

Endosymbiont-bleaching in epiphytic populations of *Sorites dominicensis*

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Abstract

Episodes of symbiont-bleaching have been documented in field studies of epiphytic populations of the dinoflagellate-bearing foraminiferan *Sorites dominicensis* from Jupiter Sound in the Indian River Lagoon, Florida, and Carrie Bow Cay and Twin Cays, Belize. In August 2003, 13–16% of the population in Jupiter Sound exhibited evidence of bleaching, with cytoplasm that was either mottled or totally white. In July 2005, 18% of the population on the reef flat off Carrie Bow Cay, and 4% of the population in the tannin-stained waters of Boston Bay, Twin Cays, exhibited signs of bleaching. Symbiont bleaching in soritid foraminiferans may be a more widespread and recurrent phenomenon than has previously been recognized. Bleaching appears to be triggered by a combination of environmental factors that are similar to the conditions that trigger bleaching in corals, such as: subaerial exposure during extreme low spring tides in the summer months, high water temperatures, increased irradiance, exposure to light in the ultraviolet or blue light spectra, and periodic disturbance by hurricanes. The endosymbionts in *S. dominicensis*, and other soritid foraminiferans, are members of the *Symbiodinium* clade of dinoflagellates that comprise the zooxanthellae in cnidarians and molluscs, thus this foraminiferal host-symbiont system has potential utility as a model system for the experimental study of the cellular and molecular mechanisms underlying coral bleaching.

Keywords: Foraminifera, epiphytes, *Thalassia testudinum*, bleaching, Florida, Belize

1. Introduction

Sorites dominicensis is a predominantly epiphytic foraminiferan that is host to dinoflagellate endosymbionts. Although rarely a dominant component of the benthic foraminiferal biota, the species is widely distributed in the shallow, tropical-subtropical waters of the Caribbean and South Florida. In August 2003, a major symbiont-bleaching event was observed during the course of a demographic study of an epiphytic population of *S. dominicensis* in Jupiter Sound, Florida. Unusually high numbers of white-colored tests that were devoid of the yellowish-brown colored cytoplasm characteristic of healthy specimens were observed in all age classes of fresh field collections. In addition to the totally bleached specimens, several specimens with mottled cytoplasm were also observed. Continued monitoring of the site during the following

spring and summer, revealed an episode of minor bleaching in late July 2004. In September 2004, the site experienced two hurricanes, after which the local population of *S. dominicensis* was decimated and has subsequently never recovered.

In July 2005, additional surveys of epiphytic populations of *S. dominicensis* were conducted at two sites in Belize, Central America: the reef flat off Carrie Bow Cay, and Boston Bay, a protected embayment located in the mangrove islands of Twin Cays. Symbiont bleaching was observed in the *S. dominicensis* populations at both sites, with the highest percentage of bleached and mottled individuals occurring in an intermittently exposed seagrass bed on the reef flat off Carrie Bow Cay (Fig. 1).

Although bleaching has been widely documented and studied in diatom-bearing species of the rotalid foraminiferal taxon *Amphistegina*, the phenomenon has not

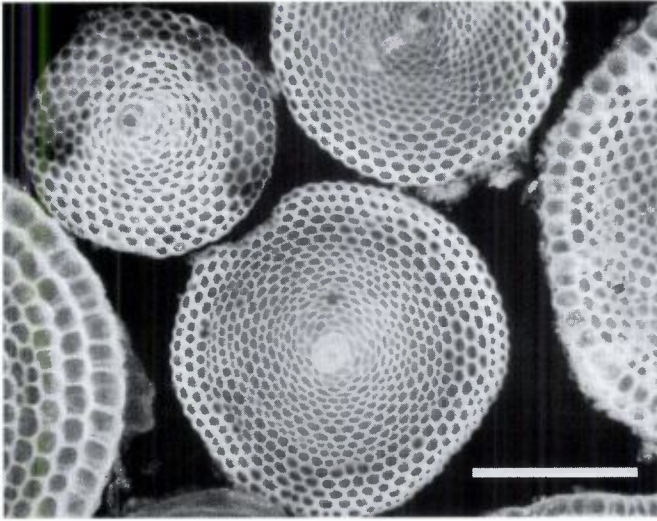


Figure 1. Photomicrograph of normal and bleached (mottled) specimens of *Sorites dominicensis* from Boston Bay, Twin Cays, Belize (July 2005). The specimen in the bottom center exhibits the characteristic coloration of a normal individual with yellowish-brown cytoplasm evenly distributed throughout the test, except for the last few chambers. The specimens in the upper right and left possess patches of bleached cytoplasm. Scale bar = 1 mm.

previously been recognized in the dinoflagellate-bearing soritid foraminiferans. The purpose of this paper, therefore, is to document and discuss the occurrence of symbiont bleaching in field populations of *S. dominicensis* from Florida and Belize. The biology, systematics, and ecology of *S. dominicensis* and its endosymbiosis with *Symbiodinium* dinoflagellates, will be reviewed, and the relevance of this host-symbiont system to studies of coral bleaching will be briefly discussed.

2. Background

Foraminifera is a monophyletic clade of predominantly marine, single-celled eukaryotes that are united by the synapomorphies of the presence of granuloreticulopodia and a set of unique insertions in the small subunit (SSU) of the ribosomal DNA (rDNA) (Habura et al., 2004). The phylogenetic position of Foraminifera relative to other eukaryotes has stabilized within the past few years, with Foraminifera consistently branching in close proximity to Cercozoa, a group that includes an eclectic assortment of single-celled eukaryotes, most of which form pseudopodia, but not granuloreticulopodia, at some stage in their life cycle, and many of which form simple, single-chambered tests (Archibald and Keeling, 2004; Longet et al., 2004; Nikolaev et al., 2004; Reece et al., 2004; Berney and Pawlowski, 2003).

Foraminifera and Cercozoa are subclades of the more inclusive clade Rhizaria (=Retaria of Adl et al., 2005), a taxon of unicellular eukaryotes that has been phylogenetically defined as “the clade containing the most recent common ancestor of *Thalassicola*, *Gromia*, *Allogromia*, *Plasmodiophora*, *Chlorarachnion*, and all of its descendants” (Nikolaev et al., 2004). Foraminiferans are unique among rhizarians in having evolved large, complex, multi-chambered tests (shells), with the largest and most complex foraminiferal tests being found in those clades that possess algal endosymbionts. Endosymbiotic associations with photosynthetic unicellular eukaryotes are observed in several modern benthic foraminiferal taxa, including Soritacea (rhodophytes, chlorophytes and dinoflagellates), Alveolinacea (diatoms), Nummulitacea (diatoms), Calcarinidae (diatoms), and Amphisteginidae (diatoms). 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 maintenance (Hallock, 1999). The algal endosymbionts presumably benefit from the mutualism as well, gaining access to nutrients that are scarce in oligotrophic environments, and refuge from predation (Hallock, 1999).

Phylogenetic relationships

Sorites dominicensis is a member of the subclade Soritida in the more inclusive clade Soritacea, a monophyletic group of large, endosymbiont-bearing Foraminifera. Soritaceans have a cosmopolitan distribution in tropical to subtropical coral reefs, and adjacent shallow-water marine benthic habitats, such as seagrass and mangrove ecosystems (Langer and Hottinger, 2000). Soritacea is a subclade within the more inclusive foraminiferal clade Miliolida, a group characterized by mineralized tests composed of high-magnesium calcite (Blackmon and Todd, 1959; Toler et al., 2001).

Photosymbiosis appears to have been the principal driving force in the evolution of the different clades of “larger” foraminiferans, such as Soritacea (Hallock, 1985; Lee, 1998; Lee and Anderson, 1991; Lee and Hallock, 1987; Lee et al., 1997, 1979; Richardson, 2001). Symbiosis with algal endosymbionts is the plesiomorphic condition for the entire clade Soritacea, with basal clades possessing unicellular rhodophyte endosymbionts (Holzmann et al., 2001; Richardson, 2001; Gudmundsson, 1994). Symbiont-switching has taken place at least twice during the evolutionary history of the clade: the first transition from basal rhodophyte to chlorophyte endosymbionts occurred prior to the diversification of the subclades Archaiasinida and Soritida (Richardson, 2001). A second transition from chlorophyte to dinoflagellate endosymbionts took place within the subclade Soritida (Richardson, 2001). Morphological and molecular analyses of Soritacea are

largely congruent; however, the branching of Eocene-aged fossil soritaceans within the derived Soritida indicates that the origination of the clade occurred prior to the Middle Eocene, in contrast to the Upper Oligocene to Early Miocene age frequently cited in the literature (Brasier, 1975; Gudmundsson, 1994; Haynes, 1981; Holzmann et al., 2001; Richardson, 2001).

Recent molecular analyses indicate that most species of *Sorites*, including *S. dominicensis*, fall within a diverse clade that branches as the sister group to *Marginopora vertebralis* (Garcia-Cuetos et al., 2006; Holzmann et al., 2001). At least 12 distinct subclades (phylotypes) (I–XII) can be resolved within the clade *Sorites*; however, the taxonomic composition of these subclades and their relationship to each other vary slightly between partial rDNA SSU and total rDNA SSU phylogenies (Garcia-Cuetos et al., 2006). Although morphologically indistinguishable, Caribbean populations of *S. dominicensis* do not comprise a monophyletic group in the analysis, and specimens from the Florida Keys branch within subclades II, III, IV, X, and XII (Garcia-Cuetos et al., 2006). Another species of *Sorites* branches as the sister clade to *Amphisorus*, indicating that *Sorites* as currently recognized may represent either a paraphyletic or polyphyletic taxon (Garcia-Cuetos et al., 2006; Holzmann et al., 2001).

Taxonomy of Sorites dominicensis

In this paper, the name *Sorites dominicensis* Ehrenberg, 1839, is applied to the Western Atlantic epiphytic populations discussed in this paper. Cushman (1927) designated *S. dominicensis* as the type species of Ehrenberg's genus *Sorites*; however, Loeblich and Tappan (1987b) later petitioned the ICZN to have *N. orbiculus* Forsskål, 1775, replace *S. dominicensis* as the type species of *Sorites*. Their petition was accepted and *Nautilus orbiculus* Forsskål was redesignated as the type species of *Sorites* Ehrenberg, 1839, in accordance with the practices of Linnean taxonomy (ICZN, 1989, Opinion 1539).

The epithet *S. dominicensis* has only been occasionally used in the literature, and has been applied to both Recent and fossil species. Specimens of *S. dominicensis* from both Belize and Florida have been compared to and have been determined to be conspecific with topotypic specimens of *S. dominicensis* from the "original probe of 1838...Insel San Domingo" (USNM 324910, National Museum of Natural History, Washington, DC) (Richardson, 2000). Earlier authors considered *S. dominicensis* to be a *nomen dubium* (Smout, 1963), and placed the species in synonymy with *S. marginalis* (Lévy, 1977; Loeblich and Tappan, 1964), or synonymized it with *S. orbiculus* (Cole, 1965; Crapon de Caprona d'Ersu and Benier, 1985; Loeblich and Tappan, 1987a, b).

Douvillé (1902, p. 294) considered *S. dominicensis* to be a Miocene-aged species from fossil deposits in the

Caribbean and Panama; however, examination of sediments from these localities has not yielded fossil specimens with the characteristics of *S. dominicensis* (S. Richardson, unpublished observations). Cushman and Ponton (1932, p. 73) postulated that the fossil species identified as *Sorites* (?) sp. (?) from the Lower Miocene Chipola Marl of Florida might be "identical with *Sorites dominicensis* Ehrenberg described from Santo Domingo, the types of which are in Berlin." Examination of soritids from the Chipola Formation of Florida has yielded two species, *Miosorites* cf. *M. americanus* (Cushman) and an undescribed smaller soritid species, neither of which are conspecific with the USNM topotypes of *S. dominicensis* (S. Richardson, unpublished data). Renz (1948, pl. 6, Figs. 8a,b) identified *S. dominicensis* as rare in Lower to Middle Miocene-aged sediments from the Agua Salada Group of Venezuela, and figured, but did not describe the species. The specimen that Renz (1948) figured shares many features in common with modern specimens of *S. dominicensis*, and thus may represent the fossil lineage of *S. dominicensis* in the Caribbean.

Recent specimens of *S. dominicensis* have been described under several different generic and specific names: *Orbitolites duplex* Carpenter, 1856 (Cushman, 1922; Doyle and Doyle, 1940), *Amphisorus hemprichii* Ehrenberg, 1839 (Cushman, 1930, 1941; Lévy 1977; Wantland, 1975), *Orbitolites (Amphisorus) hemprichii* Ehrenberg, 1839 (Hofker 1964, 1976), *Sorites orbiculus* (Forsskål 1775) (Cole, 1965; Crapon de Caprona d'Ersu and Benier, 1985; Kloos, 1980, 1981, 1984; Kloos and MacGillivray, 1978), and *Sorites marginalis* (Lamarck, 1801) (Bock, 1967; Buzas and Severin, 1982; Lévy, 1977; Müller-Merz and Lee, 1976). Recent specimens of *S. dominicensis* have been compared with, and determined to be different from, the neotypes of *S. orbiculus*, and *S. marginalis* designated by Smout (1963), that are housed in the Natural History Museum (London) (Richardson, 2000).

Ecology of Sorites dominicensis

Sorites dominicensis occupies a predominantly epiphytic mode of life, living attached to seagrasses and macroalgae throughout the Caribbean, Florida, and Bermuda (Bock, 1967; Erskian, 1972; Fujita and Hallock, 1999; Richardson, 2000; 2004; Wilson, 1998). Under optimum conditions, living tests are anchored to seagrass or macroalgae by an organic sheath and/or rope-like organic filaments (Lee et al., 1979; Kloos, 1980). As with other epiphytes on turtle grass, *S. dominicensis* must complete its life cycle within the life span of an individual blade, which for *T. testudinum*, the dominant seagrass in the Western Atlantic, is an average of 40 days (Dirnberger, 1990; Hemminga et al., 1999; Hemminga and Duarte, 2000; Phillips and Meñez, 1988).

Sorites dominicensis, like other miliolids, enlarges its

test by an accretionary mechanism, adding new chambers by terminal addition to the last-formed chamber. Tests in this species are evolutely coiled and undergo several distinctive successive ontogenetic stages. The initial chambers of the test are comprised of an oval-shaped proloculus, around which is wrapped a tubular flexostyle. The initial proloculus and flexostyle chambers are followed by a brief coiled stage (1 chamber), a flabelliform stage (1–5 chambers), a reniform stage (4–9 chambers), and a terminal annular stage that consists of numerous ring-shaped chambers (7–19 chambers) (Gudmundsson, 1994; Kloos, 1981; Richardson, 2001, unpublished data). All chambers, except for the proloculus, flexostyle, and initial coiled chamber, are subdivided by transverse septa that partition the elongated chambers into hexagonal chamberlets, giving the entire test a honeycombed appearance. Multiple rows of single or paired apertures are located along the outer periphery of the disc-shaped test. Granuloreticulopodia emerge from the apertures, and spread along the surface of the seagrass blade forming a web-like array that is used to capture food, excrete wastes, and move in response to disturbance. Live individuals that have been detached from their phytal substrate are temporarily motile and may exhibit phototaxis (Kloos, 1980; S. Richardson, unpublished observations).

Live individuals of *S. dominicensis* obtain nutrition from feeding, as well as mobile photosynthetic compounds translocated from their algal symbionts. *Sorites dominicensis* has been observed to feed on unicellular chlorophytes and a variety of diatoms in laboratory experiments (Lee and Bock, 1976). Field observations indicate that *S. dominicensis* and other epiphytic foraminiferans feed on the microbial biofilms (aufwuchs, periphyton) that coat the leaves of seagrasses and other submerged aquatic vegetation (Novak, 1984). Scanning electron micrographs of specimens that are still attached to their phytal substrate show deposits of empty diatom frustules rimming the periphery of the test (Lee et al., 1979; S. Richardson, unpublished observations).

Radioisotope studies conducted on *S. marginalis* indicate that mobile photosynthetic compounds produced by the dinoflagellate endosymbionts contribute to both the nutrition and biomineralization of the foraminiferal cell (Duguay, 1983; Lee and Bock, 1976). Light-induced stimulation of calcification has been demonstrated for *S. marginalis*, with calcium and carbon uptake rates two to three times higher in the light than in the dark (Duguay, 1983). Radioisotope tracer studies on other soritid taxa with dinoflagellate endosymbionts indicate that soluble compounds including unspecified lipids, glucose, glycerol, and polyglucan are translocated from the algal symbionts to the foraminiferal host (Kremer et al., 1980).

Prior to multiple fission, the parent cell forms from two to five brood chambers that are morphologically distinctive from the vegetative annular chambers in both size and

internal structure. In preparation for cytokinesis, the parental cytoplasm migrates into the brood chambers where it will subdivide into multiple daughter cells. In the Jupiter Sound and Belizean populations, parental tests of *S. dominicensis* have been observed to produce from 41–192 embryos during multiple fission (Fig. 2; S. Richardson, unpublished data). The *Symbiodinium* endosymbionts are vertically transmitted from parent to offspring, and visible in the nascent daughter cells prior to their calcification within the confines of the brood chambers (Doyle and Doyle, 1940; Kloos, 1981, 1984; Lee, 1983). Doyle and Doyle (1940) counted from 470–500 symbionts in the cytoplasm of *S. dominicensis* embryos collected from reproductive tests in the Dry Tortugas.

As noted by Kloos (1984) for populations in Curaçao, reproductive individuals with brood chambers have been observed throughout the year at both the Jupiter Sound and Belizean sites (Richardson, unpublished observations). Microspheric tests are rarely observed (Hofker, 1976, p. 231, Fig. 131a), and it is generally assumed that Western Atlantic populations of *S. dominicensis* are apomictic (Kloos, 1980, 1984; Kloos and MacGillavry, 1978).

Dinoflagellate endosymbionts

The dinoflagellates that comprise the endosymbionts in *S. dominicensis* and other Soritid foraminiferans are classified in the genus *Symbiodinium*, a taxon that includes the zooxanthellae of stony corals, soft corals, gorgonians, anemones, jellyfish, bivalve molluscs, nudibranchs, sponges, and ciliates (Baker, 2003; Douglas, 2003; Glynn, 1996).

Cushman (1922, p. 10) was the first worker to record observations of commensal algae in epiphytic specimens of *S. dominicensis* from the Dry Tortugas, describing the algae as brownish in color, about 6–7 μm in diameter, and noting that they “completely pack the chambers.” Cytological features of dinoflagellate endosymbionts of *S. dominicensis* specimens from turtle grass collected in the Dry Tortugas, were examined in further detail by Doyle (1934, 1935) and 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 16,000 individuals. In contrast, confocal microscopy of a 2-mm sized individual of *S. dominicensis* collected from Jupiter Sound yielded an estimated 4,000 dinoflagellates, equivalent to a density of 6.35×10^6 symbionts per cm^3 of cytoplasm (S. Richardson, unpublished data). Doyle and Doyle (1940) also described the occurrence of starch granules, calcium oxalate crystals, and pigmented oil droplets dispersed throughout the foraminiferal cytoplasm, speculating that these features were symbiont-derived.

Müller-Merz and Lee (1976) first described ultrastructural details of the dinoflagellate endosymbionts of epiphytic specimens of *S. dominicensis* living on

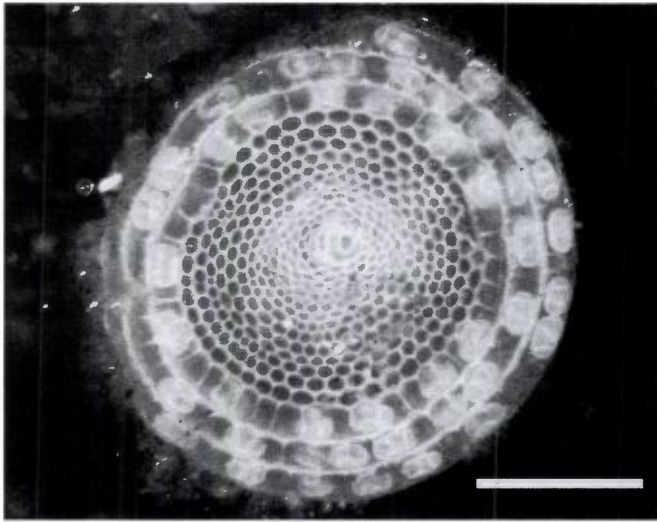


Figure 2. Photomicrograph of reproductive individual of *Sorites dominicensis* from Boston Bay, Twin Cays, Belize (July 2005). Note that most of the parental symbionts appear not have been distributed to the progeny in this specimen, as indicated by the strong cytoplasmic coloration that remains in the parent test, in contrast to the bleached appearance of the embryos in the brood chambers. Scale bar = 1 mm.

seagrasses collected from Key Largo Sound, Florida, noting the similarity in appearance of the foraminiferal symbionts to the zooxanthellae of corals. The 6- to 7- μ m sized symbionts possess the characteristically condensed chromosomes of dinoflagellate nuclei, a peripherally located, lobate chloroplast, a pyrenoid with a single stalk, storage bodies for starch, and other typical eukaryotic organelles (Müller-Merz and Lee, 1976). The symbionts appear to be surrounded by multiple membrane layers, indicating that they are located within a symbiosome, or a host-derived membrane within the host cytoplasm. Electron microscopy of the multilayered symbiosome membrane in *Symbiodinium* endosymbionts in metazoans have revealed that the symbiosome consists of a single, host-derived membrane, while the inner membrane-like layers are comprised of exudates produced by the algal cell (Wakefield et al., 2000; Wakefield and Kempf, 2001).

Inside the foraminiferal host cell, symbionts are distributed throughout the 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 (Müller-Merz and Lee 1976; S. Richardson, unpublished observations). Transcriptionally active foraminiferal nuclei are located in cytoplasmic regions with the high symbiont densities, indicating that the host may exert regulatory control over the symbiont population (Müller-Merz and Lee, 1976). As noted earlier by Doyle and Doyle (1940), an abundance of starch granules, presumably symbiont-derived, are

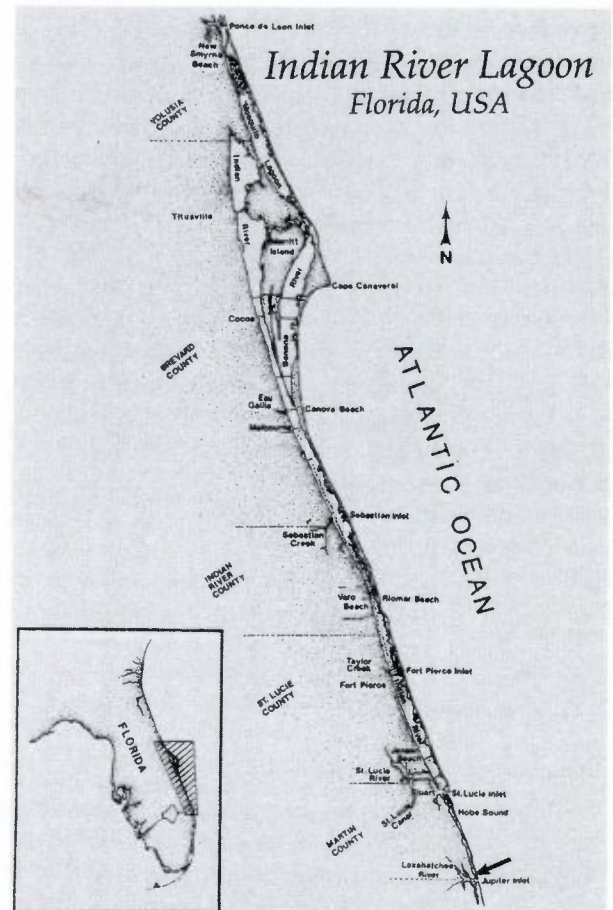


Figure 3. Map of Indian River Lagoon (IRL), Florida, USA. Inset map shows the location of the lagoon along the east coast of Florida. The lagoon stretches approximately 251 km from the Ponce de Leon Inlet, south to the Jupiter Inlet. The arrow designates the collecting site for this study, which was located just north of Jupiter Inlet in the southern portion of the IRL. Map used with permission from Grant Gilmore (Dynamac Corporation).

distributed throughout the host cytoplasm. The symbionts from specimens of *S. dominicensis* collected from the Florida Keys have been isolated and cultured, and the morphology of the vegetative cells described by Lee et al. (1979, 1997).

Originally conceived of as a single pandemic algal symbiont that was commensal with a broad range of marine taxa, *S. microadriaticum* is now known to be part of a more inclusive and diverse clade that is comprised of eight major subclades (phylogenotypes), identified by the letters A–H (Baker, 2003; Coffroth and Santos, 2005; Pochon et al., 2006; Rowan, 1999; Rowan and Powers, 1991, 1992). Symbionts from foraminiferal hosts are found in clades C, H, F, and D1 (*sensu* Garcia-Cuetos et al., 2006), with clades F and H being comprised almost exclusively of symbionts

from soritid foraminiferans (Garcia-Cuetos et al., 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., 2006; Pawlowski et al., 2001; Pochon et al., 2001, 2004, 2006). Although sequences have not yet been obtained from the symbionts of either the Belizean or Indian River Lagoon populations of *S. dominicensis*, sequences from Florida Keys specimens fall within either clades F (subclade F4) or H (Garcia-Cuetos et al., 2006; Pochon et al., 2006). In all phylogenies published to date, clade H branches as the sister group to clade C, a clade that is widely distributed in the Indo-Pacific, and appears to be more sensitive to bleaching than the symbionts in other clades (Garcia-Cuetos et al., 2006; Pawlowski et al., 2001; Pochon et al., 2001, 2004, 2006; Rowan, 1998, 2004).

3. Material and Methods

Specimens for this study were harvested from three sites; one located in the southern portion of the Indian River Lagoon, Florida (USA), and the other two located in the central region of the Mesoamerican Barrier Reef Complex, Belize, Central America (CA).

Indian River Lagoon, Florida, USA

The Indian River Lagoon study was conducted during the summers of 2003 and 2004. Epiphytic individuals of *S. dominicensis* were harvested from blades of the seagrass *Thalassia testudinum* growing in a shallow seagrass meadow located approximately 0.8 km north of the Route 707 Bridge, along the eastern shore of the lagoon off south Jupiter Island (N 26°57', W 80°05') (Fig. 3). Five of the seven species of seagrass that occur in the Indian River Lagoon have been recognized at this locality, including the endemic and endangered species *Halophila johnsonii* (Durako et al., 2003; Ridler et al., 2000; Virnstein, 1995). The seagrass samples were collected from a monospecific stand of *T. testudinum* (turtle grass), interspersed with mixed patches of *T. testudinum* and *Syringodium filiforme* (manatee grass). Estimated mean shoot densities of *T. testudinum* in 2003 were 172 ± 25 shoots/m², with an estimated leaf area index of 1–1.4 m² seagrass blade/m² seafloor (S. Richardson, unpublished data). In this region, *T. testudinum* exhibits pronounced seasonal differences in productivity and growth rates relative to more tropical areas (Gacia, 1999), due to the fact that northernmost limit of *T. testudinum* on the east coast of Florida occurs in the Indian River Lagoon (Virnstein, 1995).

The hydrology of this region is influenced by tidal exchanges through the Jupiter Inlet, which is located approximately 1.5 km to the south (Smith, 2001). The collecting site is subject to semi-diurnal tidal currents due to its close proximity to the inlet, and is protected on its western margin by an offshore sandbar (oyster bar) that baffles boat wake waves produced by traffic in the adjacent Intracoastal Waterway. The mean tidal range at this site is 0.6 m with a spring range of 0.73 m (NOAA/NOS, 2006). The samples were collected from the lower intertidal zone, although portions of the flat are partially exposed during mean spring tides, and completely exposed during extreme spring low tides (S. Richardson, unpublished observations).

The mean water temperature at this site is 25°C, the mean pH is 7.9, and the mean salinity is 33.8 (Dent et al., 2002). Water transmittance, as reported by the Loxahatchee Water District is 80–90%; however, personal observations indicate that the clarity of the water varies considerably depending on tidal currents and storm activity. The Florida Water Quality Index (FWQI) and the Trophic State Index (TSI) calculated for this site in 2000 were 18 and 15, respectively (Ridler et al., 2002). Values of FWQI below 45 and values of TSI below 49 are considered to indicate "good" water quality (Ridler et al., 2002).

The Jupiter Sound site is subject to intensive recreational use, especially on weekends. Direct anthropogenic impacts to the seagrass bed include foot traffic by human and canine waders, and boat traffic (canoes, kayaks, personal water craft, and motorboats). A county park, Coral Cove Park, is located to the east and north of the site on the Atlantic shore of the barrier island. Dense development occurs to the south of the site, with high rise condominiums and apartment buildings in a zone adjacent to the Route 707 bridge. This site has also been directly impacted by three hurricanes in the last few years: two in 2004 (Frances and Jeanne), and one in 2005 (Wilma). During both Hurricanes Frances (14 September 2004) and Jeanne (26 September 2004), the site was in the south eye wall of the storm and experienced high winds and 2-m storm surges (Beven, 2005; Lawrence and Cobb, 2005). During Hurricane Wilma (24 October 2005), the site was in the north eye wall (Pasch et al., 2006). The overall impact of repeated hurricanes on the area is only just beginning to be assessed by the local environmental agencies (M. Ridler, Loxahatchee River Water District, personal communication, April 2006).

Belize, Central America

Specimens for the Belize study were collected during July 2005 from two closely spaced sites within the central region of the Mesoamerican Barrier Reef Complex: Carrie Bow Cay (16°48'N, 88°05'W), and Boston Bay, Twin Cays (16°50'N, 88°06'W) (Fig. 4). Belize has a subtropical climate, with both wet (April–October), and dry

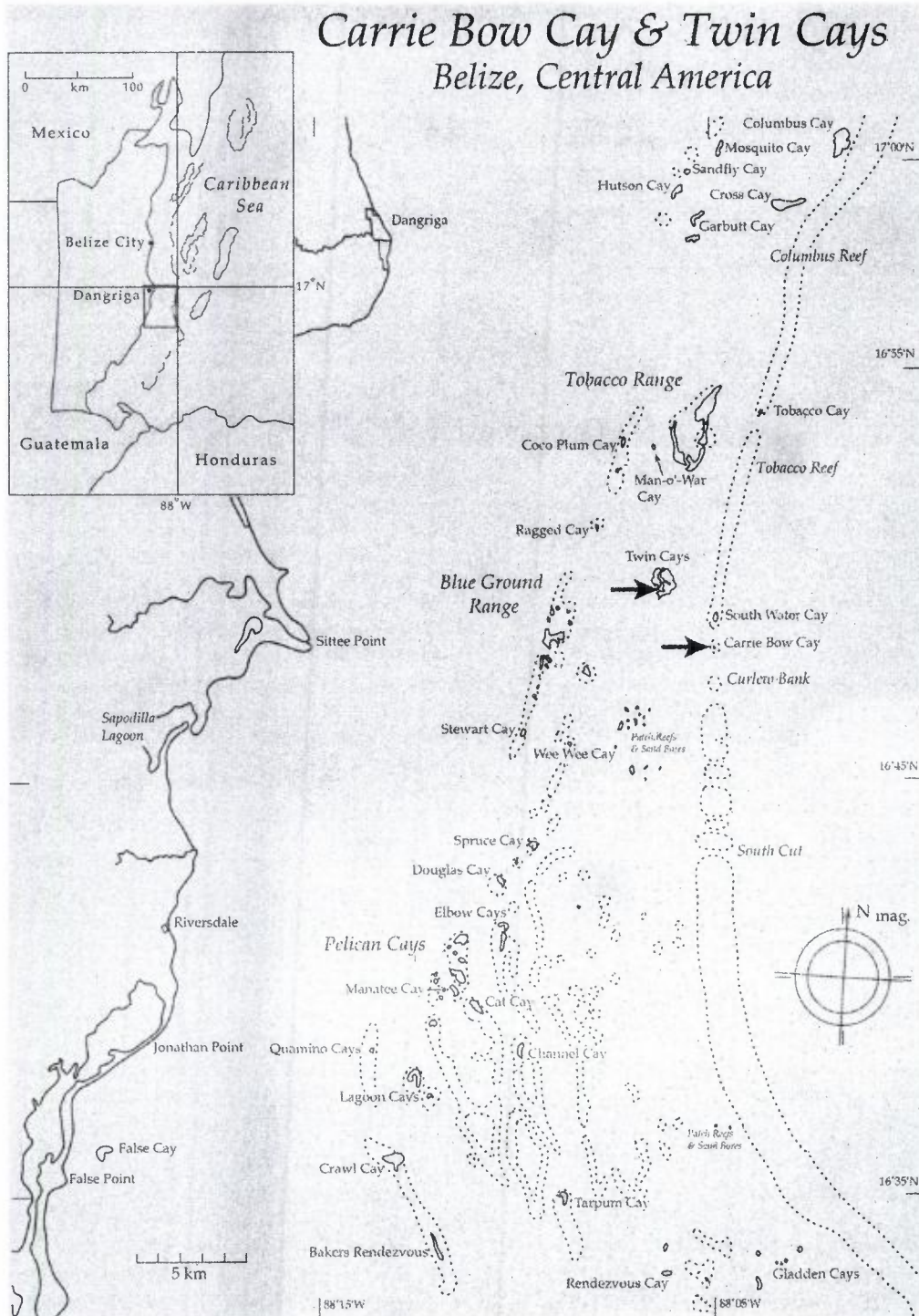


Figure 4. Map of the Carrie Bow Research Area, Belize. Inset map shows location of the research area off the coast of Belize. Arrows designate the collecting sites off Carrie Bow Cay (lower arrow) and Twin Cays (upper arrow). Map drawn by Molly Ryan and used with permission from the Caribbean Coral Reef Ecosystems Program (Smithsonian Institution).

(November–March) seasons (Koltes et al., 1998). Water temperatures off Carrie Bow range from lows of 25°C, occurring in December–January, to highs of >31°C, occurring in July–August (Opishinski, 2006). Open marine salinities characterize both sites, ranging from 33‰ in August to 37‰ in March, in both seagrass and reef habitats (Koltes et al., 1998). The tides are microtidal of the mixed semidiurnal type, with a mean range of 15 cm at Carrie Bow Cay and 20 cm at Twin Cays (Kjerfve et al., 1982; Rützler et al., 2004). Northeasterly trade winds prevail 70% of the year (Rützler and Ferraris, 1982). Hurricanes occur most frequently in the months of July through October, with Hurricane Iris (October 2001) being the most recent devastating hurricane to have directly traversed the region.

Carrie Bow Cay is a 0.4-ha sand cay that is located approximately 22 km SE of Dangriga, and 18 km from the mainland (Fig. 4). The island is situated at the rim of the barrier reef, with a shallow reef flat separating the cay from the leeward side of the reef crest (Rützler and Macintyre, 1982). The island has been inhabited since 1943, being first used as a private summer home, and is currently utilized as a field station by the Smithsonian Institution (Rützler and Feller, 1996).

The reef flat is shallow (0.2–0.5 m water depths), and overlain by clear waters with high levels of light transmittance (Koltes et al., 1998). *Thalassia testudinum* is the dominant macrophyte on the reef flat (68.5% of the total plant cover), growing on a substrate of reef-derived carbonate sand with scattered coral rubble (Shinn et al., 1982; Littler et al., 1987). The seagrass blades are subject to partial subaerial exposure during extreme low spring tides (S. Richardson, unpublished observations). Specimens for this study were collected from *T. testudinum* blades growing in a monospecific stand located approximately 5 m from shore.

The turtle blades on the reef flat are highly epiphytized and coated with a layer sediment. A diversity of encrusting organisms share space with foraminiferans on the strap-like blades of *T. testudinum*. The dominant epiphytes include: encrusting calcareous algae, spirorbid worms, and a number of different gastropod egg cases (S. Richardson, unpublished data). A total of 18 species of epiphytic foraminiferans have been identified to date from turtle grass growing off Carrie Bow Cay (S. Richardson, unpublished data). The overall densities of epiphytic foraminiferans on turtle grass are highest in summer months; for example, in June 2001, the mean density of epiphytic foraminiferans off Carrie Bow Cay was 1.49 individuals cm⁻², compared to 0.97 individuals cm⁻² in February 2002 (Richardson, 2004). The relative abundance of *S. dominicensis* in the epiphyte community is relatively low; for example, *S. dominicensis* comprised 1.8% of the epiphyte population in June 2001, and 0.16% in February 2002 (S. Richardson, unpublished data).

Twin Cays is a 9.15 ha oceanic-type mangrove island that is located approximately 2.3 km leeward of Carrie Bow Cay in the outer lagoon. Twin Cays is a complex of two large islands (East and West Islands) and four smaller islands, all of which lie in the intertidal zone. The interior ponds are regularly inundated by high spring tides, and periodically completely overwashed during storms (Rützler et al., 2004; Rützler and Feller, 1996). The offshore location of both cays ensures that neither island is subject to inundation by freshwater or influxes of terrigenous sediments. Until recently, the anthropogenic impact on both sites has been minimal. Twin Cays is occasionally used as a base by fishermen, and sections of both East and West islands are being increasingly illegally cleared of mangroves and used for dumping (I. Feller, personal communication, January 2006).

The water in Boston Bay is reddish-brown in color due to high concentrations of mangrove-derived chromophoric dissolved organic matter (CDOM), such as tannin and lignins (Calem and Pierce, 1993). Numerous individuals of the "upside-down" jellyfish, *Cassiopeia xamachana*, burrow in the sandy patches interspersed between dense patches of turtle grass. The sediment at this site consists of a thick accumulation of organic, mangrove-derived flocculent overlying a fine-grained calcareous mud (Rützler et al., 2004). The flocculent in the bay is easily disturbed and thrown up into suspension in the water from storms, tidal current flow, manatee feeding, and passing boat traffic. Water temperatures range from 18.5°C (January) to 34.5°C (July); salinities range from 22–28‰, depending on the amount of rainfall received and the tidal current flow. The site is entirely subtidal, with a mean tidal range of 20 cm (Rützler et al., 2004). During slack tides, hot, hypersaline water or cold, brackish water (during heavy rains), drains off Hidden Lake and empties into Boston Bay through Hidden Creek (Rützler et al., 2004). Specimens of *S. dominicensis* were collected from a monospecific stand of *T. testudinum* growing in approximately 1.5 m of water, located approximately one third of the way between the Main Channel and the entrance to Hidden Creek.

Estimates of the biomass of *T. testudinum* from this region are among the highest in the Caribbean, with above ground biomass ranging from 883±254 g m⁻² dry weight (August) to 731±211 g m⁻² dry weight (December) (Koltes et al., 1998; Zieman and Zieman, 1989). Areal productivity shows minimal seasonal variation, with slightly higher values of productivity recorded during August (2.86±0.96 g dry weight m⁻² day⁻¹) relative to December (2.30±0.88 g dry weight m⁻² day⁻¹), and the turnover rate for *T. testudinum* leaves averages about 2.4% per plant per day (Koltes et al., 1998).

The turtle grass blades in Boston Bay are also highly epiphytized with a more diverse array of organisms, including: cyanobacteria, encrusting calcareous algae, filamentous microalgae, hydroids, bryozoans, copepods,

spirorbids, ascidians, sponges, barnacles, and oysters (Richardson, 2004). A total of 41 species of epiphytic foraminiferans have been identified to date from turtle grass growing in Boston Bay, and collecting stations along the Main Channel of Twin Cays (Richardson, 2004). The overall densities of epiphytic foraminiferans on turtle grass have been observed to be higher in the wet season during the summer months, relative to the dry season during the winter; for example, in June 2001, the mean density of epiphytic foraminiferans in Boston Bay was 2.36 individuals cm^{-2} , compared to 0.84 individuals cm^{-2} in February 2002 (Richardson, 2004). Likewise, the highest relative abundance of *S. dominicensis* calculated for any site sampled in Belize, or elsewhere, has been for the epiphytic populations living in Boston Bay during the wet season. In June 2001, *S. dominicensis* comprised $34 \pm 0.2\%$ of the epiphytic population, compared to $11 \pm 0.6\%$ in February 2002 (Richardson, 2004).

Field and laboratory methods

Blades of the seagrass *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, measured and stored on cardboard microslides for additional study and reference material. The cytoplasmic condition (healthy, mottled, totally bleached), and reproductive state (vegetative, pre-reproductive, brood chambers, etc.) of each specimen were noted. Specimens were measured using an optical micrometer calibrated to a stage micrometer. Photomicrographs of representative individuals (healthy, mottled, and bleached) were taken using a Nikon Coolpix camera with an MCool (Martin Optics) phototube.

Individuals were recorded as having healthy cytoplasm, if the cytoplasm possessed an evenly distributed, yellowish-brown coloration (Fig. 1). Individuals were recorded as having a mottled cytoplasm, if the cytoplasm contained white-colored patches, interspersed with yellowish-brown sections of cytoplasm (Fig. 1). Specimens were recorded as being totally bleached, if the test was completely white. The tests of post-reproductive specimens were not included in the tallies of bleached specimens, as their tests were easily distinguished from the latter by the presence of fragmented brood chambers, undissemated embryos, and the close proximity of clusters of dispersed juveniles.

In Jupiter Sound, water temperatures were measured using a hand-held digital thermometer (July 2004). In Belize, water temperatures were recorded for a period of 72 h at both Boston Bay, Twin Cays, and on the reef flat off

Carrie Bow Cay, using HOBO Tidbit (Onset Computers) recorders.

4. Results

Bleaching was observed in all populations surveyed, with relatively high percentages of bleaching recorded in the Indian River Lagoon population in August 2003 (Fig. 5, Table 1), and in the Carrie Bow Cay reef flat population in July 2005 (Fig. 5, Table 2). The populations with the highest total percentage of bleached individuals were collected from shallow seagrass beds that experienced subaerial exposure during extreme low spring tides during midday in the summer. The lowest total percentages of bleached individuals were observed in Jupiter Sound in July 2004, and in Boston Bay July 2005 (Fig. 5, Table 2). Completely bleached specimens were observed in all collections, except for Jupiter Sound in late July 2004, when only mottled specimens were observed.

No water temperature data is available for Jupiter Sound in August 2004, although the water was uncomfortably hot to the touch at the time of collection (S. Richardson, unpublished observations). In July 2004, water temperatures recorded at the Jupiter Sound site ranged from 30–31°C between 1–3:30 pm in the afternoon during an extremely low spring tide that resulted in the subaerial exposure of major portions of the seagrass bed.

Table 1. Percentage of bleached tests in epiphytic populations of *Sorites dominicensis*, Jupiter Sound, Indian River Lagoon, Florida, USA, August 2003 and July 2004.

	02 Aug 2003	12 Aug 2003	29 Jul 2004
Total number of tests examined	580	147	446
% Tests with mottled cytoplasm	1%	1%	2%
% Tests with white cytoplasm	15%	12%	0%
Total % bleached	16%	13%	2%

Table 2. Percentage of bleached tests in epiphytic populations of *Sorites dominicensis*, Carrie Bow Cay and Boston Bay, Twin Cays, Belize, July 2005.

	Carrie Bow Cay	Boston Bay, Twin Cays
Total number of tests examined	797	685
% Tests with mottled cytoplasm	4%	2.5%
% Tests with white cytoplasm	14%	1.5%
Total % bleached	18%	4%

Summaries of the water temperature data recorded from 1–4 July 2005 for the Belizean sites are presented in Fig. 6. Although the overall mean temperatures were identical for both sites ($\mu=31.6^\circ\text{C}$), the reef flat off Carrie Bow Cay experienced a wider range of temperatures ($28.7\text{--}40.0^\circ\text{C}$), with higher maximum temperatures recorded during the late afternoon and lower minimum temperatures recorded at night than those recorded in Boston Bay ($30.0\text{--}34.5^\circ\text{C}$) during the same interval.

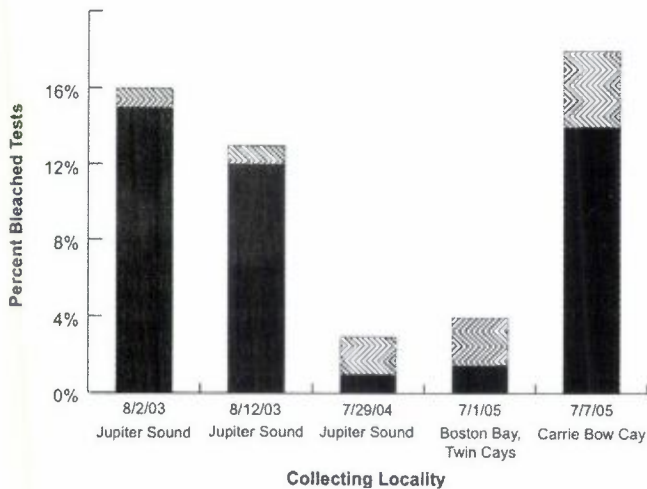


Figure 5. Bar graph showing the relative abundance of bleached specimens in epiphytic populations of *Sorites dominicensis* surveyed at Jupiter Sound, Florida (8/2/03, 8/12/03), Boston Bay, Twin Cays (7/1/05), and Carrie Bow Cay, Belize (7/7/05). The solid portion of the graph represents the abundance of totally bleached (white) specimens, and the patterned portion of the graph represents the abundance of partially bleached (mottled) specimens.

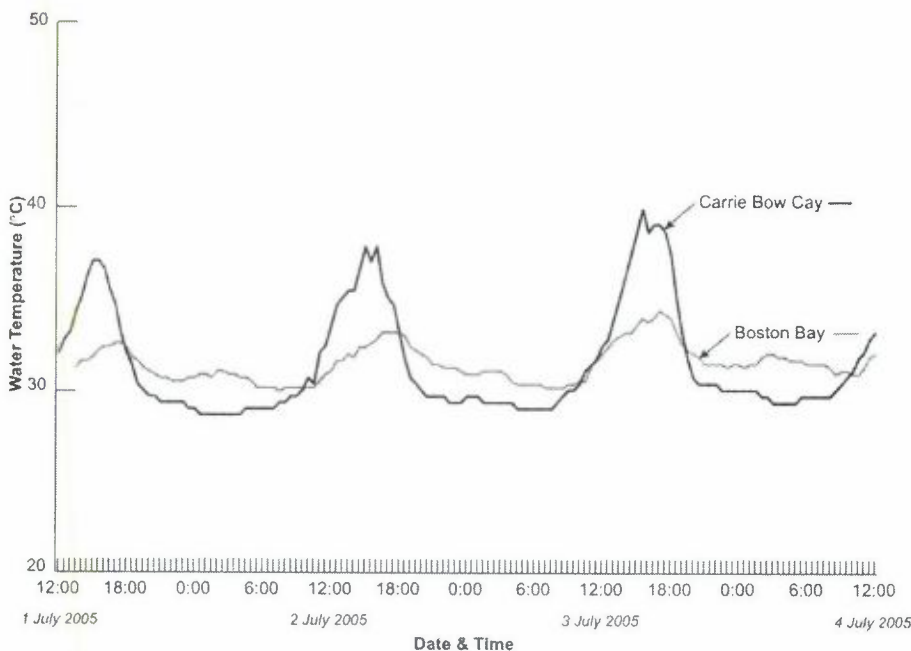


Figure 6. Plot of water temperatures recorded on the reef flat off Carrie Bow Cay, and in Boston Bay, Twin Cays, from 12 pm on 01 July 2005 to 12 pm on 04 July 2005.

5. Discussion

The most extensive observations and comprehensive studies of symbiont-bleaching in a benthic foraminiferan have been conducted on species of the diatom-bearing, rotalid taxon *Amphistegina* (Hallock, 2000; Talge and Hallock, 2003; Williams and Hallock, 2004). Field studies documented a major bleaching event in 1991 that impacted 80% of the *A. gibbosa* population in the Florida Keys (Hallock, 2000; Hallock et al., 1995). Subsequent research has shown bleaching in foraminiferans to be a seasonal phenomenon, with the highest incidence of bleaching occurring in the summer months when UV levels peak (Hallock, 2000; Toler and Hallock, 1998; Zepp, 2003). The impacts of bleaching include: decreased foraminiferal densities, increased test damage and deformities, and impaired reproduction (Toler and Hallock, 1998; Toler et al., 2001). Cytological examination of bleached individuals has shown bleaching to be accompanied by a number of cytologically recognizable events, including: symbiont loss, digestion of symbionts, deterioration of plasma and internal membranes, disintegration of organelles, and the general breakdown of cytoplasmic integrity (Talge and Hallock 1995, 2003). Experimental laboratory studies have shown that bleaching can be triggered by both photic and thermal stress, although photic stress alone (UV-B and blue light) is capable of inducing bleaching (Williams and Hallock, 2004).

The present studies represent the first documented observations of symbiont bleaching in the *Symbiodinium*-bearing foraminiferan *Sorites dominicensis*. Cushman (1922, p. 10) described symbiont-free specimens of *S. dominicensis* in the Dry Tortugas, although it is not clear

from his observations whether the specimens he observed were bleached or naturally aposymbiotic. Smith (1968) recorded observations of what may have been an entirely bleached population of the dinoflagellate-bearing soritid *Marginopora vertebralis* living on an intertidal flat in Suva Harbor, Fiji. The specimens that she observed were white in color and "attached to all types of substrata of suitable size" (Smith, 1968, p. 12). She noted that the population was exposed to "air and direct sunlight up to several hours per day as well as to torrential downpours of fresh water and to salinity variation of the bottom waters" (Smith, 1968, p. 15).

Relatively high abundances of dead (white) tests were recorded throughout most the year for an epiphytic population of another *Symbiodinium*-bearing soritid, *Amphisorus kudakajimensis*, living attached to red algae in a shallow (<1 m) reef flat in the Ryukyu Islands (Fujita et al., 2000). The highest incidence (80–100%) of dead (white) tests; however, coincided with water temperatures that ranged from 29–32°C during the summer months (June–September) (Fujita et al., 2000).

The present study indicates that bleaching in field populations of *S. dominicensis* may be triggered by a number of factors, including: subaerial exposure during extreme low spring tides in the summer months, high water temperatures, and increased irradiance. The highest percentage of bleached *S. dominicensis* tests were observed on *T. testudinum* growing on the reef flat off Carrie Bow Cay. This population experienced partial subaerial exposure, high irradiance, and high water temperatures (37–40°C) at low tide during the early afternoon for several days in early July 2005 (Fig. 6). Unusually high water temperatures (40–43°C) have also been recorded in seagrass beds growing in shallow water off Papua New Guinea (Fred Short, personal communication, January 2006). Although the water temperatures recorded in Boston Bay, Twin Cays, were not as extreme as those recorded off Carrie Bow, they still were higher than the HotSpot (28.9°C) and bleaching (HotSpot+1°C) thresholds derived by NOAA/NESDIS for Glover's Reef (Opishinski, 2006).

The Jupiter Sound population was also subjected to extreme water temperatures, high irradiance, and subaerial exposure in August 2003. Surveys of the population made the following year during an extreme low spring tide in July, however, yielded a very low percentage of mottled specimens, even though the *Thalassia* blades were burned and brown from the extended exposure. In addition, notable numbers of bleached individuals of *S. dominicensis* were not observed during 2001, when the Jupiter Sound site was monitored on a weekly basis, neither were they noted in samples collected in May–July 2003, September 2003, and May–June 2004, during demographic surveys of the *S. dominicensis* populations. The conditions leading to the bleaching event in 2003 were under investigation in 2004; however, the study concluded after the eradication of the *S.*

dominicensis population following Hurricanes Frances and Jeanne in September 2004.

The entire epiphytic foraminiferal community at the Jupiter Sound site was impacted by the 2004 hurricane season, as a result of the high winds, storm surges, and extensive freshwater inundation occurred during the storms. Dark, cloudy, turbid water continued to characterize the site for several months following the hurricanes. Goreau (1964) documented similar impacts on the coral community following Hurricane Flora in 1963. The initial post-hurricane impact on the epiphytic foraminiferal biota in Jupiter Sound included a dramatic reduction in species diversity and abundance, and high dominance, 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 extinction of the species *S. dominicensis* (S. Richardson, unpublished data). In addition, the southern portion of the Indian River Lagoon represents the northern limit of the range of *Sorites dominicensis* on the east coast of Florida (Buzas and Severin, 1982), as this region lies within the transition zone between the Western Atlantic and Carolinian biogeographic provinces (Dybas, 2002).

Factors that may buffer epiphytic *S. dominicensis* populations from extensive bleaching include the presence of chromophoric (colored) dissolved organic matter (CDOM) in the water column, such as the tannins and phenolic acids that leach from mangrove swamps into adjacent coastal waters (Dittmar et al., 2006; Otis et al., 2004; Arnold and Targett, 2002). CDOM has been shown to absorb UV radiation, producing a number of photoproducts, such as carbon monoxide, dissolved inorganic carbon, and various reactive oxygen species (Goldstone et al., 2004; Zepp et al., 1998; Moran and Zepp, 1995). The degradation of CDOM by sunlight has been implicated in the increased susceptibility of reef corals in the Florida Keys to damaging UV-B radiation and coral bleaching (Anderson et al., 2001). In Belize, the tannin-stained, tea-colored waters of Boston Bay have been shown to attenuate blue light, a wavelength that has been shown experimentally to induce bleaching in some corals and the foraminiferan *A. gibbosa* (Williams and Hallock, 2004; Fitt and Warner, 1995).

6. Summary and Conclusions

The results of these field studies indicate that symbiont bleaching in soritid foraminiferans may be a widespread and recurrent phenomenon, as evidenced by bleaching events that have been documented in successive years (Florida), at different geographic localities (Florida and Belize), and in different habitats (Carrie Bow Cay, and Twin Cays, Belize). The overall appearance of bleached

individuals of *S. dominicensis* resembles that observed in bleached specimens of *Amphistegina*, an unrelated taxon of diatom-bearing foraminiferans that undergoes bleaching in response to increased exposure to UV light. Bleaching in *S. dominicensis* may result in a mottled-looking cytoplasm in which white-colored patches of cytoplasm are interspersed with yellowish-brown symbiont-bearing regions of cytoplasm; or, it may result in tests that are totally white and bleached. Bleaching may impair the reproductive capacity of foraminiferans, as shown by the failure of the symbionts to be transmitted to the progeny via multiple fission (Fig. 2).

Episodes of bleaching in populations of *S. dominicensis* appear to be triggered by a combination of environmental factors that are similar to the conditions that trigger bleaching in corals, including: subaerial exposure during extreme low spring tides in the summer months; high water temperatures; and, increased irradiance. Bleaching may render a local population vulnerable to disturbance, such as has been observed in the apparent local extinction of *S. dominicensis* from Jupiter Sound, Florida, after the 2004 hurricane season.

The phenomenon of symbiont bleaching in foraminiferans may prove to be a useful tool for understanding the cytological aspects of coral bleaching. The small size of *S. dominicensis* facilitates microscopical observations of symbiont bleaching *in hospite*. Future research will focus on: characterizing the cytological features of bleached individuals by transmission electron and confocal microscopy, genetic characterization of bleached field populations, and experimental manipulation of bleaching in the laboratory.

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