during a three-day period of intense rain then restarted after the storms subsided. After the rainstorms, the incidence of bleaching recorded at both sites rose in all three categories (pale cytoplasm, mottled cytoplasm,

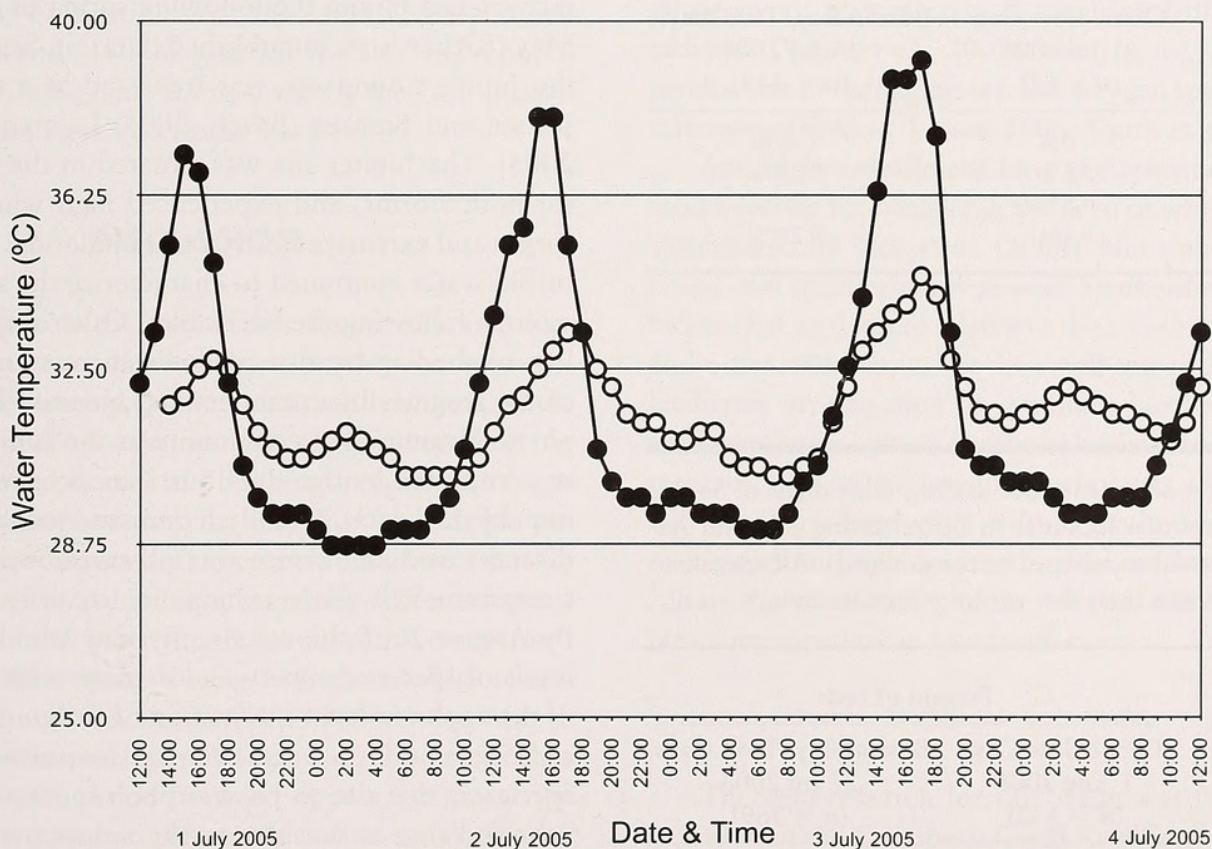


FIGURE 3. Water temperature variations on the reef flat at Carrie Bow Cay and in Boston Bay, Twin Cays, Belize, as measured at noon and every 2.5 hours thereafter during 1–4 July 2005.

TABLE 4. Relative abundance of bleached individuals of *Sorites dominicensis* from two localities in Belize during July 2005 (n = total number of tests examined).

Test condition	Percent of tests	
	Carrie Bow Cay (n = 797)	Boston Bay, Twin Cays (n = 685)
Mottled cytoplasm	4.3%	2.5%
White cytoplasm	14%	1.5%
Total bleached	19%	3.9%

TABLE 5. Relative abundance of bleached individuals of *Sorites dominicensis* from two localities in Belize during July 2006 (n = total number of tests examined). All specimens were collected before a three-day period of intense rain.

Test condition	Percent of tests	
	Carrie Bow Cay, 21 Jul 2006 (n = 62)	Boston Bay, Twin Cays, 23 Jul 2006 (n = 349)
Pale cytoplasm	0%	0%
Mottled cytoplasm	3.2%	0.29%
White cytoplasm	4.8%	0%
Total bleached	8.1%	0.29%

TABLE 6. Relative abundance of bleached individuals of *Sorites dominicensis* from two localities in Belize during July and August 2006 (n = total number of tests examined). All specimens were collected after a three-day period of intense rain.

Test condition	Percent of tests	
	Carrie Bow Cay, 1 Aug 2006 (n = 132)	Boston Bay, Twin Cays, 27 Jul 2006 (n = 369)
Pale cytoplasm	1.5%	0.27%
Mottled cytoplasm	0.76%	2.4%
White cytoplasm	8.3%	16% ^a
Total bleached	11%	19%

^a Of 60 individuals, 34 were juveniles from the same brood.

and white cytoplasm) (Table 6). Although bleaching on the reef flat at Carrie Bow Cay was slightly higher than the prestorm levels (11% vs. 8.1%), the total poststorm incidence of bleaching in Boston Bay was observed to be more than 65 times higher than that observed just a few days earlier (Table 6). Although the waters in Boston Bay are normally of open ocean marine salinities, during heavy rains and slack tides cold, brackish water drains off Hidden Lake in the Twin Cays and empties into Boston Bay through Hidden Creek (Rützler et al., 2004). Interestingly, juveniles were disproportionately impacted by the bleaching event: 34 of 60 of the tests with white cytoplasm appeared to be individuals from the same brood (Table 6).

IMPACT OF HURRICANES AND RECOVERY

Seasonal bleaching events cause increased mortality in *S. dominicensis*, resulting in compromised populations that are more sensitive to periodic disturbance by hurricanes. Monthly surveys in 2001, 2003, and 2004 indicate that *S. dominicensis* populations normally plummet in the late summer, stay low throughout the winter, and eventually recover and bloom the following spring in late April and May (Richardson, unpublished data). In September 2004, the Jupiter Sound site was traversed by two hurricanes, Jeanne and Frances (Beven, 2005; Lawrence and Cobb, 2005). The Jupiter site was situated in the south eyewall for both storms, and experienced high winds and storm surges and extensive freshwater inundation. Dark, cloudy, turbid water continued to characterize the site for several months following the hurricanes. Other impacts included loss of shading because of downed trees and overgrowth of the seagrass by cyanobacterial blooms. The entire epiphytic foraminiferal community at the Jupiter Sound site was impacted by the 2004 hurricane season (Richardson, unpublished data). Initially, a dramatic reduction in species diversity and abundance was observed, with two species comprising 92% of the community in April and May 2005. By August 2005 the community had rebounded to 2001 levels of species diversity and density, with the exception of the apparent local eradication of *S. dominicensis* (Richardson, unpublished data). *Sorites dominicensis* is the only species at this site to possess photosynthetic endosymbionts and thus is sensitive to the reduced transmission of light in the water column that resulted from the months of increased turbidity following the 2004 hurricanes.

In October 2005, Jupiter Sound was impacted by Hurricane Wilma (Pasch et al., 2006), although this time the region experienced the high winds of the north eye-

TABLE 7. Relative abundance of bleached individuals of *Sorites dominicensis* from Jupiter Sound, Florida, 4 April 2008, as determined from examination of 446 tests.

Test condition	Percent of tests (<i>n</i> = 446)
Pale cytoplasm	5.9%
Mottled cytoplasm	7.8%
White cytoplasm	9.8%
Total bleached	24%

wall of the storm. Individuals of *S. dominicensis* were not recovered from the Jupiter Sound site until the summer of 2007 and did not reach their pre-hurricane densities until April 2008 (Richardson, unpublished). A survey of 446 individuals of *S. dominicensis*, collected in April 2008, yielded a high incidence of bleached individuals (24% total), an unusual event for the spring (Table 7). The trigger for this event is unknown; the rainfall during this period was below average as the region was experiencing an extended seasonal drought. It is also not known whether the population recovered through the reproduction of relict populations of *S. dominicensis* that survived the hurricanes of 2004 and 2005 or whether the site was repopulated through immigrants transported by the Gulf Stream from the Florida Keys and/or the Caribbean.

DISCUSSION

The results from the field studies described above document the occurrence of bleaching in *Sorites dominicensis*, a dinoflagellate-bearing foraminiferan, and delineate some of the environmental stressors that trigger bleaching. As has been observed in corals, bleaching in epiphytic specimens of *S. dominicensis* may be triggered by multiple environmental factors, such as increased irradiance during subaerial exposure at low tide, increased water temperatures, influx of freshwater runoff during storm events, and catastrophic disturbance during hurricanes. The symptoms of bleaching in *S. dominicensis* include decrease in intensity of coloration (pale appearance), the patchy loss of cytoplasmic coloration (mottled appearance), and the total loss of cytoplasmic coloration (white tests). Symbiont bleaching in *S. dominicensis* can be distinguished from the loss of cytoplasmic coloration that occurs during the process of reproduction through multiple fission as the symbiont-rich cytoplasm moves from the central region of the test to the periphery where the brood chambers and

embryos will form. Studies are currently underway to link qualitative observations of bleaching in *S. dominicensis* to quantitative studies of symbiont density in bleached specimens using staining techniques that differentiate necrotic or apoptotic algal cells.

The relatively high water temperatures recorded on the reef flat at Carrie Bow Cay in July 2005 are not unusual for tropical seagrasses, which may experience annual fluctuations in seawater temperatures ranging from 19.8° to 41°C (Campbell et al., 2006). Unusually high water daily temperatures (40°–43°C) have been recorded in seagrass beds growing in shallow water off Papua New Guinea (Fred Short, University of New Hampshire, personal communication, January 2006). In addition to high temperatures, tropical seagrasses growing in shallow-water pools in the intertidal zone are subject to desiccation, extremely high levels of photosynthetically active radiation, and high levels of ultraviolet radiation (Campbell et al., 2006; Durako and Kunzelman, 2002).

Although the underlying mechanisms of bleaching in *S. dominicensis* are unknown, it is hypothesized that several of the proposed mechanisms for bleaching in corals may function in foraminiferans as well, such as reduced efficiency of photosystem II resulting from increased irradiance (Venn et al., 2008; Smith et al., 2005), and the production of damaging reactive oxygen species via several different pathways (Lesser, 2006; Smith et al., 2005).

Soritid foraminiferans have the potential to serve as a model system for bleaching, the need of which was recently emphasized by Weis et al. (2008). Not only do *S. dominicensis* and other soritids possess *Symbiodinium* endosymbionts that are closely related to the zooxanthellae in corals and other metazoans, but the small size of *S. dominicensis* facilitates investigation of symbiont bleaching *in hospite*, using methods such as in situ hybridization, immunofluorescence, and other imaging techniques. Future research will focus on developing culture methods for *S. dominicensis* and on exploring cytological methods that will facilitate the visualization of the cell processes underlying the bleaching response in foraminiferans.

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