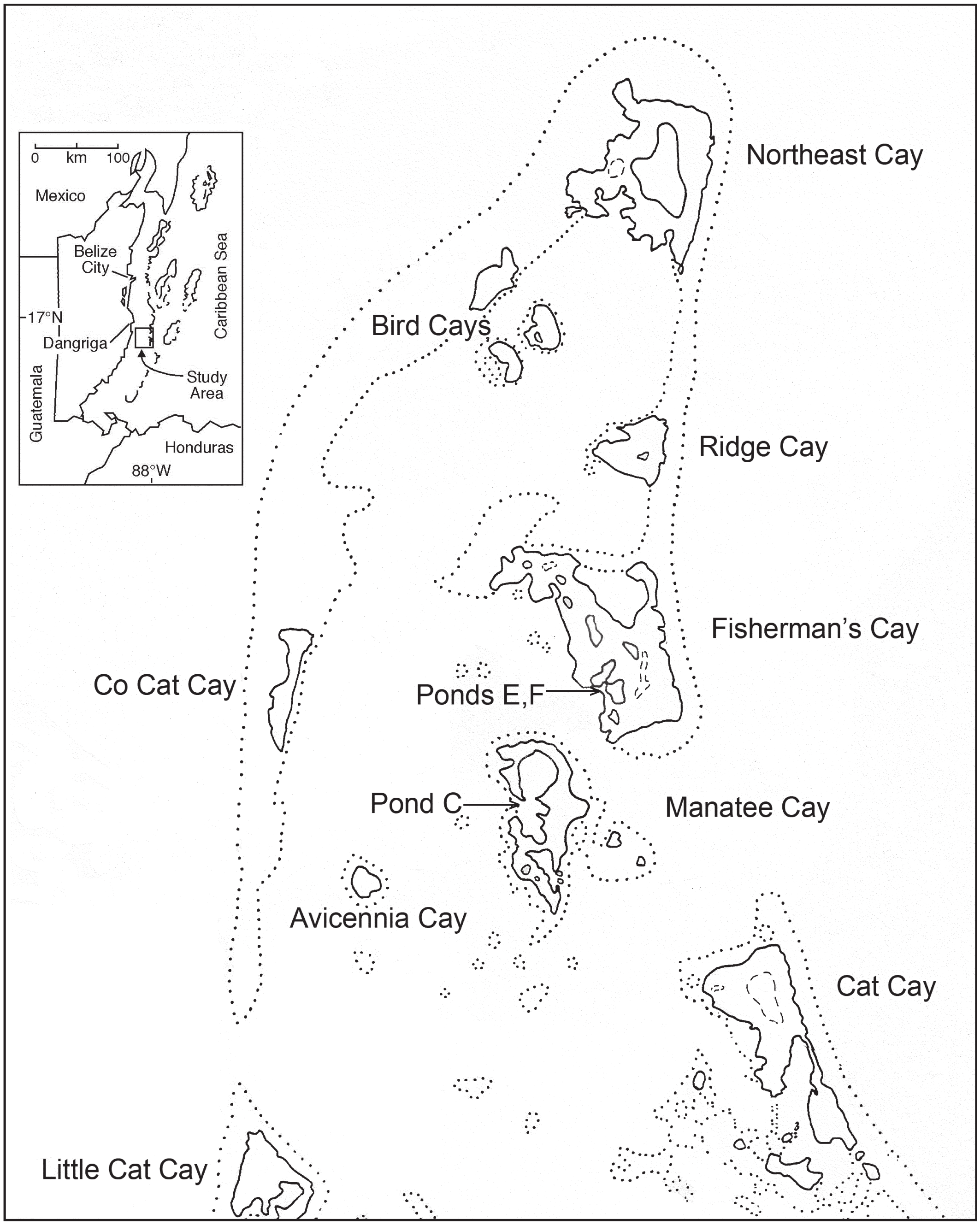

FIGURE 1. Index map showing the major mangrove islands of the Pelican Cays and their ponds.

may be 10 to 12 m deep, harbor high-diversity, low-energy environments dominated by populations of photosynthetic and filter-feeding organisms. These ponds were formed by differential coral accumulations on polygonal karst patterns of the underlying Pleistocene limestone (Macintyre et al., 2000b). The scleractinian coral *Acropora cervicornis*, which is capable of rapid accretion in response to sea-level rise (catch up), exaggerated the underlying karst topography, resulting in greater relief than that of the antecedent karst surface, and created steep-sided ridges that form the ponds. Red mangrove (*Rhizophora mangle*) communities have established on the reef ridges of this area, forming intertidal cays encircling or partially encircling the ponds. The mangrove prop roots extending into the ponds provide substrate for rich communities of sponges, ascidians, algae, corals, bryozoans, mollusks, and other organisms (Macintyre and Rützler, 2000).

Pelican Cays ponds and associated ridges support a very high level of shallow marine biodiversity within the Belize Lagoon. Examples include 70 species in 30 genera of ascidians (Figure 2A), representing 60% of all known shallow-water species in the Caribbean (Goodbody, 2000). Ten of 52 species of echinoderms found in the ponds and associated space had never been previously reported from Belize waters (Hendler and Pawson, 2000). Of 187 sponge species (Figure 2B) reported for several mangrove island groups along Belize Mesoamerican Barrier Reef, Rützler et al. (2000) found the "most diverse sponge fauna" at Pelican Cays. Of the 147 sponge species at Pelican Cays, 45% were new species or variants special to the pond environments. Manatee Cay had 95 species, Cat Cay had 77 species, and Fisherman's Cay had 90 species. Wulff (2000) attributed sponge community differences to the fact that the Pelican Cays' mangrove roots are embedded in coral reefs rather than thick peat sections as at Twin Cays (Macintyre et al., 2004) and Tobacco Range (Macintyre et al., 1995). The reef substrate may be a preferred environment for spongivorous fishes that determine the distinctive species composition of the Pelican Cays sponge community (Wulff, 2000). Richardson (2000) reported a total of 7 species of epiphytic foraminifera living on turtle grass (*Thalassia testudinum*) blades, of which 2 were new species. Littler et al. (2000) reported 152 species of marine macrophytes, of which 148 were algae and 4 were vascular plants. A total of 31 bryozoan species were found in the Pelican Cays, forming extensive colonies on the mangrove roots (Winston, 2007). Coral species on ridges and in deeper or more open areas of the ponds included *Porites furcata*, *P. divaricata*, *P. porites*, *P. astreoides*, *Acropora cervicornis*, *Siderastrea siderea*, *Agaricia tenuifolia*, *Millepora complanata*, and *Montastrea annularis* (mainly at the opening of Pond E, Fisherman's Cay; see Figure 1). Barnacles and mollusks also inhabit the ponds in significant numbers.

Faust (2000) identified 110 species in 33 genera of planktonic, oceanic, red tide-forming, benthic, and coastal dinoflagellate species from six of the Pelican Cays of great typological diversity. Approximately 50% of these appeared to be new species. Manatee Cay had 93 species, Douglas Cay, 47 species, and Cat Cay, 32 species. Waters in the Pelican Cays allow dinoflagellates to proliferate in a naturally nutrient-enriched environment, protected from prevailing winds by the surrounding mangroves and coral ridge (Faust, 2000).

In March 2000, a special issue of the *Atoll Research Bulletin* on the biology and physical characteristics of the Pelican Cays ponds was published to assist the efforts of the Government of Belize (GOB) to determine if this area should be included in the South Water Cay Marine Reserve (SWCMR). It was hoped that by bringing attention to the unique characteristics of these fragile communities they would be preserved. Based on those studies, the Pelican Cays were incorporated into the SWCMR that extends from Tobacco Cay in the north to Cat Cay in the south. The SWCMR is part of the Belize Barrier Reef Reserve System, which was inscribed on the UNESCO World Heritage List in 1996 (http://whc.unesco.org/). At that time, it was recognized by the World Heritage Committee and the GOB that, except for privately owned cays and those with preexisting leases, the cays of the SWCMR would be protected from development. In the Pelican Cays, such an exclusion would apply to a small area (<1 ha) at the southern tip of Northeast Cay. However, since 1996 most of the mangrove cays within the SWCMR have been leased for proposed resort developments. Based on our recent aerial surveys in April 2008, in most of the islands in the Pelican Cays archipelago, large sections of the mangrove forests have been cut down and covered with dredged marine sediment from the adjacent seafloor. Runoff of the fine fraction of the covering sediment has entered the interior ponds and smothered both the prop root-based and benthic seagrass communities. The extensive land clearing and filling is apparently an attempt to convert these mangrove islands into sandy cays in preparation for new tourist resorts.

METHODS AND RESULTS

Field Observations, March 2007

We visited Manatee Cay (16°39.97′N, 88°11.53′W) in mid-March 2007 to conduct reconnaissance of seagrass and prop root-based benthic communities along the perimeter of Pond C. At a point on the southeast side of Pond C (see Figure 1), we encountered an area of dead mangrove roots and a thick sediment drape covering the steep slope into the center of the pond (see Figure 2C). The seagrass communities lining the pond slope had been effectively buried by the sediment drape. At the top of the slope in this area, the ubiquitous submerged mangrove root epibenthos was conspicuously absent. At the surface, we noted a fringe of dead red mangrove trees behind which was recently cleared land covered in white marine sediment containing numerous coral fragments and mollusk shells.

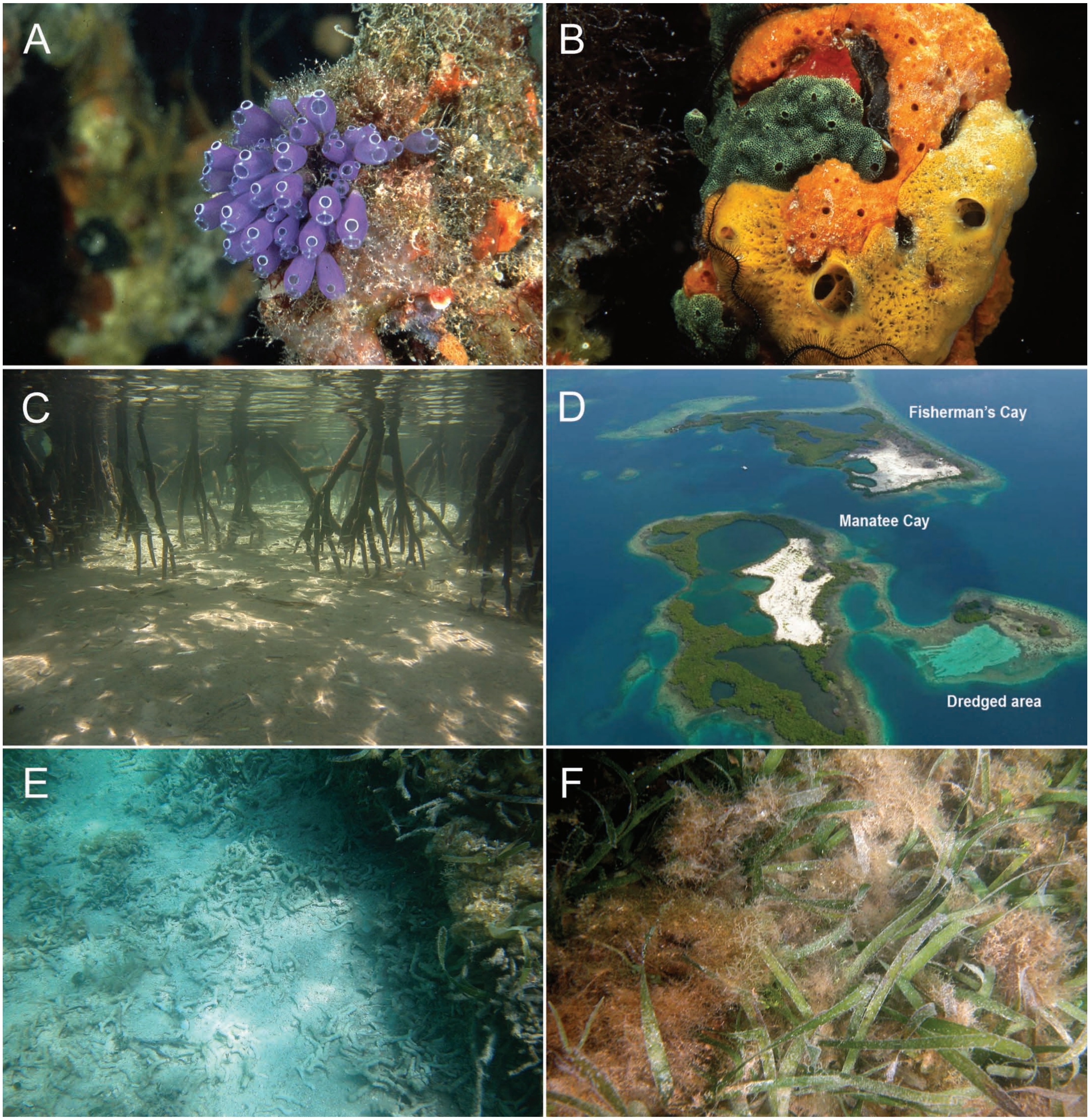

FIGURE 2. Marine communities of the Pelican Cay before (A, B) and after (C–F) dredging operations. A. Pre-dredging example of a rich encrusting community on a mangrove root that is dominated by the purple ascidian *Clavelina puertosecensis*. B. Healthy sponge community dominated by *Mycale* sp. and *Scopalina* sp. on a root before dredging. C. Spillover sediment surrounding bare dead mangrove roots in Pond C, Manatee Cay, after the deposition of dredged lagoonal sediment on clear-cut mangrove peat, March 2007. D. Aerial photograph showing the clear-cut sedimented areas of Fisherman's and Manatee Cays. Note the dredge site in the lagoon at the right of Manatee Cay. E. Dredged *Thalassia–Porites* bottom community in the lagoon east of Manatee Cay. F. Harmful toxic alga *Dictyota caribaea* overgrowing the seagrass *Thalassia testudinum* at the bottom of Pond C, August 2007.

At that time, the dredging work on Manatee Cay had been completed, but on Fisherman's Cay (16°40.25′N, 88°11.40′W), it appeared to be under way. Here, we observed similar clear-cutting and numerous large-diameter plastic pipes laid across the cleared area (Figure 3). The pipes are used to spread the sediment–water slurry over the mangrove peat and stumps. A dredging vessel was anchored just offshore of Fisherman's Cay (Figure 4).

Dredged marine sediment covered the exposed mangrove peat substrate and created the illusion of a sandy cay. However, the introduction of loose, water-laden sediment over peat resulted in runoff, which smothered and killed the mangrove root and lagoonal bottom communities along the edges of the islands. Sediment collected on the mud-covered slope in Pond C (see Figure 2C) was very fine grained (rich in the clay-size fraction), which caused turbidity when it washed off the island. Along the outer edges of the island, runoff of the sediment slurry carried these fine sediments into nearshore waters. In one case, it smothered shallow-water head coral communities along the windward side of Fisherman's Cay and created a muddy plume that extended into the pass between Fisherman's and Manatee Cays. More detailed studies are needed to establish the changes that have occurred in the pond communities as a result of the dredging activity. A brief visit in August 2007 indicated a marked increase in macroalgae, most notably *Dictyota caribaea*, a bushy and toxic brown alga (Littler et al., 2006; see Figure 2F). In addition, further studies of the dredged lagoonal seafloor areas should undertaken to assess the damage. A seagrass–*Porites* community to the east of Manatee Cay had been dredged down to 2 to 3 m below the shallow surface (Figure 2E). We estimate that such destruction will take decades to recover, as indicated by the still bare but shallower seismic line depressions in seagrass beds surveyed in the 1960s between Carrie Bow Cay and Twin Cays.

AERIAL PHOTO SURVEYS, APRIL 2007

Aerial photos taken in April 2007 indicated extensive clearing of mangroves and dredge-spoil filling over the exposed mangrove peat on Manatee and Fisherman's Cays

FIGURE 3. Stumps of clear-cut mangroves being covered with lagoonal sediment transported by the black pipes (arrow) in the background, March 2007.

FIGURE 4. Dredge boat operating off Fisherman's Cay, March 2007.

(see Figure 2D). An area of disturbed, bare seabed (see Figure 2E) was visible where the dredge removed the sediment near Manatee Cay. The time series of aerial photos since 2003 indicated that Northeast Cay had been partially cleared and had buildings on it before March 2003. Manatee, Fisherman's, Ridge, Bird, and Cat Cays had not yet been cleared in March 2003, but clearing had begun on all but one of the Bird Cays by April 2006. With the pumping of dredge spoil over the exposed mangrove peat and truncated roots, sediment spillover and runoff has resulted in extensive nearshore turbidity, which was also visible from the air along the edges of the ponds and the outer shorelines.

As of April 2007, approximately 15.4 ha (of 53.3 ha, or 29% of the total) of mangrove forests in the Pelican Cays had already been cleared, burned, and filled. Additional survey lines, which are typically the first evidence of development activity, were visible on both Fisherman and Manatee Cays in the aerial photographs taken in April 2007.

PHYTOPLANKTON SAMPLING ALONG THE NORTH SIDE OF POND C

In May 2007, we conducted a preliminary survey at Manatee Cay to determine the effect of mangrove clearing and dredging in the Pelican Cays on the phytoplankton populations dominated by dinoflagellates, which may form red tides and visibly discolor the water (Morton and Villareal, 2001). Manatee Cay Pond C (see Figure 1) is large, semi-enclosed, separated from open water by coral ridges (Figures 1, 2D), and has distinct hydrographic, chemical, and biological characteristics. With little water exchange from the ocean side, the pond is warmer and more saline than the surrounding waters. This environmental setting allows microplankton, filter feeders, and corals to proliferate (Villareal et al., 2000). We observed that dying mangrove trees edged the pond and the water surface was highly turbid. Dinoflagellates and associated microplankton were collected in the center of Pond C via a vertical tow with a 20 μm pore size plankton net. Specimens were examined in the laboratory with an Axiophot Carl Zeiss light microscope, and dinoflagellate species were identified (Faust, 2000). The water sample included a total of 14 species representing six genera. Oceanic species included *Ceratium* (2), *Protoperidinium* (5), and *Pyrophacus* (2). Coastal planktonic species included *Gymnodinium* (3) and *Peridinium* (2). Benthic species included *Prorocentrum* (3) (Table 1).

TABLE 1. Number of species in the dinoflagellate genera recorded in Manatee Cay, Pond C, Pelican Cays, collected in May 1996 and May 2007.

	Number of species	
Dinoflagellate genus	**1996**	**2007**
Amphidinium	2	–
Bepharocysta	1	–
Bysmatrum	1	–
Ceratium	10	2
Cochlodinium	1	–
Coolia	1	–
Corythodinium	1	–
Dinophysis	3	–
Diplopelta	1	–
Diplopsalis	3	–
Diplopsalopsis	1	–
Gambierdiscus	3	–
Gonyaulax	6	–
Gymnodinium	3	3
Heteraulacus	1	–
Lingolidinium	1	–
Ostreopsis	5	–
Peridiniella	1	–
Peridinium	3	2
Phaeopolykrikos	1	–
Plagodinium	1	–
Prorocentrum	1	3
Protoceratium	2	–
Protoperidinium	15	5
Pyrodinium	2	–
Pyrophacus	2	2
Scrippsiella	2	–
Zygabikonidium sp.	1	–
Total genera: 28	75	17

Live dinoflagellate cells were fewer than expected. Table 1 provides a comparison of the biodiversity and species associations of dinoflagellate assemblages before (May 1996) and after (May 2007) the clearing. In 1996, dinoflagellates included 28 genera and 83 species. In contrast, in 2007 only 6 genera and 14 species were present, and all were reduced in numbers of individuals present.

DISCUSSION

Despite repeated demonstration of their ecological and economic importance, mangroves are one of the world's most threatened ecosystems (Valiela et al., 2001; Alongi, 2002; Rivera-Monroy et al., 2004). Overall, 50% of the world's mangrove forests have been lost in the past 50 years, with at least 35% lost in just the past two decades (Valiela et al., 2001). Duke et al. (2007) predicted the current rate of loss would lead to mangrove extinction in 100 years. Loss of mangroves is occurring faster in some areas. For example, 29% of Guatemala's mangroves were lost in just 6 years between 1992 and 1998 (Abt Associates Inc., 2003). Most of that loss is directly attributed to unfettered clear-cutting for shrimp farm aquaculture, agriculture, mining, and development (Alongi, 2002). Based on growing evidence from around the world, the clearing and filling of mangrove forests for waterfront property to meet the demands of the leisure and tourism market for seaside resorts and retirement homes are also contributing significantly to this loss (Ellison and Farnsworth, 1996; Curran and Cruz, 2002; Barbier and Cox, 2003; Naylor et al., 2002; Choong, 2005). In the Gulf of Honduras along the Caribbean coast of Central America, mangroves have been destroyed to make way for hotels and other tourism infrastructure (CZAI, 2000). In these low-lying areas, such development requires fill material that is dredged from the seabed of nearby subtidal habitats. This action not only destroys corals and seagrass directly but also causes the suspension of sediments (turbidity), reduces light penetration, smothers seagrass and corals, increases nutrient levels, and releases contaminants (Rambøll Consulting Engineers, 2000). In addition, the inadequately disposed solid waste and untreated sewage associated with this coastal development enter waterways and increase unwanted nutrients, thus decreasing water quality. Similar building efforts have been observed all along the Belize mainland coastline where many acres of mangroves have been cut down to make room for numerous large private homes and resorts. In addition, many acres of mangroves have been removed to create extensive areas of shrimp ponds.

Although tourism is the second largest foreign exchange earner for the countries of Belize, Honduras, and Guatemala in the region, this type of development is counterproductive because loss of mangroves leads to a reduction in income from tourism and fisheries, changes in employment, loss of aesthetic value, loss of cultural heritage, conflicts between user groups, and loss of recreational opportunities (Abt Associates Inc., 2003).

Although mangrove forests are apparently considered of little value, recent studies have demonstrated the vital role of mangroves as nursery habitat for several species of reef fish (Mumby et al., 2004; Mumby, 2006). As stated by Mumby et al. (2004; specifically concerning Belize and Mexico), "Current rates of mangrove deforestation are likely to have severe deleterious consequences for the ecosystem function, fisheries productivity and resilience of coral reefs." In particular, the availability of mangroves for fish nursery habitat (intermediate between seagrass beds and coral reefs) is highly correlated to the numbers of reproducing adults and even the continued existence of certain species. According to these authors, parrotfish, which are important herbivores on reefs, have become locally extinct as a consequence of mangrove removal. Commercial species biomass has been effectively halved in areas of mangrove removal. Thus, the health of coral reefs and of fisheries, both essential for both tourism and local livelihood, are deleteriously affected by mangrove loss.

Despite the legislated restrictions on leasing government-owned lands within the Belize Barrier Reef World Heritage Site and the SWCMR, most of these cays have been leased or sold to foreign developers since 1996 by following standard procedures. These procedures involve locating a suitable site and having it surveyed; this requires a permit from the Lands & Surveys Office in Belmopan, Belize, which has apparently ignored the legal protection status afforded areas in marine protected areas. Separate permits from government departments are required to clear the leased areas delineated by survey lines. After the areas have been cleared, a developer must obtain another permit from the government to dredge material from the adjacent seabed to fill the leased areas.

The areas of mangrove clearing and filling with lagoonal sediments on Manatee and Fisherman's Cays (and other islands in the group) are extensive, exposing most of the available island surfaces. As such, sufficiently large areas have been cleared on these cays to account for potentially extensive development of seaside resorts. Disturbingly, the thin veneer of sediment laid over mangrove peat, especially where the mangroves themselves have been cleared, will not prevent significant subsidence as the underlying peat decomposes and compacts. The substrate will then further subside because of the pressure of any load placed upon it, pilings notwithstanding, which will prove to be a significant long-term problem for construction on mangrove substrate.

In addition to these obvious problems, construction on and habitation of these islands will ensure perpetual pollution of the ponds from continued sediment runoff combined with the eventual addition of sewage outflow and solid waste. Turbidity in the water column from runoff of dredge spoil will continue to deleteriously affect marine communities adjacent to the affected islands. Along the outer shorelines of Manatee and Fisherman's Cays, numerous nearshore coral heads and patch reefs will eventually be smothered by the sediment load noted along the shorelines and in the passes between the Cays. In the Ponds, the rich benthic communities inhabiting the ridges upon which the islands are built and in the seagrass beds lining the slopes of the ponds have been locally decimated by direct sediment runoff. The water column in Pond C is now generally turbid, and it is anticipated that further sediment pumping, runoff, construction waste, and eventually untreated sewage outfall will further impact the pond habitats and cause eutrophication of the water column, which could lead to further losses of species, particularly photosynthetic organisms.

The Pelican Cays, although small in geographic scale, are characterized by great topological diversity in coral reef–mangrove habitats. Biological communities within this system vary markedly from one pond to another. Because of this complexity, some important details about the associations of dinoflagellate species in this ecologically diverse environment have come to light as a result of long-term studies in Pelican Cays (Faust, 2000). Dinoflagellates and microalgae are the primary food source for zooplankton, their primary consumer, including filter feeders and juvenile fish (Frenchel, 1988). Dinoflagellates and zooplankton proliferate in response to their unique physical, chemical, and biological needs (Villareal et al., 2000).

Species associations of dinoflagellates is another important indicator of certain stability in mangrove communities that are constantly threatened. Studies targeting processes in the Caribbean have examined benthic and epiphytic dinoflagellates in the coral reefs of the Virgin Islands (Tindall and Morton, 1998). Mangrove detritus, a unique microcosm, maintains a reservoir of diverse microalgae and meiofauna at Twin Cays, Belize (Faust, 1996). Most species tend to show preference for one habitat, either on sessile macroalgae or free-floating in the water column (Faust, 2004), although some species are found in a wide range of habitats.

Microbial communities can be damaged and species driven to local extinction by external factors; however, the damage is not immediately apparent to the human eye. Recent field observations of microscopic microalgae and zooplankton signaled significantly altered dinoflagellate populations, dead cells, and a greatly changed microscopic food web in Manatee Cay Pond C (see Table 1). This is yet another example of the continuing trend in the Belizean coral reef–mangrove ecosystem observed over 25 years (beginning in 1982) indicating declining abundances of dinoflagellate and zooplankton in the microbial food web caused by human activities (Faust, 2004). This finding in itself has important implications for the ecology and economy of the Belizean Barrier Reef, in that dinoflagellate populations are the primary food source of zooplankton, including fish larvae and juvenile fish.

CONCLUSIONS

Despite the location of Pelican Cays within the SWCMR and the World Heritage Site, development has been accomplished by following a sequence of procedures involving several separate jurisdictions. Investigations began recently into the process of mangrove cutting, clearing, and filling in the Pelican Cays, and it appears that some of this activity was illegal (Melanie McField, Smithsonian Marine Station at Fort Pierce, personal communication, April 2008).

It is highly questionable that the proposed highly vulnerable tourist resort on the Pelican Cays will survive the subsidence related to rotting peat or storms. Indeed, these sea-level structures will be readily destroyed by severe storms, leaving abandoned communities both on land and in the sea in an area originally noted for its unique and unusually high biological diversity.

The future of the unique ecology of the mangrove and seagrass communities in the Pelican Cays appears to be very bleak. The dredging barge is no longer operating off Fisherman's Cay, and a Caribbean Island Brokers website is now offering 37 acres of cleared mangrove on this cay for US $1,750,000. Given this situation, all mangrove islands in this area will be cleared and developed, so that the ponds adjacent to cleared areas will likely suffer the same fate as Pond C of Manatee Cay, as will nearshore marine communities along the outer perimeters of these islands. Lack of foresight, which is disrupting the connectivity between mangroves and the health of the nearshore marine realm, will result in economic losses following the reduction of commercial and recreational fisheries that rely on mangroves. Much of this collapse is related to the dramatic loss of dinoflagellate assemblages, which provide the base of food webs supporting fisheries in Belize.

Tourism losses will subsequently occur as coral reefs decline without mangroves to support the mangrove-dependent fish species essential to reef herbivory and commerce. Thus, the short-term economic gains from construction will lead to long-term environmental disruption, ecological degradation, local species extinction, and the consequent economic collapse of the tourism and fishing industries all along the Belizean coast and similarly affected areas of Mesoamerican reefs. The government of Belize has instituted a mangrove clearing moratorium to evaluate the situation.

ACKNOWLEDGMENTS

We thank Gary Peresta for field assistance; LightHawk (Michele Gangaware) for providing the plane and pilot for aerial surveys; Molly Ryan of the Smithsonian National Museum of Natural History (NMNH) for preparing the index map; Chip Clark of the Smithsonian NMNH for photographs (Figure 2A,B); and finally Klaus Rützler, Janet Gibson, Isaias Majil, Melanie McField, and John Tschirky for providing advice and information for this manuscript. This is contribution number 831 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Fund.

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Using the Panama Canal to Test Predictions about Tropical Marine Invasions

Gregory M. Ruiz, Mark E. Torchin, and Katharine Grant

ABSTRACT. As humans alter the landscape of the Earth and economic globalization expands, biological invasions increasingly homogenize the world's biota. In temperate marine systems, invasions are occurring at a rapid pace, driven by the transfer of organisms by vessels and live trade (including aquaculture and fisheries activities). In contrast, little is known about patterns and processes of tropical marine invasions, although the same species transfer mechanisms are in operation. This disparity may be the result of limited studies of invasions in the tropics relative to temperate regions. Alternatively, the tropics may be less susceptible to invasion than temperate regions for reasons of environmental unsuitability and biotic interactions. This paper provides a brief summary of the current but limited information of marine invasions across latitudes, focusing particular attention on the eastern Pacific north of the Equator. Within this latitudinal framework, the Panama Canal provides an especially important model system for testing predictions about marine invasions in the tropics for reasons of (a) the high level of shipping traffic since the Canal opened in 1914; (b) the permeability of the Canal as a conduit for marine invaders, despite the apparent freshwater barrier; and (c) the current expansion of the Canal that is expected to increase the size and number of ships visiting the region.

INTRODUCTION

Biological invasions are common in coastal marine ecosystems around the world (Cohen and Carlton, 1995; Orensanz et al., 2002; Fofonoff et al., 2008). In fact, reports of new invasions are increasing exponentially in many well-studied regions (Cohen and Carlton, 1998; Ruiz et al., 2000; Hewitt et al., 2004). Although invasions can result from natural dispersal, most contemporary invasions derive from human-mediated transfer associated with a variety of activities. As economic globalization continues to expand, creating a high degree of connectivity through the movement of commodities and people, opportunities for new invasions also increase. Bays and estuaries have been the most invaded marine systems, probably because they are hubs for shipping, aquaculture, and other human endeavors known to transfer organisms (Ruiz et al., 1997; Wasson et al., 2005).

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To date, most human-mediated invasions (hereafter introduced species) in marine habitats have been reported in temperate latitudes (Ruiz and Hewitt, 2008, and references therein). Relatively few introduced species have been reported from tropical or polar regions. This difference across latitudes may result partly from historical research effort and taxonomic knowledge, which are greatest in the temperate zone. However, a small but growing literature for high latitudes suggests that marine invasions may be limited in polar regions by a combination of current low temperatures and low propagule supply (Barnes et al., 2006; Aronson et al., 2007; Ruiz and Hewitt, 2008).

It is evident that marine invasions can occur in tropical marine systems (Agard et al., 1992; Guerrero and Franco, 2008), but the extent to which they occur remains largely unexplored. Few studies have evaluated marine invasions in the tropics. The exceptions are extensive analyses of introduced species on the Hawaiian Islands and Guam (Eldredge and Carlton, 2002; Paulay et al., 2002). It is uncertain whether these island ecosystems are broadly representative of the tropics, including especially mainland sites that may differ from islands in susceptibility to invasion (Elton, 1958; MacArthur and Wilson, 1967; Sax, 2001).

In a preliminary analysis of marine invasion patterns for mainland Australia, Hewitt (2002) reported an increase in introduced species richness with increasing latitude. The study included four tropical and four temperate sites, spanning 13°–38°S latitude. Despite a significant relationship with latitude, there is uncertainty about the taxonomic identification and biogeographic origin of many tropical species, resulting from limited information and relative lack of study for low latitude biotas. For this reason, Hewitt urges some caution and underscores the need for further analyses to interpret the observed pattern. It is nonetheless intriguing that this preliminary analysis provides results similar to those reported for tropical terrestrial systems, where relatively few exotic species of birds, mammals, and plants are established (Sax, 2001).

We have begun to explore latitudinal patterns of marine invasions for the mainland (continental) habitats within the Americas. To date, most of our analyses have focused on bays and estuaries within the United States, particularly on the Pacific Coast. We are currently initiating a research program to compare the number of introduced species, scale of vector operations (propagule supply), and ecology of invasions across temperate and tropical latitudes. Here, we briefly review the current state of knowledge about invasions and invasion processes along the Pacific Coast of the Central and North America and discuss the potential significance of Panama as a model system to evaluate regional and latitudinal patterns of marine invasion.

LATITUDINAL PATTERN OF INVASIONS ALONG THE NORTHEASTERN PACIFIC

Outside of the tropics, there is a clear increase in the number of nonnative species reported with decreasing latitude, from Alaska to California, 61°–32°N (Ruiz et al., 2006a). An extensive review and synthesis of the literature indicate that more than 250 nonnative species of invertebrates and algae are established in coastal waters of California (NEMESIS, 2008). Most of these invasions are attributed to commercial shipping and live shipments of organisms, especially oysters and their associated biota (Cohen and Carlton, 1995; Miller, 2000; Ruiz et al., unpublished data). Some of the California invasions have spread northward through natural dispersal, and other species have been introduced independently to the north. However, compared to California, far fewer nonnative species are known from Oregon, Washington, and Alaska (Cohen et al., 1998; Wonham and Carlton, 2005; Ruiz et al., 2006a).

Although this latitudinal pattern of invasion could result from reporting biases in the literature, particularly in the level of research (search effort) among regions, recent surveys suggest that the pattern is robust for sessile invertebrates in hard substrate fouling communities. Using standardized surveys to sample sessile invertebrates, deRivera et al. (2005) and Ruiz et al. (2006a) found that the number of introduced species increased with decreasing latitude from Alaska to southern California. It appears that the northern spread of many nonnative species from California may have been limited by dispersal as a result of the relatively low level of human activities (and, thus, species transfer opportunities) that have been present historically (Ruiz and Hewitt, 2008).

Similar analyses are not yet available to extend this comparison to lower latitudes along the eastern Pacific. Although there have been some studies reporting introduced marine species in Central America (Rubinoff and Rubinoff, 1969; Lambert and Lambert, 2003; Wysor, 2004, Roche and Torchin, 2007; Roche et al., 2009; Bastida-Zavala, 2008), standardized, quantitative community-level comparisons are lacking. In particular, synthetic studies focused within bays and estuaries of Central America targeting those taxonomic groups for which invasions are often most prevalent do not exist. Even where syntheses from the literature have been attempted, the paucity of available data limits conclusions about the scope of invasions. For example, Cohen (2006) provides a useful summary of available information on invasions surrounding the Panama Canal, which has received considerable attention for a tropical system. Despite the historical interest on biotic exchange in Panama, Cohen characterizes the current state of knowledge as follows: "The Panama Canal lies in a region of the world where the marine biota is both diverse and relatively poorly known, and there has been remarkably little investigation of the effect that the Canal has had on the distribution of that biota."

With a broad goal to evaluate patterns and processes in marine invasions using a latitudinal framework, we have initiated a research program in Central America (a) to compile available data from the literature on nonnative marine species, as part of our database (NEMESIS, 2008), and (b) to conduct standardized surveys at multiple sites. Our approach will allow direct comparisons with more than two dozen sites surveyed on the Pacific and Atlantic coasts of the USA. Our initial effort is focused primarily on sessile invertebrates (including ascidians, barnacles, bryozoans, hydroids, mussels, and sponges), which comprise a large proportion of marine introductions, are relatively well studied, and are conducive to standardized, quantitative field surveys.

A preliminary review of the literature for barnacles suggests the number of introduced species increases from Alaska to Panama (Figure 1A), consistent with an increase in the magnitude of shipping (see next section). At least four nonnative species of barnacles are reported to occur on the Pacific coast of Panama, including *Amphibalanus amphitrite*, *A. reticulatus*, *Balanus trigonus*, and *Fistulobalanus pallidus* (Matsui et al., 1964; Jones and Dawson, 1973; McCosker and Dawson, 1975; Laguna, 1985). Three introduced barnacles are known from California: *Amphibalanus amphitrite*, *A. eburneus*, and *A. improvisus* (Carlton, 1979; Carlton and Zullo, 1969; Cohen and Carlton, 1995; Cohen et al., 2002). *Amphibalanus reticulatus* has also been detected in recent surveys in southern California, but it is not yet known to be established (Ruiz, unpublished data). Only one introduced barnacle, *A. improvisus*, is reported in Oregon and Washington (Carlton, 1979; Wonham and Carlton, 2005), and there are no introduced barnacles known from Alaska (Ruiz et al., 2006a). It is noteworthy that the reported number of nonnative barnacle species in Panama exceeds that along the western USA, considering the latter is relatively well surveyed. Thus, we expect that strength of this inverse relationship with latitude may increase with additional information.

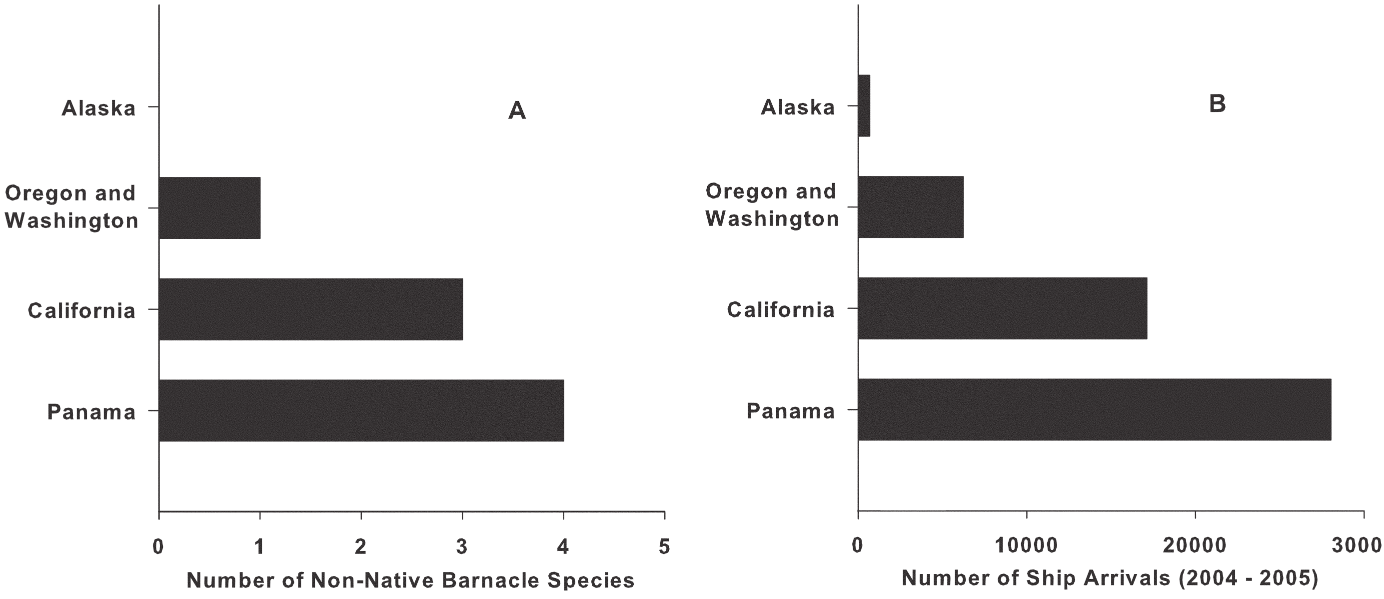

FIGURE 1. A. Number of nonnative barnacle species established by geographic region. Shown are the numbers of nonnative barnacle species reported to be established from Alaska to Panama (see text). B. Number of vessel arrivals by geographic region. Shown are the numbers of commercial vessel arrivals from overseas to different geographic regions, from Alaska to Panama, over a two-year period (2004–2005). Coastwise domestic traffic is excluded from arrivals to U.S. locations. (Data from Miller et al., 2007; ACP, 2008b.)

At the present time, the relationship between introduced species richness and latitude is poorly resolved for the northeastern Pacific and other global regions. The pattern presented in Figure 1A should be considered as preliminary, and it may change with further research. We also caution that these data are restricted to barnacles, a very small subset of species present in the fouling community.

PANAMA: A TEST CASE FOR TROPICAL MARINE INVASIONS

Panama is a potential hotspot for tropical marine invasions, because of the country's historic significance as a hub of world trade since the fifteenth century, expanding greatly since construction of the Panama Canal. The Canal created a new shipping route between the Atlantic and Pacific basins, resulting in a large influx of commercial ships, which have been an important source of introduced species in North America (Cohen and Carlton, 1995; Cohen et al., 1998, 2002; Ruiz et al., 2000; Wonham and Carlton, 2005; see discussion below). Figure 1B compares the magnitude of commercial shipping to several major port systems, indicating that ship arrivals to Panama exceed those to major port systems in the western United States by a large margin. Over the two-year period 2004–2005, nearly twice as many vessels arrived to Panama as overseas vessels arrived to California. In fact, Panama receives more ship arrivals than any of the largest ports in the United States (Ruiz et al., 2006b; Miller et al., 2007).

Since its opening in 1914, the number of Canal transits increased rapidly, with the exception of a brief interruption during WW II, until reaching capacity in 1970 (ACP, 2008a; Figure 2). Currently, the Canal is operating at 90% of its theoretical maximum capacity, servicing 12,000 to 14,000 vessels and carrying approximately 5% of the world's cargo annually (Reagan, 2007). More than 800,000 ocean-going commercial vessels have passed through the Canal since its completion (Ruiz et al., 2006b).

While the number of transits has leveled off, the average size of ships transiting the Canal has continued to increase, allowing for a continued increase in the volume of cargo passing through the Canal (ACP, 2008a; see Figure 2). The average tonnage (based on CPSUAB, a universal system of tonnage for the Panama Canal, or Canal ton, which is equivalent to approximately 100 cubic feet of cargo) per transit has increased from 4,832 in 1955 to 21,963 in 2005 (ACP, 2008a). This change in cargo capacity reflects an increase in the size of vessels over time; these changes are the topic of a future analysis that will characterize changes both in vessel size and in underwater surface area available for colonization by organisms. In recent years, however, the size of vessels has been constrained by the lock dimensions and has been relatively static, with the Panamax ships designed specifically as the largest vessels able to transit the locks (see next section).

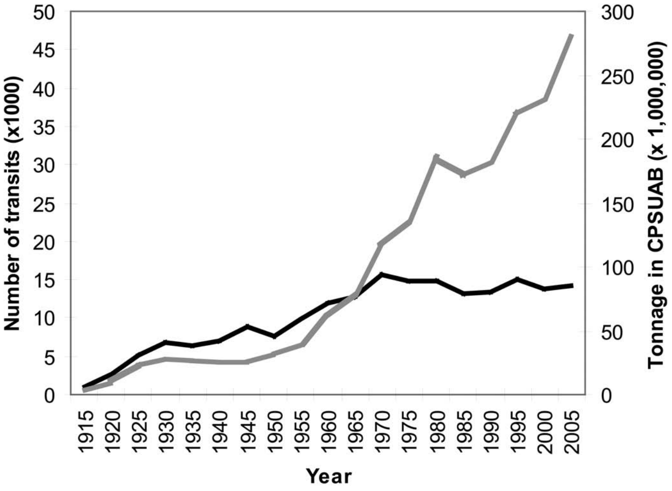

FIGURE 2. Number of commercial vessel transits (black line) through the Panama Canal and associated cargo tonnage (gray line); CPSUAB is a universal system of tonnage for the Panama Canal, or Canal ton, which is equivalent to approximately 100 cubic feet of cargo. (Figure modified from ACP, 2008a.)

Likely consequences of the Panama Canal and ports located at both entrances are an increase in (a) the global transfer of marine organisms, as the canal provides a conduit for worldwide shipping, and (b) regional biological invasions in Central America. Commercial shipping is a major pathway for the movement of species and appears largely responsible for a dramatic increase in the rate of known invasions for many regions in recent time (Ruiz et al., 2000; Fofonoff et al., 2003; Hewitt et al., 2004). Ships move organisms associated primarily with hull and sea chest fouling and with ballasted materials, as an unintended result of normal operations (Carlton, 1985; Minchin and Gollasch, 2003). In general, the likelihood of invasions increases with increasing propagule supply, including the magnitude and frequency of organisms delivered (Ruiz and Carlton, 2003; Lockwood et al., 2005). Thus, the chance of colonization by introduced species in Panama is likely to have increased over time with the high frequency of vessels arriving to Panama from around the globe.

Given the high number of vessel arrivals, we might also expect the relative magnitude of propagule supply and invasions to be high in Panama. However, this remains to be tested, and there are several reasons why this may not be the case. First, different ship types and operational behaviors vary in their potential to transfer marine organisms (Verling et al., 2005; Miller et al., 2007; NBIC, 2008). Second, independent of propagule supply, some sites are less susceptible to invasion for reasons of either environmental conditions or biological interactions (Lonsdale, 1999; Ruiz et al., 2000; Roche et al., 2009).

Past studies have certainly highlighted the potential significance of vessels as a source of invasions to the Panama Canal and surrounding waters (see Cohen, 2006, and references therein for recent review). For example, Chesher (1968) discusses the potential importance of ballast water. Menzies (1968) considers the capacity of vessels to transfer fouling organisms. Hay and Gaines (1984) suggest that small pleasure boats may be especially important in the transfer or organisms across the Isthmus of Panama. A few studies also test the capacity of marine organisms to survive freshwater exposure for the duration of a transit through the Canal (Chesher, 1968; Hay and Gaines, 1984). Despite the long interest and recognition in ship-mediated transfer, the estimates given above are limited to few (if any) data on species composition or direct quantitative estimates of propagule supply (abundance) on vessels. Surprisingly few data exist on biota associated with ballast water or hulls of vessels associated with the Canal. Instead, there are only coarse data available on general operational aspects of vessels that may affect species transport opportunities.

Most commercial ships arriving to Panama will transit the Canal, but some will have considerable time at anchorage before entering the Canal. From 2000 to 2005, the average service time (from arrival to complete transit) of ships passing through the Canal was 16 hours when holding reservations. However, many ships have not had reservations, and average service times for these ships can reach 57 hours (Table 1). Although the proportion of ships holding reservations has increased in recent years, half of all ships still experienced some delay. Such increased residence time is likely to also increase the opportunity for reproduction and colonization of organisms associated with ships' hulls (Minchin and Gollasch, 2003; Davidson et al., 2008), relative to shorter residence times. It is evident that some organisms arrive to Panama on the hulls of vessels (Figure 3). However, a lack of quantitative information on the biota associated with outer surfaces of vessels transiting the Panama Canal and surrounding ports limits any detailed analyses.

For ballast water, we are not aware of any reliable estimates of the historical patterns of ballast water management and discharge of vessels arriving to Panama, including those ships delivering cargo to the terminals and those simply transiting the Canal. Even a coarse estimate of volume is challenging, given large differences in operations among vessels (Verling et al., 2005; but see Chesher, 1968). Presumably, ballast water discharge today is rather limited because many vessels conduct ballast operations to compensate for loading or off-loading cargo. In addition, Panama prohibits ballasting operations in the Canal under most circumstances (ACP, 2008b).

Despite the limited information available, we surmise that propagule supply has been relatively high in Panama, compared to many other temperate and tropical sites. Based solely on the large number of vessel arrivals and their relatively long residence times (see Figure 2, Table 1), it is likely that Panama has received large inocula of nonnative organisms associated with the vessels' hulls and sea chests, which have been historically important sources of invasions in

TABLE 1. Comparison of service time for ships with and without reservations transiting the Panama Canal; *n* = number of ships. (Source: Modified from ACP, 2008a.)

	Mean transit time (hours) through canal					
Year	**Reservation (*n*)**		**No reservation (*n*)**		**Could not get reservation (*n*)**	
2000	16.7	(1,944)	35.7	(6,864)	42.1	(121)
2001	15.7	(5,008)	26.3	(6,590)	43.7	(306)
2002	16.1	(5,692)	29.0	(5,134)	57.1	(1,062)
2003	16.2	(5,527)	24.9	(4,596)	45.1	(1,361)
2004	16.4	(6,419)	30.5	(3,568)	49.8	(2,531)
2005	16.5	(6,972)	27.3	(3,406)	45.8	(2,270)

FIGURE 3. Photograph of a vessel hull upon arrival to Panama showing associated biofouling organisms. Inset: Close up of bow with barnacles.

other regions (Coutts, 1999; Coutts et al., 2003; Coutts and Taylor, 2004; Hewitt et al., 2004).

As a result of its shipping history, Panama provides a unique opportunity to test hypotheses about patterns and processes of invasions to tropical marine systems. If propagule supply drives invasion patterns, we predict that Panama may be a hotspot for invasions. If tropical systems are inherently less susceptible to invasions (Elton, 1958; Sax, 2001), we would expect to see low introduced species richness despite high historical propagule supply. Our current research seeks to estimate nonnative species richness and advance our understanding of historical propagule supply in Panama, in the context of a broader latitudinal comparison as discussed above.

EVALUATING FUTURE CHANGES IN PANAMA

In October 2006, the Republic of Panama passed a referendum to expand the capacity of the existing Canal. The modernization will include (a) two new sets of locks, one at the Pacific entrance and one at the Atlantic; (b) two new navigational channels to connect the locks to existing channels; and (c) deeper and wider shipping lanes (Reagan, 2007). The expansion project is now under way and is scheduled to be completed by 2015 (Reagan, 2007).

When the expansion is completed, the Panama Canal Authority estimates that Canal transits will most likely increase from 12,700 per year in 2005 to approximately 19,600 in 2025, with an optimistic forecast as high as 22,100 transits per year (Figure 4). Further, the largest vessels currently capable of transiting the Canal are Panamax ships reaching 320 m in length that can carry 65,000 tons of cargo. After the completion of the new locks, the Canal will accommodate vessels up to 425 m long, carrying about twice the amount of cargo of today's ships (Gawrylewski, 2007; Reagan, 2007).

While efforts have been made to evaluate potential environmental effects of the Panama Canal expansion (ACP, 2008a), the possible effects of this expansion on invasion dynamics have not received much attention to date. One might expect an increase in propagule supply associated with the increased number and size of vessels transiting the

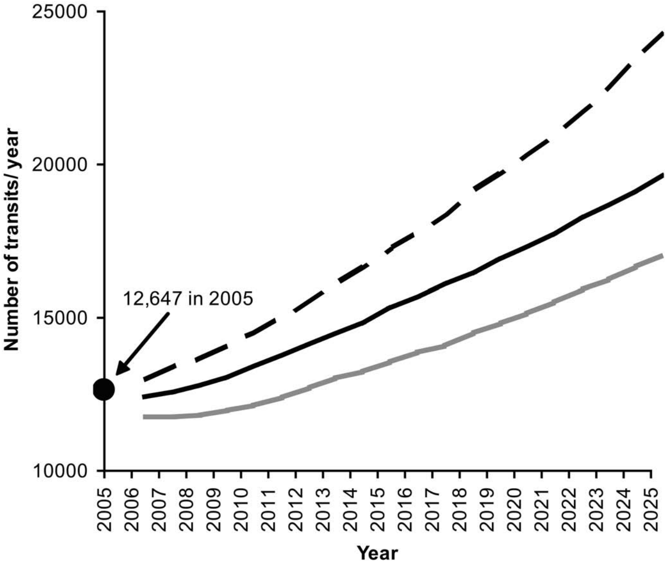

FIGURE 4. Forecast of demand for Canal transits. Solid black line = probable demand, dashed line = high (optimistic) demand, and shaded gray line = low (pessimistic) forecast demand. In 2005, there were 12,647 recorded Canal transits (solid circle). (Figure modified from ACP, 2008a.)

Canal. There may also be shifts in trade routes that could expand the species pool associated with ships' arrivals, resulting from either new markets or previous constraints on the size of vessels that could previously use this corridor. Alternatively, the service time of vessels may decrease as the capacity to accommodate more transits increases. This decrease could reduce the establishment probability of organisms attached to the hulls of arriving vessels, as residence time and likelihood of invasion are thought to be positively correlated (Davidson et al., 2008).

Potential changes in environmental conditions associated with both the ships and the Canal entrances could also influence future invasions. With the international ban on tributyl tin as an antifouling coating now coming into force, some have suggested that biofouling of ships' hulls, and hence ship-mediated propagule supply, may increase (Nehring, 2001). Additionally, changes in the salinity regimes will probably occur at both Pacific and Atlantic entrances to the Canal, as well as in areas within the Canal near the lockages, as a result of increased freshwater discharges into the oceans and potential seawater intrusion into the Canal. Such changes in salinities could alter the susceptibility to invasion for arriving organisms. However, any predictions about directional changes in propagule supply and susceptibility are currently speculative at best, as sufficient information presently is not available.

There is also a regional context for the Panama Canal that deserves consideration. Although the Canal provides a critical corridor across the Isthmus of Panama for global trade, Panama's ports are becoming increasingly important hubs for the regional distribution of commodities. More specifically, cargo that is delivered to Panama's ports is often transferred secondarily by other vessels to surrounding countries in the region. As Panama is a distribution center, any increase in introduced species increases the chances for ship-mediated dispersal to surrounding ports. Conversely, increased commerce with the other countries in the region also enhances the opportunity for delivery of organisms to Panama. The potential significance of such regional dispersal through this hub-and-spoke system of shipping has not been evaluated for the past, present, or future.

We are currently working with the Panama Canal Authority and the University of Panama to evaluate the role of the Panama Canal in regional and global marine invasions. Although the major focus of our efforts is to evaluate past and current levels of invasion, as well as to obtain some coarse estimates of propagule supply to the region, we hope to provide the baseline needed to forecast and evaluate potential impacts of future changes on invasion risks.

CONCLUSIONS

Panama provides exceptional opportunities to test hypotheses about invasions in tropical marine systems. The presence of the Canal and the magnitude of shipping to the region have undoubtedly increased the supply of nonnative species delivered to the shores of Panama. While there is limited information on actual propagule delivery, the Panama Canal Authority has maintained historical records on the number and characteristics of transiting vessels. This information provides a unique view of the magnitude of shipping and changes through time and could be used as an initial coarse proxy for propagule supply. We predict that invasions are common in Panama relative to surrounding regions as a result of the intensity of shipping in the area. If propagule supply is positively correlated to introduced species richness, as the literature suggests, we predict a relatively high number of invasions have occurred. However, if relatively few introduced species are detected in Panama, this suggests that some combination of environmental conditions and biotic resistance may limit invasions in this tropical region.

We have focused attention on Panama as a model system to understand marine invasion dynamics, but a robust analysis must also include comparisons to other locations that differ in the intensity of shipping and other transfer mechanisms. Ideally, such comparisons should be replicated across latitudes. Such a comparative approach is key to untangling patterns of marine invasions in tropical and temperate regions and, ultimately, in determining the processes that drive these patterns.

ACKNOWLEDGMENTS

We thank Michael Lang for organizing the Smithsonian Marine Science Symposium and for providing us the opportunity to participate. For discussions on the topic, we thank James Carlton, Ian Davidson, Richard Everett, Paul Fofonoff, Chad Hewitt, Anson Hines, Julio Lorda, Valentine Lynch, Whitman Miller, Ira Rubinoff, and Mark Sytsma. For comments and improvements to the manuscript, we thank James Carlton, Daniel Muschett, John Pearse, and Brian Wysor. We also acknowledge assistance from the Panama Canal Authority (ACP) and funding from the National Sea Grant Program, Smithsonian Institution, Secretaría Nacional de Ciencia Tecnología y Innovación de Panamá (SENACYT), and the U.S. Coast Guard.

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Ciguatera Fish Poisoning in the Caribbean

Patricia A. Tester, Rebecca L. Feldman, Amy W. Nau, Maria A. Faust, and R. Wayne Litaker

ABSTRACT. Ciguatera fish poisoning (CFP) is a significant illness in the Caribbean. Local fishers and natives attempt to avoid CFP by applying traditional knowledge concerning where and when certain fish species are likely to be ciguatoxic, but this knowledge is incomplete. Evidence gathered over the past decades indicates that CFP events are increasing and becoming more unpredictable, thereby posing a greater threat to local inhabitants as well as tourists. The current understanding of CFP distribution is from studies nearly a decade old and generated largely by self-reported CFP incidents to a call-in "hotline" in Miami, Florida. To better guide resource allocation and focus future research, an active survey method was used to uniformly query public health professionals and fisheries officials on the occurrence of CFP. Points of contact from each of these two groups were compiled for the 24 Caribbean island countries and territories and 9 mainland countries bordering the Caribbean. An outcome of this project will be to provide public health agencies, resource managers, and others with information they can use in developing CFP tracking systems and effective public education programs. The long-term goal of associated efforts is to provide accurate and affordable monitoring tools for predicting the onset of CFP events.

PREFACE

Ciguatera fish poisoning (CFP) occurs in tropical regions worldwide and is globally the most common nonbacterial food-borne illness (Tester, 1994; CDC, 2007; Figure 1A). The toxic organisms most commonly associated with CFP are benthic dinoflagellates reported to produce ciguatoxins or maitotoxins (Yasumoto et al., 1977; Durand-Clement, 1987; Satake, 2007). Ciguatoxins bioconcentrate in the food chain and reach their highest levels in top predators such as barracuda or other tropical reef fish. These toxins have been found in more than 400 fish species, including groupers, snappers, jacks, mackerels, triggerfish, and surgeonfish (Bagnis et al., 1970). Consumption of tainted fish can lead to gastrointestinal distress followed by neurological (perioral numbness, tingling, temperature sensory reversal) and cardiovascular (arrhythmia, bradycardia, tachycardia, reduced blood pressure) symptoms and, in rare cases, death. The chronic phase of CFP can persist for weeks, months, or years (Freudenthal, 1990), and repeated exposure to ciguatoxins exacerbates the symptoms.

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Manuscript received 9 June 2008; accepted 20 April 2009.

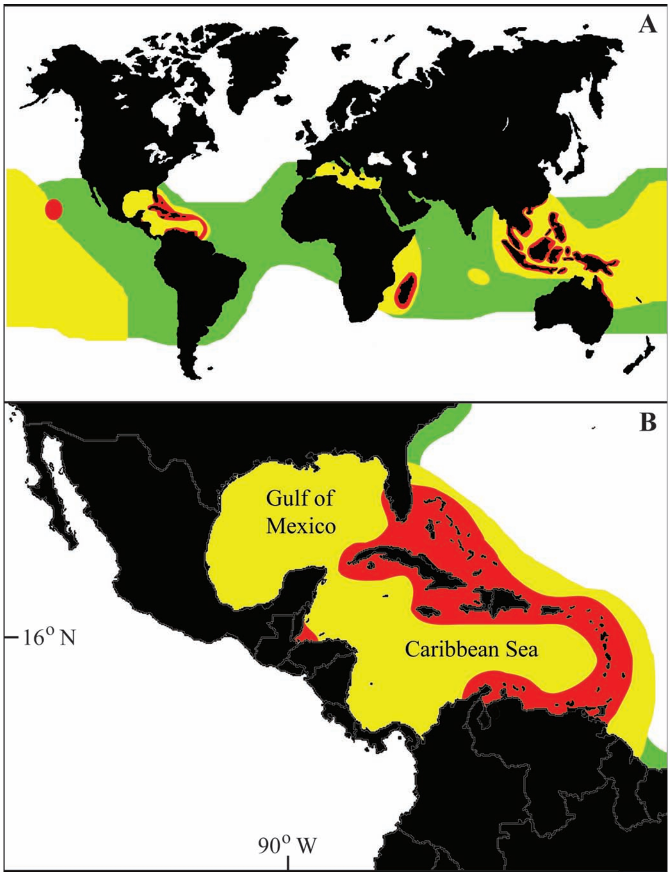

FIGURE 1. A, Potential global distribution of ciguatera fish poisoning (CFP). Red areas indicate regions with a high CFP prevalence, yellow indicates moderate potential exposure, and green indicates regions where the dinoflagellates responsible for the disease are found and represent a potential problem. This map represents a composite of the data obtained from an aquatic biotoxins review by Huss et al. (2003), the CFP distribution map maintained by the journal *Harmful Algae* (WHOI, 2008), and Lewis (2006). B, Potential distribution map of CFP in the Caribbean, as modified from Stinn et al. (2000), combined with some recent incident reports showing the presumed distribution of ciguatera fish poisoning in the Caribbean, mostly collected by passive means; that is, a self-reporting CFP hotline in Miami ("Cigualine" at 1-888-232-8635). Red areas indicate high frequency of CFP reports; yellow indicates regions where CFP is reported less frequently; green indicates infrequent reports of CFP. These maps may not accurately portray the actual CFP distribution because many cases go unreported.

This paper provides the justification for and an overview of our recent efforts to conduct an active survey of public health officials and fishery management professionals on the incidence of CFP in the Caribbean. We currently lack an accurate picture of CFP in the Caribbean because of the difficulty in diagnosing CFP and the absence of uniform reporting criteria or any entity responsible for maintaining this information. Previous information gathered on the incidence of CFP in the Caribbean has relied heavily on self-reporting mechanisms, such as calls to a "hot-line" in Miami, Florida. Because people living closer to Miami are more likely to know about the hot-line, the reported incidence rates could reflect a geographic bias (Figure 1B). Another important aspect of this research has been to focus the joint research efforts of the National Oceanic and Atmospheric Administration (NOAA) and Smithsonian Institution scientists who are working on the molecular and morphological characterization of the toxic dinoflagellates responsible for CFP. Both groups have strong interests in understanding how changes in the distribution and abundance of ciguatera-associated dinoflagellate species relate to the occurrence and severity of CFP.

An important outcome of this project will be to provide public health agencies, resource managers, and others with information that they can use in developing CFP tracking systems and effective public education programs. The long-term goal of associated efforts is to provide accurate and affordable monitoring tools for predicting the onset of CFP events.

INTRODUCTION AND BACKGROUND

Ciguatera fish poisoning is a common disease in the Caribbean, caused by the ingestion of a wide variety of fishes that contain toxins accumulated from the marine food web (Lewis and Holmes, 1993) (Figure 1B). The ultimate sources of these toxins (ciguatoxins and maitotoxins) are small benthic microalgae belonging to the dinoflagellate genera *Gambierdiscus*, *Coolia*, *Ostreopsis*, and *Prorocentrum* (Figure 2) (Steidinger and Baden, 1984). Although ciguatera fish poisoning (CFP) is a threat to public health throughout the Caribbean, it is generally managed by local, traditional knowledge of the native fishers. However, their knowledge of the seasonality of occurrence and locations of ciguatoxic reefs may no longer be accurate because of changing environmental conditions (Tester, 1994; Tosteson, 2004). These environmental changes in turn alter the distribution and abundance patterns of the cells that cause CFP. Some evidence exists that ciguatoxicity may vary seasonally, but not all studies support this view (de Fouw et al., 2001). Tosteson (2004) argued that seasonality of CFP and the correlation of dinoflagellate abundance with CFP intoxications evident before 1990

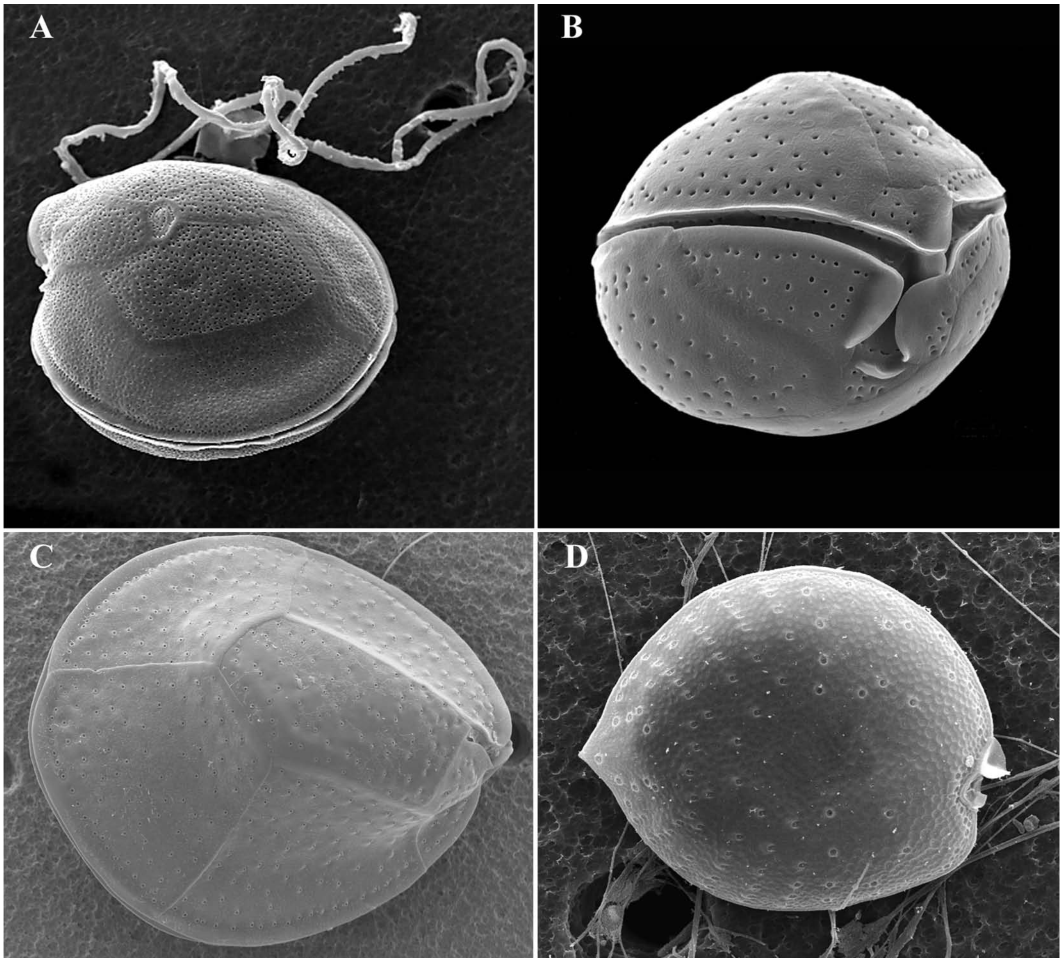

FIGURE 2. Scanning electron micrographs of ciguatera-associated dinoflagellates: A, *Gambierdiscus*; B, *Coolia*; C, *Ostreopsis*; D, *Prorocentrum*.

was not observed in data from 1990–2000. He suggested these changes appeared to be associated with increasing periods of elevated sea-surface temperatures in the Caribbean. Further, the potential for a greater number of people to be exposed to CFP has increased because of more intense exploitation of fisheries and the depersonalization of markets (Olsen et al., 1984). Both trends have been accelerated by tourism and rapidly growing resident populations (CIA, 2008).

The average number of tourist days (excluding ships' passengers) in the Caribbean, 174 million, dwarfs the 38.8 million residents and represents a significant exposure of a naive population to CFP. The most common route of exposure is through consumption of locally harvested fish. Currently, the annual total Caribbean fishery landings exceed 1.6 million metric tons (CRFM, 2008; FAO, 2005, 2008; WRI, 2007), making a strong argument for focused studies on CFP occurrence and on the environmental factors that affect the distribution and abundance of CFP-associated organisms.

As part of its commitment to understand and characterize the diversity, distribution, and abundance of organisms throughout the Caribbean, the Smithsonian Institution has carried out extensive studies on dinoflagellates over the past 20 years (Faust and Gulledge, 2002). Because of this pioneering work, much of the background information and expertise needed to characterize the diversity of ciguatera-causing dinoflagellates are already in place. During the past five years, NOAA (National Oceanic and Atmospheric Administration) and Smithsonian scientists have collaborated to isolate, identify, and genetically characterize the ciguatera-causing dinoflagellates of the Caribbean, as well as to develop species-specific molecular assays for assessing their abundance. As part of this work, four new *Gambierdiscus* species have been discovered and are being described (Tester et al., 2008; Litaker et al., in press).

We are now in a position to begin systematic studies of the incidence of CFP and distribution and abundance of CFP-causing dinoflagellates throughout the Caribbean. To identify areas of concern from both public health and marine resource perspectives, and to focus the effectiveness of environmental sampling, we needed to identify areas where CFP was most common. Consequently, we initiated active surveys of local fishery managers and public health officials. By examining the CFP incidences among the 24 islands and the 9 mainland countries surrounding the Caribbean, additional insights can be gained into factors that govern the spatial and temporal variations in the prevalence of CFP.

A second objective of this study was to determine how CFP was being monitored and reported throughout the Caribbean, where more than 46% of the tourists are from the United States (United Nations Statistics Division, 2004; CTO, 2008; Figure 3) and the average length of stay is 8.7 days (United Nations Statistics Division, 2004; CTO, 2008; Figure 4). This project represents the first steps toward an assessment of community vulnerability by the identification of susceptible populations and serves as a framework for developing human dimensions research as a cross-cutting priority of ecosystem science supporting marine resource management (Bauer, 2006).

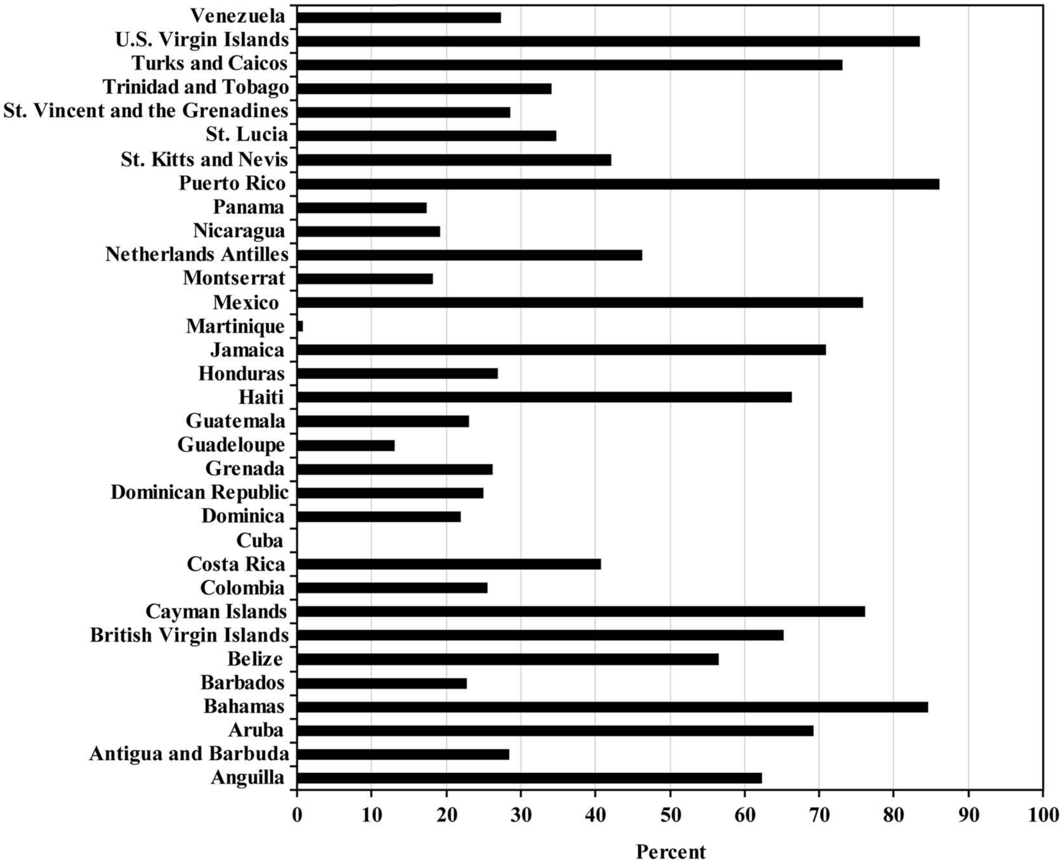

FIGURE 3. Average percentage of American tourists visiting the Caribbean by country (1996–2005). Only data from Cancun and Cozumel were used for Mexico. On average, 46% of tourists who visited all Caribbean countries came from the United States. On average, not counting visits from passengers on cruise ships, tourists spend over 174 million tourist days in this region each year (OAS, 1997; ACS-AEC, 2003; UNSD, 2004; CIA, 2008; CTO, 2008).

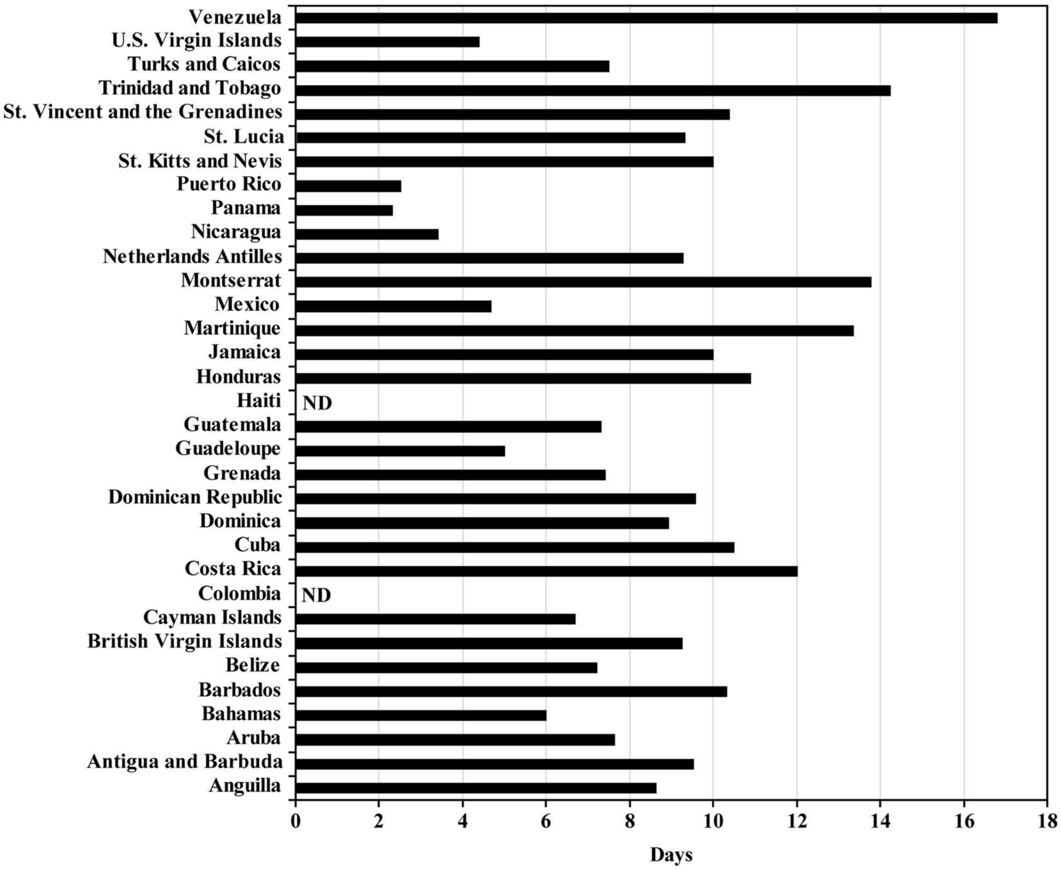

FIGURE 4. Average length of stay for all tourists visiting the Caribbean during 1996–2005, by country. Only data from Cancun and Cozumel were used for Mexico. The average length of stay for all tourists was 8.7 days (OAS, 1997; ACS-AEC, 2003; UNSD, 2004; CIA, 2008; CTO, 2008). ND = no data.

Our ultimate goal is a comprehensive assessment of the environmental, sociocultural, and economic impacts of CFP in the Caribbean and the development of effective detection and monitoring tools to support management decisions and improve inter-island communications among public health officials, marine resource managers, Caribbean residents, and tourists.

METHODS

Based on published cases and self-reporting, it appears that CFP is more prevalent in the eastern Caribbean than the western Caribbean (Stinn et al., 2000; see Figure 1B). To assess whether this is the case or whether the pattern derives from reporting bias, we used an active method to query public health officials and fisheries managers about the occurrence of CFP from 1996 through 2006 in 24 Caribbean island nations and territories and 9 mainland countries bordering the Caribbean. Fisheries and public health officials were contacted separately. One or both agencies could be involved in the surveillance of and response to CFP, although often within different administrative units. Querying two separate agencies was intended to allow corroboration of the data and to measure information-sharing between agencies. The questionnaires used in this study were vetted by a panel of experts with experience in designing human health surveys (see Acknowledgments).

Initial contact was made with public health and fisheries department staff persons by telephone. Introductory conversations were conducted in English, Spanish, or French, depending on the preference of the official contacted. The following preliminary information and questions were provided during these telephone calls before sending the survey:

- The focus of the project is to gather information about where and how many people are poisoned by eating fish contaminated with ciguatera toxin (ciguatoxin) throughout the Caribbean, including in ___________ *(name of country)*. People who eat fish carrying this toxin can develop ciguatera fish poisoning, an illness that affects primarily the digestive and nervous systems.
- Does your office compile information about fish that transmit ciguatera or cases of ciguatera fish poisoning in ___________ *(name of country)*?
  (If No) Do you know of another office that does?
  (If Yes) What is the name of that office?
  (If No) Do you know anyone who might be able to help me locate an office that compiles information about ciguatera fish poisoning?

A long-term goal of the research project is to better understand where ciguatera fish poisoning occurs, which could improve the use of resources to monitor and respond to it. The results of our research throughout the Caribbean will be summarized in a report, documented in a database, and displayed on maps that will be available to you and others interested in the project. We will not be collecting names, addresses, or other personal information from people who have ciguatera fish poisoning.

- Are you the best person in your office to provide information about ciguatera in ___________ *(name of country)*?
  (If referred to another person or agency) Do you have any contact information for the person you recommend I speak with?

We are asking for your voluntary assistance with our research.

- Would you be willing to answer a few questions?
  (If Yes) Thank you! I would greatly appreciate being able to e-mail you some specific questions I have. May I do so?
  (If No) Why not?

Once an appropriate contact was identified, a written copy of the questionnaire was provided in the appropriate language (or languages, as some participants received the questionnaire in both Spanish and English or French and English). Both questionnaires (the fisheries department version and the public health department version) included the 11 core questions listed in Appendix I, as well as 4 questions that applied to only the fisheries department (Appendix II) or the public health department (Appendix III). Efforts were made, in designing the questionnaire, to allow respondents to qualify how confident they were of the completeness of the data they were providing.

RESULTS AND DISCUSSION

To date, results are preliminary, as not all the questionnaires have been returned. However, some trends have begun to emerge, and it is possible to provide a brief synopsis of these. One of the most striking results was the wide range of concern and knowledge about CFP. Some government agencies have simply asserted that CFP cases do not occur in their jurisdictions and declined to receive or complete the questionnaire. Other agencies acknowledged that a potential problem exists but have been hampered by insufficient resources to institute an organized monitoring system. Still other governments reported making progress toward bringing CFP surveillance programs online, sometimes in response to a recent outbreak of CFP cases.

Some countries had a well-developed mandatory protocol for reporting CFP, including information on the name of the patients, symptoms, and diagnosis. In some instances, public health officials have a high degree of confidence that they are finding 90% or more of the cases, but most public health officials who have responded to date are less confident in their statistics. In some countries, when clusters of CFP cases are observed, the health department issues a press release. At the same time, the department may do a public service announcement for radio and TV about the risk of consuming barracuda.

A wide range of opinions were offered about how aware and concerned local populations and fishers are about the risk that eating certain types of locally caught fish could result in developing CFP. These responses ranged from “Not aware” or “Not concerned,” to “Somewhat aware” or “Somewhat concerned,” to “Very aware” or “Very concerned.” One respondent commented that native-born citizens had a higher level of awareness and concern than people who recently moved to the region. Perceived levels of risk might depend more on being educated about the problem rather than an actual risk of exposure. At least in some regions where CFP is well known, most people seem to understand that if they feel tingling or prickling on their tongues when they are eating fish, they should stop eating it to minimize the risk of becoming sick.

In some countries, the data also suggest a trend toward increasing numbers of CFP cases with time. Public health officials on a few islands attributed this not to environmental change, but to population growth, in some cases as rapid as a doubling of the population in 20 years. As the population has grown, so too has the demand for fish, which could result in an increase in the number of people exposed to CFP. It is generally agreed that CFP is underreported and that this lack could be attributable to a variety of reasons (e.g., because its symptoms resemble those of other diseases when the poisoning is mild). This apparent increase may also be attributable to increased reporting because of heightened awareness, or it may reflect an actual increase in new cases of CFP.

Several public health departments have compiled and reported the months and years when people ate ciguatoxic fish and were diagnosed with CFP. From these limited data it appears that the number of CFP episodes was distributed evenly throughout the year but that the number of cases (people diagnosed with CFP) per episode was greater in September and October (Figure 5).

Overall, public health and fisheries officials indicated that consumption of contaminated barracuda was the most common cause of CFP. Other species frequently identified with CFP include jack, grouper, snapper, hogfish, and mackerel. Some fishermen discard barracuda that do not "put up a fight" when caught, believing that if a fish does not fight, it is sick. However, it should be noted that ciguatoxic status cannot be discerned visually; seemingly healthy fish can be quite toxic. One positive outcome of this research was that some countries provided data indicating geographic locations where ciguatoxic fish were frequently found. This information will guide future sampling efforts.

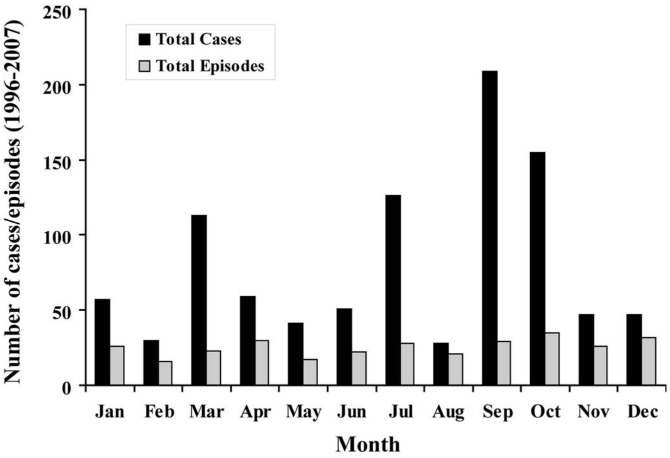

FIGURE 5. Ciguatera episodes and cases in the Caribbean by month from 1996 to 2007. Episodes indicate multiple cases (usually defined by zip code) during the same week.

CONCLUSIONS

The data currently available from Caribbean countries suggest there is wide variability in the amount of attention given to CFP. This variability is probably not entirely attributable to how prevalent CFP is in various areas. The reasons for this include differences in (1) how significant a problem CFP is thought to pose, (2) awareness of the risk of CFP, (3) whether central reporting of CFP cases is mandatory, and (4) resources available for CFP monitoring and education.

Active surveys, such as the one described in this study, can help countries quantify potential risks and establish training and monitoring systems for CFP. This study also provides unique insights into human dimensions of CFP, including perceptions of how significant the risks are in different areas and how frequently health and fisheries departments exchange information concerning CFP. The data from this study were also detailed enough, in some cases, to suggest specific regions in the Caribbean where CFP occurrences are elevated or are relatively rare. This information will facilitate identification of specific sampling sites for future investigations of the factors that affect the temporal and spatial variability in exposure to CFP. The fruitful partnership between the Smithsonian Institution and NOAA continues the Smithsonian's tradition of documenting the diversity of life on earth and NOAA's mission to bring state-of-the-art management tools to the marine community.

ACKNOWLEDGMENTS

We thank Drs. Nathalie Valette-Silver, David Johnson, and Michael Dowgiallo and Mr. Joseph Schittone of the National Ocean Service (NOS), NOAA, for facilitating this study. Dr. Richard Appledorn, Director of the Caribbean Coral Reef Institute, provided guidance for field sampling. Mr. Michael Carpenter, National Museum of Natural History (NMNH), kindly provided logistic support. Mr. Scott Whittaker (Head) and Mr. Don Hurlbert of the Smithsonian's NMNH Imaging and Photography Department generously gave us technical assistance. We appreciate the guidance from Leonard Young, Public Health Scientist, Eastern Research Group; Dr. MaryBeth Bauer, NOAA National Centers for Coastal Ocean Science; Dr. Chris Ellis and Ms. Lauren Smith, Human Dimensions Program, NOAA Coastal Services Center; and Dr. Janna Shakeroff, Duke University Marine Laboratory, in the development of the questionnaire used in this study. We are especially grateful to Dr. Klaus Ruetzler and the Caribbean Coral Reef Ecosystem Program and the NOS International Program Office for funding. This is contribution number 851 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Fund.

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APPENDIX 1

The following core questions were used in both fisheries and health department questionnaires:

1. a. What information does your office compile about cases of ciguatera fish poisoning (for example, number of people diagnosed, locations of people diagnosed, locations where fish were caught, etc.)?
   b. If your office does not compile such information, is there another governmental office or agency that does, and what is its name? ___ Yes ___ No ___ I'm not sure
   Name of other office or agency:
   c. If yes, what types of information do you think that office might have?
   d. Please provide contact information for someone in that office, if possible (contact name, e-mail address, phone number, and fax number).

2. If you receive reports of ciguatera fish poisoning, from whom do the reports come? (*Please check ALL that apply.*)
   ___ Doctors ___ Clinics and Hospitals ___ Fisheries Department [for the health department survey] ___ Fishermen ___ Health Department [for the fisheries department survey]/Other Health Agencies [for the health department survey] (please specify jurisdiction represented and contact person, if available) ___ Restaurants ___ Hotels ___ Individual Citizens ___ Other Sources (please list)

3. Please indicate the total number of reported ciguatera fish poisoning cases per calendar year from January 1, 1996, through December 31, 2006.
   [A table containing one line for each year, a column for the number of cases reported, and a column for any comments was provided here.]

4. To the extent available, please provide the following information for each episode of ciguatera fish poisoning. (For this study, an episode is defined as an occasion when one or more people were poisoned on the same day by one or multiple fish of the same variety, caught in the same place.)
   a. Number of people poisoned
   b. Date of episode (list season and year if date or month is not known)
   c. Date of diagnosis, if date of poisoning (B) is not known
   d. City where fish with ciguatera was eaten
   e. Home city of patient(s), if city where fish was eaten (D) is not known
   f. Type of fish with ciguatera (common name or scientific name)
   g. Describe where fish with ciguatera was caught, in as much detail as possible (with latitudes and longitudes, if available)

5. At this time, is reporting any information about fish transmitting ciguatera or cases of ciguatera fish poisoning voluntary or mandatory? ___ Voluntary ___ Mandatory ___ I'm not sure
   If reporting is mandatory:
   a. What information must be reported?
   b. When did it become mandatory?
   c. What agency receives these reports initially?

6. a. What percentage of ciguatera fish poisoning cases diagnosed each year in ___________ (*name of country or territory*) do you think are reported to your office?
   b. How confident are you of this estimate? ___ Very confident ___ Somewhat confident ___ Slightly confident ___ Not at all confident ___ I'm not sure

continued

Appendix 1 continued

7. a. To your knowledge, has your agency or another governmental agency issued any advisory warnings related to consuming fish that might carry ciguatera, such as barracuda or large reef fish?
___ Yes ___ No ___ I'm not sure
b. If yes, please indicate which office issued the advisory.
c. If applicable, please include or attach the wording of each such advisory and indicate when it was issued. Attach additional pages, if necessary.
d. If your agency has not issued an advisory, who or what agency would be most appropriate to consult for information on advisories? (Please list the agency name and the following, if available: a contact name, e-mail address, phone number, and fax number.)

8. How often do your department and fisheries department officials [for the health department survey]/health department officials [for the fisheries department survey] exchange information about episodes of ciguatera fish poisoning?
___ As cases occur ___ Every month ___ Every 3 months ___ Every 6 months ___ Every year ___ Never
___ Other (please specify):

9. How aware do you think local citizens are of the risk that eating certain types of fish could cause them to develop ciguatera fish poisoning? ___ Very aware ___ Somewhat aware ___ Not very aware ___ Not aware
___ I'm not sure

10. To what extent do you think local citizens are concerned about ciguatera fish poisoning?
__ Very concerned __ Somewhat concerned __ Slightly concerned __ Not concerned __ I'm not sure

11. Please provide your contact information for future reference. Thanks again for your assistance!
Government represented:
Agency and office:
Name and title of person completing questionnaire:
Telephone number, with city code:
Fax number, with city code:
e-mail address:
Date information provided:
Would you like to receive notification of the results of the study? ___ Yes ___ No

APPENDIX 2

The following questions were directed only to officials representing fisheries departments:

1. a. Is information usually communicated to you about where fish suspected of carrying ciguatera were caught?
___ Yes ___ No
b. Is information usually communicated to you about what types of fish have carried ciguatera?
___ Yes ___ No
c. If yes to either (a) or (b), and if you do not have information in the format provided in Question 4, please provide any information you have about the types of fish, and the locations involved in episodes of ciguatera fish poisoning reported to you, for the years 1996 to 2006. [A table was provided with the following headings: Year, Common or scientific names of fish reported, Locations of fish reported (latitudes/longitudes, if possible, or place names, in as much detail as possible).]

2. Please provide any information you have on economic losses resulting from ciguatera fish poisoning, either quantitative or qualitative (for example, if fishing had ceased at a particular reef because of the suspected presence of ciguatera toxins, there might be an annual loss of $10,000 to the fishing industry). Please include the year(s) your data reflects and note your data sources.

3. To what extent do you think fishermen are aware of the risk of catching certain types of fish that could cause people to develop ciguatera fish poisoning? ___ Very aware ___ Somewhat aware ___ Not very aware ___ Not aware ___ I'm not sure

4. To what extent do you think fishermen are concerned about catching certain types of fish that could cause ciguatera fish poisoning? ___ Very concerned ___ Somewhat concerned ___ Slightly concerned ___ Not concerned ___ I'm not sure

APPENDIX 3

The following questions were directed only to officials representing health departments:

1. Is any information available to you on the cost per year to your government of monitoring or documenting the incidence of ciguatera fish poisoning? ___ Yes ___No
   If yes, please provide the information below and note your data sources.

2. Is any information available to you on the cost per year of medical treatments in ___________ (*name of country or territory*) for ciguatera fish poisoning, as an average per person affected by ciguatera fish poisoning and/or annually for ___________ (*name of country or territory*)? ___ Yes ___No
   If yes, please provide it below, specify whether it reflects a total or an average per person, and note your data sources.

3. Is any information available to you related to the number of days people have been unable to work due to ciguatera fish poisoning per year in ___________ (*name of country or territory*)? ___ Yes ___No
   If yes, please provide it below, specify whether it reflects a total or an average per person, and note your data sources.

4. Would you rank ciguatera fish poisoning as one of the 10 most severe food-borne illnesses in ___________ (*name of country or territory*)? ___ Yes ___No ___ I'm not sure
   If yes, would it rank in the top ___ 1 to 5 or ___ 6 to 10?

History of Reef Coral Assemblages on the Rhomboid Shoals of Belize

Richard B. Aronson, Ian G. Macintyre, Anke M. Moesinger, William F. Precht, and Michael R. Dardeau

ABSTRACT. Coral assemblages of the rhomboid shoals of the Belizean barrier reef have undergone dramatic, historically unprecedented changes over the past several decades. Before the late 1980s, the flanks of the shoals exhibited a distinct biological zonation, with branching *Porites* spp. dominant in a shallow zone (0–3 m water depth); the staghorn coral *Acropora cervicornis* dominant in an intermediate zone (3–15 m depth); and large, plating agariciids and the lettuce coral *Agaricia tenuifolia* dominant in a deep zone (15–30 m depth). *Acropora cervicornis* died off catastrophically from white-band disease after 1986 and was replaced by *Agaricia tenuifolia* in the intermediate zone. Push-cores extracted from intermediate depths in previous studies showed that *Acropora cervicornis* was the dominant space occupant and primary framework builder for millennia before the phase shift to *Agaricia tenuifolia*. Cores extracted from the shallow zone showed that *Acropora cervicornis* dominated until several centuries ago, when the tops of the reefs reached approximately 2 m water depth and branching *Porites* spp. replaced it. In contrast, three cores extracted from the deep zone in the present study showed that for millennia the subsurface coral assemblage, like the assemblage on the modern deep-reef surface, was dominated by large, plating agariciids and *Agaricia tenuifolia*. Because white-band disease only affects acroporid corals, the unprecedented phase shift that followed the outbreak was confined to the intermediate zone. High sea temperatures in the summer of 1998 caused coral bleaching and mortality, especially of agariciids in the intermediate and deep zones, but to date this event has not left a geologic signature in the Holocene record.

INTRODUCTION

Coral reef ecosystems are collapsing at an accelerating rate, jeopardizing the ecosystem services that they provide (Hughes et al., 2003; Wilkinson, 2006; Carpenter et al., 2008). The common presumption that mortality of hard corals (Scleractinia and Milleporina) commenced earlier and was more severe in the Caribbean and eastern Pacific than in other tropical and subtropical regions may not be correct (Bruno and Selig, 2007). Nevertheless, the causes and consequences are best understood for the Caribbean and eastern Pacific.

Coral mortality has been elevated in the Caribbean since the late 1970s (Gardner et al., 2003). The impacts of global change, including increasing sea temperatures, increasing cyclone intensity, and declining aragonite saturation

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state (Kleypas et al., 1999; Buddemeier et al., 2004; Hoegh-Guldberg et al., 2007), are sources of grave concern, but coral assemblages throughout the Caribbean have already been severely affected by outbreaks of infectious marine diseases (Aronson and Precht, 2001b; Sutherland et al., 2004; Weil et al., 2006). In particular, white-band disease (WBD), a bacterial infection that is specific to acroporid corals, decimated *Acropora palmata* (elkhorn coral) and *Acropora cervicornis* (staghorn coral) on reefs throughout the western Atlantic from the late 1970s through the early 1990s (Aronson and Precht, 2001a, 2001b). Acroporid populations have been reduced so drastically that the two species are now listed as threatened under the U.S. Endangered Species Act (Hogarth, 2006) and are classified as critically endangered according to the Red List criteria of IUCN, the International Union for Conservation of Nature (Carpenter et al., 2008). Hurricanes, temperature-induced bleaching, declining herbivory, nutrient loading, and predation by corallivores have had additional, interacting impacts on coral mortality and the scope for population recovery (Aronson and Precht, 2006). Emergent diseases, for example, could be related to or exacerbated by global warming and nutrient loading (Harvell et al., 2002; Rosenberg and Ben-Haim, 2002; Bruno et al., 2003, 2007; Sutherland et al., 2004; Kline et al., 2006). Recent changes on Caribbean reefs were novel events in at least the last 3,000 to 4,000 years (Aronson et al., 2002a, 2004, 2005a; Wapnick et al., 2004; Hubbard et al., 2005; Greer et al., 2009), and Pandolfi et al. (2006) drew a similar conclusion about Holocene reef dynamics in Papua New Guinea.

Aronson and Precht (2001a, 2001b, 2006; Precht and Aronson, 2006) argued that because WBD was the primary cause of recent mortality of *Acropora palmata* and *Acropora cervicornis* in the Caribbean, and because the two species were the dominant space occupants at depth ranges of 0–5 and 5–25 m, WBD was clearly one of the most important causes of recent coral mortality in the region. Mass mortality of the acroporids was followed by two types of phase shifts. Where coral mortality exceeded the capacity of herbivores to respond to algal growth on the space that had been opened, macroalgae rose to dominance (Ostrander et al., 2000; Aronson and Precht, 2001a, 2006; Williams et al., 2001; Rogers and Miller, 2006). Where herbivory was sufficient to control the algae, brooding, self-fertilizing corals, primarily of the families Agariciidae and Poritidae, replaced the acroporids (Aronson and Precht, 1997; Greenstein et al., 1998; Bythell et al., 2000; Knowlton, 2001; Green et al., 2008). The shift to macroalgal dominance has not been as widespread as previously supposed (Bruno et al., 2009).

An important exception to the overall Caribbean trend is the Flower Garden Banks (FGB) in the northwestern Gulf of Mexico, where coral cover has held steady at 40%–60% at depths of 17–26 m from the 1970s to the present. Aronson et al. (2005c) explained the persistently high coverage of living corals based on the historical absence of the cold-sensitive acroporids. Coral mortality has been far lower at the FGB than elsewhere in the Western Atlantic region because no acroporids were present to die of WBD. The appearance of *Acropora palmata* at the FGB in the past few years could be related to global warming (Precht and Aronson, 2004).

An ecosystem-level version of this biogeographic argument is that reef zones historically not dominated by acroporids should not have undergone phase shifts at the same time as the adjacent *Acropora*-dominated zones. In this study we examined the millennial-scale history of the coral assemblage near the bases of the rhomboid shoals in the central shelf lagoon of the Belizean barrier reef. We cored the deep-reef framework of two of the shoals, reconstructed the history of the coral assemblage during the late Holocene, and completed a model of reef development over the last several thousand years from present sea level down to the bases of the shoals. Although *Acropora cervicornis* dominated at intermediate depths for millennia until the late 1980s, acroporids apparently did not dominate the deep zone for at least the past 1,500 to 2,000 years, providing an opportunity to test our hypothesis of the occurrence and timing of phase shifts.

ZONATION AND PALEOECOLOGY OF THE RHOMBOID SHOALS

The rhomboid shoals are uncemented, atoll-like reefs lying within the central shelf lagoon of the Belizean barrier reef. The sloping outer flanks of the rhomboid shoals displayed a clear pattern of coral zonation from at least as far back as the early 1970s, when the first rigorous ecological observations were made, until 1986 (Westphall, 1986; Aronson and Precht, 1997; Aronson et al., 1998). A shallow zone (0–3 m water depth) was dominated by branching *Porites* spp., primarily *Porites furcata* and *Porites divaricata*, mixed with the hydrocoral *Millepora alcicornis*. *Acropora cervicornis* dominated an intermediate-depth zone (3–15 m depth), with the blade-forming lettuce coral *Agaricia tenuifolia* as the subdominant. (*Agaricia tenuifolia* recently has been revised to *Undaria tenuifolia*; however, we will retain *Agaricia* as the generic designation in this paper.) A deep zone, extending from 15 m to the lagoon floor at 22–30 m depth, was dominated by large colonies of plating agariciids (*Agaricia lamarcki*, *Agaricia grahamae*, *Agaricia undata*, and *Leptoseris cucullata*) and *Agaricia tenuifolia*, with scattered massive corals. The total hard-coral fauna consisted of approximately 25 species, most of which were rare (Aronson and Precht, 1997).

In the decade following 1986, the dominant coral at intermediate depths, *Acropora cervicornis*, succumbed to WBD and was replaced by *Agaricia tenuifolia*. This phase shift was mediated by an abundant, herbivorous sea urchin, *Echinometra viridis*, which limited macroalgal growth and promoted the recruitment and opportunistic growth of agariciids on the dead skeletons of *Acropora cervicornis* (Aronson and Precht, 1997). *Agaricia tenuifolia* was the fastest growing of the agariciids that recruited and, therefore, it became the new dominant.

To determine whether the transition was historically unique, Aronson et al. (2002a) extracted push-cores at 5–10 m water depth from stations distributed over a 375 km^2 area of the lagoon (Figure 1). Analysis and radiocarbon dating of the cores revealed continuous dominance of *Acropora cervicornis* and upward growth of the reef for at least 3,000 years before the late 1980s. Spines of *Echinometra viridis* were present throughout the cores, indicating continuously high herbivory. During the past three millennia *Agaricia tenuifolia* grew in small patches (of the order of square meters), which appeared as subsurface layers of skeletal plates that were isolated in time and space (Aronson et al., 2002a). The recent, area-wide phase shift, in contrast, was preserved at the tops of the cores as a layer of *Agaricia tenuifolia* plates overlying a thin layer of taphonomically degraded *Acropora cervicornis*. This signature persisted in the Holocene record despite subsequent hurricanes and bleaching events (Aronson et al., 2000, 2002b, 2005b). Coring in a lagoonal habitat at Discovery Bay, Jamaica, showed that a more common phase shift, in which *Acropora cervicornis* was killed by WBD and replaced by macroalgae as the result of limited herbivory, was similarly unprecedented on a millennial time scale (Wapnick et al., 2004).

Cores extracted from the rims and ridges of the shoals near the present sea level revealed that *Acropora cervicornis* dominated the shallowest portions of these reefs for at least several millennia until approximately 500 years ago (Westphall, 1986; Aronson et al., 1998, 2005a; Macintyre et al., 2000). At that time the reef tops grew to within 2 m of sea level, and branching *Porites* spp. replaced *Acropora cervicornis* as the dominant coral taxon. Since then, the *Porites*-dominated assemblage has kept up with the slowly rising sea level, forming the shallow zone. The shallowing-upward, successional sequence in the shallow zone contrasts with the post-1986, disease-induced replacement of *Acropora cervicornis* by *Agaricia tenuifolia* at intermediate depths.

As part of the worldwide reef-bleaching event of 1997–1998 (Wilkinson, 2000), which was related to the El Niño–Southern Oscillation and probably augmented by global warming, a high-temperature anomaly in the summer of 1998 bleached almost all corals in the intermediate and deep zones of the rhomboid shoals (Aronson et al., 2000, 2002b). *Agaricia tenuifolia* is particularly prone to temperature-induced bleaching (Robbart et al., 2004), and populations of this coral at intermediate and deeper depths experienced nearly complete mortality. Mortality rates were lower, but still very high, for plating agariciids. The dead coral skeletons were colonized primarily by thin algal turfs and the sponge *Chondrilla* aff. *nucula* (Aronson et al., 2002b), which Rützler et al. (2007) have now described as *Chondrilla caribensis*. Agariciid populations had not recovered as of December 2008 (W. F. Precht, personal observation). Branching *Porites* corals in the shallow zone were less affected by the 1998 thermal anomaly. These corals did not bleach to the extent the agariciids did, and as a result they did not experience large-scale mortality (W. F. Precht and R. B. Aronson, personal observation).

MATERIALS AND METHODS

In April 2008, we extracted six push-cores in water depths of 14.0–19.5 m from the reefs at Channel and Elbow Cays, in the center of our 375 km^2 study area (see Figure 1). Push-coring requires less equipment than mechanical techniques such as rotary drilling and percussion vibracoring. By eliminating the need for tripods and other heavy equipment, push-coring offers easier logistics, greater mobility, and a much lower cost per core. Penetration and recovery of cores dominated by branching and foliose corals have been excellent in the shallow and intermediate-depth zones of the rhomboid shoals, as well as on uncemented lagoonal reefs in Panama and Jamaica (Dardeau et al., 2000; Aronson et al., 2004; Wapnick et al., 2004). Rotary drilling is not an option because branching and foliose corals generally are broken up and flushed out of the core barrel. As a result, recoveries are poor in lagoonal and fore-reef environments dominated by fragile corals (Glynn and Macintyre, 1977; Halley et al., 1977; Macintyre et al., 1981; Shinn et al., 1982).

Dardeau et al. (2000) described the push-coring method in detail. Briefly, aluminum tubes, 5 m long and

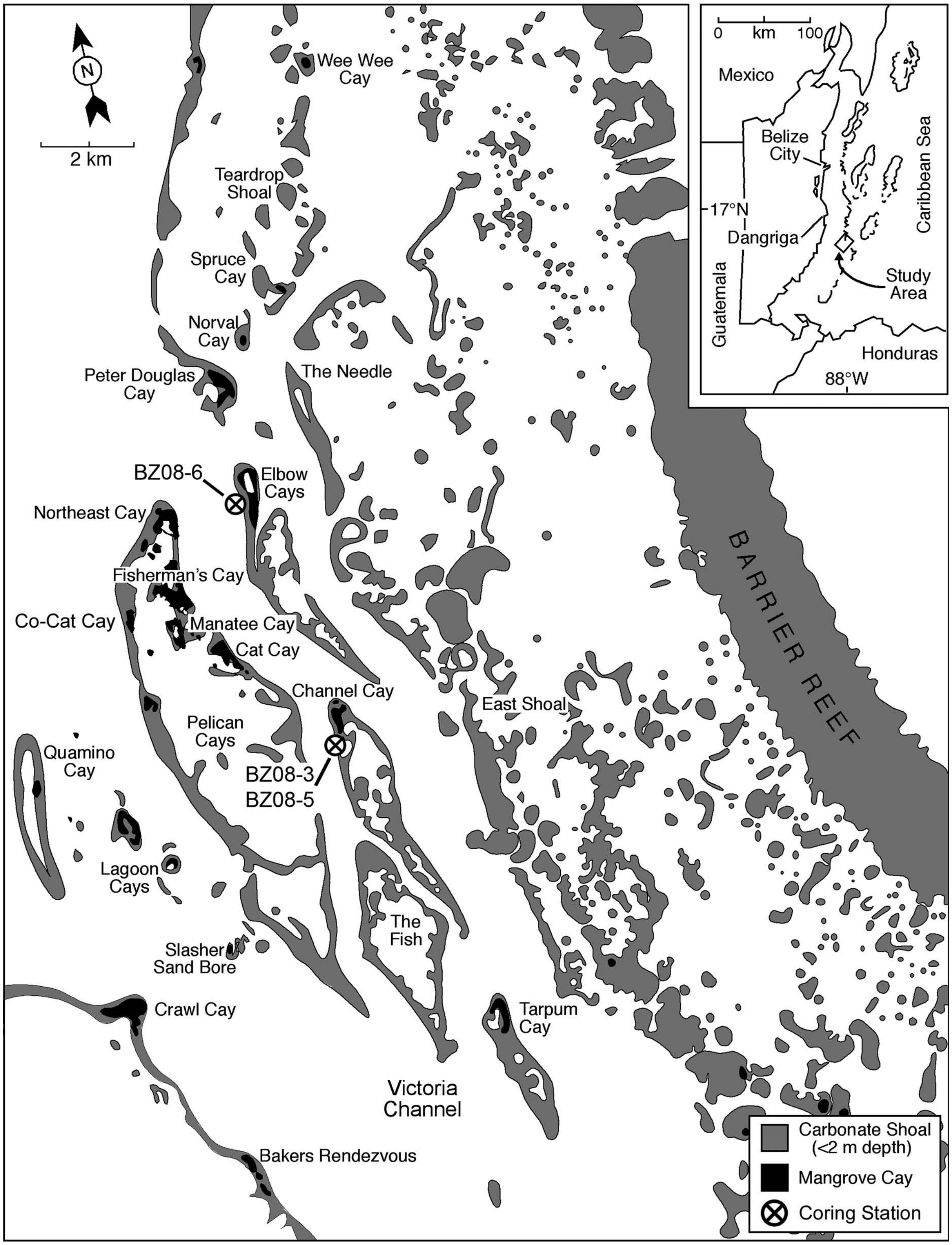

FIGURE 1. Map of the central shelf lagoon of the Belizean barrier reef, showing the rhomboid shoals and the locations of the two coring stations. Three of the six cores extracted were analyzed for this study, as noted on the map. (Modified from Aronson et al., 2002a.)

7.6 cm (3 in.) in diameter with teeth cut into their leading ends, were driven by hand into the uncemented reef framework. The tubes were rotated in using adjustable core slips with handles and tapped with a sliding hammer-weight, sleeved over the top, to aid in penetration. The tubes cut through, penetrated, and captured the loose framework of branching and foliose coral skeletons, and they cored through most massive coral heads as well. Although head corals are rare in the subsurface at shallow and intermediate depths, they are more common in the deep zone. The cores were sealed with plastic caps and electrical tape, extracted from the reef, and transported to the laboratory for analysis.

Estimates of recovery were obtained at intervals during the coring process by dropping a weighted fiberglass measuring tape down the open core barrel. In previous studies these measurements, along with simultaneous measurements of penetration, confirmed that material entered the tubes continuously as they were forced into the reef. In some cases in the present study the tube cored through a massive coral and was plugged by it, preventing further recovery as the tube was forced deeper into the uncemented framework. We used the penetration depth at the point at which the tube was plugged to calculate percent recovery. Comparison of final recoveries measured before extraction with recoveries measured after extrusion in the laboratory showed that little or no material was lost from the bottoms of the tubes during extraction. Of course no material was lost from cores that were plugged at their bases by massive corals.

There were no indications of significant voids in the reef framework. In no case did the tube suddenly drop vertically while we were driving it into the reef. We also saw no reversals in the in situ estimates of recovery, which would have indicated episodic compaction during coring.

Three of the extruded cores were analyzed at intervals of 5 cm. The constituents of each interval retained on a 5 mm sieve were cleaned of matrix, sorted to species, dried to a constant mass, and weighed to the nearest milligram. In earlier studies, we showed from regression analysis that, for the coral constituents, log(mass) was a strong predictor of log(volume), as measured by water displacement.

In the manner described previously by Wapnick et al. (2004), we assessed the degree of taphonomic degradation of the *Acropora cervicornis* material—encrustation, surficial erosion, and internal boring—using a modified version of the rank scales of Greenstein and Moffat (1996). The average taphonomic condition of each coral fragment was rated as good, intermediate, or poor. The good rating was applied to fresh-looking pieces that had little or no encrustation, retained essentially all their surface sculpture, and showed little to no evidence of internal boring. Poor fragments were those with extensive encrustation, surficial erosion, and/or boring; degradation was extensive enough that the structure of the corallites was completely obscured. Fragments were rated as intermediate if their condition, averaged over the three categories, fell between good and poor. A coral taxon, or a taxon in a particular taphonomic condition, was considered dominant in a 5 cm interval if its mass exceeded the mass of each of the other taxa/conditions in that interval.

A coral sample from the bottom of each core was radiocarbon dated by Beta Analytic, Inc. (Miami, Florida), using standard techniques. Measured dates were corrected for isotopic fractionation to generate conventional dates, which are expressed as radiocarbon years before 1950 (^{14}C year). Conventional dates were calibrated to calendar years before 1950 (CalBP).

RESULTS

The cores captured the framework of loose coral skeletons surrounded by a light gray watery matrix of sandy mud. The matrix was almost entirely carbonate, with only a trace of noncarbonate material. It was less compact than the matrix in cores collected from the shallow and intermediate zones (Aronson et al., 1998; Macintyre et al., 2000; Aronson et al., 2002a). X-ray diffraction analysis of sediment samples revealed a notable lack of high magnesium calcite in the sand and silt fractions. The majority of high magnesium calcite was found in the clay fraction, corroborating our earlier conclusion of active precipitation of micritic high magnesium calcite without significant cementation (Macintyre and Aronson, 2006). Spines of *Echinometra viridis* in the matrix indicated that those herbivores were present during the time interval represented by the cores.

Three of the six cores we collected provided penetrations, recoveries, and bottom dates sufficient to analyze temporal trends in the coral assemblage of the deep zone (Table 1). Cores BZ08-3 and BZ08-5 from Channel Cay were both plugged by heads of *Porites astreoides* at penetration depths of 2–3 m. Core BZ08-6 from Elbow Cays penetrated nearly 3.5 m. Bottom samples consisting of *Porites astreoides* from the bases of cores BZ08-3 and BZ08-5, and plating *Agaricia* from the base of BZ08-6, were radiocarbon dated. The remaining three cores yielded recoveries of 65 cm or less and were not analyzed.

TABLE 1. Summary statistics for the three cores.

Core	Water depth (m)	Site	Penetration (cm)	Recovery (cm)	Percent recovery	Basal radiocarbon dates[a]	
						Conventional date (^{14}C year ± SE)[b]	Calibrated date (CalBP)[c]
BZ08-3	14.5	Channel	256	81	31.6%	2,730 ± 50	2,420 (1,860–1,560)
BZ08-5	16.2	Channel	216	78	36.1%	2,130 ± 60	1,710 (2,650–2,320)
BZ08-6	15.3	Elbow	347	109	31.4%	1,290 ± 60	840 (940–700)

[a] Radiocarbon dates are of coral samples from the bases of the cores.

[b] Conventional dates are measured dates corrected for isotopic fractionation, expressed as radiocarbon years before 1950 (^{14}C year) and accompanied by standard errors (SE).

[c] Calibrated dates (CalBP) are expressed as calendar years before 1950, with 95% confidence intervals in parentheses.

The mean recovery for the three cores analyzed was 33.0% of penetration depth (±1.53 SD). This figure is slightly lower than the mean of 35.9% obtained for cores from intermediate depths on the rhomboid shoals and considerably lower than the mean of 62.3% for cores from intermediate depths in Bahía Almirante, a coastal lagoon in Panama (Dardeau et al., 2000). The low recoveries in the present study probably reflect the open reef framework of the rhomboid shoals (compared to Bahía Almirante), combined with the low sediment content of the matrix in the deep zone (compared to intermediate depths on the rhomboid shoals).

All three cores were dominated by agariciid corals (Figure 2). These corals were primarily large, plating forms, which characterized the living community until 1998 and that now characterize the modern, postbleaching death assemblage in the deep zone. *Agaricia tenuifolia* was more common near the tops of cores BZ08-5 and BZ08-6 than lower in those cores. The agariciids were in mixed taphonomic condition, with most intervals containing both intermediate and poor material. The skeletons from the top 20 cm of the cores were in neither better nor worse condition than those further down.

Slope angles in the vicinity of the coring sites, measured with an inclinometer (Aronson et al., 2002a), were 36°–39°. Those slopes were less steep than the critical angle of 45°, above which *Agaricia tenuifolia* skeletons are transported downslope (Aronson et al., 2002a). The critical angle of 45° probably applies to the dead, fragmented skeletons of plating agariciids as well.

Core BZ08-3 contained a layer of *Acropora cervicornis* branch fragments in poor taphonomic condition. This layer could have been the result of downward transport from intermediate depths. On the other hand, *Acropora cervicornis* is less sensitive to slope angle than *Agaricia tenuifolia* (Aronson et al., 2002b), so an autochthonous layer cannot be ruled out. Other coral taxa, including branching *Porites* spp. and *Porites astreoides*, *Montastraea annularis* species complex, *Colpophyllia natans*, *Madracis auretenra* (formerly *Madracis mirabilis*; Locke

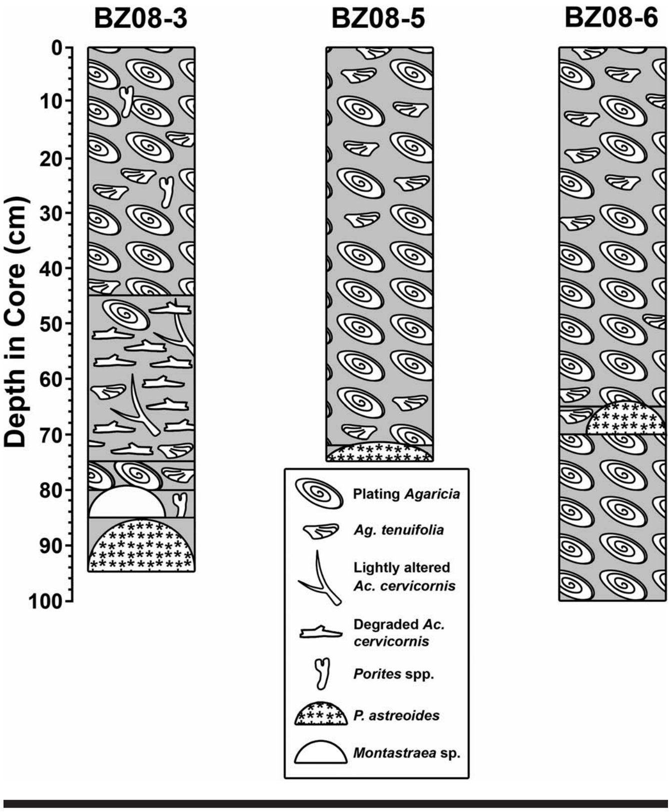

FIGURE 2. Schematic diagrams of the three extruded cores. The lengths of the cores depart slightly from recoveries estimated in the field (Table 1). Gray shading indicates a matrix of watery, sandy mud; *Ag.* = *Agaricia*; *Ac.* = *Acropora*; *P.* = *Porites*.

et al., 2007), and *Stephanocoenia intersepta*, were rare in the cores. None of the cores recorded millennial-scale intervals of actively accreting *Acropora cervicornis* framework, which were represented in the intermediate-zone cores by thick accumulations of *Acropora cervicornis* in good taphonomic condition.

DISCUSSION

Shinn et al. (1979; see also Westphall, 1986) extracted cores from the flanks of the Channel Cay shoal, including one from the base of the reef near our coring station (see Figure 1). Their general statement, that the cores were dominated by *Acropora cervicornis* with agariciids as the subdominants, did not draw distinctions between cores extracted from the different zones. We found that agariciids were the dominant framework constituents in the deep zone.

Core BZ08-3, which contained a layer of taphonomically degraded *Acropora cervicornis* underlying a thick uppermost layer of agariciids, could represent a deepening-upward sequence. This scenario seems unlikely, however, considering that sea level has risen only approximately 2 m during the past 3,000 years (Toscano and Macintyre, 2003). Furthermore, the other two cores showed no such *Acropora cervicornis*-dominated layer. Regardless, none of the three cores suggests a recent transition from millennia of fast-growing and rapidly accumulating *Acropora cervicornis* framework to dominance by agariciid corals, as was observed in the cores from intermediate depths. The layer of *Acropora cervicornis* in BZ08-3 is more likely derived from material that was transported downslope, forming debris fans at the bases of the shoals.

Aronson et al. (2005a) compared late Holocene reef development between the rhomboid shoals and the uncemented reefs of Bahía Almirante in Panama. The shallow and intermediate zones had been cored extensively in both locations, providing an accurate picture of stasis and change in the dominant coral taxa. In both cases, however, the deep zones were poorly characterized. The dearth of push-cores from the bases of the reefs has been primarily a consequence of the greater densities of core-occluding massive corals in the subsurface, compared to the subsurface of the shallow and intermediate zones.

The cores analyzed in this study allow us to present a more comprehensive model of the history of the coral assemblages of the rhomboid shoals (Figure 3). In the shallow zone, catch-up dynamics gave way to keep-up dynamics: the *Acropora cervicornis* that had dominated for millennia during the catch-up phase was replaced centuries ago by branching *Porites* spp. during the keep-up phase. *Acropora cervicornis* was also dominant for millennia at intermediate depths, but in the late 1980s it was nearly extirpated by white-band disease and then replaced by *Agaricia tenuifolia*. The deep zone, in contrast, appears to have been dominated by agariciids for at least 1,500 to 2,000 years. No recent transitions were evident in the deep zone, a result consistent with the hypothesis that such shifts were predicated on the prior dominance and subsequent mortality of acroporids.

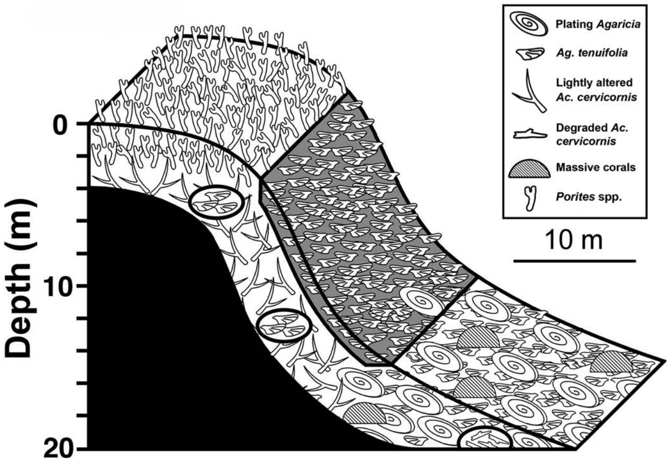

FIGURE 3. Model of reef development on the rhomboid shoals of Belize over the last several thousand years. Gray shading indicates that the coral assemblages at intermediate water depths experienced a recent transition. Black fill represents earlier Holocene and antecedent Pleistocene reef framework at depths not penetrated by the cores. Horizontally oriented, subsurface ellipses indicate spatially isolated layers of *Agaricia tenuifolia* and taphonomically degraded *Acropora cervicornis*. (Modified from Aronson et al., 2005a.)

Thus, only the intermediate zone was affected when *Acropora cervicornis* died off regionally in the late 1980s to the early 1990s. The subsequent bleaching event in 1998 killed most of the agariciids on the rhomboid shoals. Cores extracted from the intermediate zone in 2004 did not display a taphonomic signature of that mass mortality event, which would have appeared as a discrete, uppermost layer of taphonomically degraded agariciid skeletons (Aronson et al., 2005b). Similarly, because of the mixed taphonomic character of the subfossil agariciid material in the deep zone, the expected signature of the 1998 event had not been observed in the Holocene record of that zone as of April 2008.

ACKNOWLEDGMENTS

We thank M. E. Parrish for assistance with the fieldwork and R. M. Moody and T. J. T. Murdoch for drafting the illustrations. Fieldwork was supported by a grant from the Smithsonian Institution's Caribbean Coral Reef Ecosystems (CCRE) program, and laboratory analysis was funded by the Dauphin Island Sea Lab (DISL). K. Rützler and M. Carpenter of the CCRE facilitated our fieldwork, which was based at the Smithsonian's Carrie Bow Cay research station and carried out under a research permit from the Belize Department of Fisheries. This is contribution number 833 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Fund; DISL contribution number 393; and contribution number 8 from the Institute for Adaptation to Global Climate Change at the Florida Institute of Technology.

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Climate and Hydrological Factors Affecting Variation in Chlorophyll Concentration and Water Clarity in the Bahia Almirante, Panama

Rachel Collin, Luis D'Croz, Plinio Gondola, and Juan B. Del Rosario

ABSTRACT. Water clarity and productivity are fundamentally important for the distribution of tropical marine organisms. In the Caribbean, changes in nutrient loading that result from rapid development are thought to have caused increased planktonic productivity, reduced water clarity, and reduced reef and seagrass health. Here we analyze chlorophyll *a* concentration and water clarity from eight years of environmental monitoring in Bocas del Toro, Panama. Chlorophyll *a* concentrations did not vary significantly among the six sampled sites and showed no significant temporal changes, despite the recent rapid development in the region, accompanied by scant wastewater treatment. In contrast, water clarity increased significantly during the study period. Because chlorophyll *a* does not vary closely with water clarity, Secchi depths are likely to reflect changes in suspended particulate matter rather than in phytoplankton biomass. Secchi depths decreased with rainfall and wind speed but increased with solar radiation, supporting the idea that clarity was not tightly linked to phytoplankton biomass. The decrease in annual rainfall, but not wind speed, over the past eight years suggests that the long-term trend in Secchi readings is the result of changes in rainfall patterns.

INTRODUCTION

Water clarity and productivity are fundamentally important to the distribution of tropical marine organisms, especially corals. Ocean primary productivity is also important for global geochemistry and carbon sequestration (Falkowski et al., 1998). Global warming and increase in atmospheric CO_2 are expected to influence the distribution of the biota, as well as its abundance, and the photosynthetic activity of phytoplankton (Falkowski et al., 1998). SeaWiFS satellite imagery shows that worldwide oceanic chlorophyll *a* concentrations are about 0.2 mg/m^3 (Yoder et al., 1993) and can reach 5 mg/m^3 in coastal upwelling zones (Falkowski et al., 1991; Walsh et al., 1978). It is difficult to use this method to obtain information on chlorophyll *a* concentrations for many onshore tropical areas because accurate remote sensing is difficult in coastal areas with large sediment input and because many tropical regions have high frequencies of cloud cover. In such areas field measurements of water clarity and chlorophyll *a* concentrations are vital for assessing short-term variation and ground-truthing remote measurements.

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Coral reef environments are particularly sensitive to changes in water quality, especially changes in nutrients, sediment load, and productivity. The paradigm of coral reef biology is that reef development and coral health are greatest in areas with low sedimentation, low primary productivity, low abundances of zooplankton, and high water clarity. These habitats are most conspicuous in the Indo-Pacific and the offshore islands in the Caribbean. In many locations these habitats are suffering from reduction of water quality associated with coastal development (Bell, 1992; Lapointe, 1992). In the Caribbean, most studies of reefs and their waters are conducted in the Bahamas, Puerto Rico, Netherlands Antilles, and other offshore islands (Gilbes et al., 1996; Otero and Carbery, 2005; van Duyl et al., 2002; Webber et al., 2003). In addition there have been some studies of the unusual upwelling sites along the coast of Venezuela and Colombia (Franco-Herrera et al., 2006) and the strongly freshwater-influenced regions around the Yucatan (Herrera-Silveira et al., 2002). However, few studies have examined heavily terrestrially influenced systems without these unusual features in the Caribbean. Here we report the results of eight years of physical climatic and water quality monitoring in Bahia Almirante, an enclosed Caribbean archipelago that is highly terrestrially influenced.

STUDY LOCATION: BOCAS DEL TORO, PANAMA

Three bodies of water surround the Bocas del Toro Archipelago on the Caribbean coast of Panama: the Bahia Almirante and the Laguna de Chiriquí on the landward side, and the Caribbean Sea on the exposed coastal side (Figure 1). The mainland surrounding the region is largely forested, although the completion of a road linking Costa Rica to Bocas del Toro and the rest of Panama in the year

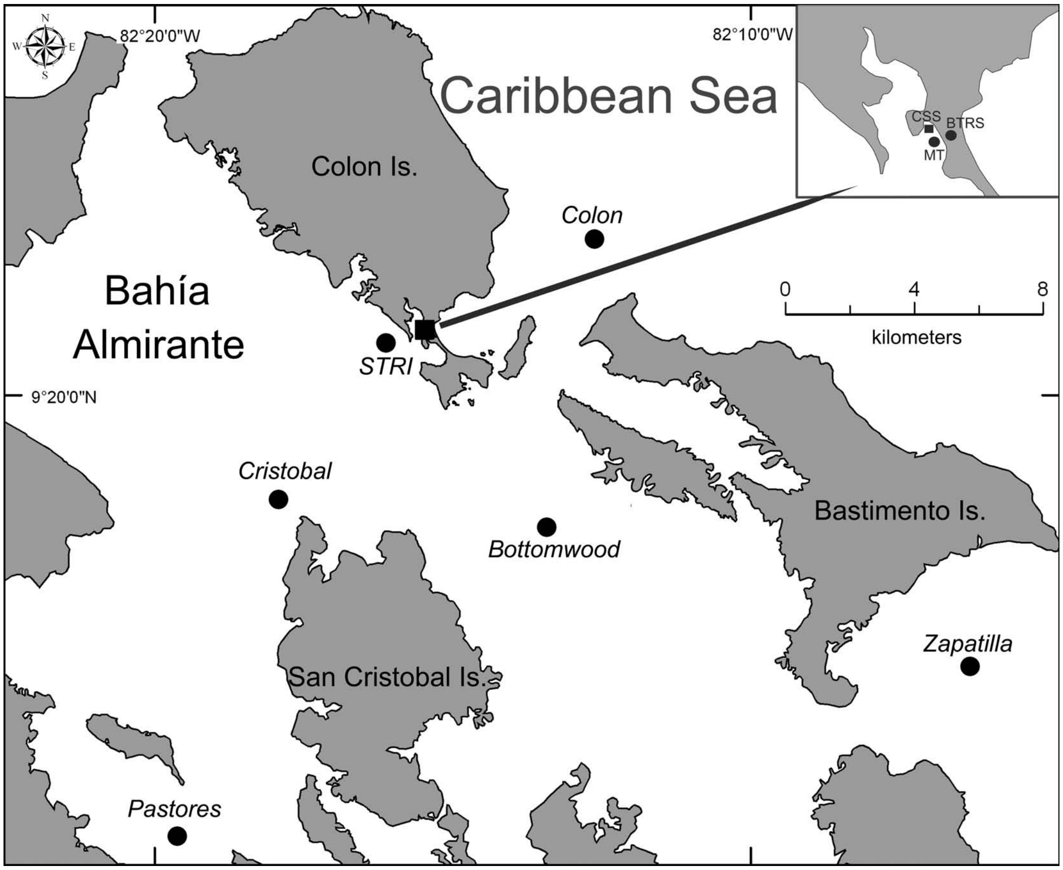

FIGURE 1. Map of the Bahia Almirante region with sampling sites indicated. BTRS = Bocas del Toro Research Station; CSS = CARICOMP seagrass site; MT = instrument platform; STRI = Smithsonian Tropical Research Institute.

2000 has resulted in increased lowland deforestation, as well as land development for small farms and tourism. The landward sides of the islands are fringed with largely intact red mangrove forests, although these are also being cleared from the landward side. The Laguna de Chiriquí, which receives twice the freshwater runoff of Bahia Almirante, has higher nutrient loads and limited coral reef development (D'Croz et al., 2005) and is not discussed further here.

The Bahia Almirante has significantly more oceanic influence than the Laguna de Chiriqui and supports well-developed coral reefs. It receives runoff from only two rivers of any note. High rainfall (about 3 m/year) and runoff from the San San Pond Sac peat swamp forest often result in pronounced haloclines with low-salinity waters (which are often cold) overlying full-salinity bottom waters (Kaufmann and Thompson, 2005). Surface salinities are generally 30–34 PSS (practical salinity scale) but can drop as low as 20 PSS after heavy rains (Kaufmann and Thompson, 2005). Other conditions are relatively aseasonal, with mean sea surface temperatures varying from 27.5°C (January–February) to 29.7°C (September–October). Average wind speed is about 7 km/h but occasionally exceeds 20 km/h (Kaufmann and Thompson, 2005). Despite the high levels of runoff, N:P was always recorded to be below Redfield ratios in a previous survey of the area (D'Croz et al., 2005). This observation suggests that primary productivity could be nutrient limited and that inputs from freshwater runoff or wind mixing could fertilize primary productivity in the Bahia Almirante.

The Smithsonian Tropical Research Institute's Bocas del Toro Research Station is on the Bahia Almirante side of Isla Colon. As part of the development of the scientific knowledge base of the station, and as part of the CARICOMP program, various physical and biological features of the surrounding environment have been monitored since 1999. Here we examine these data (1) to develop a baseline to which future studies can be compared, (2) to determine if the recent rapid development of the region has had an effect on water clarity and phytoplankton biomass, and (3) to explore the physical data to understand what factors influence the variation in these parameters.

MATERIALS AND METHODS

MONITORING HISTORY

Isla Colon is the site of the Smithsonian Tropical Research Institute's Bocas del Toro Research Station. At its inception in 1998 a long-term physical and biological monitoring program was initiated. Physical records of air and water temperature, rainfall, salinity, solar radiation, and wind speed have been kept since 1999 (reviewed in Kaufmann and Thompson, 2005). Monitoring of Secchi depths and chlorophyll *a* concentrations was conducted approximately biweekly at five sites (see Figure 1) from 1999 until 2001. The sampling intervals were not equal (ranging from 7 to 28 days), so these data were not appropriate for time-series analyses.

The Secchi depths and chlorophyll *a* monitoring was reinitiated at three of these sites and at an additional site in 2006 and continues to be measured weekly. At one of these, the CARICOMP reef monitoring site (described in Guzmán et al., 2005), the Secchi depths have been recorded weekly since 2000. At the CARICOMP seagrass site, horizontal Secchi readings have been taken weekly since 1999. During the entire period, measurements were made by the same three-person team.

SAMPLING LOCALITIES

Sampling sites (Figure 1; Table 1) were chosen in 1999 to include a range of environments. In 2006 sites were chosen to include an onshore–offshore gradient, in which we expected more oceanic conditions on one end and terrestrially influenced conditions on the other end.

- Colon, 6.3 km northeast of Bocas del Toro Town, is the most exposed site. The bottom at 20.5 m is muddy. Rough conditions occasionally made it impossible to take measurements in this location.
- Cristobal, in the middle of the Almirante Bay, is a site 7 km from the mainland and surrounded by patch reefs. The bottom at 25 m is muddy.
- Pastores is a semienclosed bay, 500 m from the mainland. It is more heavily influenced by continental runoff and creek discharge than the other sites. Depth at the sampling site is 26 m but a nearby coral reef slopes from 5 to 16 m. Jellyfishes are abundant at this site.
- Smithsonian Tropical Research Institute (STRI) is the site closest to the Bocas del Toro Research Station, 500 m from the shore. This site serves as the water monitoring site for the CARICOMP reef site, which is onshore of this location, over a reef that slopes from 5 to 20 m. The bottom is muddy and sandy with isolated patches of coral.
- Bottomwood, between Solarte and San Cristobal Islands, is protected from oceanic influence. The sampling site is near mangrove islets, sand cays, and a shallow coral reef. The reef slopes to a fine sand bottom at 16 m.

- Zapatillas has the highest diversity and abundance of coral and octocoral species of any of our sampling sites. The bottom at about 15 m is mostly covered by patch reefs and fine sand.
- The CARICOMP seagrass site is several hundred meters along the shore to the northwest of the Bocas del Toro Research Station. This shallow (2 m depth) location has extensive *Thalassia* cover, and the small bay is fringed by red mangroves.

HYDROLOGICAL MEASURES

Water temperature and salinity were recorded with an YSI 85 multiparameter probe (Yellow Springs Instruments, Yellow Springs, Ohio, USA) at the same time and depth as the seawater was sampled. Measurements were taken at approximately 50 cm. Dissolved oxygen was also measured in 2006–2008. Salinity is expressed in the practical salinity scale (PSS) and dissolved oxygen in milligrams per liter.

CLIMATE RECORDS

Rainfall, solar radiation, and wind speed are monitored continuously at the Bocas del Toro Research Station, as described by Kaufmann and Thompson (2005). These measurements are taken close to the STRI site (see Figure 1). For the purposes of this study average rainfall, solar radiation, and wind speed were calculated for 3 days and 6 days before each sampling day. We chose these periods because Beman et al. (2005) showed that phytoplankton blooms can peak 3 to 5 days after nutrient input from terrestrial runoff.

Annual rainfall was obtained in two ways. First, an hourly tipping bucket measured rainfall from 2002. Because data are incomplete for three of the years (including 2008), we calculated the average daily rainfall to standardize across the years. The second estimates were from the Bocas del Toro airport. These records extend to 1999 and were also converted to annual daily averages.

SECCHI DEPTHS

Water clarity was measured by lowering a 30 cm diameter Secchi disk into the water until it was no longer seen and then raised until it reappeared. The Secchi depth was measured according to the length of the submerged rope. This operation was repeated three times at each site during each measurement. At the seagrass site the Secchi was measured horizontally, underwater at 0.5 m depth, and was read with a dive mask.

CHLOROPHYLL *A*

Three replicate water samples were collected by hand at 50 cm below the surface in polyethylene bottles and placed in a cooler for the return to the laboratory. Two liters of each replicate were vacuum filtered on Whatman GF/F (0.7 μm pore size). Filters were wrapped in aluminum foil and stored frozen (−20°C). A Teflon pestle was used

TABLE 1. Study site locations and the data available for each site.

Site	Location	Secchi depths	Chlorophyll *a*
Colon	9°22′37″N	1999–2001	1999–2001
	82°12′37″W	2006–2008	2006–2008
Cristobal	9°18′15″N	2006–2008	2006–2008
	82°17′55″W	–	–
Pastores	9°12′36″N	1999–2001	1999–2001
	82°19′37″W	2006–2008	2006–2008
STRI [a]	9°20′40″N	2000–2008	1999–2001
	82°16′39″W	–	2006–2008
Bottomwood	9°17′47″N	1999–2001	1999–2001
	82°13′25″W	–	–
Zapatilla	9°15′27″N	1999–2001	1999–2001
	82°06′19″W	–	–
CARICOMP seagrass	9°21′06″N	1999–2008	–
	82°15′29″W	Horizontal	

[a] STRI, Smithsonian Tropical Research Institute.

to grind the filters in 5 mL 90% aqueous acetone solution. The slurry was transferred to 15 mL polypropylene screw-cap centrifuge tubes and filled to 10 mL with acetone. The tubes were kept in the dark at −20°C for 24 h. Extracts were centrifuged at 3,000 rpm, and the supernatant was analyzed for chlorophyll *a* following the nonacidification fluorometric method (Welschmeyer, 1994).

STATISTICAL ANALYSIS

Correlation analyses and multiple regression analyses were used to describe the relationships between the variables of interest (Secchi depth and chlorophyll *a* concentration) and the hydrological data and the climate data. Student's *t* test, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) were used to test for differences between sites and sampling periods. Because it is likely that there is a lag in the response of phytoplankton to the input of nutrients from river runoff or turbulence, we looked for correlations between Secchi depths or chlorophyll *a* concentrations and the average of rainfall, solar radiation, and wind speed over the previous 3 and 6 days. Because the 3 day and 6 day results did not differ substantively, only the results using the 3 day average are reported here. Because rainfall and cloud cover are patchy on a local scale, we only examined climatic variables for the STRI and CARICOMP seagrass sites. Time-series autocorrelation analyses were applied to Secchi depth and chlorophyll *a* data. The few weeks of missing data were filled with the averages values for the time series under analysis.

RESULTS

A number of complex relationships were demonstrated between the hydrological parameters, Secchi depths, and chlorophyll *a* concentrations at the different sites. Several of these relationships vary among the sites, and there are a number of interactions between factors; however, the following generalizations can be made. (1) Secchi depths increased with temperature, salinity, and solar radiation, and decreased with rainfall, wind speed, and chlorophyll *a* concentration. (2) Correlations between any hydrological characteristic and Secchi depths or chlorophyll *a* were low (r^2 rarely exceeding 0.10) but were higher for all the climatic variables (rain and solar radiation had r^2 up to 0.22). (3) Chlorophyll *a* concentrations showed no consistent temporal or spatial patterns. (4) Secchi depths were not tightly correlated with chlorophyll *a* concentrations. (5) Secchi depths increased and rainfall decreased throughout the study.

HYDROLOGICAL CONDITIONS AT EACH SITE

Hydrological parameters varied somewhat among the six sites (Table 2, Figure 2). Salinity was significantly different at all sites (ANOVA with post hoc *t* test; Table 2), with the lowest average salinity in Pastores, the most inland site, and the highest average salinity in Colon, the most oceanic site. For 1999–2001 the average temperature at Pastores was significantly higher than the other sites and the temperature at Colon was significantly lower. The temperature

TABLE 2. Summary of physical and biological data from 1999–2001 and 2006–2008.

Site	Years	Temperature, °C (SD)	Salinity,[a] PSS (SD)	Dissolved oxygen, mg/L (SD)	Secchi depth, m (SD)	Chlorophyll *a*, mg/m³ (SD)	Significant changes between periods (*t* test)
Colon	1999–2001	28.1 (1.26)	33.0 (1.70)	–	9.1 (3.6)	0.44 (0.19)	Temperature increased
	2006–2008	28.6 (0.89)	33.5 (1.31)	5.80 (0.43)	10.0 (3.6)	0.47 (0.23)	
Cristobal	2006–2008	28.8 (0.95)	32.9 (1.46)	5.83 (0.49)	12.4 (3.2)	0.46 (0.25)	NA
Pastores	1999–2001	28.6 (1.29)	31.9 (2.15)	–	11.0 (3.3)	0.46 (0.24)	Temperature and Secchi depth increased
	2006–2008	29.2 (0.98)	32.4 (1.76)	5.81 (0.51)	13.2 (3.0)	0.49 (0.28)	
STRI	1999–2001	28.3 (1.16)	32.9 (1.33)	–	10.9 (3.9)	0.37 (0.24)	Temperature and Secchi depth increased
	2006–2008	28.7 (0.91)	33.0 (1.34)	5.78 (0.49)	13.2 (3.6)	0.43 (0.23)	
Bottomwood	1999–2001	28.3 (1.24)	32.7 (1.43)	–	11.9 (3.7)	0.36 (0.19)	NA
Zapatillas	1999–2001	28.3 (1.28)	33.0 (2.78)	–	11.3 (2.6)	0.46 (0.22)	NA

[a] PSS = practical salinity scale.

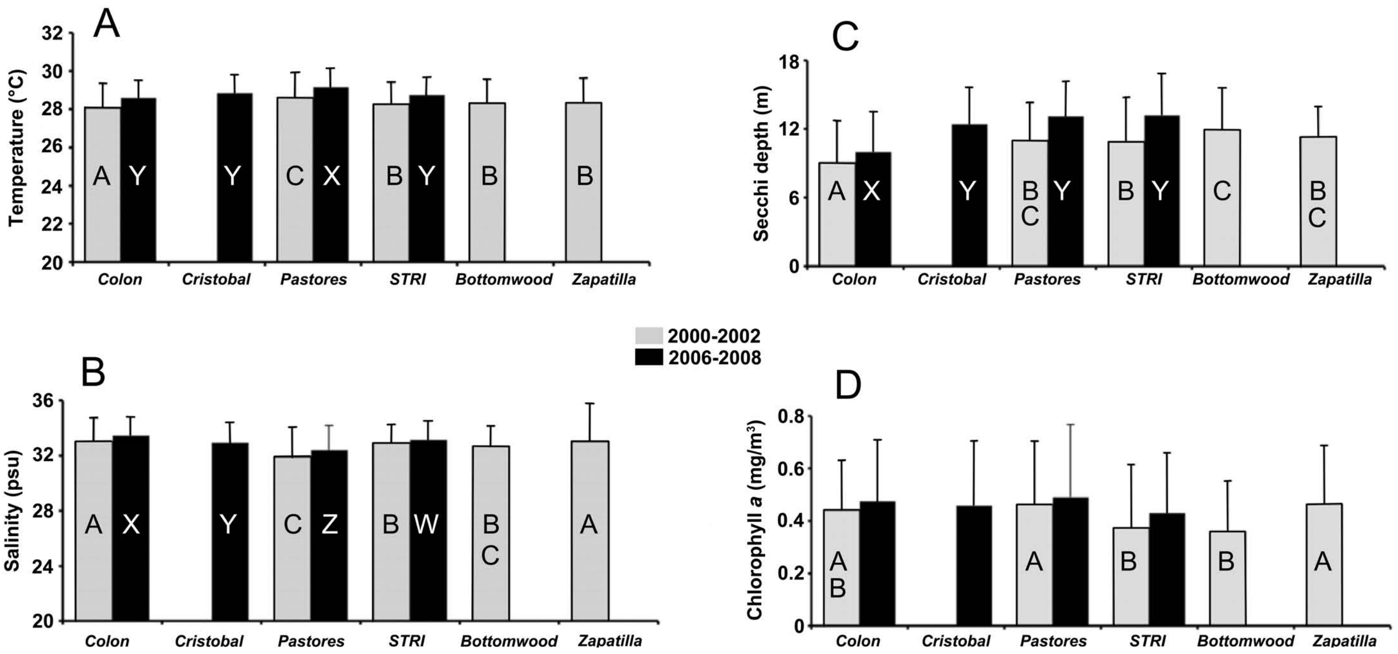

FIGURE 2. Averages of temperature (A), salinity (B), Secchi depths (C), and chlorophyll concentration (D) from the two sampling periods (1999 data excluded). Student's *t* tests showed significant increases in temperature between periods at Colon, Pastores, and STRI and increases in Secchi depth at Pastores and STRI. Single-factor analysis of variance (ANOVA) detected significant ($P < 0.01$) site effects. Significant differences between groups of sites within either sampling period are indicated with letters, so that bars both labeled with "A" are not significantly different from each other but are different from those otherwise labeled with post hoc tests. Specific letters were assigned arbitrarily, but A–C refer to 2000–2002 data and W–Z refer to 2006–2008 data. Bars = one standard deviation (1 SD) of the mean. (Salinity is expressed in the practical salinity scale, PSS.)

at Pastores was also significantly higher than at the other sites in 2006–2008, but there were no significant differences between the remaining sites. Dissolved oxygen did not differ between sites.

Temperature increased significantly between the two time periods at the three sites for which data were available over both periods (*t* test, $P < 0.002$ for each site), despite an overall temperature decrease during the 2006–2008 period. Salinity did not show a significant temporal trend during either time period nor did it differ between the two periods. Dissolved oxygen was only measured for the 2006–2008 period, where it showed no temporal trend. Eight years of data from climatic monitoring at the Bocas Research Station instrument platform shows a downward trend in rainfall, but little change in average solar radiation or average wind speed (Figure 3).

FACTORS AFFECTING SECCHI DEPTHS

Secchi depths ranged from 2 to 22 m, and the depths varied substantially from week to week (Figure 4). Secchi depths showed significant effects of site, and significant associations with temperature, salinity and chlorophyll *a* concentrations during both the 1999–2001 and 2006–2008 periods (ANCOVA; Table 3). The correlation of any one variable with water clarity was low, with

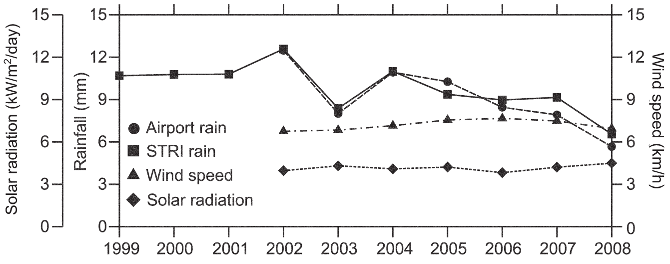

FIGURE 3. Long-term trends in climatic variables. Yearly averages for rainfall, solar radiation, and wind speed during the past 8 years show the decline in average daily rainfall. Daily averages are used because missing data prevent the use of cumulative data. (Rainfall is mm/d.)

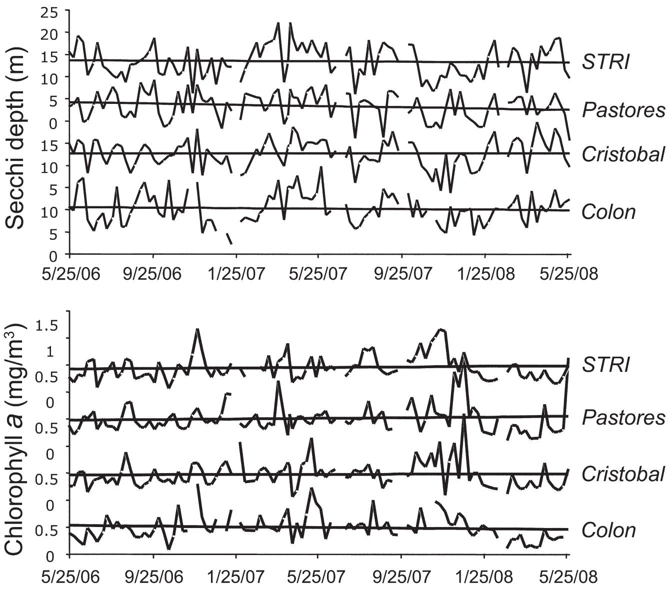

FIGURE 4. Variation in Secchi depths (top graph) and chlorophyll *a* (bottom graph) concentrations over time for the 2006–2008 dataset. Straight line is the trend line of depth or concentration on that date. Superimposed lines show individual variation.

the highest r^2 value for temperature at 0.13–0.17. Secchi depths increased with temperature (Ordinary Least Squares regression [OLS]: 1999–2001, $r^2 = 0.13$, $P < 0.001$; and 2006–2008, $r^2 = 0.17$, $P < 0.001$), and salinity (OLS: 1999–2001, $r^2 = 0.10$, $P < 0.001$; and 2006–2008, $r^2 = 0.06$, $P < 0.001$) and decreased with chlorophyll *a* concentration (OLS: 1999–2001, $r^2 = 0.09$, $P < 0.0001$; and 2006–2008, $r^2 = 0.06$, $P < 0.001$). The average Secchi depth was significantly lower for the exposed Colon site than for the other sites in both time periods (see Table 2, Figure 2). Analysis of the data from the two different periods showed different combinations of interaction effects (see Table 3).

Climatic variables were more tightly correlated with Secchi depth than were the seawater variables. Using the six years of complete climate data from the STRI site, we found that Secchi depths at the STRI site show significant effect of year ($P < 0.0001$), a marginal effect of rainfall ($P = 0.056$), and significant effects of solar radiation ($P = 0.002$) and wind speed ($P < 0.001$), but no significant interactions between these factors. For the CARICOMP seagrass site there was no effect of year, but rainfall and wind speed over the prior 3 days were significant ($P < 0.01$), as well as the interaction between rainfall and solar radiation ($P < 0.0008$). Secchi depth decreased with the amount of rainfall ($r^2 = 0.22$ and 0.23, respectively, with $P < 0.001$) and wind speed ($r^2 = 0.21$; $P < 0.001$) at both sites and increased with solar radiation ($r^2 = 0.21$ and 0.15, respectively, with $P < 0.0001$) at the STRI site but was only significant by its interaction with rainfall in the seagrass site. The interaction at the seagrass site showed that Secchi distances decreased more quickly with rainfall at high levels of solar radiation than at low solar radiation.

Secchi depths increased over the long term: they increased from 1999–2001 to 2006–2008 at Pastores and STRI (*t* test, $P < 0.0001$ for both) but not at Colon. Least squares regression showed a significant increase in Secchi depths ($r^2 = 0.02$; $n = 381$; $P < 0.0002$; slope = 0.3) with date over the 8 years of weekly sampling at STRI. The horizontal Secchi data from the nearby CARICOMP

TABLE 3. Analysis of covariance (ANCOVA) effects of physical variables on chlorophyll *a* concentration and Secchi depth in 1999–2001 and 2006–2008 data after stepwise removal of nonsignificant variables.

Source	*df* [a]	Sum of squares	*F* ratio	*P*
Secchi depth, 1999–2001				
Site	4	235.03	6.78	<0.0001
Temperature	1	100.97	11.65	0.0008
Salinity	1	290.63	33.53	<0.0001
Chlorophyll *a* concentration	1	150.82	17.40	<0.0001
Site*salinity [b]	4	104.02	3.00	0.02
Salinity*temperature [b]	1	67.31	7.76	0.006
Secchi depth, 2006–2008				
Site	3	556.41	21.77	<0.0001
Temperature	1	454.35	53.33	<0.0001
Salinity	1	216.91	25.46	<0.0001
Oxygen	1	2.86	0.33	0.56
Chlorophyll *a* concentration	1	47.15	5.53	0.02
Site*temperature [b]	3	70.34	2.75	0.04
Temperature*oxygen [b]	1	49.58	5.82	0.02
Chlorophyll *a*, 1999–2001				
Site	4	0.38	2.30	0.06
Temperature	1	1.24	30.11	<0.0001
Salinity	1	0.06	1.43	0.23
Site*salinity [b]	4	0.55	3.34	0.01
Salinity*temperature [b]	1	0.31	7.58	0.006
Chlorophyll *a*, 2006–2008				
Temperature	1	0.26	4.90	0.03
Salinity	1	2.41	45.35	<0.0001
Oxygen	1	0.25	4.67	0.03

[a] *df* = Degrees of freedom.

[b] * = Run with only two-way interactions.

seagrass site show no long-term trend. When these values are binned by month, there is a marginal effect of month on the Secchi depths in the seagrass site ($P = 0.07$) and a significant effect of month at the reef site ($P = 0.0007$). Greater Secchi depths were recorded from drier months and sunnier months (Figure 5), a result also found by Kaufmann and Thompson (2005).

FACTORS AFFECTING CHLOROPHYLL A CONCENTRATIONS

Chlorophyll *a* concentration varied between 0.04 and 1.66 mg/m^3. Similar to Secchi depths, concentrations varied substantially from week to week and with no clear seasonal component to the variation (see Figure 4). During the first 14 sampling dates of the 1999–2001 study period, chlorophyll *a* concentrations were measured with a spectrophotometer. An ANOVA testing for effects of site and method showed that the results from the spectrophotometer were significantly higher (site: $F = 3.96$; $df = 4$; $P < 0.005$; method: $F = 26.8$; $df = 1$; $P < 0.0001$; $n = 328$). Therefore values obtained from the spectrophotometer were excluded from the subsequent analyses and this dataset included only data from 2000–2001 or 2006–2008.

Although the average chlorophyll *a* concentrations did not differ between the two periods (*t* test, $P > 0.05$), there were different patterns for the two sampling periods. The only common results were that chlorophyll *a* concentration decreased with temperature, and that the variables examined explained no more than 10% of the variance in chlorophyll *a* concentrations. Data from 2000–2001 showed a significant effect of temperature and a marginal effect of site, but no effect of salinity (ANCOVA; see Table 3). There were significant interactions between site and salinity and between site and temperature (Table 3). Overall, chlorophyll *a* concentrations decreased with temperature (OLS: $n = 328$; $r^2 = 0.06$, $P < 0.0001$). Results from 2006–2008 were different: there were significant effects of temperature and salinity, but not of site or oxygen concentration, nor were there significant interactions (Table 3). Chlorophyll *a* concentrations decreased with temperature (OLS: $n = 402$; $r^2 = 0.03$, $P = 0.002$) and salinity ($r^2 = 0.11$, $P < 0.0001$) but these factors explained very little of the variation.

Climate data were poorly linked to chlorophyll *a* concentrations. Average wind speed for the 3 days before sampling was positively correlated with chlorophyll concentration ($r^2 = 0.19$, $P < 0.005$) but this appeared to be caused by a few periods with extremely high winds. Chlo-

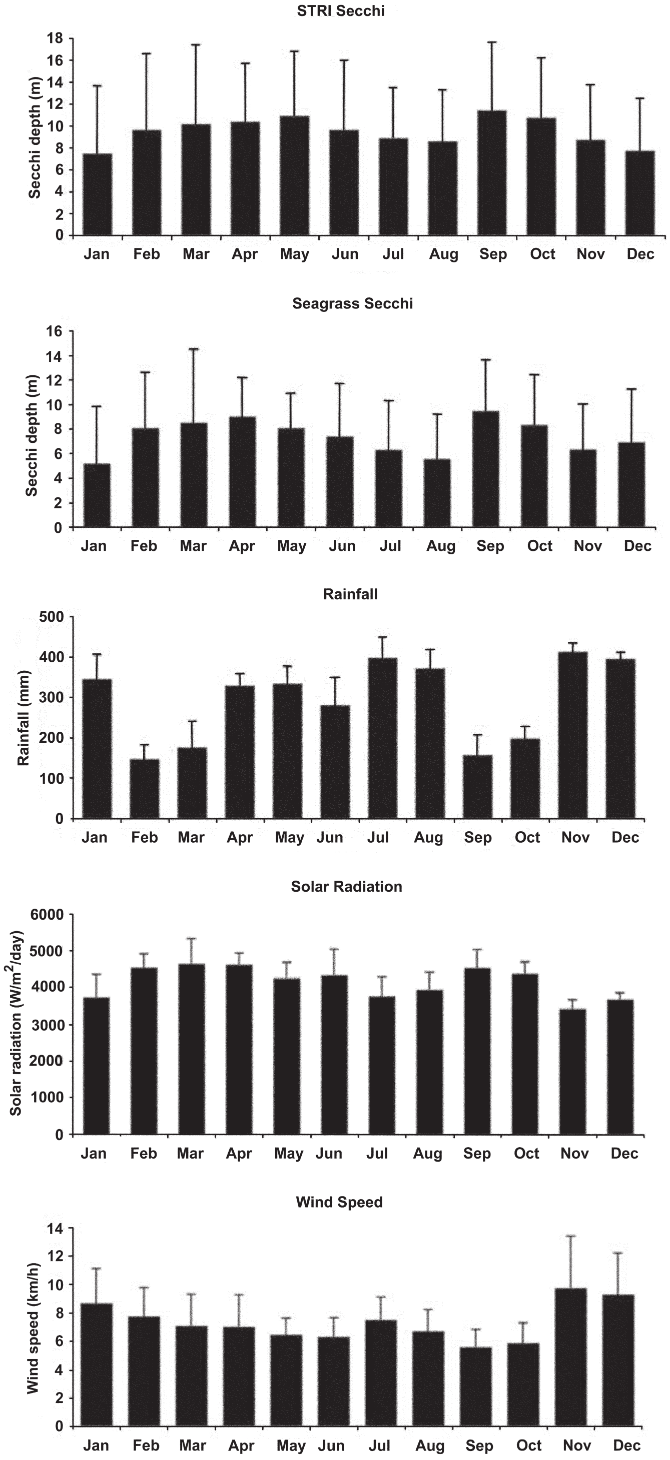

FIGURE 5. Bar graph with monthly averages of Secchi depths, rainfall, solar radiation, and wind speed for the 8-year dataset showing that months with higher average Secchi depths also had lower average rainfall. Bars = 1 SD of the mean.

rophyll *a* concentration was independent of both rainfall over 3 days prior and average solar radiation over the 3 days before the measurements.

TIME SERIES

Both the Secchi depths and chlorophyll *a* concentrations varied considerably from week to week (see Figure 4). To determine if this variation has a temporal autocorrelation, we conducted a time-series analysis. For 1999–2008 Secchi depth is temporally auto-correlated at both the CARICOMP seagrass and the STRI sites (seagrass: Fisher's kappa = 9.9, $P < 0.01$; for coral: Fisher's kappa = 12.2, $P < 0.001$). Over the shorter period, 2006–2008, Secchi depth was temporally auto-correlated at Colon (Fisher's kappa = 8.59, $P < 0.01$), Cristobal (Fisher's kappa = 7.39, $P < 0.02$), and STRI (Fisher's kappa = 6.91, $P < 0.04$) but not Pastores ($P > 0.05$). Chlorophyll *a* concentrations, on the other hand, showed an autocorrelation only for Colon ($P < 0.005$). Examination of the autocorrelation function shows that, over the short term (lag of up to several months), the autocorrelation function appears stationary (Figure 6). However, a peak around the 52 week lag (Figure 6) is evidence of seasonal externally driven periodicity and suggests an annual cycle that is not obvious from plots of the raw data (see Figure 4).

DISCUSSION

The overall values for the data presented here are similar to those reported for the Bahia Almirante by D'Croz et al. (2005), Kaufmann and Thompson (2005), and Carruthers et al. (2005). We report some long-term trends that were not detected by Kaufmann and Thompson, who closely examined the patterns of daily

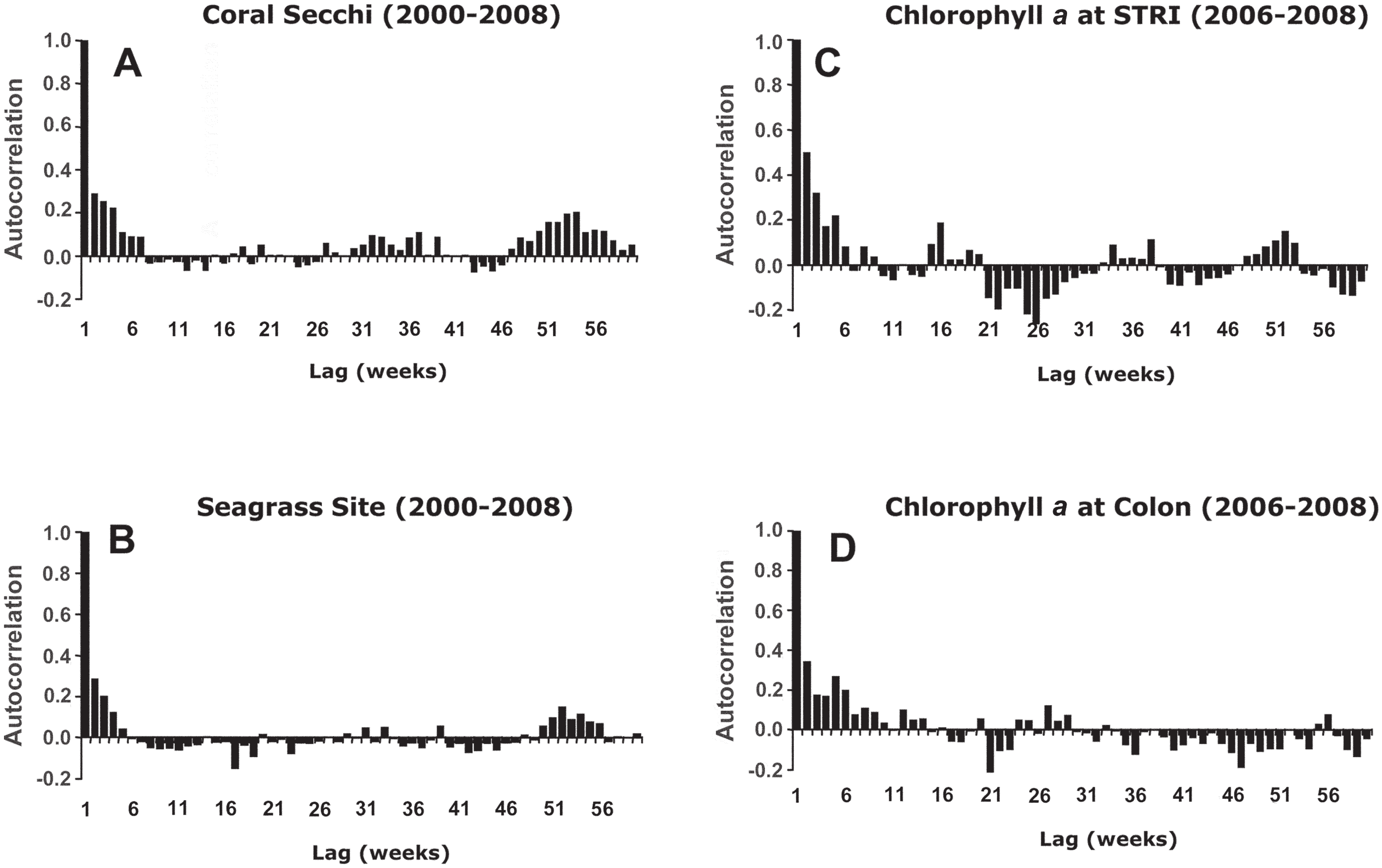

FIGURE 6. Autocorrelation function for 8 years of Secchi data for STRI and CARICOMP seagrass sites and chlorophyll *a* concentrations for 2 years for Colon (significant autocorrelation) and STRI (no significant autocorrelation) sites.

and monthly variation in physical parameters. Comparing the YSI 85 probe measures of temperature and salinity between the 2000–2002 sampling period and the 2006–2008 period, we found significant increases in water temperature and salinity. This finding appears to be associated with the recent trend toward lower rainfall in the region.

Annual rainfall is typically high, in excess of 3,000 mm, in the Bahia Almirante, and the mean freshwater runoff is approximately 1,600 mm per year (IGNTG, 1988). However, average daily rainfall per year dropped from 12.48 mm in 2002 to 7.91 mm in 2007 (see Figure 3). Reduced rainfall likely affected the hydrological conditions in Bahia Almirante, which result from the interaction between river discharge and ocean intrusion (D'Croz et al., 2005). During the 1999–2001 sampling period, rainfall was high and salinity showed the typical increasing trend from Pastores, the site nearest the mainland, to the ocean-exposed sites at Colon and Zapatilla. This pattern in surface salinity is consistent with the expected high dilution at nearshore sites resulting from river discharge into the bay. The inshore-to-offshore salinity gradient was not apparent during the 2006–2008 sampling period, presumably because of the reduction of river discharge and consequent greater influence of salinity from open ocean waters (see Figure 2).

Long-Term Trend in Secchi Depths

The most striking long-term trend we detected was the surprising increase in Secchi disk depths. During the 8 years of monitoring, visibility has increased by 2 m (a rate of 0.25 m/year) for several of the sites. Long-term trends of *decreased* Secchi depths have been reported for monitoring in other areas. For example, in a dataset from the Baltic Sea spanning 77 years, Secchi depths have decreased 0.05 m/year (Sandén and Håkansson, 1996), and a decrease of 0.03 m/year was reported in the Menai Strait in Wales (Kratzer et al., 2003). The few reports of increased Secchi depths were associated with bioremediation or efforts to reduce untreated sewage outfall. For example, Secchi depths increased at 0.05 m/year in Narragansett Bay, Rhode Island, coincident with reductions in anthropogenic total suspended solids (Borkman and Smayda, 1998), as at one of several sampled sites in the Southern California Bight (Convers and McGowan, 1994). Our measures show a much more rapid change in Secchi depths than these previous studies.

The observed changes in Secchi depths were not in the expected direction. A number of complicated, interacting factors can influence water clarity, as measured by Secchi disk, but many of them would indicate a decrease in Secchi depth. The ongoing rapid development of tourism in Bocas del Toro, particularly on Isla Colon, is accompanied by an increase in wastewater input to the Bahia Almirante. Changes in Secchi readings can reflect changes in particulate matter (from runoff or wind-induced turbidity) but can also be caused by changes in phytoplankton biomass or yellow pigments (mostly humic and fulvic acids) in the water. Deforestation and coastal development can affect all three of these factors. Inputs from untreated wastewater as well as runoff from deforested areas can increase the nutrients, particulate matter, and yellow pigments in the water. In addition, increased nutrients often lead to increased primary productivity, which can result in higher standing phytoplankton biomass. These anthropogenic effects have been increasingly affecting coral reef habitats throughout the Caribbean, where wastewater disposal is the leading cause for eutrophication and decreased water clarity (Szmant, 2002). We had expected to see a long-term reduction in water clarity as a result of similar changes in Bocas del Toro.

Secchi depth is often strongly correlated with chlorophyll *a* concentration and has been used as a proxy for productivity in highly seasonal upwelling zones or temperate lakes. This method is often favored because it is cheaper, faster, and easier to obtain than a quantification of chlorophyll *a* concentration. Sandén and Håkansson (1996) reviewed four studies as well as their own data that showed a relationship between Secchi depths and chlorophyll *a* concentrations. The relationships are reported as power functions and show chlorophyll *a* to scale with Secchi depth to the 1.47–2.6 power. Megard and Berman (1989) showed that the proportion of light attenuation caused by chlorophyll concentration differed between neritic and pelagic seawater, but there were clear relationships nonetheless. Here we found that chlorophyll *a* concentration explained only 6%–9% of the variance in Secchi depths. In addition, mean chlorophyll *a* concentrations were relatively low in the Almirante Bay, near 0.5 mg m^{-3}, which is the suggested threshold value for oligotrophic conditions required for coral reef development (Bell, 1992). Therefore, these measures are not consistent with the presence of phytoplankton blooms resulting from anthropogenic nutrient enrichment. They do, however, suggest that even small increases in nutrients or chlorophyll *a* concentrations in this region could result in a shift from coral-dominated to algal-dominated benthic communities.

It seems unlikely to us that there has been a drop in the load of anthropogenic suspended solids and/or nutrients during the past eight years, despite the probable decrease in the volume of runoff. In fact, it appears that, if anything, these inputs have increased. So, what is the cause of the long-term trend in Secchi depth? The correlation analysis and the monthly trends (see Figure 5) both suggest that rainfall and solar radiation are the most closely associated with Secchi depth. However, rainfall is the only variable showing a strong annual trend consistent with the increased Secchi depths, and rainfall over the three days before the measurements was the variable most highly correlated with Secchi depths of any hydrological or climate variable examined. Solar radiation, although it is positively correlated with Secchi depths on the reef, does not show the pronounced long-term trend that rainfall does. The effect of wind on Secchi depth similarly does not explain the long-term trend. It could, however, explain the fact that Colon, the most exposed site, with the highest winds had consistently lower Secchi depths than the other sites. Wind-induced turbidity, which resuspends bottom sediment, is the likely cause of the limited water clarity at this site.

CONCLUSION

The baseline data reported here will be useful for future studies of anthropogenic effects in the unique Bocas del Toro archipelago. Rapid local development is progressing in the face of little information on the impact of such development and the factors affecting such impacts (e.g., water residence time or currents in the Bahia Almirante). It is likely that anthropogenic inputs of nutrients and suspended particulate matter will contribute to eutrophication of some areas. This study suggests that despite the impact of development, patterns of water clarity and chlorophyll *a* concentrations in the region are currently driven mainly by large-scale climate patterns. There is little evidence of a tight relationship between these measures and features of the local water mass, nor is there evidence of eutrophication at the sites we sampled. Future sampling closer to highly developed areas is necessary to document and monitor the impact of development on water quality.

ACKNOWLEDGMENTS

We thank Arcadio Castillo for help in the field, James Roper for comments on the manuscript, the Hunterdon and Johnson Oceanographic Research Endowments for financial support, and Empresa de Transmisión Eléctrica Panamá for supplying the rainfall data from the Bocas del Toro airport.

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Nutrient and Chlorophyll Dynamics in Pacific Central America (Panama)

Luis D'Croz and Aaron O'Dea

ABSTRACT. Strong wind jets from the Caribbean and the Gulf of Mexico cross Central America through topographic depressions in the cordillera during the boreal winter, pushing Pacific coastal waters offshore, lowering sea levels at the coast, and causing coastal upwelling. Where high mountains impede the winds, this phenomenon does not occur. The Panamanian Pacific shelf is an excellent example of this variability. The coast is divided into two large areas, the Gulf of Panama and the Gulf of Chiriquí. To investigate hydrological conditions between the two gulfs, we sampled the water column during upwelling and non-upwelling seasons in each region. In both gulfs during non-upwelling conditions, surface-level nutrients are poor, and the chlorophyll maximum occurs around 30 m where the thermocline intersects the euphotic zone. Oxygen-poor waters (<2 ppm) commonly occurred below the thermocline. During the dry season, wind strength increased and strong upwelling was observed in the Gulf of Panama. The thermocline rose and surface waters became nutrient enriched and chlorophyll *a* levels increased. Well-oxygenated waters were compressed to shallow depths. In the Gulf of Chiriquí, wind strength was weaker, surface waters did not become enriched with nutrients, and surface chlorophyll *a* remained low. We did observe a shallowing of the thermocline in the Gulf of Chiriquí, but in contrast to the Gulf of Panama, wind mixing was not strong enough to result in sea-surface cooling and nutrient enrichment. We postulate that the convergence of a shallow thermocline and internal waves in the Gulf of Chiriquí is the likely mechanism that causes pockets of deep water to occasionally migrate into surface waters, leading to restricted and ephemeral upwelling-like conditions. Although its effects upon shallow-water communities remain to be studied, we propose that the process may be more likely to occur during the boreal winter when the thermocline is shallower.

INTRODUCTION

One of the most pervasive hydrological events to influence the shelf waters of Pacific Central America is upwelling. Intermittent or seasonal upwelling develops in the gulfs of Tehuantepec (Mexico), Papagayo (Costa Rica), and Panama (Legeckis, 1988; McCreary et al., 1989; Xie et al., 2005), driving extensive planktonic productivity and shaping the secondary production of biological communities (Jackson and D'Croz, 1997; O'Dea and Jackson, 2002).

The shelf waters along the Pacific coast of Panama are among the most dynamic in the region. Here, the coastal shelf is naturally divided into two large gulfs by the Azuero Peninsula: the Gulf of Panama (shelf area, 27,175 km^2) and the Gulf

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of Chiriquí (shelf area, 13,119 km^2) (Figure 1). The Gulf of Panama experiences strong seasonal upwelling while the Gulf of Chiriquí exemplifies a non-upwelling environment (Dana, 1975; Kwiecinski and Chial, 1983). This distinction is customarily explained using geographic differences between the two gulfs. Seasonal upwelling in the Gulf of Panama develops during Panama's dry season, corresponding to the boreal winter, when northeast trade winds cross to the Pacific over low areas in the isthmian mountain range, pushing warm and nutrient-poor coastal surface water offshore, lowering the nearshore sea level, and causing the upward movement of colder and nutrient-richer deep water (Smayda, 1966; Forsbergh, 1969; Kwiecinski et al., 1975; D'Croz et al., 1991; D'Croz and Robertson, 1997). The established model proposes that because western Panama has higher mountain ranges that block the winds, surface waters in the Gulf of Chiriquí are not displaced out to the Pacific, and no upwelling as such occurs there.

The structure of shallow biological communities between the two regions supports this inference. Coral reefs, which respond poorly to upwelling conditions, are more extensive in size in the Gulf of Chiriquí than in the Gulf of Panama (Glynn, 1977; Glynn and Maté, 1997), whereas small pelagic fish species from the Gulf of Panama represent a large proportion of the total estimated fishery resource in the country (NORAD, 1988). Satellite imagery shows both wind speeds and chlorophyll content of surface waters to be lower in the Gulf of Chiriquí than the Gulf of Panama during the dry seasons (Pennington et al., 2006).

However, the statement that upwelling does not occur in the Gulf of Chiriquí is supported by sea-surface data derived from satellite imagery analysis or from the measurement of properties in the shallow section of the water column. Hydrological profiles of the water column have documented the shoaling of the thermocline in the Gulf of Chiriquí, yet there appears to be no clear association between the physical forcing of this event with the wind-induced upwelling in the Gulf of Panama. Nevertheless, the movement of pockets of cool water that bring nutrients into the upper layer may be a more common occurrence in the Gulf of Chiriquí than previously suspected (D'Croz and O'Dea, 2007).

It is therefore essential that we obtain detailed and comparable hydrological data from both gulfs if we wish to explain variability in biological communities along the Pacific coast of the Isthmus of Panama today and through geologic time (O'Dea et al., 2007). In this paper we expand the information presented in our previous study (D'Croz and O'Dea, 2007), adding new hydrological and biological data from the Gulf of Chiriquí and the Gulf of Panama, and we further discuss the issue of whether upwelling takes place in the Gulf of Chiriquí.

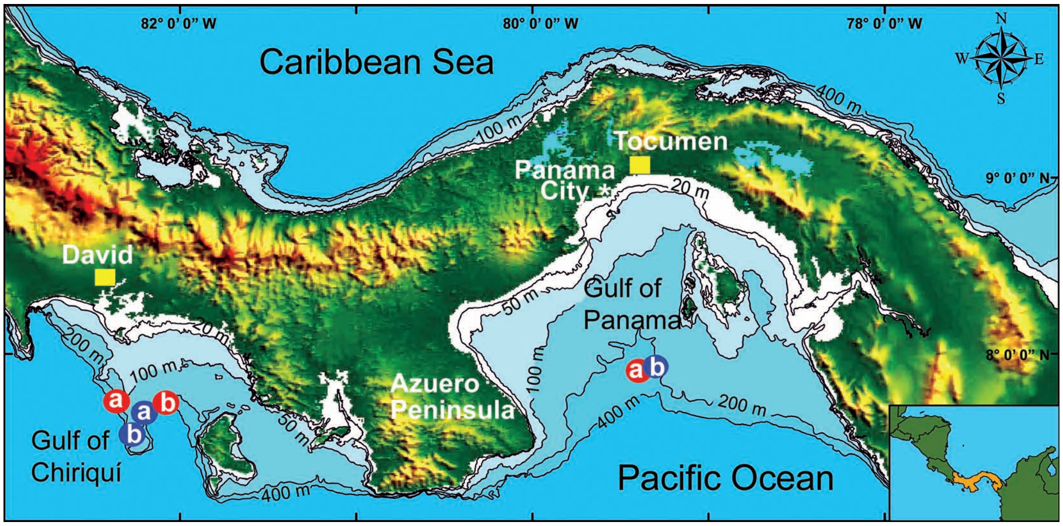

FIGURE 1. Map of the Republic of Panama showing sampling sites. Red dots represent the location of the rainy season samplings in the Gulf of Panama (a = 18 December 2004) and in the Gulf of Chiriquí (a = 13 July 2003; b = 17 December 2004). Blue dots represent the location of the dry season samplings in the Gulf of Panama (a = 29 February 2000) and in the Gulf of Chiriquí (a = 1 March 2000; b = 13 April 2007). Yellow squares indicate the location of the meteorological stations.

MATERIALS AND METHODS

STUDY AREA

Panama's Pacific shelf is located from 07°30′ to 09°01′N and 78°10′ to 82°52′W. The shelf is predominantly occupied by low-salinity surface water, similar to the water mass found over the center of the tropical Pacific Ocean at about 10°N (Wyrtki, 1967; Fiedler and Talley, 2006). The climatology is governed by the Inter-Tropical Convergence Zone (ITCZ), the position of which defines the seasonal pattern of rainfall and winds. The rainy season develops between May and December when the ITCZ is located over or slightly to the north of Panama and winds are light and variable in direction. The dry season develops between January and March when the ITCZ moves south of Panama, a time period characterized by predominating intense northeast trade winds. The mean annual rainfall recorded at meteorological stations near the coast (1999–2004) was 2,760 mm in the Gulf of Chiriquí (David) and 1,880 mm in the Gulf of Panama (Tocumen). Approximately 94% of the annual rainfall in both areas corresponded to the rainy season, the months of September and October being the rainiest in both regions. The estimated sizes of the drainage basins are 11,846 km^2 in the Gulf of Chiriquí and 33,828 km^2 in the Gulf of Panama. River discharges into both gulfs typically follow the seasonal trend described for rainfall. Detailed discussions on wind-stress, rainfall, and river discharge patterns are presented in D'Croz and O'Dea (2007). The tidal regime is semidiurnal, and the sea-level difference during spring tides is 6 m (Glynn, 1972).

SAMPLING PROCEDURES

Sampling research cruises were conducted in the gulfs of Panama and Chiriquí using the Smithsonian Tropical Research Institute's R/V *Urracá* (see Figure 1). Samplings were scheduled to correspond with different times of the year, representing contrasting hydrological conditions (upwelling and non-upwelling). Surface-to-bottom profiles for salinity, temperature, dissolved oxygen, and chlorophyll *a* were recorded with a CTD (conductivity, temperature, depth) multiparameter profiler (Ocean Seven 316, Idronaut Srl, Milano, Italy). Hydrological casts with the CTD corresponding to the dry season were carried out in both gulfs on 29 February 2000 and 1 March 2000 and in the Gulf of Chiriquí on 13 April 2007. Rainy season CTD casts were carried out in the Gulf of Chiriquí on 13 July 2003 and in both gulfs during 17 and 18 December 2004. The water column was sampled at discrete levels to study nutrient and chlorophyll *a* concentrations. Water samples were collected using Niskin bottles during the dry season of the year 2000 (29 February to 1 March) and during the rainy season of the year 2004 (17 and 18 December). Three replicate water samples per selected depth were collected at each site. Two liters of each individual replicate water sample were immediately sieved through Nitex (350 μm) to exclude zooplankton and vacuum filtered on Whatman GF/F filter (0.7 μm pore size) for chlorophyll *a* analysis. An aliquot from each filtrate was set apart for the determination of dissolved inorganic nutrients. Filters and water samples were stored frozen (−20°C) until analysis. Salinity is expressed using the Practical Salinity Scale (pss) indicated by UNESCO (1981). Results from the chlorophyll *a* analyses were used to check the calibration of the CTD's fluorometer. The depth of the euphotic zone (1% incident radiation) was estimated from Secchi disk readings (Parsons et al., 1984). The light attenuation coefficient was calculated as K_d = f/zs where zs is the Secchi depth and f = 1.4.

ANALYSIS OF SAMPLES

Not later than two weeks after sampling, filters holding the phytoplankton were analyzed for chlorophyll *a* using the non-acidification fluorometric method (Welschmeyer, 1994). Water samples were analyzed for $NO_3^- + NO_2^-$ (nitrate + nitrite), $Si(OH)_4$ (silicate), and PO_4^{3-} (phosphate) by colorimetric methods using an Alpkem Flow Solution IV automated analyzer. Minimum detection limits were 0.02 μM for nitrate, 0.01 μM for nitrite, 0.12 μM for silicate, and 0.02 μM for phosphate.

ANALYSIS AND PRESENTATION OF DATA

Water quality variables, namely temperature, salinity, dissolved oxygen, dissolved inorganic nutrients, and chlorophyll *a*, are presented graphically as profiles of the samplings. Overall differences in between the two gulfs were assessed with the Mann–Whitney test (*U*) by taking the median of each variable from samples collected in the top 30 m of the ocean where the highest hydrological variability occurred (Table 1). Water transparency data were compared using the paired *t* test. We followed the practice of taking the position of the 20°C isotherm to represents the depth of the center of the permanent thermocline in the eastern Pacific Ocean (Wyrtki, 1964; Fiedler et al., 1991; Xie et al., 2005). Pearson correlations with Bonferroni adjustment were used to test statistical relationships among variables.

TABLE 1. Average value of hydrological variables in the top water column (30 m) in the gulfs of Panama (GP) and Chiriquí (GC); SE = standard error of the mean. Statistical tests were either Mann–Whitney *U* test or paired *t* test ($^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, ns = nonsignificant).

Hydrological variables	Dry season values			Rainy season values		
	GP (Mean ± SE)	GC (Mean ± SE)	Statistical value [a,b]	GP (Mean ± SE)	GC (Mean ± SE)	Statistical value [a,b]
Temperature (°C)	17.97 ± 0.92	27.17 ± 0.92	16.0* [a]	26.75 ± 0.54	28.61 ± 0.05	18.0 ns [a]
Salinity (pss) [c]	34.18 ± 0.29	32.98 ± 0.29	12.0* [a]	31.67 ± 0.64	30.48 ± 0.38	3.0 ns
Chlorophyll *a* (μg L^{-1})	1.82 ± 0.65	0.83 ± 0.65	4.0* [a]	0.23 ± 0.13	0.18 ± 0.06	8.5 ns [a]
Dissolved oxygen (ppm)	3.45 ± 0.27	4.78 ± 0.27	13.0* [a]	3.98 ± 0.16	4.38 ± 0.01	4.0 ns [a]
NO_3^- (μM)	14.37 ± 2.48	3.72 ± 2.48	1.0** [a]	0.99 ± 0.34	0.36 ± 0.02	2.5 ns [a]
PO_4^{3-} (μM)	1.08 ± 0.21	0.39 ± 0.21	1.0** [a]	0.43 ± 0.07	0.24 ± 0.03	4.0 ns [a]
N:P ratio	12.82 ± 1.10	7.77 ± 1.10	1.0** [a]	2.11 ± 0.36	1.49 ± 0.10	3.0 ns [a]
$Si(OH)_4$ (μM)	8.99 ± 1.03	4.40 ± 1.03	5.0* [a]	5.40 ± 0.71	4.87 ± 0.47	13.0 ns [a]
Secchi depth (m)	4.20 ± 0.00	14.80 ± 0.00	−1591.0*** [b]	20.00 ± 0.00	19.00 ± 0.00	2.0 ns [b]
Euphotic zone (m)	13.8 ± 0.00	48.63 ± 0.00	−1394.2*** [b]	65.71 ± 0.00	62.43 ± 0.00	188.4 ns [b]

[a] Mann–Whitney *U* test.

[b] Paired *t* test.

[c] pss = practical salinity scale.

RESULTS

THERMOHALINE STRUCTURE

Both the Gulf of Panama and the Gulf of Chiriquí exhibit the typical tropical coastal ocean water structure of cool deep waters leading upward to a shallow thermocline topped by warm surface waters. However, significant differences occur between the two gulfs with respect to climatic variability. During the rainy season, the thermal structure in both gulfs is remarkably similar (see Table 1). Sea-surface temperatures (SSTs) are invariably warm (27°–28°C), and the thermocline sits at approximately 60 m (Figure 2).

During the dry season, thermal conditions become dissimilar between the two regions (Table 1). In our observations, the thermocline in the Gulf of Panama rose sharply and nearly broke at the surface, resulting in a significant cooling of surface waters to 22°C (Figure 3a). Simultaneously, the thermocline in Gulf of Chiriqui rose to around 30 m, compressing warm SSTs into shallow waters (Figure 3b). However, the shoaling of the thermocline in Chiriquí was not as intense as that seen in the Gulf of Panama and did not result in SST cooling.

In general, salinity profiles in both regions revealed a sharp gradient from high-salinity deep water to fresher surface waters. Seasonal variability in surface salinities in both gulfs was very similar (Table 1). During the rainy season, both regions experienced high freshwater dilution in the upper-layer waters, with surface salinities below 30 on the pss (see Figure 2). The halocline was located at 60 m depth, coinciding with the thermocline. During the dry season, lower rainfall led to increased salinities in the surface waters of both gulfs (Figure 3). However, the effect was more striking in the Gulf of Panama as the halocline shoaled and salinity in surface waters reached 34.

In April 2007, the thermohaline structure in the Gulf of Chiriquí departed drastically from the typical condition as the thermocline/halocline shoaled to 20 m. Despite this condition, however, SSTs remained warm (Figure 3c).

CHLOROPHYLL

Concentrations of surface chlorophyll were always below 0.30 μg/L in both gulfs during the rainy season (Table 1), but a deep chlorophyll maximum developed from 30 m to 50 m, lying above the thermocline (Figure 2). The deep chlorophyll maximum contained most of the chlorophyll *a* in the water column in both gulfs, concentrations reaching 1 μg/L during the rainy season. The dry season upwelling changed this pattern in the Gulf of Panama, as the chlorophyll maximum moved into shallower waters, where concentrations surpassed 4 μg/L (Figure 3a). Surface chloro-

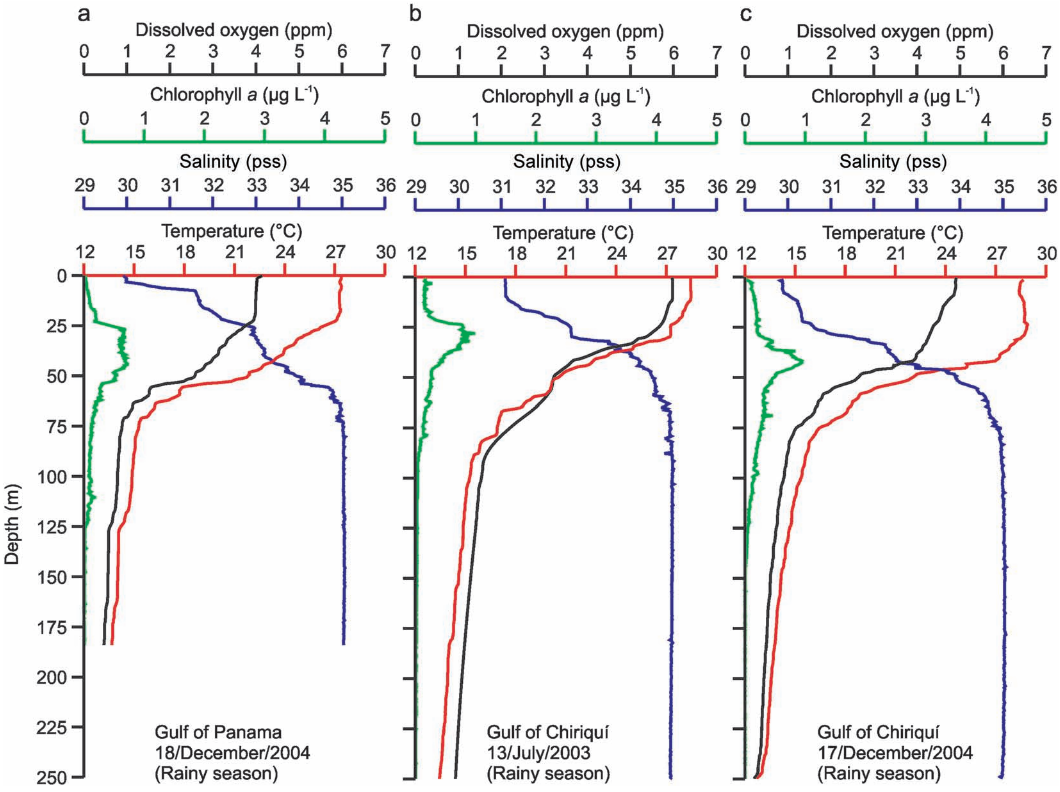

FIGURE 2. Profiles of dissolved oxygen, chlorophyll *a*, salinity, and temperature in the Gulf of Panama and the Gulf of Chiriquí during the rainy season. a = Gulf of Panama, 18 December 2004; b = Gulf of Chiriquí, 13 July 2003; c = Gulf of Chiriquí, 17 December 2004.

phyll *a* remained at very low values in the Gulf of Chiriquí during the dry season, but the deep chlorophyll maximum became remarkably intense at 30 m where concentration reached 3 µg/L (Figure 3b).

DISSOLVED OXYGEN

Dissolved oxygen profiles followed the typical pattern of well-oxygenated surface waters lying on top of deeper oxygen-poor waters. During the rainy season, severe hypoxic conditions (<2 ppm) were recorded below the strong oxycline, at 50 m and nearly coincident with the thermocline (see Figure 2). Oxygen concentrations in waters above the thermocline were strongly correlated with temperature in both the Gulf of Panama ($r = 0.91$; $P < 0.001$) and the Gulf of Chiriquí ($r = 0.89$; $P < 0.001$) during the rainy season. This arrangement, however, had strong seasonal variation in the Gulf of Panama during the dry season, as the oxycline rose to 25 m and compressed the oxygenated waters into shallow depths (Figure 3). Dissolved oxygen below this depth rapidly declined to less than 1 ppm (Figure 3a), whereas waters in the Gulf of Chiriquí only became hypoxic below the 50 m oxycline (Figure 3b). No correlations were confirmed between dissolved oxygen and temperature in any of these regions during the dry season.

DISSOLVED NUTRIENTS

Both gulfs exhibit a strong vertical gradient of upwardly decreasing nutrient concentrations. Nitrate in surface waters was depleted in both gulfs during the rainy season, with values below 0.5 µM (Figure 4). During the dry season, nitrate concentrations at the surface were observed to increase 10 fold in the Gulf of Panama when the nutricline shoaled to around 10 m (Figure 5a). No similar surface enrichment was detected in the Gulf of Chiriquí, where a strong nutricline was developed at 60 m (Figure 5b).

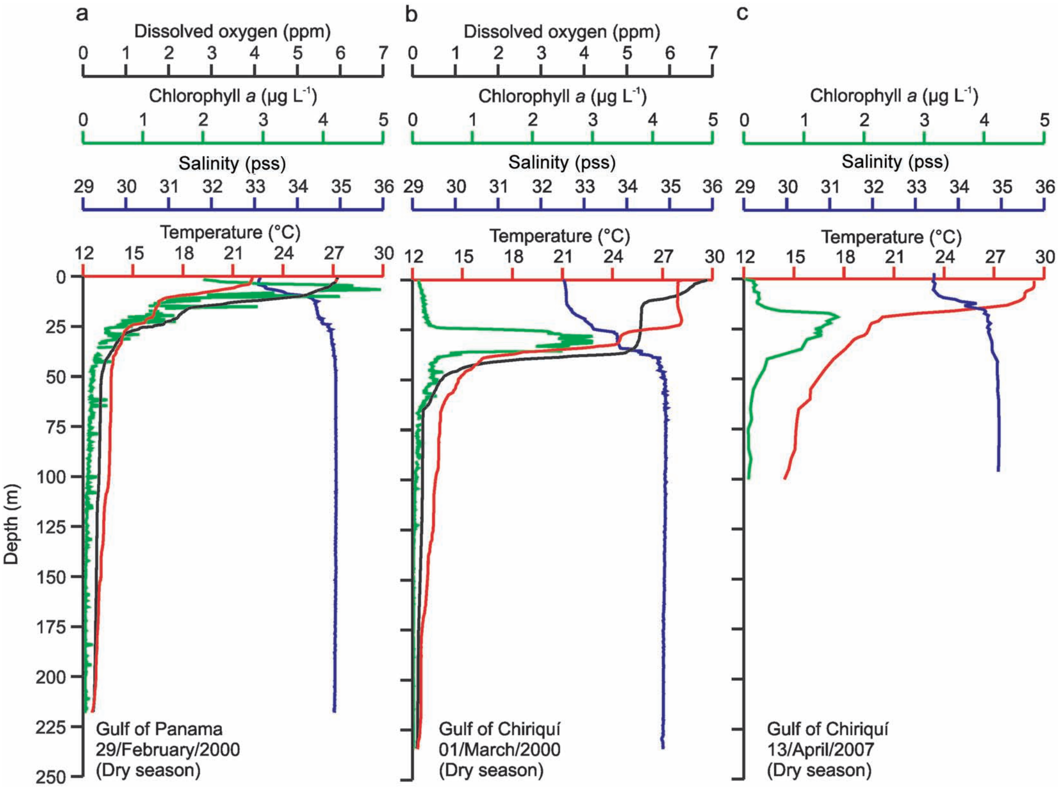

FIGURE 3. Profiles of dissolved oxygen, chlorophyll *a*, salinity, and temperature in the Gulf of Panama and the Gulf of Chiriquí during the dry season. a = Gulf of Panama, 29 February 2000; b = Gulf of Chiriquí, 1 March 2000; c = Gulf of Chiriquí, 13 April 2007.

Overall, the patterns of phosphate resembled those of nitrate, but concentrations were lower by an order of magnitude. Concentrations of phosphate in excess of 1 µM were usually found below 30 m depth. Phosphate concentrations in surface waters remained relatively low (<0.3 µM) in the Gulf of Chiriquí during both climatic seasons (Figures 4b, 5b). However, phosphate enrichment of surface waters clearly occurred in the Gulf of Panama during the dry season when the nutricline shoaled and phosphate concentrations in the top of the water column reached about 1.0 µM (Figure 5a).

Silicate profiles followed similar trends to that of the nitrate and phosphate (Figures 4, 5). Although silicate concentrations were similar in surface waters in both gulfs during the rainy season, they doubled in the Gulf of Panama during the dry season (Table 1).

Dissolved nutrients in the upper 50 m had a high degree of relationship with temperature and salinity. During the rainy season, nitrate concentrations were inversely correlated to temperature in both the Gulf of Chiriquí (r = –0.78; $P < 0.001$) and the Gulf of Panama (r = –0.97; $P < 0.002$). In the dry season, nitrate in the Gulf of Panama was negatively correlated to temperature (r = –0.98; $P < 0.044$) and directly related to salinity ($r = 0.98$; $P < 0.049$). Nitrate was negatively correlated to temperature in the Gulf of Chiriquí during the dry season (r = –0.89; $P < 0.016$), but not to salinity ($r = 0.67$; $P > 0.159$). Phosphate was negatively correlated to temperature during the dry season in the Gulf of Panama (r = –0.98; $P < 0.038$) and in the Gulf of Chiriquí (r = –0.97; $P < 0.036$). Dry season phosphate was also correlated to salinity in the Gulf of Chiriquí ($r = 0.98$; $P < 0.05$).

The extremely low nitrate to phosphate ratios (N:P) suggest that phytoplankton growth in both regions was under severe nitrogen limitation during the rainy season (Figure 6). The N:P ratio was below 2:1 in surface water and increased with depth, surpassing the value of 10:1 below the depth of 50 m. During the dry season, N:P ra-

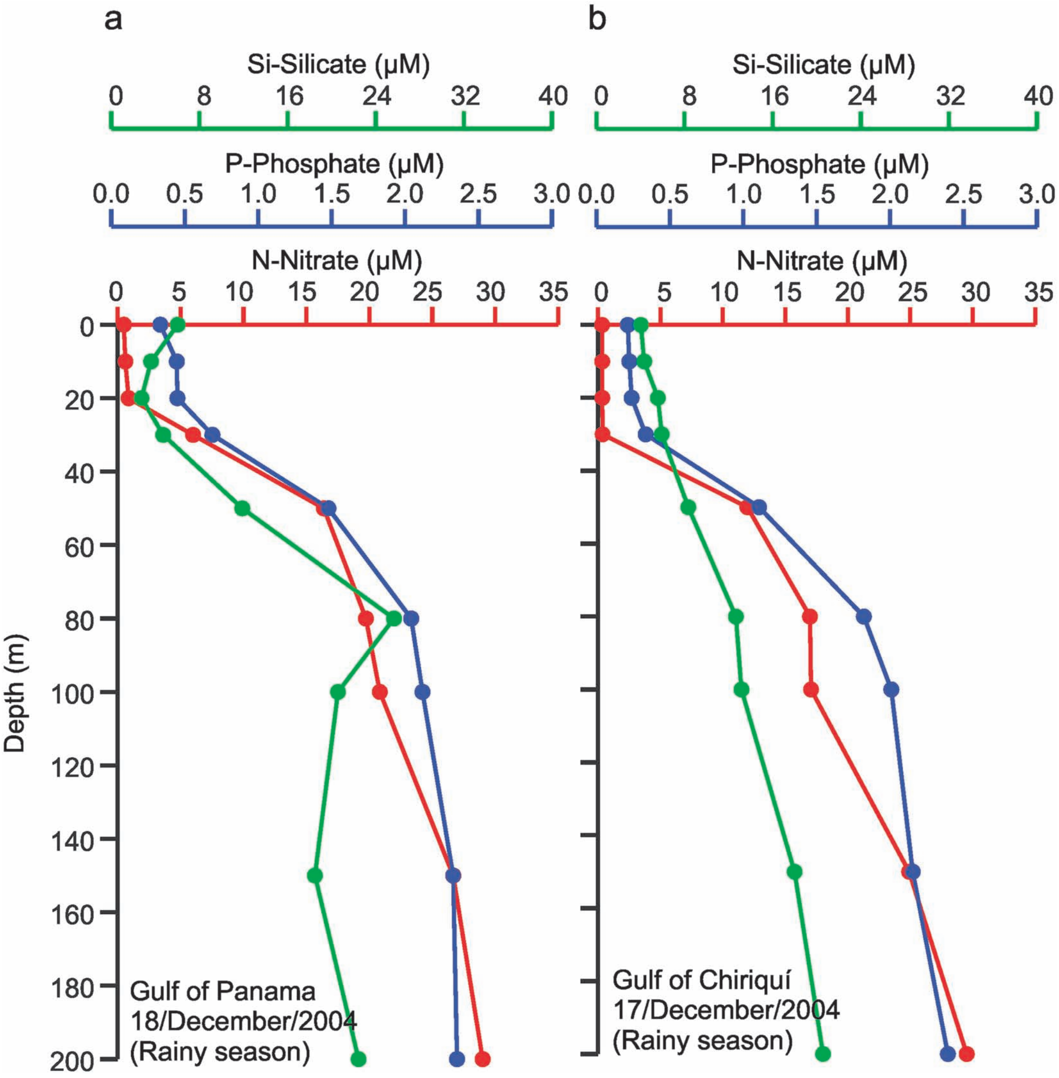

FIGURE 4. Mean profiles of silicate (Si), phosphate (P), and nitrate (N) in the Gulf of Panama and the Gulf of Chiriquí during the rainy season. a = Gulf of Panama, 18 December 2004; b = Gulf of Chiriquí, 17 December 2004.

tios within the euphotic zone largely increased in both regions, becoming closer to the N:P ratio of 16:1 suggested as favorable for phytoplankton growth (Redfield, 1958).

WATER TRANSPARENCY

Water transparency was seasonably stable in the Gulf of Chiriquí but varied considerably in the Gulf of Panama (see Table 1). Water transparency in both gulfs was higher during the rainy season when the euphotic zone was approximately 60 m deep, in contrast to the limited transparency and shallow euphotic zone (14 m) observed in the Gulf of Panama during the dry season upwelling.

DISCUSSION

Our data on bottom-to-surface profiles reveal the dynamics of hydrological conditions along the Pacific coast of Panama during times of both upwelling and non-upwelling. During the non-upwelling rainy season, both gulfs exhibit extremely similar hydrological structures dominated by the

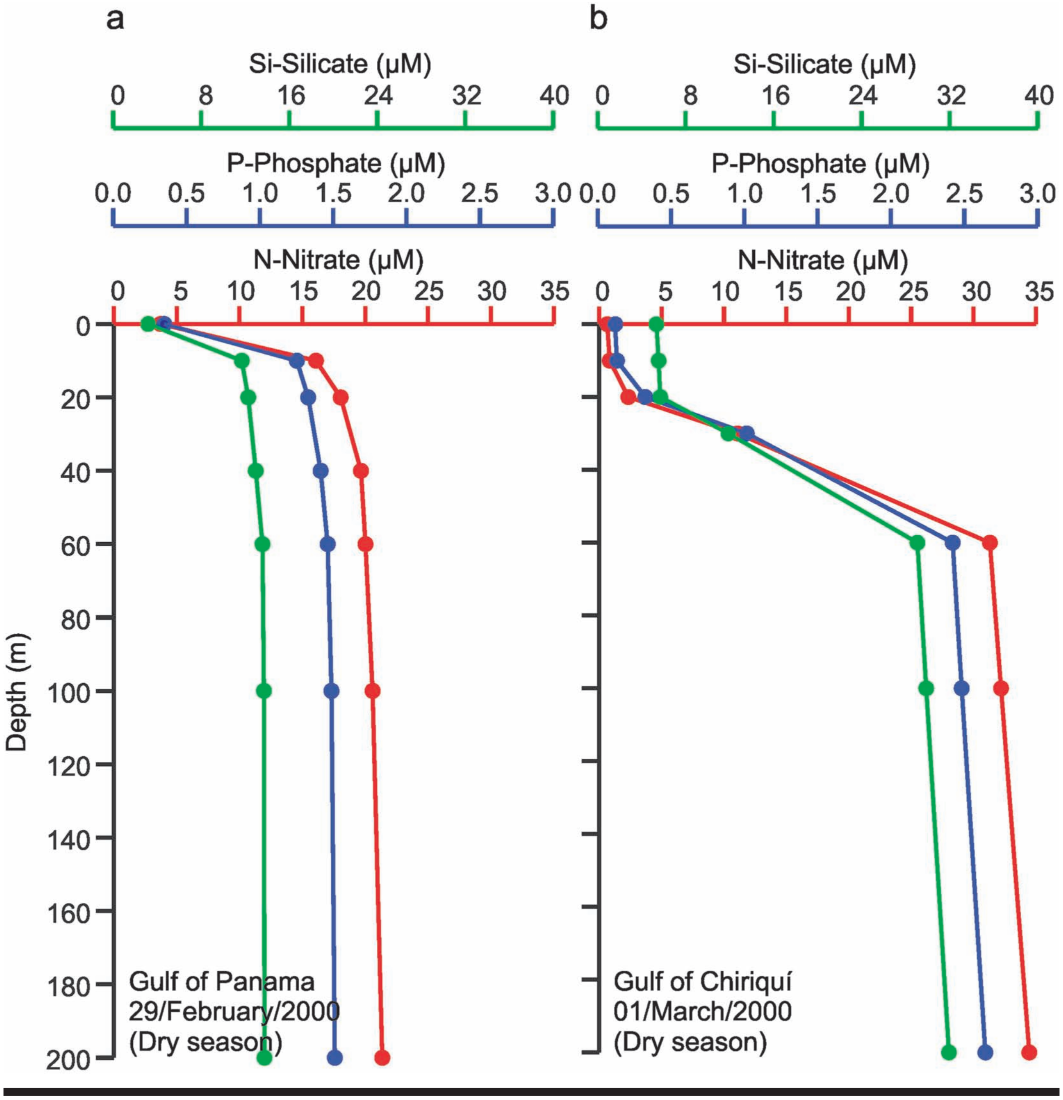

FIGURE 5. Mean profiles of silicate (Si), phosphate (P), and nitrate (N) in the Gulf of Panama and the Gulf of Chiriquí during the dry season. a = Gulf of Panama, 29 February 2000; b = Gulf of Chiriquí, 1 March 2000.

development of an intense thermocline at approximately 60 m. Surface waters tend to have low salinities and are warm and nutrient depleted. Low N:P ratios in surface waters during the rainy season suggest that phytoplankton growth is strongly nitrogen limited. Consequently, the standing stock of chlorophyll *a* is maintained at relatively low levels in surface waters. Phytoplankton does however peak at subsurface levels as the nutrient-rich thermocline waters intersect the euphotic zone, increasing N:P ratios and favoring algal growth. The strong inverse correlation between nutrients and sea temperature is consistent with the coincidence of a shallow thermocline and strong nutricline typical of the eastern tropical Pacific Ocean (Enfield, 2001). As such, the seasonal movement of the thermocline represents a key source of nutrients for phytoplankton. Our sampling sites were far offshore and therefore silicate concentrations were not as high as previously reported for the inner shelf (D'Croz and O'Dea, 2007) even though the concentration of silicate in the Gulf of Panama is reported to be the highest in the eastern Pacific as a consequence of the intense runoff in the area (Pennington et al., 2006).

During the dry season, the hydrological patterns of the two gulfs become dissimilar. In the Gulf of Panama strong upwelling of cold deep waters into coastal and surface wa-

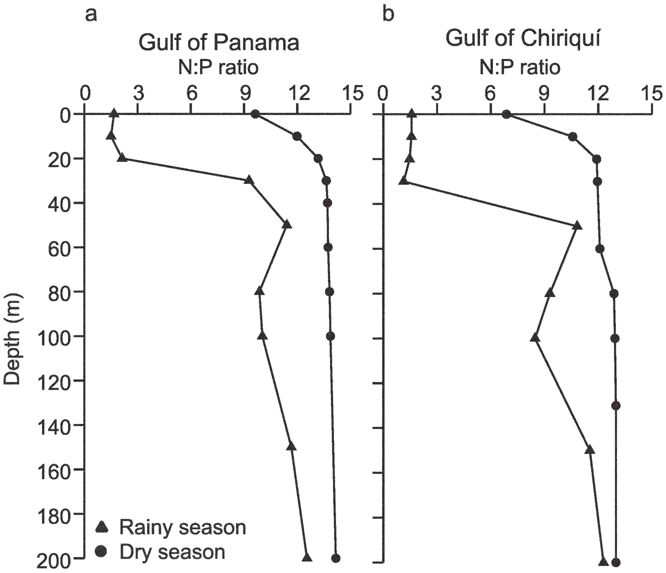

FIGURE 6. Profiles of average nitrate to phosphate ratios (N:P) in rainy (triangles) and dry (circles) seasons: a = Gulf of Panama; b = Gulf of Chiriquí.

ters drives significant changes in the hydrological properties of the water column. The thermocline migrates vertically upward, leading to cooling, increased salinity, and nutrient enrichment on surface waters. Surface N:P ratios become closer to the Redfield value and, as a result, phytoplankton growth intensifies, leading to a reduction in water clarity. A shallow oxycline also develops and oxygen concentration below the oxycline is reduced, often leading to severe hypoxic conditions. In contrast, the oxycline in the Gulf of Chiriquí is deeper and deep water remains hypoxic. Low oxygen minima are nonetheless typical in the eastern tropical Pacific as a combination of high algal growth at the surface, a strong pycnocline that impedes the ventilation of waters below, and the sluggish circulation of deep waters (Fiedler and Talley, 2006). The report of large filamentous *Thioploca*-like sulfur bacteria on shallow sediments in both regions strongly suggests that the inner shelf is exposed to episodes of reduced oxygen (Gallardo and Espinoza, 2007).

A significant relationship between wind-stress index (calculated from the sum of northerly winds) and sea level provides an explanatory mechanism for upwelling in the Gulf of Panama (Schaefer et al., 1958; Legeckis, 1988; Xie et al., 2005). Surface waters are displaced into open ocean by strong northerly winds during the dry season, and deep waters move vertically upward to replace them (Fleming, 1940; Smayda, 1966; Forsbergh, 1969). Consequently, wind stress is inversely related to SST in the Gulf of Panama during the dry season but not during the rainy season (D'Croz and O'Dea, 2007).

Data from the Gulf of Chiriquí are scant but did suggest that upwelling does not occur, because wind stress during the dry season is normally one-third of that of the Gulf of Panama (Kwiecinski and Chial, 1983) and it does not displace surface waters offshore. High mountain ranges running along western Panama impede the flow of northerly winds across to the Gulf of Chiriquí (see Figure 1), whereas mountain ranges in central Panama are low, allowing strong wind jets to form toward the Gulf of Panama. Despite this clear distinction, our data show that similar hydrological changes to those that occur in the Gulf of Panama do take place in the Gulf of Chiriquí. During the dry season, and concurrent with strong upwelling in the Gulf of Panama, we observed deeper waters rise toward shallower depths in the Gulf of Chiriquí. This movement led to a substantial compression of the mixed layer and the corresponding rise of available nutrients within the euphotic zone, shifting the chlorophyll maximum above the shallow thermocline. Although direct evidence of prolonged surface water cooling was not observed, we postulate that cooling and nutrient-enrichment episodes in the Gulf of Chiriquí may occur and that their intensity is dependent upon the depth to which the thermocline reaches in the eastern Pacific during the boreal winter. Nonetheless, the process is clearly much less intense than that in the Gulf of Panama. Despite substantial shifts in deeper water conditions in the Gulf of Chiriquí, surface waters remain warm and nutrient poor, presumably because wind stress is not strong enough to cause the advection of deep, cool, and nutrient-rich waters to the surface (D'Croz and O'Dea, 2007). However, ocean forces such as internal waves might change the oceanographic structure in the Gulf of Chiriquí, causing brief periods of advection of deep cold water to the surface layer (Dana, 1975). Long-term records from data loggers deployed in coral reefs give evidence of such brief SST drops in the Gulf of Chiriquí that are possibly related to internal waves (D'Croz and O'Dea, 2007). This effect might be more evident as the internal waves approach the shallow coasts around the islands in the Gulf of Chiriquí and may be more likely to occur during times of thermocline shallowing.

In conclusion, although the Gulf of Chiriquí does not experience the intense seasonal upwelling characteristic of the Gulf of Panama, deeper waters do migrate upward in synchrony with Gulf of Panama upwelling. This movement is probably caused by an overall shallowing of the thermocline across Central America. The difference in intensity of upward movement of the thermocline between the two gulfs strongly influences the phytoplankton community, with seasonal blooms occurring in the Gulf of Panama but not in the Gulf of Chiriquí. Deeper waters do nonetheless experience similar patterns of seasonal hydrographic change, and shallow waters of the Gulf of Chiriquí can be exposed to brief pulses of cold and nutrient-rich waters by advection. However, the effects of thermocline migration and advection on the shallow-water communities of the Gulf of Chiriquí remain to be studied in detail.

ACKNOWLEDGMENTS

Juan B. Del Rosario, Plinio Góndola, and Dayanara Macías assisted in the collection and processing of the samples. Sebastien Tilmans and Juan L. Maté reviewed the manuscript. Rainfall data were kindly provided by Empresa de Transmisión Eléctrica S.A., Panama. We acknowledge the participants, skipper, and crew of the R/V *Urracá* for their assistance during the cruises. The Government of the Republic of Panama granted the permits for the collections.

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Growth and Nutrient Conservation in *Rhizophora mangle* in Response to Fertilization along Latitudinal and Tidal Gradients

Ilka C. Feller, Catherine E. Lovelock, and Cyril Piou

ABSTRACT. Mangroves form heterogeneous marine ecosystems with spatial differences in structural complexity, biodiversity, biogeochemistry, and hydrology that vary at local and regional scales. Although mangroves provide critical ecosystem goods and services, they are threatened globally by human activities, including nutrient over-enrichment. Our goal was to determine if enrichment with nitrogen (N) or phosphorus (P) interacts with forest structure and latitude to alter growth and nutrient dynamics. We established a series fertilization experiments across more than 2,000 km and 18° of latitude from the Indian River Lagoon (IRL), Florida, to Twin Cays, Belize, to Bocas del Toro, Panamá. At each site, we fertilized individual trees with one of three treatment levels (control, +N, +P) in two intertidal zones (fringe, scrub) and measured their responses for four years. We tested the effects of nutrient over-enrichment on growth, resorption efficiency, and resorption proficiency of the red mangrove *Rhizophora mangle*. All sites were nutrient limited, but patterns of nutrient limitation varied by zone and latitude. At IRL, growth was N limited; at Twin Cays, the fringe was N limited, but the scrub forest was P limited; at Bocas del Toro, the fringe was N limited, but the scrub forest was both N- and P limited. Nutrient enrichment had dramatic and complex effects on nutrient conservation. Adding nutrients to mangrove ecosystems affected growth and the nutrient recycling, but the pattern depended on location, site characteristics, and the nature of nutrient limitation. Predicting how forests will respond to nutrient over-enrichment requires an assessment of spatial heterogeneity at multiple scales of response.

INTRODUCTION

Mangrove ecosystems are coastal wetlands dominated by woody plants that span gradients in latitude (30°N to 37°S), tidal height (<1 m to >4 m), geomorphology (oceanic islands to riverine systems), sedimentary environment (peat to alluvial), climate (warm temperate to both arid and wet tropics), and nutrient loading (oligotrophic to eutrophic). Throughout their distribution, mangroves are critical not only for sustaining biodiversity in these intertidal forests but also for their direct and indirect benefit to human activities. As a detritus-based ecosystem, the leaf litter from these trees provides the basis for adjacent aquatic and terrestrial food webs (Odum and Heald, 1975). Mangroves function as nurseries for many of the sport and commercial fishes found in deeper waters and provide feeding grounds

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for large reef fishes (Nagelkerken et al., 2000; Mumby et al., 2004). As a result, mangrove-assimilated energy and nutrients are exported to surrounding coral reefs (Dittmar and Lara, 2001). Besides supporting and renewing coastal fishing stock, mangroves also benefit human economic development by stabilizing shorelines. This stabilization is a critical function in tropical coastal areas that may be battered periodically by tropical storms, hurricanes, and tsunamis (Danielson et al., 2005; Barbier, 2006).

Despite repeated demonstration of their ecological and economic importance, mangroves are one of the world's most threatened ecosystems (Valiela et al., 2001; Alongi, 2002; Barbier and Cox, 2003; Rivera-Monroy et al., 2004; Duke et al., 2007). In addition to direct destruction, increasing input of human-caused nutrient pollution is widely recognized as one of the major threats to mangroves and other marine environments worldwide (NRC, 1995, 2000, 2001; Duce et al., 2008). However, system-specific attributes may lead to large differences among coastal and estuarine systems in their sensitivity and susceptibility to these increasing nutrient levels (Cloern, 2001). The complex suite of direct and indirect responses in coastal systems to nutrient over-enrichment include changes in water chemistry, distribution and biomass of plants, sediment biogeochemistry, decomposition processes, nutrient cycling, nutrient ratios, phytoplankton communities, habitat quality for metazoans, and ecosystem functions.

Relatively little is known about how the structure and function of mangrove ecosystems are altered by nutrient enrichment. In temperate salt marshes and mangroves, ecological processes have been shown to be nitrogen- (N) limited (Valiela and Teal, 1979; Feller et al., 2003b). The few tropical and subtropical mangrove wetlands that have been studied were shown to be both phosphorus- (P) and N limited (Boto and Wellington, 1984; Feller, 1995; Feller et al., 1999, 2003a, 2003b; Lovelock and Feller, 2003; Lovelock et al., 2004). Because mangroves are responsive to processes operating at multiple spatial scales, comparisons along a broad latitudinal gradient in climate and across narrow tidal gradients will improve our understanding of the relative impacts of global versus local factors on the structure and function of these ecosystems. In this study, we focused on the mangrove *Rhizophora mangle* (red mangrove), an evergreen tree that has a large geographic range throughout the Atlantic-East Pacific region (Duke, 1992). Along the Atlantic coasts of North and South America, its distribution is continuous and spans almost 60° of latitude from its northern limit along the coast of Florida at 29°42.94′N (Zomlefer et al., 2006) to its southern limit along the coast of Brazil at 27°53′S (Shaeffer-Novelli et al., 1990). In this study, our goals were to determine how nutrient availability varies among *R. mangle* forests spanning a temperate to tropical gradient and how nutrient over-enrichment affects plant growth and nutrient conservation. We manipulated nutrient availability and measured responses of trees fertilized with nitrogen (+N) or phosphorus (+P) growing along intertidal gradients in similar habitats at three locations along this latitudinal gradient to test the following hypotheses.

1. Nutrient availability varies along a latitudinal gradient with a decreasing supply of P relative to N toward the tropics (Vitousek, 1984; Vitousek and Sanford, 1986; Crews et al., 1995). This hypothesis predicts increasing P limitation in mangrove forests at lower latitudes and N limitation at higher latitudes (Güsewell, 2004; McGroddy et al., 2004; Reich and Oleksyn, 2004; Kerkhoff et al., 2005).
2. Delivery, uptake, or assimilation of P is more strongly affected by tidal flushing and concomitant factors that vary spatially than is that of N (Smith, 1984; McKee et al., 2002). This hypothesis predicts differences in N versus P limitation within mangrove forests at different intertidal elevations (Ross et al., 2006). Specifically, N limitation is predicted for the low intertidal where tidal flushing is greater (residence time is shorter) than in the high intertidal where P limitation is predicted.
3. Because of difference in growth rates along climatic gradients, the mechanisms used by plants to recycle and conserve nutrients will be more efficient at higher latitudes (Oleksyn et al., 2003). This hypothesis predicts increased nutrient conservation by mangroves growing near their temperate limit (Lovelock et al., 2007).
4. As nutrient availability increases, nutrient conservation mechanisms become less efficient (Shaver and Melillo, 1984; Vitousek, 1984; Schlesinger et al., 1989; Escudero et al., 1992). This hypothesis predicts that the effects of nutrient loading on mangrove forests will differ depending on whether a system is N- or P limited, with the expectation that the limiting nutrient will be more efficiently and tightly conserved (Feller et al., 1999).

MATERIALS AND METHODS

Site Descriptions

We compared the effects of nutrient over-enrichment on plant growth and nutrient dynamics in *Rhizophora mangle* L. at three locations along the Atlantic and Caribbean coasts from Florida to Panamá spanning a climatic gradient of more than 2,000 km and 18° of latitude (Figure 1):

FIGURE 1. The three study sites used in this study span more than 18° of latitude and extend from the Indian River Lagoon (IRL), Florida, in the north, to Twin Cays, Belize, and to Bocas del Toro, Panama, in the south.

(1) Indian River Lagoon (referred to hereafter as IRL), Florida; (2) Twin Cays, Belize (referred to hereafter as Twin Cays); and (3) Bocas del Toro, Republic of Panamá (referred to hereafter as Bocas) (Table 1). Table 2 provides a summary of the characteristics for the three locations (Koltes et al., 1998; McKee et al., 2002; Feller et al., 2003a; Feller and Chamberlain, 2007; Lovelock et al., 2005). Forest structure at the three locations was heterogeneous and characterized by complex gradients in tree height that included a narrow seaward fringe of uniformly tall (~4 m) trees dominated by *R. mangle*, varying in width from 5 to 20 m (Figure 2). Tree height decreased rapidly to landward with interior areas dominated by old-growth stands of low stature, or "scrub," trees (~1.5 m) (Table 3). The black mangrove (*Avicennia germinans* L.) and the white mangrove (*Laguncularia racemosa* (L.) Gaertn. f.) were also present in each of these locations, typically near the landward ecotone. The hydrogeomorphic settings were variable among the three locations. IRL and Bocas were continental in contrast with Twin Cays, which is a low oceanic island. However, Twin Cays and Bocas were more similar in mineralogy (Phillips et al., 1997; Macintyre et al., 2004; Coates et al., 2005), with mangrove forests atop a carbonate platform and deep peat deposits. All sites were microtidal with mixed semidiurnal tides (Kjerfve et al., 1982; Kaufmann and Thompson, 2005). The fringe zones at the three locations were similarly well flushed, but the hydrological conditions of the scrub zones varied. At Twin Cays, these interior portions of the forest were completely inundated and waterlogged (McKee et al., 2007). In contrast, the Bocas scrub zone drained completely at low tide (Lovelock et al., 2005). At IRL, the scrub zone drained completely at low tide during the summer but remained inundated for days during the winter (Feller et al., 2003b).

In the IRL, our experimental sites were situated on the lagoonal side of two barrier islands. The fringe site was in Avalon State Park on North Hutchinson Island, St. Lucie County; the scrub site was in the Hobe Sound National Wildlife Refuge on Jupiter Island, Martin County. In this area, soil was composed primarily of marine sand with mangrove forests adjacent to coastal strand vegetation and maritime hammocks. Descriptions of forest

TABLE 1. Hydrogeomorphic characteristics of the study sites along a latitudinal gradient from the Indian River Lagoon (IRL), Florida, to Twin Cays, Belize, to Bocas del Toro (Bocas), Panama.

Characteristic	IRL	Twin Cays	Bocas
Latitude	27°33′N, 80°13′W	16°50′N, 88°06′W	9°09′N, 82°15′W
Freshwater inflow	Medium	Low	High
Type of landscape	Continental	Oceanic	Continental
Topographic relief	Medium	Low	High
Nutrient flux	High	Low	Medium
Mineralogy	Siliclastic/carbonate	Peat/limestone	Peat/limestone
Annual rainfall	1.3 m	2.8 m	3.5 m
Mean temperature range [a]	12.4°–23.6°C (w) 22.6°–31.9°C (s)	18.3°–29.9°C (w) 22.2°–31.3°C (s)	20.1°–31.1°C (w) 21.9°–31.8°C (s)
Mean tidal range	37 cm	34 cm	19 cm
Major disturbances	Anthropogenic, hurricanes	Anthropogenic, hurricanes	Anthropogenic, flooding

[a] w = winter; s = summer.

TABLE 2. Characteristics of the mangrove forest structure in the fringe and scrub zones at the Indian River Lagoon (IRL), Florida, to Twin Cays, Belize, to Bocas del Toro (Bocas), Republic of Panama. Data are from Koltes et al. (1998), McKee et al. (2002), Feller et al. (2003a), Lovelock et al. (2005), and Feller and Chamberlain (2007).

Location	Zone	Salinity (‰) (mean ± SE)	Species	Tree height (m) (mean ± 1 SE)	DBH (cm) (mean ± 1 SE)	Stem density (stems·0.1 ha^{-1})	Basal area (m^{2}·0.1 ha^{-1})
IRL	Fringe	32.7 ± 0.7	*Rhizophora mangle*	3.9 ± 0.1	4.5	3,9536.4	
			Laguncularia racemosa	3.2 ± 0.3	6.1	1,3433.9	
			Avicennia germinans	3.8 ± 0.3	4.8	6711.2	
	Scrub	32.4 ± 0.5	*Rhizophora mangle*	1.7 ± 0.1	2.5 ± 0.2	2,3861.5	
			Laguncularia racemosa	4.5 ± 0.4	4.6 ± 0.7	4771.0	
			Avicennia germinans	1.6 ± 0.0	1.2 ± 0.0	730.01	
Twin Cays	Fringe	36.9 ± 1.2	*Rhizophora mangle*	3.2 ± 0.2	7.3 ± 0.4	4012.1	
			Laguncularia racemosa	2.2[a]	2.9[a]	3[a]0.2[a]	
			Avicennia germinans	2.2[a]	4.0[a]	3[a]0.01[a]	
	Scrub	39.4 ± 1.2	*Rhizophora mangle*	0.8 ± 0.1	2.4 ± 0.2	8970.4	
Bocas	Fringe	34.4 ± 0.6	*Rhizophora mangle*	3.9 ± 0.1	5.3 ± 0.6	8501.6	
	Scrub	33.3 ± 1.9	*Rhizophora mangle*	0.7 ± 0.1	1.5 ± 0.1	3,3570.7	

[a] Based on occurrence of a single tree in each zone.

structure, hydro-edaphic conditions, growth, nutrient dynamics, and photosynthesis at the Avalon State Park site were previously reported (Feller et al., 2003a; Lovelock and Feller, 2003).

At Twin Cays, our fringe and scrub sites were located on the two largest islands of this 92-ha mangrove archipelago, 10 km offshore. Descriptions of forest structure, biogeochemistry, ecophysiology, growth, and nutrient dynamics were previously reported (Rützler and Feller, 1996; McKee et al., 2002; Feller et al., 2003b, 2007; Lovelock et al., 2006a, 2006b, 2006c, 2006d). These oceanic mangroves islands are underlain by deep deposits of mangrove peat 8 to 12 m thick (Macintyre et al., 2004; McKee et al., 2007).

At Bocas, fringe and scrub sites were located on three islands (San Cristobal, Solarte, Isla Popa) in Almirante Bay and the Chiriqui Lagoon in a vast network of mangrove islands and mainland peninsulas covering approximately 2,885 km^{2} (De Croz, 1993; Guzman and Guevara, 1998; Guzman et al., 2005; Lovelock et al., 2004, 2005). Here, mangroves occurred adjacent to tropical rainforests and grew on peat approximately 5 m deep atop ancient coral reef limestone (Phillips and Bustin, 1996; Phillips et al., 1997). This location was outside the hurricane belt, but flooding was common. Earthquakes are episodic (Phillips et al., 1994, 1997; Phillips and Bustin, 1996) and are likely to be the major nonanthropogenic disturbance regime influencing these forests.

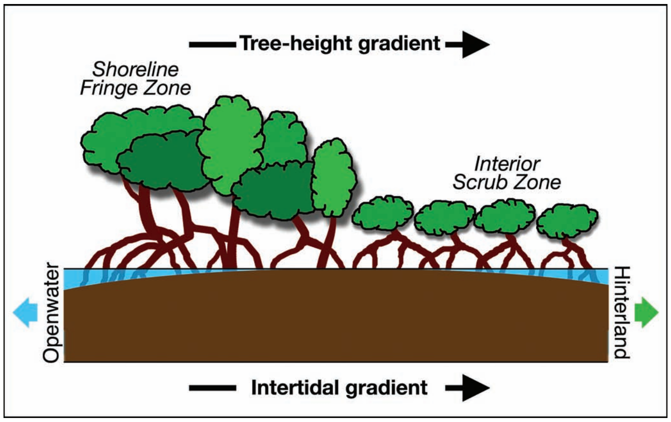

FIGURE 2. Mangrove forests at each of our study sites are characterized by a distinctive tree-height gradient with tall trees fringing the shoreline and scrub trees in the interior.

EXPERIMENTAL DESIGN

Fertilization experiments were set up at IRL in January 1997, at Twin Cays in January 1995, and at Bocas in January 1999. To compare responses, we used a three-way factorial analysis of variance (ANOVA) design (i.e., 3 nutrient enrichment treatment levels [Control, +N, +P] × 2 zones [fringe, scrub] × 3 locations [IRL, Twin Cays, Bocas] × 3 sites per location × 3 replicate trees per site, for a total of 162 trees). Nutrient treatment was randomly as-

TABLE 3. Three-way factorial analysis of variance (ANOVA) results on the seven response variables: shoot elongation (Growth), N-, P-, and K-resorption efficiencies (NRE, PRE, KRE), and N-, P-, and K-resorption proficiencies (NRP, PRP, KRP). The kind of transformation conducted on response variables for normalization and homogeneity of variances is given in the second line of column headings. Results are in the form of *F* statistical values for each effect and the corresponding level of significance: $^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$; and $\sim$ for $P < 0.1$.

		Growth *Log(x)*		**NRE** *Exp(x)*		**PRE** *Exp(4x)*		**KRE** *Exp(x)*		**NRP** *Log(x)*		**PRP** *Log(1000x)*		**KRP** *Log(x)*	
Factor	***df***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***	***F***	***P***
Location (L)	2	24.2	***	28.6	***	126	***	16.5	***	86.1	***	373	***	18.9	***
Zone (Z)	1	0.11		65.2	***	4.57	*	0.96		75.4	***	0.29		5.18	*
Treatment (T)	2	23.4	***	10.4	***	75.4	***	14.6	***	40.3	***	108	***	36.8	***
L × Z	2	12.0	***	3.21	*	1.21		0.78		2.88	~	7.15	**	1.98	
L × T	4	12.9	***	4.37	**	12.5	***	5.60	***	2.16	~	23.6	***	8.13	***
Z × T	2	17.8	***	3.27	*	4.36	*	8.97	***	4.77	**	13.4	***	25.0	***
L × T × Z	4	4.9	**	4.35	**	1.30		4.27	**	7.95	***	4.21	**	8.61	***
Residuals	140														

signed within each zone and site. Trees were amended with 150 g N as NH_4 (45:0:0), or P fertilizer as P_2O_5 (0:45:0), per centimeter diameter breast height, as described in Feller (1995). Doses (150 g) of fertilizer were sealed in dialysis tubing and placed in each of two holes 30 cm deep, cored into the substrate on opposing sides of a tree beneath the outermost margin of its canopy, and sealed. Experiments at IRL and Twin Cays were fertilized twice per year. Because of limited access, the Bocas experiment was fertilized once per year. Thus, growth responses were normalized to the annual rate of fertilizer application. For controls, holes were cored and sealed but no fertilizer was added. Direct fertilizer application to the root zone of our target trees was used because all sites were flooded at high tides and fertilizer broadcasted on the surface would have washed away.

Tree Growth

To quantify growth, we measured the length of five initially unbranched shoots in sunlit positions in the outer part of the canopy of each tree at the three locations. To compare growth responses among the three locations, we calculated the annual shoot elongation based on the amount fertilizer added per location (cm · year^{-1} kg^{-1}).

Leaf Nutrient Dynamics

To determine the relative effects of nutrient over-enrichment on the ability of *R. mangle* to conserve nutrients invested in foliage, we measured N, P, and potassium (K) concentrations in green and senescent leaves. For green leaves, we sampled the youngest, fully mature green leaves from penapical stem positions in sunlit portions of the canopy. Fully senescent yellow leaves with well-developed abscission layers were taken directly from the trees. Leaf area was determined with a Li-Cor 3000 Leaf Area Meter (Lincoln, Neb., USA). Leaf samples were dried at 70°C in a convection oven and ground in a Wiley Mill to pass through a 40 mesh (0.38 mm) screen. Concentrations of carbon (C) and N were determined with a Model 440 CHN Elemental Analyzer (Exeter Analytical, North Chelmsford, Mass., USA) at the Smithsonian Environmental Research Center, Edgewater, Md. Concentrations of P and K were determined using an inductively coupled plasma spectrophotometer by Analytical Services, Pennsylvania State University, Pa. Nutrient concentrations expressed on a leaf area basis ($\text{mg} \cdot \text{cm}^{-2}$) were used to calculate N, P, and K resorption efficiencies (NRE, PRE, KRE), as below (Chapin and Van Cleve, 1989):

$$\text{resorption efficiency} = \frac{\text{N, P, or K } (\text{mg} \cdot \text{cm}^{-2})_{\text{green leaf}} - \text{N, P, or K } (\text{mg} \cdot \text{cm}^{-2})_{\text{senescent leaf}}}{\text{N, P, or K } (\text{mg} \cdot \text{cm}^{-2})_{\text{green leaf}}} \times 100$$

The absolute levels to which N, P, and K were reduced (% dry mass) in senesced leaves (indicated as $\%N_{\text{senesced leaf}}$, $\%P_{\text{senesced leaf}}$, and $\%K_{\text{senesced leaf}}$, respectively) were used directly as indices of N, P, and K resorption proficiencies (NRP, PRP, KRP), as below (Killingbeck, 1996):

resorption proficiency = the level to which N, P, or K has been reduced in senescent leaves (% dry mass).

Note that low levels for $\%N_{\text{senesced leaf}}$, $\%P_{\text{senesced leaf}}$, and $\%K_{\text{senesced leaf}}$ are indicative of high resorption proficiency whereas high levels indicate low resorption proficiency. Concentrations less than 0.7% are considered complete resorption for N and concentrations less than 0.04% are considered complete resorption for P (Killingbeck, 1996). Higher values indicate incomplete resorption. In this study, we considered values less than 0.3% N and less than 0.01% P as the ultimate resorption potential for *R. mangle*, as proposed by Killingbeck (1996). Comparable values for K resorption potential have not been determined.

STATISTICS

Our data were grouped by nutrient treatment (Control, +N, +P) × zone (fringe, scrub) × location (IRL, Twin Cays, Bocas), to compare seven response variables of *R. mangle*, including growth responses, N-, P-, and K-resorption efficiencies, and N-, P-, and K-resorption proficiencies. Three-way factorial analyses of variance (ANOVA) were applied for each response variable. When an ANOVA found significant effects, Tukey's honestly significant difference (HSD) tests were applied to examine pairwise differences within and among the treatment levels. To respect the assumptions of heterogeneity of variances and normality, the response variables were transformed using logarithms and exponentials. To investigate relationships between nutrient content of green and senescent leaves as well as among nutrient resorption proficiencies, we used the Spearman rho (ρ) correlation test on the ranked row values. These analyses were conducted using the R software 2.7.0 (R Development Core Team, 2008).

RESULTS

TREE GROWTH

There was a significant three-way interaction of nutrient enrichment × location × zone on growth rates of *R. mangle* trees (see Table 3; Figure 3). For control trees in the fringe zone, the rate of shoot elongation at IRL was signifi-

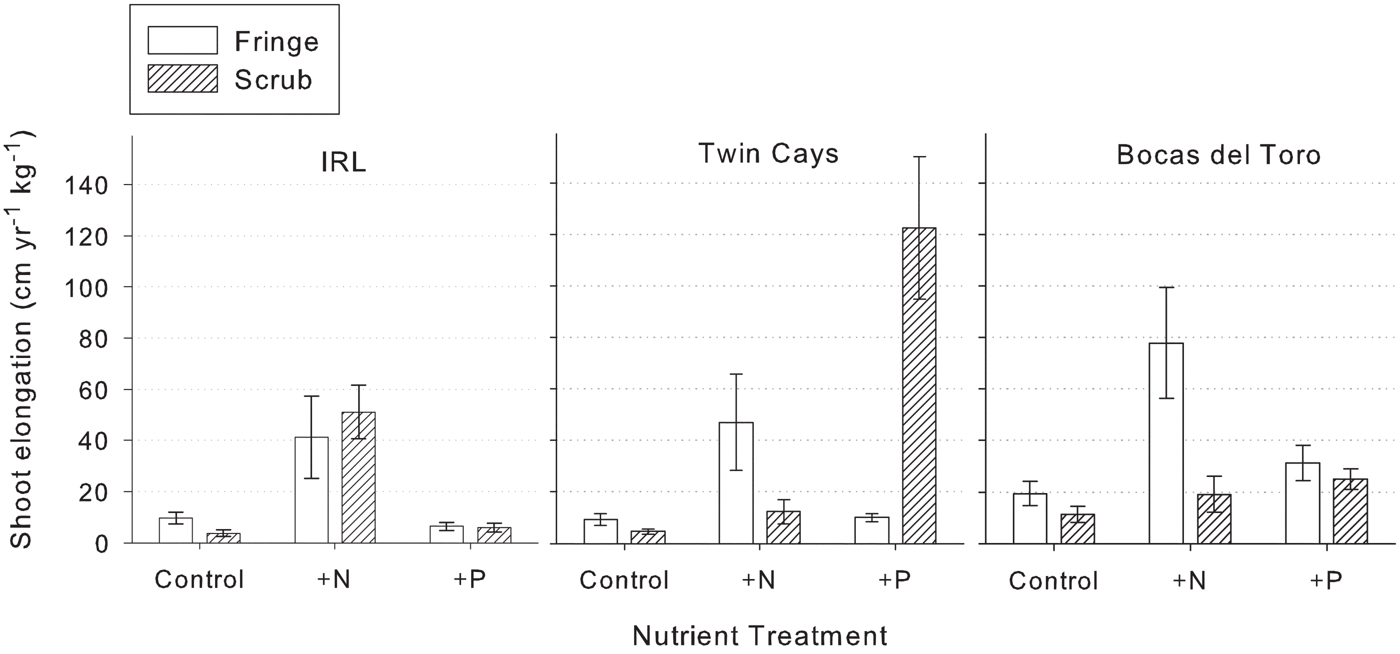

FIGURE 3. *Rhizophora mangle* growth (cm · year^{-1} · kg^{-1}) measured as elongation of individual shoots per year (normalized to fertilizer application at each site) at Indian River Lagoon (IRL), Twin Cays, and Bocas del Toro, in two zones (fringe, scrub), and in response to nutrient enrichment with nitrogen (+N) or phosphorus (+P). (IRL and Twin Cays data from Feller et al., 2003a, 2003b).

cantly lower than at Bocas (HSD adjusted $P < 0.001$) but similar to those at Twin Cays (HSD adjusted $P = 0.070$), which had similar values. There were no significant differences in shoot elongation rates for control trees in the scrub zone among all the locations. +N caused significant increases in shoot elongation rates for fringe and scrub trees at IRL, but only for fringe trees at Twin Cays and Bocas. However, shoot elongation for +N fringe trees in the IRL was lower than observed at Bocas (HSD adjusted $P = 0.089$). +N caused similar increases in shoot elongation in the fringe at Bocas and Twin Cays. In the scrub zone, +P increased growth at Twin Cays (HSD adjusted $P < 0.001$) and Bocas (HSD adjusted $P = 0.095$), although the rates were much higher for Twin Cays (HSD adjusted $P = 0.047$). +P had no effect on growth in either fringe or scrub zones at IRL. The +N treatment had no effect on growth rates in the scrub zones at Twin Cays and Bocas.

NUTRIENT CONSERVATION

The impact of fertilization on N-, P-, and K-resorption efficiencies varied by location and zone (Figure 4a–c). For N-resorption efficiency (NRE), there was a significant three-way interaction among location, zone, and nutrient enrichment (see Table 3; Figure 4a). Values ranged from 26% to 68%. In control trees at all locations, NRE was consistently highest for the fringe. At IRL, +N caused a slight decline in values for fringe but not scrub trees. At Twin Cays, +N had no effect on NRE in the fringe where growth was N limited. However, +P caused an approximately 40% increase in NRE for the P-limited scrub trees (HSD adjusted $P < 0.001$). Although +N had no effect on the growth of scrub trees at Twin Cays, it did result in a slight increase in NRE. Overall, values for NRE were lowest at Bocas.

There were significant two-way interactions among nutrient enrichment × location and nutrient enrichment × zone on P-resorption efficiencies. However, the three-way interaction among nutrient enrichment × location × zone was not significant (see Table 3, PRE; Figure 4b). PRE values ranged from 36% to 80%. Overall, IRL had the lowest PRE. Here, values for control fringe and scrub trees were approximately half those at Twin Cays and Bocas where values were similar. +N caused a slight increase in PRE for IRL fringe and scrub trees. At Twin Cays and Bocas, +N had no effect in either zone, but +P caused an approximately 50% decrease in PRE for scrub trees and an approximately 25% decrease for fringe trees.

For K-resorption efficiency (KRE), we found a significant three-way interaction of nutrient enrichment × location × zone (see Table 3; Figure 4c). In the IRL, values were uniformly low but positive in both zones, and nutrient enrichment had no effect. For control fringe trees at all locations, KRE was consistently positive. Overall, the lowest KRE values occurred at Twin Cays. The negative values for senescent foliage from control scrub trees at Twin Cays and Bocas indicated that K accumulated in leaves rather than being resorbed by the plant during senescence. At Twin Cays and Bocas, +P caused a significant increase in KRE by scrub trees, but had little effect on fringe trees. However, +N had no significant effect on KRE in either zone.

Fertilization also had striking and complex effects on resorption proficiencies, measured as the $\%N_{\text{senesced leaf}}$, $\%P_{\text{senesced leaf}}$, and $\%K_{\text{senesced leaf}}$, that varied by location and zone (Table 3; Figure 5a–c). Concentrations of N, P, and K in senesced leaves were positively associated with their concentrations in green leaves (Spearman ρ values for N, P, and K = 0.52, 0.87, and 0.65, respectively, all significantly different than 0 with $P < 0.0001$). There was no relationship between $\%N_{\text{senesced leaf}}$ and $\%P_{\text{senesced leaf}}$ (Spearman $\rho = 0.03$, $P = 0.66$), but $\%K_{\text{senesced leaf}}$ was significantly correlated with $\%N_{\text{senesced leaf}}$ (Spearman $\rho = 0.19$, $P = 0.02$) and with $\%P_{\text{senesced leaf}}$ (Spearman $\rho = -0.43$, $P < 0.0001$). For NRP, there was a significant three-way interaction among location, zone, and nutrient enrichment (see Table 3; Figure 5a). The $\%N_{\text{senesced leaf}}$ ranged from a low of 0.28% for +P scrub trees at Twin Cays to a high of 0.91% in +N fringe trees at Bocas. For control trees from the fringe and scrub zones, values were similar at IRL and Bocas but were significantly lower at Twin Cays, which indicated increased NRP. +N caused an increase of 20% in $\%N_{\text{senesced leaf}}$ from the fringe at IRL but had little effect on fringe trees at the other locations. In the scrub zone, +N had no effect on $\%N_{\text{senesced leaf}}$ at IRL and Twin Cays, but significantly higher values at Bocas resulted in a decrease in NRP. +P had little effect on either fringe or scrub zones at IRL and Bocas, but it caused a dramatic decrease in $\%N_{\text{senesced leaf}}$ and a corresponding increase in NRP in scrub trees at Twin Cays.

We found the highest levels of $\%P_{\text{senesced leaf}}$ (~0.06%) in the control trees in both zones at IRL, which indicated low PRP compared to Twin Cays and Bocas. Fertilization with +N or +P had no detectable effect on these levels at IRL (Figure 4b; all HSD adjusted $P > 0.5$). Very low levels (~0.01%) of $\%P_{\text{senesced leaf}}$ in both zones at Twin Cays and Bocas indicated high PRP in the range of maximal P resorption (Figure 6). +N had no effect on values in either zone at Twin Cays or Bocas. +P caused the most dramatic increase in $\%P_{\text{senesced leaf}}$, with a concomitant decrease in

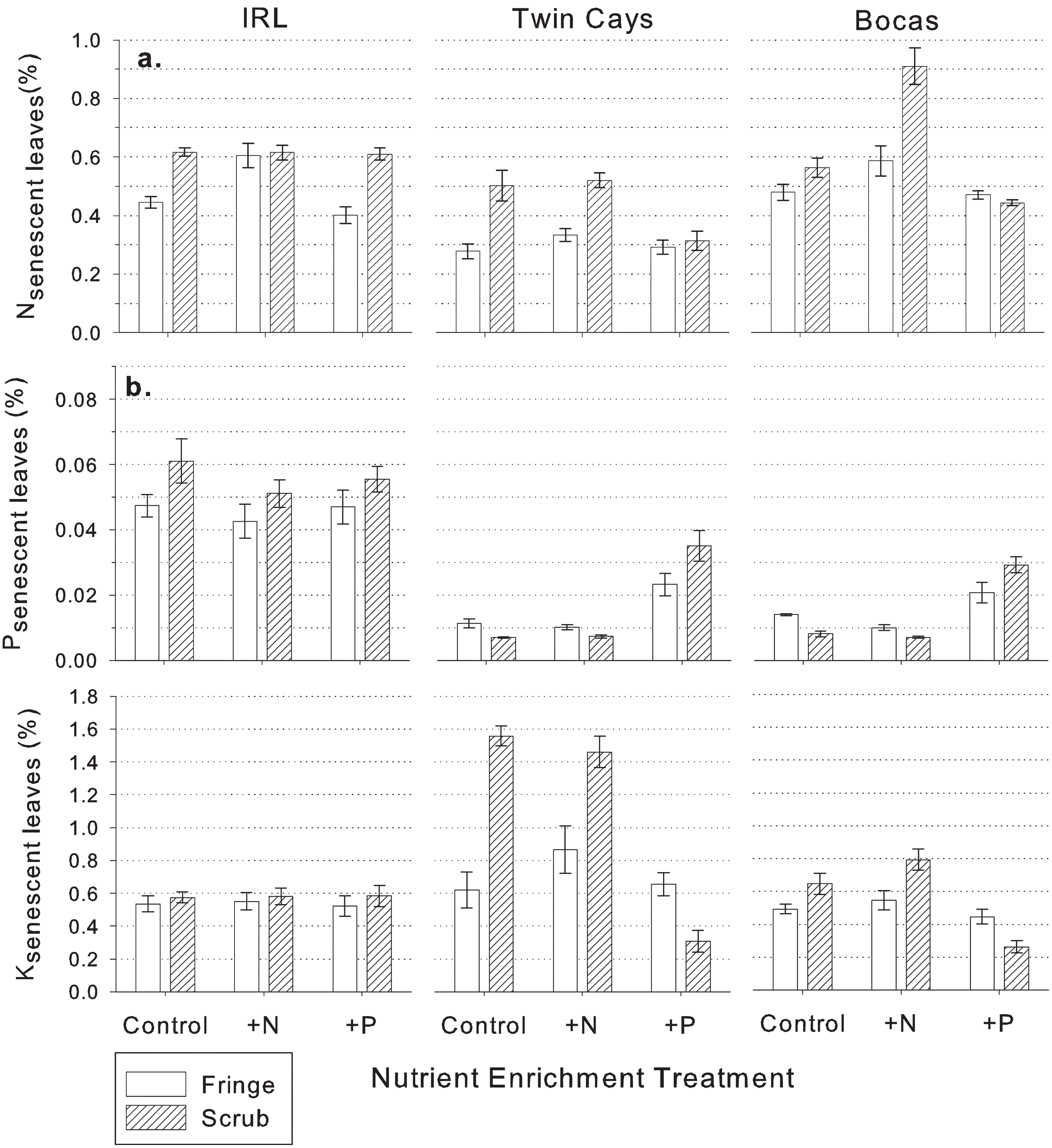

FIGURE 4. Resorption efficiencies for (a) nitrogen (N), (b) phosphorus (P), and (c) potassium (K) at Indian River Lagoon (IRL), Twin Cays, and Bocas del Toro (Bocas) in two zones (fringe = open bars, scrub = hatched bars), and in response to nutrient enrichment with nitrogen (+N) or phosphorus (+P). (IRL and Twin Cays data from Feller et al., 2003a, 2003b).

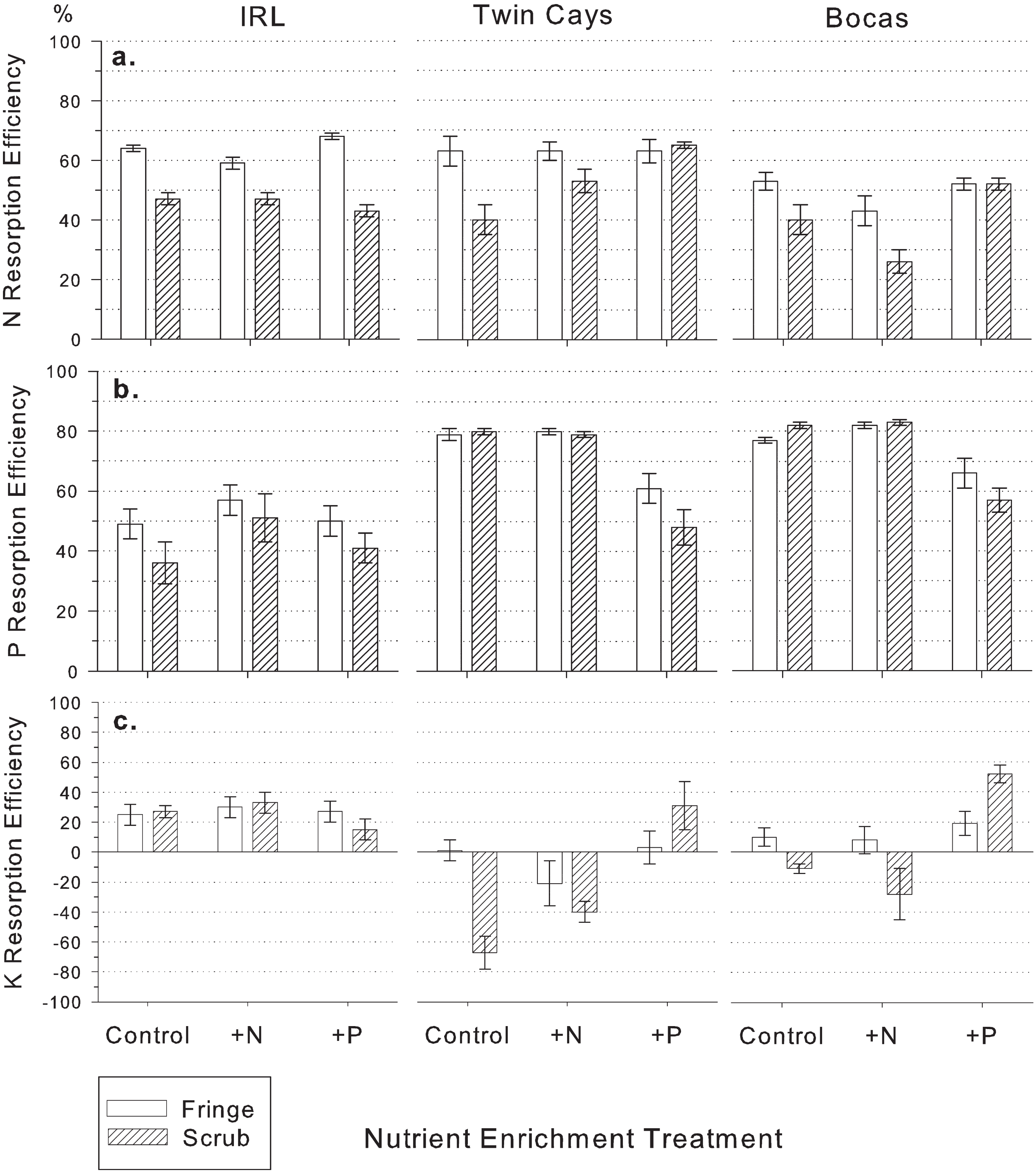

FIGURE 5. Resorption proficiencies for (a) nitrogen, (b) phosphorus, and (c) potassium at Indian River Lagoon (IRL), Twin Cays, and Bocas del Toro (Bocas) in two zones (fringe, scrub), and in response to nutrient enrichment with nitrogen (+N) or phosphorus (+P).

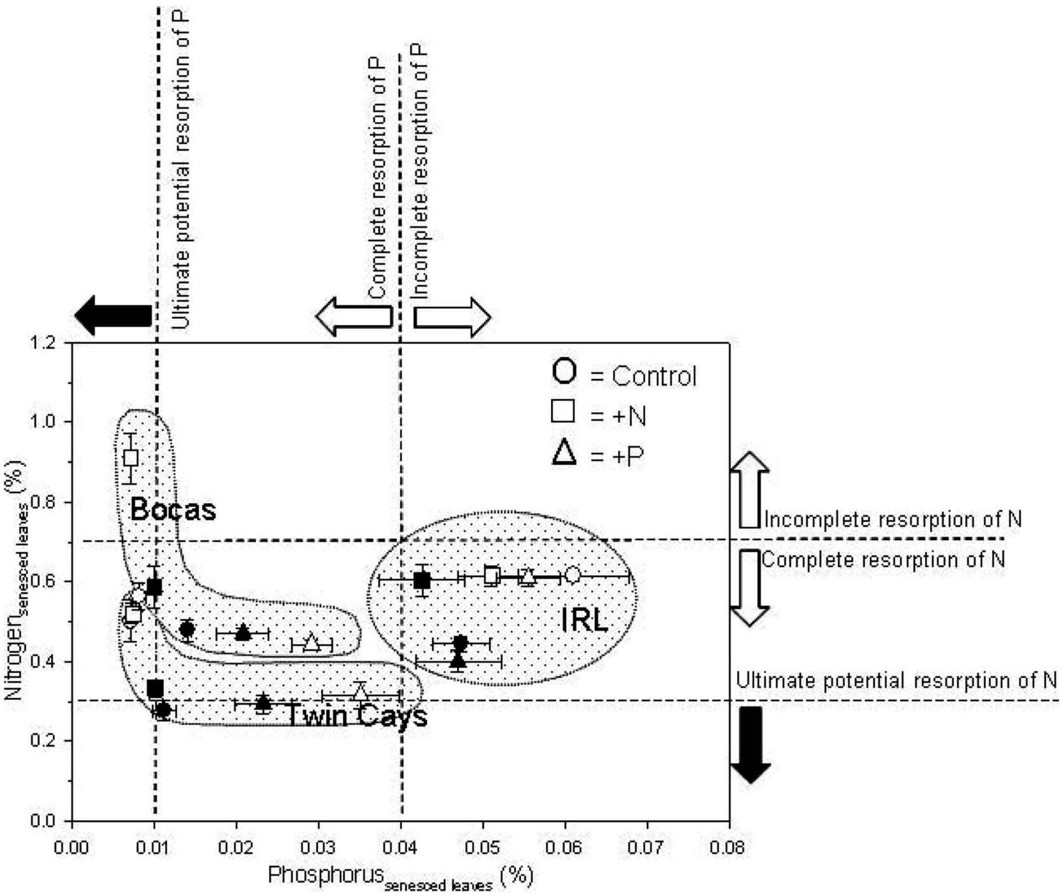

FIGURE 6. N-resorption proficiency (%$N_{\text{senesced leaf}}$) versus P-resorption proficiency (%$P_{\text{senesced leaf}}$) for *Rhizophora mangle* by location (Indian River Lagoon [IRL], Twin Cays, Bocas del Toro), nutrient enrichment treatment level (control [○], +N [□], +P [△]), and intertidal zone (fringe [closed symbols] or scrub [open symbols]).

PRP, for both the fringe and scrub zones at Twin Cays (both HSD adjusted $P < 0.001$). At Bocas, there was a similar increase in %$P_{\text{senesced leaf}}$ with +P in the scrub zone (HSD adjusted $P < 0.001$), whereas the response in the fringe zone was comparatively smaller and not significant (HSD adjusted $P = 0.694$).

There was also a significant three-way interaction among location, zone, and nutrient enrichment on KRP (see Table 3; Figure 5c). Values for control trees in both zones at IRL and Bocas were similar with no differences between zones. Neither +N nor +P had any effect at IRL, but +P caused a significant decrease in %$K_{\text{senesced leaf}}$ in both zones at Bocas. The %$K_{\text{senesced leaf}}$ ranged from a low of 0.26% for +P scrub trees at Bocas to a high of 1.56% in control scrub trees at Twin Cays, which was more than double the K concentrations in senescent foliage of fringe trees. In the Twin Cays scrub zone, +P caused a fourfold decrease in %$K_{\text{senesced leaf}}$, resulting in an associated increase in KRP.

DISCUSSION

Long-term fertilization experiments at IRL, Twin Cays, and Bocas del Toro demonstrated that these three locations, which were arrayed along a latitudinal gradient, were nutrient limited. However, system-specific attributes resulted in significant differences in patterns of nutrient limitation and responses to fertilization. Although the mangrove ecosystems at these locations exhibited similar tree-height gradients dominated by *Rhizophora mangle*, they differed in several hydrogeomorphic and structural features (see Tables 1, 2). The locations also differed in substrate types; that is, the soil at IRL was composed of Pleistocene marine sands while the soils at Twin Cays and Bocas site were deep deposits (6–12 m) of mangrove peat formed during the Holocene (Phillips and Bustin, 1996; Lovejoy, 1998; Macintyre et al., 2004). Our experimental site in the IRL was in a young forest, less than 40 years old, in an abandoned mosquito impoundment (Rey et al., 1986). In contrast, the experiments at Twin Cays and Bocas were in old-growth forests. Although no data are available for a direct comparison, it is likely that the forests at Bocas are older than at Twin Cays because of differences in their exposures to hurricanes (Stoddart, 1963; Carruthers et al., 2005). Overall, stem density was lowest at Twin Cays. Stem density in the IRL fringe was approximately 10 times greater than at Twin Cays and 4 times greater than at Bocas. On the other hand, the density of trees in the scrub forest was highest at Bocas.

Growth of *R. mangle* stems, which we used as a bioassay of nutrient limitation in our fertilization experiments, varied among IRL, Twin Cays, and Bocas. However, the responses did not support Hypothesis 1 of increasing P limitation toward the tropics (Vitousek, 1984; Vitousek and Sanford, 1986; Crews et al., 1995). This hypothesis predicted that P limitation would be greatest at Bocas, which was located at the lowest of the three latitudes compared in this study. Instead, shoot elongation indicated an order that ranged from N limitation in both fringe and scrub zones at IRL, to N limitation in fringe and scrub as well as P limitation in scrub at Bocas, and to N limitation in fringe and P limitation in scrub at Twin Cays. The magnitude of the growth responses to fertilization with the limiting nutrient at each location was also consistent with this order, that is, IRL < Bocas < Twin Cays, with the most severe P limitation and the greatest growth response to P fertilization in the scrub zone at Twin Cays.

The differences in growth responses that we observed at the three locations suggest that nutrient limitation within and among mangrove ecosystems is likely determined by several features of their geomorphology, including sediment/nutrient flux, tidal range, and substrate type. These findings contrast with other studies that attribute P limitation in the tropics mainly to differences in the age of soils between tropical and temperate regions, with the most P-limited forests on the oldest soils (Vitousek, 1984; Vitousek and Sanford, 1986; Crews et al., 1995; Güsewell, 2004; McGroddy et al., 2004; Reich and Oleksyn, 2004; Kerkhoff et al., 2005).

Based on findings from Twin Cays (Feller, 1995; Feller et al., 2003a, 2007), McKee et al. (2002) hypothesized that the shift from N limitation in fringe zone around the periphery of the island to severe P limitation in scrub zone in the interior was the result of differences in factors associated with tidal flushing. Our results from the other two locations compared in this study partially support this hypothesis. Although all locations were N limited in the fringe, growth in the scrub zone at Bocas was limited by both N and P. This finding again differs from the IRL where growth was N limited in both zones (Feller et al., 2003b). These patterns along tidal gradients indicate that differences in nutrient limitation among the three locations are the result of variations in tidal flushing, external nutrient supply, substrate, and endogenous biological processes. The scrub forests in the interior areas have a low tidal exchange and a low supply of exogenous nutrients, whereas the fringe zones are well flushed with a higher net exchange of nutrients. Mangroves at the IRL and Bocas locations are in continental settings with medium to high relief, freshwater inflow, and nutrient flux. However, their tidal regimes and underlying soils differ dramatically. In contrast with IRL where mangroves are growing on sandy soils, mangroves at Twin Cays and Bocas are growing on peat. Although both of these locations are associated with low-nutrient coral reef ecosystems, Twin Cays receives negligible terrigenous inputs of freshwater or sediments whereas Bocas mangroves experiences a high flux of nutrients from several rivers draining into the archipelago. In addition, patterns of nutrient limitation in these systems may be affected by local patterns of N_2 fixation (Joye and Lee, 2004; Borgatti, 2008).

Resorption of phloem-mobile nutrients from leaves during senescence is an important nutrient conservation strategy for plants that influences many ecological processes, including primary production, nutrient uptake, competition, and nutrient cycling (Chapin, 1980). To resolve the relative degree to which latitude and nutrient enrichment affect the ability of *R. mangle* to conserve nutrients invested in foliage, we examined resorption of N, P, and K. Across location, zone, and nutrient treatment levels, our results indicate that a major control of the nutrient concentrations in senesced leaves was nutrient concentration in green leaves, which is consistent with a global dataset compiled by Kobe et al. (2005). Specifically, concentrations of N, P, and K in senesced leaves were positively associated with their concentrations in green leaves. In contrast to Oleksyn et al. (2003), who predicted that nutrient resorption efficiencies should increase with latitude, we found the lowest efficiencies at IRL, our northernmost location, consistent with Lovelock et al. (2007). We also found the most efficient nutrient conservation for

N and P at Twin Cays, the location positioned at the intermediate latitude. Although the levels to which nutrients were conserved varied by nutrient, location, and zone, the patterns did not fall clearly along a latitudinal gradient. All experimental trees at the three locations, except for the +N trees in the scrub zone at Bocas, had less than 0.7% N concentrations in their senescent leaves, which is within the range of complete resorption in the model proposed by Killingbeck (1996) (see Figure 6). In the Twin Cays fringe and the +P-fertilized scrub trees, the N concentration in senesced leaves was less than 0.3%, which was found to be the maximal level to which N can be reduced in senescent leaves of evergreen species and is regarded by Killingbeck (1996) as the ultimate potential resorption for N. In Killingbeck's model, less than 0.04% $P_{\text{senesced leaf}}$ represents complete resorption of P for evergreens. All experimental trees at Twin Cays and Bocas had values below this threshold and thus exhibited complete P resorption. Moreover, control and +N trees in the scrub and fringe zones at Twin Cays and Bocas had 0.01% $P_{\text{senesced leaf}}$ or less, which is the maximal level to which P can be reduced in senescent leaves in evergreens representing the ultimate potential resorption of P. Comparable levels of $\%P_{\text{senesced leaf}}$ have been reported for mangroves elsewhere (Alongi et al., 2005). In contrast, all the trees at IRL had values for $P_{\text{senesced leaf}}$ greater than 0.04%, which represents incomplete resorption. In contrast to suggestions by Aerts and Chapin (2000), the results presented here indicate there are nutritional controls on nutrient resorption in *R. mangle*. Nutrient enrichment clearly altered resorption of N and P at Twin Cays and Bocas but had no effect at IRL. Enrichment with +P resulted in increases in N and K resorption efficiency and proficiency at Twin Cays and Bocas but had the opposite effect on P resorption. Similarly, +N decreased N resorption, but only in the N-fertilized trees in the scrub zone at Bocas. These findings suggest that P enrichment may have either increased the requirements for N and K in *R. mangle* or it may have increased its physiological capacity to conserve these nutrients during leaf senescence. Increased resorption of N and K in response to +P may also indicate that under P-limiting conditions these nutrients become limiting when P is added to the system. Although we found no relationships between growth and N or P concentrations in green leaves, we did observe a weak but significant relationship between $\%K_{\text{green leaf}}$ and growth rates ($r = 0.230$, $F = 8.723$, $P < 0.01$). These results indicate that K availability may be important to the structure and function of some mangrove forests (Kathiresan et al., 1994), which warrants further study.

In conclusion, our results indicate that nutrient overenrichment of the coastal zone will alter forest structure and nutrient dynamics in mangrove ecosystems. We showed that fertilization altered growth and nutrient conservation in *R. mangle*, but the patterns did not correspond with a latitudinal gradient. Growth was consistently N limited for trees in fringing forests, which have higher water exchange rates compared to scrub forests, supporting the hypothesis of Smith (1984) and McKee et al. (2002) that open systems are more likely to be N limited than P limited. In the IRL, scrub trees in the interior of the forest were also N limited. Patterns of nutrient limitation became more complex at lower latitudes. Phosphorus limitations characterized the scrub zone at Twin Cays whereas both N and P limitations were widespread in the scrub zone at Bocas. Our results clearly indicated that the phenotypic potential of *R. mangle* to resorb N, P, and K from senescing leaves varied as a function of nutrient availability, which was driven by differences in hydrology and substrate along latitudinal and tidal gradients.

ACKNOWLEDGMENTS

We thank the Governments of Belize and Panamá for permission to use study sites at Twin Cays and at Bocas del Toro; Klaus Rützler, Valerie Paul, and Rachel Collin for support and permission to work at the Smithsonian marine laboratories at Carrie Bow Cay, Fort Pierce, and Bocas del Toro; Michael Carpenter, Woody Lee, and Gabriel Jacome for logistical arrangements; Anne Chamberlain for assistance in the laboratory and in the field. Financial support was provided by the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution; the Smithsonian Marine Station at Fort Pierce (SMSFP); and the National Science Foundation DEB-9981535. This is contribution number 842 of the CCRE, supported in part by the Hunterdon Oceanographic Research Fund, and SMSFP contribution no. 757.

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Underwater Spectral Energy Distribution and Seagrass Depth Limits along an Optical Water Quality Gradient

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ABSTRACT. We measured in situ inherent optical properties and seagrass maximum depth distribution in widely differing optical water types, including turbid green waters of the Indian River Lagoon (IRL, Florida, USA), a mix of turbid and clear waters in Panama, and very clear waters in Belize. We used Hydrolight to model in situ spectral energy distributions and measured leaf absorbance spectra (*Thalassia testudinum*) to distinguish between photosynthetically available radiation (PAR) and photosynthetically usable radiation (PUR). Attenuation coefficients for PAR and PUR were nearly indistinguishable in Belize and Panama and differed only slightly in the IRL. Grass grew to depths of penetration of 33% of PAR in the IRL, 14% in Panama, and approximately 5% in Belize, although we expect the value for Belize is an underestimate because conditions more turbid than are typical were prevailing at the time of the measurements. Corresponding percentages for PUR were 27%, 12%, and 5% for IRL, Panama, and Belize, respectively. These regional differences in light requirements were striking, and less than half of the difference could be attributed to latitudinal variations in incident light. We conclude that factors other than spectral energy distribution that covary with water clarity control site-specific light requirements of seagrasses. Possibilities include epiphytes and sediment quality.

INTRODUCTION

Seagrasses are important primary producers that play a role in the stability, nursery function, biogeochemical cycling, and trophodynamics of many coastal and estuarine ecosystems and as such are important for sustaining a broad spectrum of organisms (Hemminga and Duarte, 2000). Seagrasses are potentially sensitive indicators of declining water quality because of their high light requirements (11%–37% surface irradiance) compared to those of other aquatic primary producers with much lower light requirements (<1%) (Dennison et al., 1993; Zimmerman, 2003). Seagrass communities have declined in coastal regions worldwide (Orth et al., 2006), which is usually attributed to reductions in water clarity brought about, at least initially, by accelerated eutrophication in the coastal zone (Krause-Jensen et al., 2008).

Management efforts aimed at preserving and restoring seagrass systems generally focus on improving water clarity (Batiuk et al., 2000; Kenworthy and Haunert, 1991; Steward and Green, 2007), based on the high light requirements

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Manuscript received 23 July 2008; accepted 20 April 2009.

of seagrasses and the reduction in light penetration associated with eutrophication (Ralph et al., 2007). Deciding on the extent of water quality improvements (or limit of allowable deterioration) requires more detailed knowledge of the wavelength-specific light requirements of seagrasses. Based on a survey of available literature, Carter et al. (2000) determined that mesohaline and polyhaline submerged grass communities in Chesapeake Bay require a long-term average of 22% of surface irradiance at the deep edge of the grass meadow for survival. Gallegos and Kenworthy (1996) determined a similar requirement for mixed beds of *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme* in the Indian River Lagoon (IRL) near Ft. Pierce, Florida. In contrast, Steward et al. (2005) found 20% to be near the minimum for the IRL, while the average light requirement was 33% of annual incident irradiance, similar to the wide range (24%–37%) reported for the southern Indian River Lagoon (Kenworthy and Fonseca, 1996). More recently, Duarte et al. (2007) analyzed 424 reports of seagrass colonization depths and light attenuation and found generally higher light requirements for plant communities growing in shallow, turbid waters than in clear, deep waters. The authors suggested that large differences in light requirements between shallow- and deep-growing seagrasses may be partially attributed to differences in the quality of light. Seagrasses may grow deeper in clear water because there is more high-energy blue light available for photosynthesis, whereas in shallow turbid water the shorter blue wavelengths are rapidly attenuated.

The wavelength specificity of light absorption by seagrasses has implications for setting water quality requirements needed to protect or restore these plants in eutrophic waters that are dominated by inefficient green wavelengths. The absorption of light by the complement of pigments (chlorophyll *a* and chlorophyll *b*) in seagrasses is highly wavelength selective, with absorption peaks in the blue (centered around 450 nm) and red (centered around 670 nm) regions of the visible spectrum, and a broad absorption minimum in the green between 500 and 600 nm (Drake et al., 2003; Zimmerman, 2003). Wavelengths of light that are poorly absorbed by the plant are relatively inefficient at driving photosynthesis (Drake et al., 2003; Falkowski and Raven, 2007).

Light requirements of seagrasses that have been determined to date (Batiuk et al., 2000; Kenworthy and Fonseca, 1996) have been based on photosynthetically available radiation (PAR, 400–700 nm) because of the widespread availability of underwater quantum sensors. PAR measurements weight quanta of all visible wavelengths equally. By contrast, measurements of photosynthetically *usable* radiation (i.e., PUR; see Morel, 1978) weight quanta in proportion to the efficiency with which they are absorbed. There are no sensors for direct measurement of PUR; it must be calculated from the underwater spectrum (measured or modeled) weighted by the relative absorption spectrum of the plant of interest.

Using a bio-optical model of light penetration in the mesohaline Chesapeake Bay, Gallegos (1994) determined that the 22% surface PAR requirement for seagrasses occurred at the same depth as the penetration of 16% of surface PUR. The distinction is potentially important because the penetration of PUR is more sensitive to the concentration of phytoplankton chlorophyll (i.e., eutrophication) than is the penetration of PAR, for the reason that phytoplankton chlorophyll absorption selectively removes those same wavelengths most efficiently used in photosynthesis by seagrass. Thus, by basing light requirements on PUR rather than on PAR, we would predict greater restoration benefit from chlorophyll reduction, and greater seagrass losses from chlorophyll increases, than by light requirements based on PAR (Gallegos, 1994).

The objective of this work was to determine whether the distinction between PAR and PUR requirements could be determined from in situ depth distributions of seagrass communities. The distinction cannot be drawn from depth distributions at a single site such as Chesapeake Bay or the IRL, because within these systems the underwater spectrum is peaked in the green, and thus there is insufficient spectral variability in available light to differentiate between depth limits based on PAR compared with PUR. The gradient of optical water quality types across locations of the Smithsonian Marine Science Network, however, offers a potentially ideal scenario for making this determination. All three of the dominant seagrass species found in the IRL also occur in the tropical waters of Carrie Bow Cay, Belize, and Bocas del Toro, Panama. In optically clear waters, the underwater spectrum peaks in the blue, near an absorption peak of chlorophyll *a* or *b*. In blue water, therefore, PUR penetrates deeper than PAR, and plants should grow to relatively deeper depths in blue tropical waters if PUR rather than PAR is the determining factor. To investigate this distinction, we surveyed seagrass distributions and measured inherent optical properties (IOPs), from which we calculated underwater light spectra at the deep edges of grass beds, to test the hypothesis that across the optical water quality gradient seagrass would grow to a consistent depth of penetration of PUR but a variable percentage of PAR.

METHODS

STUDY SITES

Station locations are shown in Figure 1. We occupied stations in the clear tropical waters off Carrie Bow Cay, Belize (station Blue Ground Range, BGR), and in Bahia Almirante, Panama (station STRI [Smithsonian Tropical Research Institute]), a station receiving colored-water discharge from a nearby creek in Panama (station SN03), and the more eutrophic waters of the Indian River Lagoon, Florida (ICW194; see Figure 1). Detailed characteristics of these sites are given by Lang (2009) in the Introduction to this volume.

OPTICAL PROPERTIES

We measured in situ profiles of IOPs, the spectral absorption and beam attenuation coefficients, at nine wavelengths (412, 440, 488, 510, 532, 555, 650, and 715 nm) using a WETLabs ac-9 instrument with a 0.1 m pathlength, equipped with a pressure sensor to measure depth. A Seabird SBE-5T pump provided water flow to the ac-9 and a WETLabs MPAK unit that controlled pump and instruments and logged data.

Measured absorption and beam attenuation coefficients were corrected for temperature according to the manufacturer's protocols. We corrected absorption coefficients for scattering errors (Kirk, 1992) by the Zaneveld et al. (1994) algorithm that subtracts a fraction of measured scattering coefficient from absorption (Equation 1):

$$a_{t-w}(\lambda) = a_m(\lambda) - \varepsilon(c_{t-w}(\lambda) - a_m(\lambda)) \tag{1}$$

where $a_{t-w}(\lambda)$ is the scattering-corrected absorption coefficient less pure water absorption at wavelength λ, a_m is the measured non-water absorption coefficient subject to scattering error, c_{t-w} is the measured non-water beam attenuation coefficient, and ε is a coefficient that accounts

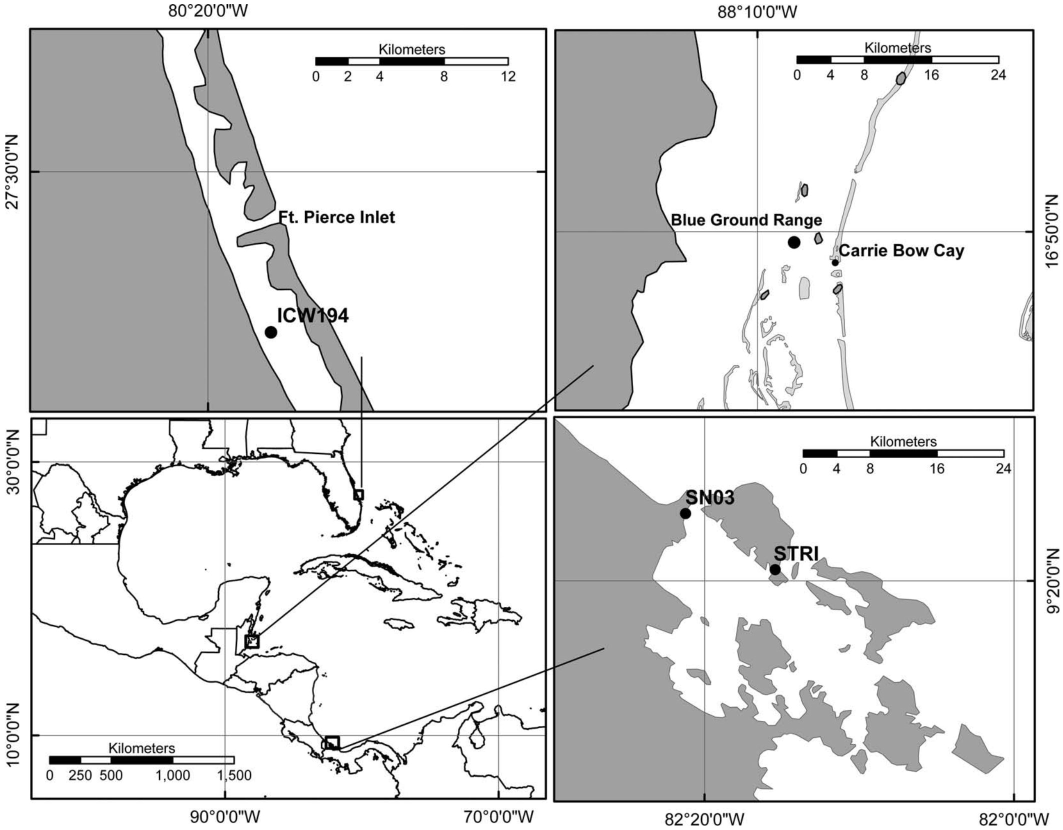


FIGURE 1. Locations of stations in the Indian River Lagoon, Florida (upper left), Belize (upper right), and Panama (lower right). Lower left panel shows overview of Caribbean. Light gray shading in Belize panel indicates coral reef habitat.

for overall errors with the reflective tube absorption meter of the ac-9 that result from a failure to collect all scattered light (Kirk, 1992). In this work we verified the assumption that non-water absorption at the longest ac-9 wavelength (715 nm) was not measurable in the laboratory (Tzortziou et al., 2006). Thus, we calculated ε by Equation 2:

$$\varepsilon = \frac{a_m(715)}{c_{t-w}(715) - a_m(715)} \tag{2}$$

We measured the absorption spectrum of *Thalassia testudinum* leaves in an integrating sphere (LICOR 1800-12S) interfaced to an Ocean Optics USB2000 spectrometer. A clean segment of leaf was placed on a microscope slide over the opening to the sphere and illuminated with a fiberoptic microscope light source. Black tape on the slide obscured the portion of the opening not covered by the leaf. Percent transmittance (%T) of the leaf was calculated referenced to the slide and tape without a leaf in place. Absorbance was calculated as −ln(%T), and the spectrum was normalized to the value at the absorption peak at 675 nm. Measurements on eight leaves collected from the deep edge at the site in Belize were averaged. Similar measurements made in Panama had similar results.

RADIATIVE TRANSFER MODELING

To calculate spectral diffuse attenuation coefficients and underwater light spectra, we used the commercially available radiative transfer model, Hydrolight 4.2, which is extensively documented by Mobley (1994). User input consists of specifications for IOPs, boundary conditions, and assumptions on inelastic scattering processes. We used the pure-water absorption coefficients of Pope and Fry (1997) and pure-water scattering coefficients for freshwater from Buiteveld et al. (1994). We used in situ estimates of absorption, attenuation, and scattering coefficients binned at 0.5 m intervals. Following Tzortziou et al. (2006), we used the Fournier–Forand scattering-phase function, the shape of which was shown by Mobley et al. (2002) to be well specified by the backscattering ratio. We omitted inelastic scattering processes because our interest is in downwelling irradiance, and these processes primarily affect only calculations of upwelling radiance. For incident irradiance and the distribution of total irradiance between direct and sky irradiance we used the built-in RADTRAN routine for the time, location, and estimate of approximate cloud cover.

From the simulations of spectral downwelling irradiance we calculated PAR according to its definition (Equation 3):

$$PAR(z) = \int_{400}^{700} Q(\lambda, z)\, d\lambda = \int_{400}^{700} \frac{E_d(\lambda, z)}{h\eta} d\lambda \tag{3}$$

where Q is the quantum flux, E_d is the spectral downwelling irradiance in energy units, h is Planck's constant, λ is the wavelength and $\eta = 2\pi c/\lambda$ is the frequency of light, and c is the speed of light in vacuum. PUR was calculated in an analogous manner, weighted by the plant absorption spectrum, measured at the deep edge of the Belize site:

$$PUR(z) = \int_{400}^{700} Q(\lambda, z)\tilde{a}_{Th}(\lambda)\, d\lambda \tag{4}$$

where $\tilde{a}_{Th}$ (λ) is the absorption spectrum of *T. testudinum* normalized to its peak at 675 nm and to unit sum. For comparison of attenuation rates, PAR and PUR were both normalized to their values at the surface.

SEAGRASS SURVEYS

At each sampling site a pair of scuba divers entered the water to visually confirm the seagrass bed (*T. testudinum*) deep edge, defined as the visible transition between vegetated and unvegetated bottom. Once the physical boundaries of the meadow edges were identified underwater, the divers laid out two 10 m long transects parallel to the edge of the seagrass bed. At 1.0 m intervals along each transect, the divers visually estimated seagrass cover in a 0.25 m^2 quadrat using the Braun-Blanquet scale (1965). The Braun-Blanquet cover abundance scale is a visual assessment technique for estimating the canopy cover. Values are 0.1 = solitary shoot, with small cover; 0.5 = few shoots, with small cover; 1 = numerous, but less than 5% cover, 2 = 5%–25% cover, 3 = 25%–50% cover, 4 = 50%–75% cover, and 5 = more than 75% cover.

At the same location each diver counted the number of seagrass short shoots in either a 0.25 m^2 or 0.0625 m^2 quadrat, depending on the shoot density. Short shoot counts were multiplied by the appropriate scaling factor and averaged for the 10 quadrats to obtain an estimate of the number of short shoots per square meter. For comparison of deep edge seagrass characteristics, we also surveyed relatively shallow sites at the Blue Ground Range station in Belize (2.4 m) and the STRI station in Panama (1.8 m). At SN03 in Panama we only surveyed at the deep edge. Deep edge data for the IRL are from annual surveys by the South Florida Water Management District (http://my.sfwmd.gov/gisapps/sfwmdxwebdc/dataview.asp?query=unq_id=1797).

RESULTS

SEAGRASS DEPTH LIMITS

At the Blue Ground Range station in Belize, the deep edge of the *Thalassia testudinum* meadow was located at 10–11 m. The deep edge was a distinct transition from a sparse cover of *T. testudinum* to unvegetated, fine carbonate mud. Recently germinated seedlings of the small opportunistic species *Halophila decipiens* were observed just outside of the deep edge of the *T. testudinum* meadow. Braun-Blanquet cover values ranged from 0.5 (a few individual short shoots) to 1 (<5%). *Thalassia testudinum* short shoot densities ranged from 0 to 48 shoots m^{-2}, averaging 22.4 shoots m^{-2}. At the shallow Blue Ground Range transect, *T. testudinum* Braun-Blanquet scores ranged from 3 to 4, indicating that cover generally varied from 25% to 75%, while densities ranged from 176 to 416 shoots m^{-2}, averaging 310 shoots m^{-2}. At the shallow station *T. testudinum* was 14 times more dense than at the deep edge. No other seagrass species were observed at this station.

At the STRI station in Panama we located the deep edge of the *T. testudinum* at 8.5 m. The transition edge of the *T. testudinum* meadow was distinct; however, there was considerably more *H. decipiens* just downslope of the edge than there was at the Blue Ground Station in Belize. *Thalassia testudinum* short shoot densities ranged from 0 to 56 shoots m^{-2}, averaging 18 shoots m^{-2}, similar to the deep edge at the Blue Ground Range Station in Belize. Braun-Blanquet values ranged from 0 to 1, indicating that cover was generally less than 5%. We also observed three quadrats with a relatively sparse cover of *Halodule wrightii*. At the shallow STRI station (1.8 m), *T. testudinum* densities ranged from 160 to 528 shoots m^{-2} with an average of 465, 25 times the density at the deep edge and more dense than the shallow station at Blue Ground Range in Belize. Braun-Blanquet values ranged from 3 to 4, similar to the shallow station at Blue Ground Range (BGR) in Belize.

At the SN03 site in Panama, the deep edge of the *T. testudinum* bed was located at 2.4 m. Short shoot densities ranged from 0 to 288 m^{-2}, with a mean value of 114. The deep edge of the *T. testudinum* meadow was marked by a transition from *T. testudinum* to unvegetated sediment. Braun-Blanquet scores ranged from 0 to 3, indicating cover values less than 50%.

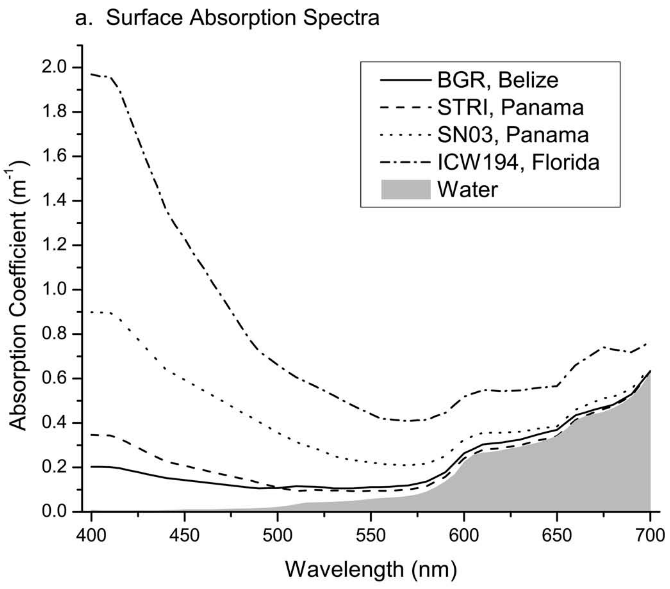
Seagrass depth limits in the IRL at the site where optical measurements were made in 2001 were reported as 0.92 m for beds described as continuous and dense, with a lower limit of 50% to 60% cover.

OPTICAL PROPERTIES

A wide range of optical properties was observed among the four sites (Figure 2a). Based on absorption spectra, Belize had the clearest water while the most turbid water occurred in the IRL. The two sites in Panama were intermediate. The rank order of sites was different for scattering coefficients (Figure 2b), with scattering coefficients at the Panama shallow site (SN03) being the highest and the Panama deep site (STRI) the lowest.

ABSORPTION SPECTRUM

Normalized absorption by *T. testudinum* was similar to measurements by other investigators (Zimmerman, 2003), having peaks in the red wavelengths (~680 nm), a broad maximum at blue wavelengths (400–490 nm), and a trough at green wavelengths (~525–625 nm) (Figure 3, solid line). This spectrum was used to calculate PUR from simulated downwelling spectral irradiance according to Equation 4. However, even at the local minimum at 555 nm, measured absorption was still 37% of the red peak. On considering that *T. testudinum* has no chlorophyll pigments that absorb green wavelengths (Zimmerman, 2003), we also constructed a hypothetical photosynthetic action spectrum based on chlorophyll absorption alone, consisting of Gaussian curves with peaks at 410, 430, 455, 642, and 680 nm for an alternate calculation of PUR (see Figure 3, dashed line). The hypothetical action spectrum is expected to produce the maximal separation between PAR and PUR, especially in turbid green water, because the trough in the hypothetical chlorophyll absorption spectrum at green wavelengths is much more pronounced compared with the measured absorption spectrum, which includes an unquantified contribution by photosynthetic carotenoids. This hypothetical chlorophyll-based action spectrum serves as a site-independent sensitivity test for the greatest possible difference between PAR and PUR for a higher plant. We did not measure absorption spectra in the IRL, so they are unknown. The hypothetical spectrum allows a comparison among sites in the absence of measurements at all sites.



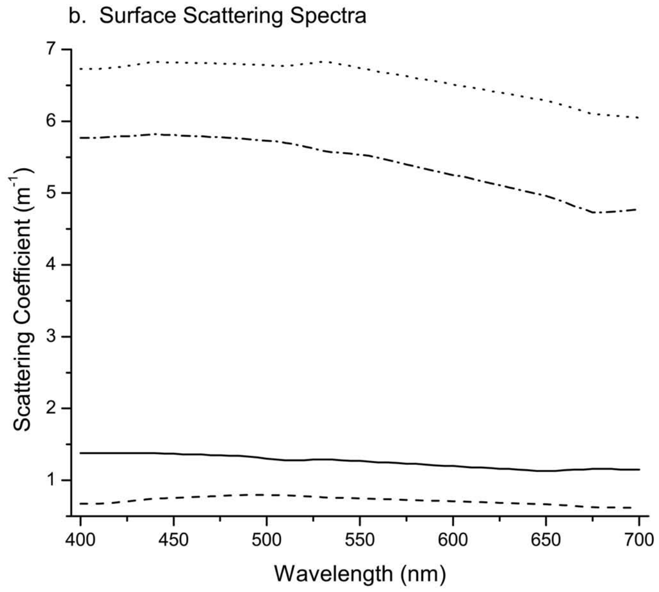


FIGURE 2. Surface water absorption spectra (a) and surface water scattering spectra (b) at sites sampled in Belize, Panama, and Florida.

PAR and PUR Profiles

Profiles of normalized downwelling PAR and PUR based on the measured absorption spectrum (PURm) and PUR based on the hypothetical action spectrum (PURh) are shown for the stations having the least and the most separation between PAR and PUR in Figure 4. The diffuse attenuation coefficients for each of the three quantities are reported for all stations in Table 1. At the Blue Ground Range station in Belize, diffuse attenuation coefficients for PAR and PURm were indistinguishable, while that for PURh was only 7% higher than for PAR (Table 1). The largest differences among the three attenuation coefficients occurred at the IRL. The relative differences between attenuation coefficients for PAR and PURm (13%) and between PAR and PURh (31%) were similar for the IRL and SN03 site in Panama, although the absolute coefficients were smaller at SN03 (Table 1).

The percentages of surface light remaining at the deep edges of the seagrass beds varied widely among the locations, from about 5% at the Blue Ground Range site in Belize to about 30% at the IRL (see Table 1). The percentages based on PUR were, as expected, lower than those based on PAR, but the differences among sites was still large (Table 1). Because of the extremely large differences among sites in the percentage of light at the seagrass bed deep edge, the calculation of PUR did not yield a consistent value across sites. The overall range was, however, somewhat smaller for PUR than for PAR (Table 1). Spectra of downwelling irradiance at the deep edges calculated by Hydrolight are shown in Figure 5. The overall fraction of surface irradiance remaining at the deep edges at the different locations follows the percentages in Table 1. Qualitative differences in the spectra of light remaining at

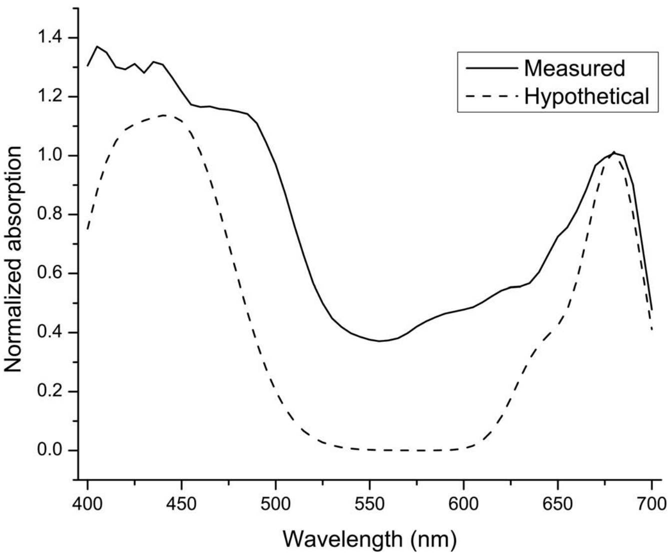


FIGURE 3. Normalized absorption spectra used for calculating photosynthetically usable radiation, based on absorption spectrum measured on *Thalassia testudinum* leaves (solid line), and a hypothetical action spectrum derived by assuming only light absorbed by chlorophylls *a* and *b* drive photosynthesis in *Thalassia* (dashed line).

the deep edges also occur. Because of absorption by water, virtually no light is present at wavelengths greater than 600 nm at the BGR location in Belize and very little at STRI in Panama. Increasing amounts of red wavelengths are present at the SN03 and IRL sites as a result of the shallower depths of the deep edges. The peaks of the in situ spectra shift progressively toward green wavelengths along the progression from BGR to IRL, and the greatest similarities are at 400 to 410 nm, where the percentage of surface irradiance remaining ranges from 2% to 6%.

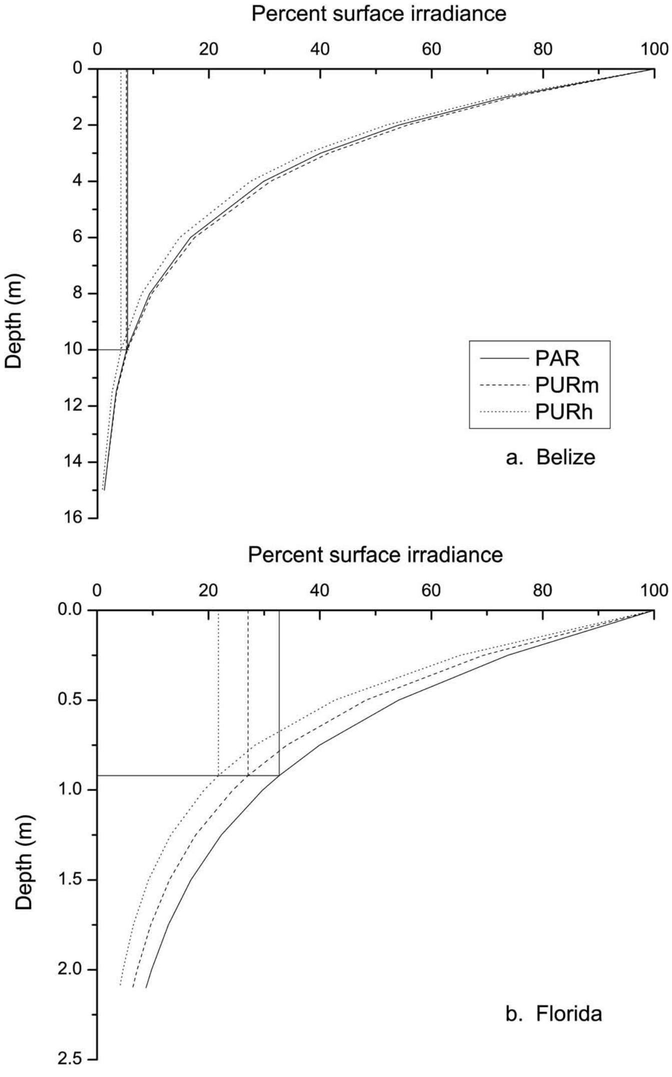


FIGURE 4. Vertical profiles of photosynthetically active radiation (PAR, solid line), and photosynthetically usable radiation (PUR) based on measured absorption spectrum (PURm; dashed line) and hypothetical action spectrum (PURh; dotted line) in (a) Belize and (b) the Indian River Lagoon (IRL), Florida. Profiles were normalized to the irradiance incident at the surface (100%).

TABLE 1. Depths of seagrass deep edge (Z_{max}) and attenuation coefficients for photosynthetically active radiation (K_{PAR}) and photosynthetically usable radiation (PUR) weighted by measured absorption spectrum of *Thalassia testudinum* leaves (K_{PURm}) or weighted by a hypothetical action spectrum (K_{PURh}; see Figure 2). Percentage of surface light penetrating to the seagrass deep edge is given in parentheses.

Site [a]	Z_{max} (m)	K_{PAR} (m^{-1})	K_{PURm} (m^{-1})	K_{PURh} (m^{-1})
BGR, Belize	10	0.293 (5.2%)	0.293 (5.4%)	0.314 (4.2%)
STRI, Panama	8.5	0.232 (13.6%)	0.247 (12.0%)	0.304 (7.4%)
SN03, Panama	2.4	0.836 (14.1%)	0.945 (11.0%)	1.098 (7.7%)
IRL, Florida	0.92	1.157 (32.7%)	1.301 (27.1%)	1.52 (21.8%)

[a] BGR, Blue Ground Range; STRI, Smithsonian Tropical Research Institute; SN03, Panama creek station; IRL, Indian River Lagoon.

DISCUSSION

At all three study sites we were able to locate a distinct deep edge of the *Thalassia testudinum* meadows, characterized by a transition from moderate and sparsely vegetated seagrass to either unvegetated substrate or patches of the smaller, low light adapted seagrass *Halophila decipiens*. Where we were able to sample shallower sites in Belize and Panama, there were substantially higher densities of *T. testudinum*. The presence of *H. decipiens* at the Blue Ground Range (BGR) station in Belize and the STRI site in Panama further confirmed that we were sampling at light-limiting edges of the *T. testudinum* distribution. *Halophila decipiens* is a small, ruderal species of seagrass commonly found growing in deep or turbid water and has lower light requirements than *T. testudinum* (Kenworthy, 2000; Gallegos and Kenworthy, 1996; Kenworthy et al., 1989). The presence of *H. decipiens* at these two stations was a good indication of light-limiting conditions for *Thalassia*. Although we did not record *H. decipiens* at SN03 in Panama, a thorough visual examination by divers at deeper depths than the observed *T. testudinum* distribution confirmed there were no seagrasses growing beyond 2.4 m depth.

Attenuation coefficients for PAR and PUR were nearly indistinguishable in Belize and Panama and differed only slightly in the IRL. Based on these one-time profiles, we calculated that seagrass grew to depths of penetration of

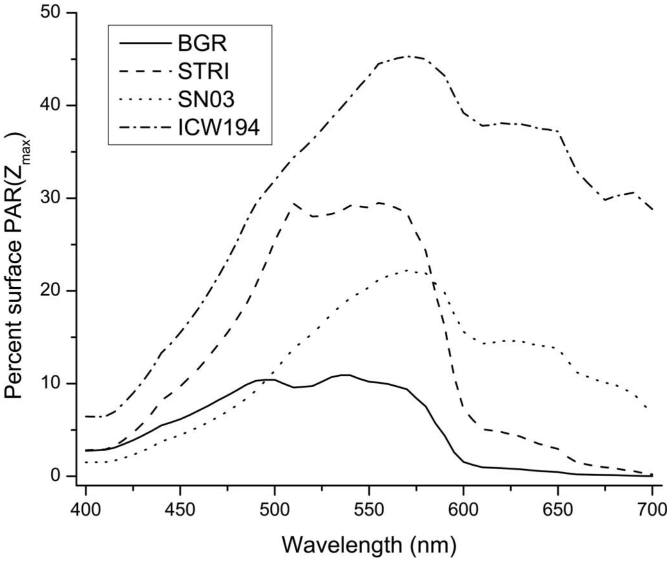


FIGURE 5. Spectra of photosynthetically active radiation (PAR) at the depth of the seagrass deep edge (Z_{max}) in Belize (BGR, solid line), Panama (STRI, dashed line, and SN03, dotted line), and Florida (IRL [ICW194], dot-dashed line).

33% of PAR in the IRL, 14% in Panama, and approximately 5% in Belize. Corresponding percentages for PUR were 27%, 12%, and 5% for IRL, Panama, and Belize, respectively. The accuracy of these estimates depends on the degree to which the profiles were measured under conditions that are typical for their respective growing seasons. We are fairly certain this was *not* the case in Belize, where strong northerly winds, atypical for the season, blew for several days before and on the day of sampling. Horizontally sighted Secchi disk visibility at a seagrass bed near Twin Cays was 5.5 m during the time of our measurements, compared with annual means of 10.1 m (±0.38 m SE) for 2004 and 8.9 m (±0.25 m SE) for 2005 (see Koltes and Opishinski, 2009: fig. 6, this volume). If the water column were more strongly stirred with higher than typical concentrations of particulate matter, then our estimates for Belize would be biased low, as we suspect they are. The estimated PAR light requirements for the IRL are, however, based on more frequent visits and are in agreement with other published estimates (Kenworthy and Fonseca, 1996; Steward et al., 2005). The limitation of our approach was the inability to determine the integral of light requirements for the whole growing season from only a few days of measurements. Because of this limitation, it is unlikely that the observed depth distribution of the seagrasses is fully captured by PAR and PUR percentages calculated, and repeating this study during another season could yield different percentages.

Nonetheless, assuming that the light requirements for seagrasses at Belize are similar to those in Panama, the regional differences in light requirements between the IRL and the two tropical sites remain striking. Qualitatively, the differences are consistent with the observations of Duarte et al. (2007) that seagrasses growing in shallow, turbid waters (e.g., IRL) have higher light requirements than those growing in clear, deep water (Panama, Belize). Calculation of PUR closed the gap only slightly, leading us to conclude that factors other than spectral energy distribution contribute substantially to site-specific light requirements of seagrasses, especially at the deep edges. An extended growing season in the more tropical locations of Belize and Panama could possibly account for some of the difference. The tropical sites receive about 7% more incident radiation annually than the IRL site, most of which occurs during winter months (November through February) when temperatures are also more favorable in the tropics. Other possible differences between sites include leaf-shading epiphytes, sediment quality (e.g., grain size or organic matter content), and possible periods of low oxygen in thermally stratified deeper waters. These latter factors have management implications because they are all affected by coastal eutrophication. Improved understanding of the factors accounting for site-specific differences in seagrass light requirements is, therefore, urgently needed.

ACKNOWLEDGMENTS

We gratefully acknowledge the Smithsonian Marine Science Network for Pilot Project funds to conduct these studies. We thank Sam Benson for diving assistance in Belize and Amy Lewis for help with optical data reduction and analysis. This is contribution no. 844 of the Caribbean Coral Reef Ecosystem Program (CCRE), supported in part by the Hunterdon Oceanographic Research Fund, and Smithsonian Marine Station at Fort Pierce contribution no. 787.

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Interannual Variation in Gelatinous Zooplankton and Their Prey in the Rhode River, Maryland

Eileen S. Graham, Danielle M. Tuzzolino, Rebecca B. Burrell, and Denise L. Breitburg

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ABSTRACT. The lobate ctenophore *Mnemiopsis leidyi* is an important predator of zooplankton and ichthyoplankton both within and outside its native range, and it is a dominant consumer within the Chesapeake Bay food web. We sampled the Rhode River, a subestuary of Chesapeake Bay, during 2004 and 2005 to quantify the abundances of *M. leidyi*, its scyphomedusan predators, and its mesozooplankton prey, and conducted ctenophore egg production experiments in 2004. Despite low mesozooplankton densities, ctenophores produced up to 9,380 eggs individual^{-1} day^{-1}. Temporal patterns, as well as peak abundances, of copepods, ctenophores, and sea nettles (*Chrysaora quinquecirrha*; the major predator of *M. leidyi*) varied considerably between years. This interannual variation may have been caused by direct and indirect effects of physical factors, especially low salinities during 2004, on all components of the food web. In 2004, zooplankton abundances peaked in June, *M. leidyi* abundances steadily increased throughout the summer, and *C. quinquecirrha* was rare. In contrast, during 2005, *C. quinquecirrha* density increased during midsummer. As this medusa increased in abundance, *M. leidyi* numbers declined and copepod abundances increased. Shallow systems with salinities near the minimum threshold for *C. quinquecirrha* ephyra production may exhibit more extreme interannual variability than deeper, higher-salinity systems and may serve as models to provide insight into factors controlling gelatinous zooplankton dynamics.

INTRODUCTION

The lobate ctenophore *Mnemiopsis leidyi* is native to Atlantic and Caribbean estuaries and coastal waters from Massachusetts to southern Argentina and has been introduced to several Eurasian systems including the Black, Caspian, Baltic, and North Seas (Purcell et al., 2001; Kube et al., 2007). *Mnemiopsis leidyi* can tolerate a wide range of temperatures, salinities, and dissolved oxygen (DO) concentrations. It occurs in waters with salinities ranging from less than 5 to more than 36 (Purcell et al., 2001; Purcell and Decker, 2005) and can survive exposure to DO concentrations of 0.5 mg L^{-1} for at least 4 d (Decker et al., 2004). Optimal temperatures for *M. leidyi* reproduction are approximately 18°–20°C (Costello et al., 2006).

In late spring and early summer, *M. leidyi* can be abundant in Chesapeake Bay and its tributaries, where it is a dominant consumer, potentially capable of clearing much of the daily standing stock of zooplankton and ichthyoplankton

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(Cowan et al., 1992; Cowan and Houde, 1993; Purcell et al., 1994; Purcell and Decker, 2005). In mesohaline portions of the Chesapeake Bay system, the major predator of *M. leidyi*, the scyphomedusa *Chrysaora quinquecirrha*, usually becomes abundant in early July and persists through the end of summer (Cargo and King, 1990). As *C. quinquecirrha* population densities increase, *M. leidyi* abundances typically decline and zooplankton populations rebound (Purcell and Cowan, 1995). However, in years when *C. quinquecirrha* populations are low, *M. leidyi* may exert much greater and prolonged control within the food web. *Chrysaora quinquecirrha* polyps are generally found in salinities of 7 to 20 and strobilate when temperatures exceed 17°C (Cargo and Schultz, 1967; Cargo and King, 1990). Medusae are most abundant at salinities of 10–16 (using the Practical Salinity Scale) and temperatures of 26°–30°C (Decker et al., 2007). Thus, interannual variation in salinity and temperature can strongly affect the timing and spatial distribution of *C. quinquecirrha* and its control of *M. leidyi*.

The Rhode River is a small, shallow subestuary on the western shore of Chesapeake Bay (Figure 1) characterized by summer salinities that vary interannually in both absolute maxima and timing of these maxima. Similar to other tributaries in the Chesapeake Bay system, this estuary supports a gelatinous zooplankton food web throughout late spring and summer months. The most abundant gelatinous species are the zooplanktivorous *M. leidyi* and its scyphomedusan predator and competitor *C. quinquecirrha*. Average spring–summer salinity in the Rhode River is near the lower limit required for strobilation by *C. quinquecirrha*. In addition, interannual variation in water temperature has the potential to cause variation in the timing of initial and peak occurrences of these gelatinous species and their prey. As a result, the Rhode River can have two distinct gelatinous food webs: one in which the top predator (*C. quinquecirrha*) exerts control over the intermediate consumer (*M. leidyi*) and one in which the intermediate consumer is not controlled by predation.

The objectives of this study were to examine temporal and spatial patterns in abundances of *M. leidyi* and *C. quinquecirrha* within and near the Rhode River and to examine how those patterns varied in relationship to water temperature, salinity, and the abundance of mesozooplankton prey. We also examined temporal and spatial variation in egg production by *M. leidyi*. This study was conducted during the summers of 2004 and 2005, years with very different temporal patterns of *M. leidyi* and *C. quinquecirrha* densities.

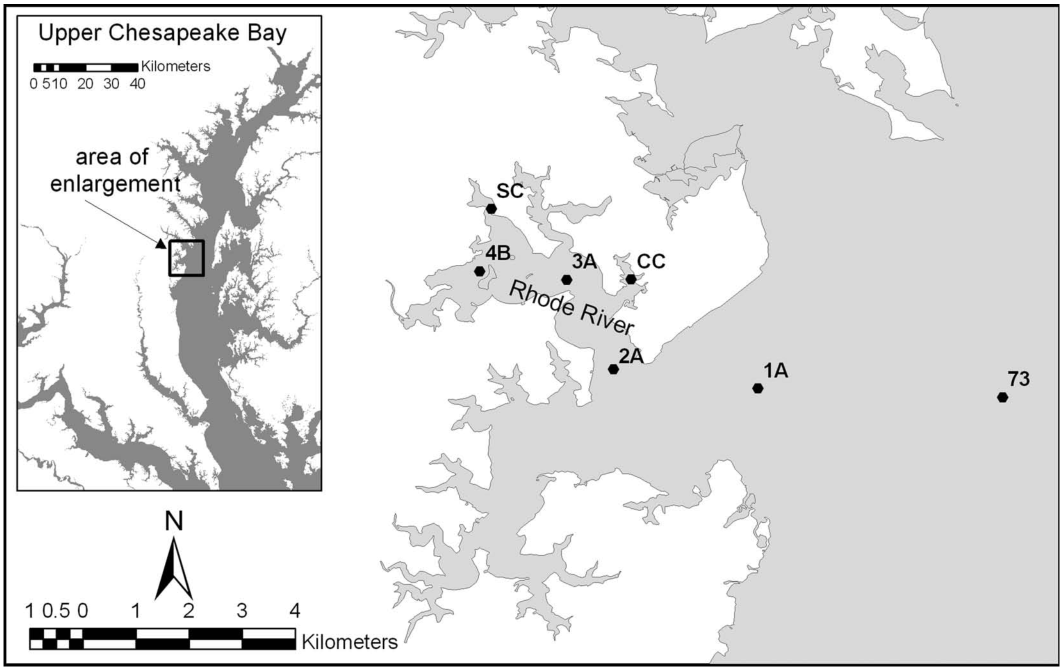


FIGURE 1. The Rhode River and its location in the Chesapeake Bay. Dots indicate location of sampling sites; the SERC dock is located directly inshore (northwest) of site 4B.

METHODS

We sampled seven sites: six within the Rhode River and one just beyond the mouth of the river in the mainstem Chesapeake Bay. Sites were chosen based on prior research conducted in the Rhode River and designed to cover its entire length. At each site, weather conditions were noted and temperature, DO, and salinity were recorded at the surface and subsequent 1 m depth intervals with a YSI 600QS meter. Additional temperature, DO, and salinity data were available from the monitoring station located at the dock of the Smithsonian Environmental Research Center (SERC) in the Rhode River, which was equipped with a YSI 6600 meter (C. Gallegos, SERC, unpublished data).

Gelatinous zooplankton samples were collected in duplicate 3 min stepped oblique tows using a 0.5 m diameter, 202 μm mesh hoop plankton net towed at approximately 2 knots and equipped with a General Oceanics flowmeter (model 2030). Excess water was strained from the sample, total volume of gelatinous zooplankton was measured, and all individuals were identified to species and enumerated. Bell diameters of *C. quinquecirrha* and the oral to aboral lengths of up to 15 *M. leidyi* were recorded. Remaining specimens of *M. leidyi* were classified as either larger than or equal to or less than 3.0 cm.

Mesozooplankton samples were collected using 0.3 m diameter, 202 μm mesh paired hoop nets. Samples were rinsed through a 2 mm sieve to remove gelatinous zooplankton and preserved with 10% buffered formalin; mesozooplankton species were subsequently identified and enumerated.

Whole water column chlorophyll data were collected by another research group (C. Gallegos, SERC) at the four central Rhode River sites (1A, 2A, 3A, 4B; see Figure 1) on different days during each sampling week. Chlorophyll *a* (chl *a*) was measured with a Spectronics Genesis 5 spectrophotometer and converted into micrograms per liter ($\mu g\ L^{-1}$).

Mnemiopsis leidyi egg production assays were conducted in 2004 using established methodology (Kremer, 1976; Grove and Breitburg, 2005). Undamaged individuals covering the size range from each site (3–8 cm) were randomly assigned to jars containing 3 L filtered Rhode River water and left overnight at ambient water temperatures. At approximately 0900 the following morning, adult ctenophores were removed and lengths and volumes recorded. Water from each jar was strained through a 35 μm sieve, preserved with 10% acid Lugol's solution (Sullivan and Gifford, unpublished data; Grove and Breitburg, 2005), and eggs were enumerated. Egg production was normalized by ctenophore volume to facilitate comparisons among individuals.

Data were analyzed using analysis of variance (Proc GLM: SAS v. 9.1) on rank-transformed data. Student–Newman–Keuls tests were used for a posteriori comparisons. Regression models were used to examine the effects of ctenophore volume, site, date, and interactions between these factors on egg production. Nonsignificant interaction terms with $P \geq 0.25$ were dropped from statistical models.

RESULTS

PHYSICAL PARAMETERS

Temperature, salinity, and DO all varied among sites and between years (Table 1; Figure 2; two-way analysis of variance [ANOVA]). Surface water temperature varied among sites ($F = 38.21$, $P < 0.01$), and was cooler adjacent to, and near the mouth of, the Rhode River and at the deeper sites. Surface salinity also varied significantly among sites ($F = 3.55$, $P < 0.01$), and was generally highest at the Bay site (Site 73) and at sites near the mouth of the Rhode River. Minimum DO concentration varied among sites ($F = 7.33$, $P < 0.01$) and was significantly lower at the Bay site than elsewhere.

Measurements at the SERC dock indicated that surface water temperatures reached 25°C more than 3 weeks earlier in 2004 than in 2005 but exceeded 30°C only during 2005. Salinity remained below 8 except for a brief period in 2004 but exceeded 8 for most of the summer in 2005. Daytime low DO concentrations (<2 mg L^{-1}) were occasionally recorded in the bottom waters during cruises; all low daytime DO measurements in 2004 and all but one in 2005 were recorded at the Bay site. The continuous YSI 6600 monitor at the SERC dock indicated that low DO concentrations occurred near the surface within the Rhode River in the early morning hours of both years (C. Gallegos, SERC, personal communication, 2004). Analysis of our weekly sampling data indicated that temperature ($F = 5.38$, $P = 0.02$), salinity ($F = 135.18$, $P < 0.01$), and DO concentrations ($F = 6.39$, $P = 0.01$) were all significantly higher in 2005 than in 2004.

2004 BIOTA

Chlorophyll *a* concentrations peaked in early June, declined, and then rose continually during the period sampled from mid-June through early September 2004 (see

TABLE 1. Mean environmental conditions measured at each site sampled for 2004 and 2005. See Figure 1 for site locations. Chlorophyll *a* concentrations are whole-water integrated values (C. Gallegos, SERC); minimum dissolved oxygen (DO) values are based on near-bottom measurements; temperature and salinity are from surface waters (<1 m depth); NA = site not sampled.

	2004				2005			
Site	Chlorophyll *a* (μg L^{-1})	Minimum DO (mg L^{-1})	Temperature (°C)	Salinity	Chlorophyll *a* (μg L^{-1})	Minimum DO (mg L^{-1})	Temperature (°C)	Salinity
73[a]	NA	2.31	25.40	7.76	NA	3.46	26.26	9.79
1A	24.55	5.20	25.95	8.20	21.37	6.61	26.64	9.26
2A	24.76	5.77	26.66	8.04	37.02	6.88	27.58	9.44
CC	NA	4.70	29.14	7.35	NA	5.14	28.91	9.10
3A	32.43	4.73	27.54	7.94	28.20	5.21	28.00	8.87
SC	NA	4.23	28.09	7.78	NA	5.31	27.97	9.38
4B	44.34	5.22	28.41	7.29	32.29	5.19	28.62	9.08

[a] Because of sea conditions, site 73 was not sampled during mid- to late summer 2004 as frequently as other sites; thus, averages are not necessarily representative of physical conditions at site 73 relative to other sites measured on the same dates.

Figure 2). Mesozooplankton samples in both years were dominated (>95% of individuals) by the calanoid copepod *Acartia tonsa*. During 2004, mesozooplankton densities varied significantly among dates ($F = 6.28$, $P < 0.01$). Peak densities of 4–7 individuals L^{-1} occurred on 21 June and 7 July and then declined to approximately 1.0 individuals L^{-1} for the rest of the season (see Figure 2).

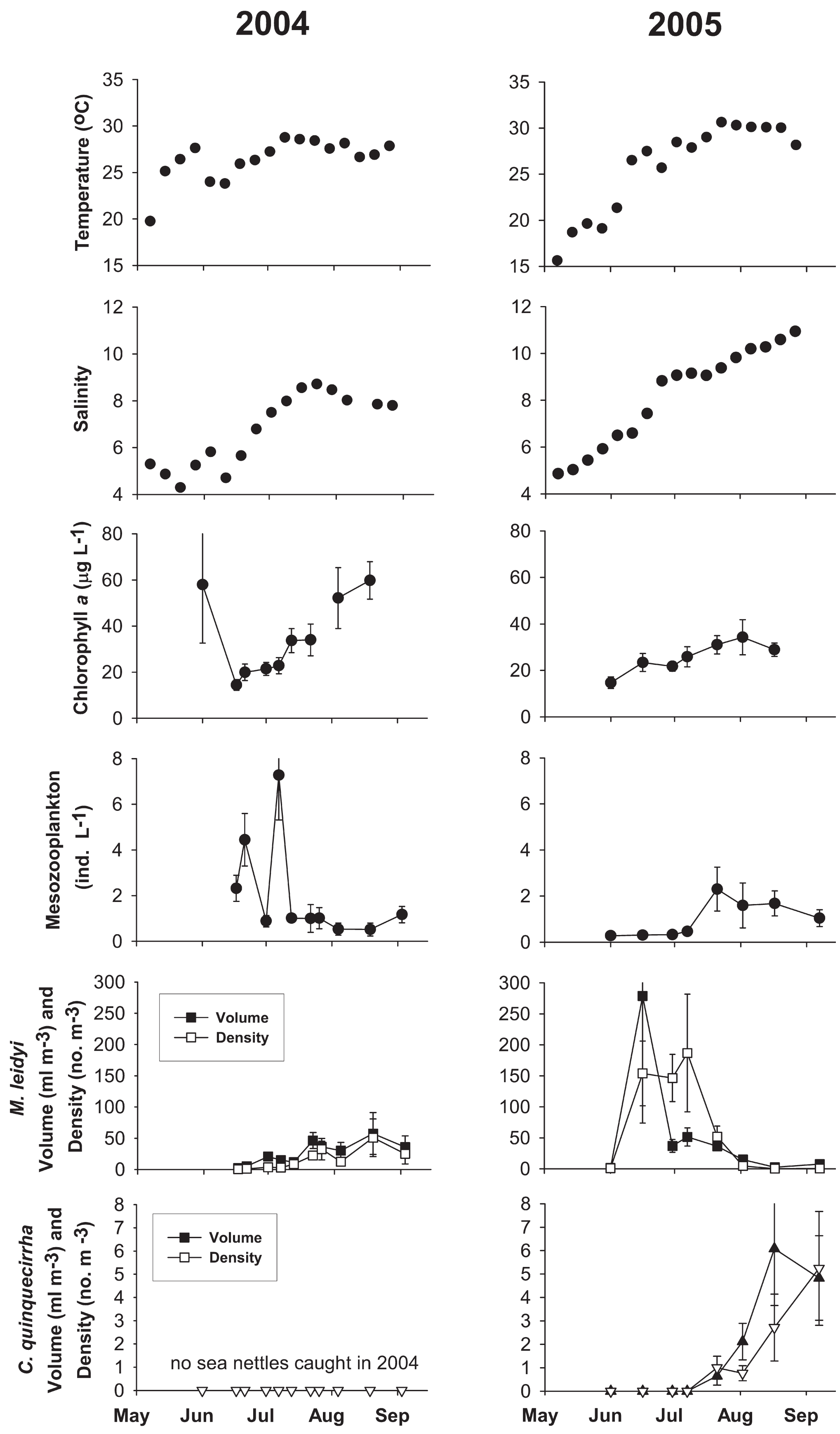
Mnemiopsis leidyi volumes also varied significantly among dates (one-way ANOVA on ranks; $F = 6.08$, $P < 0.01$). Numerical densities and volumes were lowest in mid-June ($\leq 0.62 \pm 0.25$ individuals m^{-3} and $\leq 2.3 \pm 0.77$ mL m^{-3}, respectively), and then gradually increased to a maximum of 51 ± 30.2 individuals m^{-3} and 58 ± 33.5 mL m^{-3} on 19 August (see Figure 2), the date that coincided with highest densities of "recruits" (individuals ≤1 cm in length). Regression analyses indicated a significant relationship between the zooplankton density of the prior week and both *M. leidyi* volume ($r^2 = 0.13$, $P < 0.01$) and the density of recruits ($r^2 = 0.21$, $P < 0.01$). However, the previous week's chl *a* concentration explained a greater percentage of the variation in both these measures of *M. leidyi* abundance for the sites at which chl *a* data were available (1A, 2A, 3A, 4B) (volume: $r^2 = 0.33$, $P < 0.01$; density of new recruits: $r^2 = 0.25$, $P < 0.01$). *Chrysaora quinquecirrha* abundances were low during 2004. A few medusae were seen in the field during August and early September but were never caught with either the 0.5 m diameter hoop net or the larger 1 m^2 neuston net, which was deployed in an attempt to more accurately sample the low-density *C. quinquecirrha* population.

2005 BIOTA

Temporal patterns and peak abundances of most biota in 2005 differed from those in 2004 (see Figure 2). Mid-June chl *a* concentrations in 2005 were similar to those in the corresponding time period in 2004, and as in 2004 generally increased during the remainder of the season. However, sampling did not detect an early June chl *a* peak in 2005, and maximum chl *a* concentrations in late summer 2005 reached only about two-thirds the concentrations reached in 2004 (Figure 2). Mesozooplankton densities varied among dates (one-way ANOVA on ranks, $F = 4.87$, $P < 0.01$). The 21 July peak density of 2.3 individuals L^{-1} was both later and lower than peak densities in 2004. Early June through early July mesozooplankton densities remained below 1 individual L^{-1} and were similar to mid-July–early September densities in 2004.

The timing of the increase in mesozooplankton densities in 2005 corresponded to a decrease in *M. leidyi* densities and the appearance of *C. quinquecirrha*. *M. leidyi* densities varied significantly among dates (one-way ANOVA on ranks: $F = 13.98$, $P < 0.01$). Peak *M. leidyi*

FIGURE 2. (*facing page*) Weekly mean temperature (°C) and salinity at the SERC dock (C. Gallegos, unpublished data), and river-wide mean (±SE) chlorophyll *a* concentration (μg L^{-1}), mesozooplankton abundance (number L^{-1}), and *Mnemiopsis (M.) leidyi* and *Chrysaora (C.) quinquecirrha* abundance (volume, mL m^{-3}; density, number m^{-3}) for 2004 (left) and 2005 (right).


2004
2005
Temperature (ºC)
35
30
25
20
15
Salinity
12
10
8
6
4
Chlorophyll a (µg L-1)
80
60
40
20
0
Mesozooplankton (ind. L-1)
8
6
4
2
0
M. leidyi Volume (ml m-3) and Density (no. m-3)
300
250
200
150
100
50
0
Volume
Density
C. quinquecirrha Volume (ml m-3) and Density (no. m -3)
8
7
6
5
4
3
2
1
0
no sea nettles caught in 2004
May
Jun
Jul
Aug
Sep

densities were higher and occurred earlier in 2005 than in 2004. Volumes peaked on 16 June (279 ± 205 mL m^{-3}), declined substantially by the 21 July sample date, and then remained low throughout the rest of the season (Figure 2). Medusae of *Chrysaora quinquecirrha* were first caught in our sample nets on 18 July 2005, and numbers continually increased over the season, reaching a maximum on the last sample date, 7 September (Figure 2). *Mnemiopsis leidyi* densities declined as *C. quinquecirrha* abundances increased. Regression analysis was run on *C. quinquecirrha* density and the prior week zooplankton density and chl *a* concentrations. Partial r^2 values indicated that *C. quinquecirrha* number explained 41% of the variation in the number of *M. leidyi* recruits whereas prior week zooplankton explained only 17% and 13% of the variation in number of recruits and *M. leidyi* volume, respectively.

MNEMIOPSIS LEIDYI EGG PRODUCTION

Egg production assays were performed on three dates in July 2004. *Mnemiopsis leidyi* produced between 0 and 668 eggs mL^{-1} of ctenophore. There was a significant positive correlation between *M. leidyi* volume and the number of eggs produced, both on each date and for the three dates combined (Figure 3). Egg production on each date in 2004 differed significantly from all others. Egg production was highest on 7 July, 355 ± 28.2 eggs mL^{-1} ($n = 36$); lower on 1 July, 274 ± 25.7 eggs mL^{-1} ($n = 33$); and lowest on 22 July, 50 ± 8.71 eggs mL^{-1} ($n = 35$) (see Table 2).

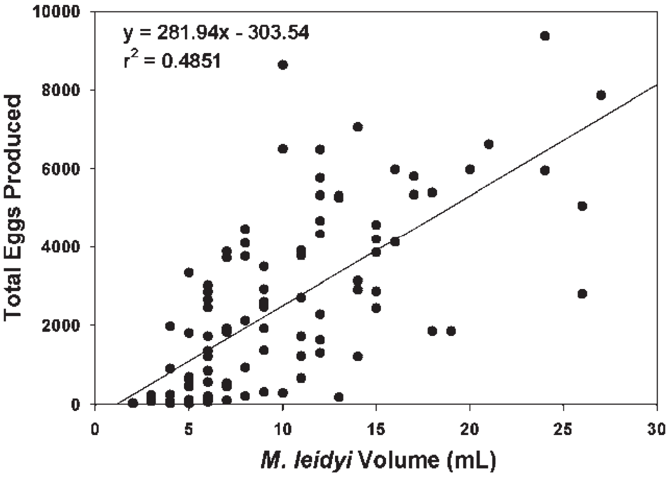


FIGURE 3. Total number of eggs produced and volume (mL) of each *M. leidyi* in all three reproduction experiments.

TABLE 2. Mean egg production rate (eggs mL^{-1} ctenophore ± SE) and 2-week mean mesozooplankton density (number L^{-1} ± SE) for each reproduction study date.

Date	Egg production	Zooplankton density
1 July	274 (± 25.7)	2.72 (± 0.56)
7 July	355 (± 28.2)	4.13 (± 1.03)
22 July	50 (± 8.7)	1.03 (± 0.34)

Mesozooplankton prey density during the week leading up to the reproduction assays was estimated by averaging mesozooplankton densities measured in samples collected on the day of the egg production assay and from the previous week to include food immediately available as well as prey quantity potentially affecting prior growth and reproduction. Two week average zooplankton densities were 4.13 ± 1.03 ($n = 6$), 2.72 ± 0.56 ($n = 7$), and 1.03 ± 0.34 ($n = 7$) individuals L^{-1} for 7 July, 1 July, and 22 July, respectively (see Table 2). These zooplankton densities corresponded directly with the ranked egg production rates on these dates. ANOVA indicated that the total number of eggs produced per individual increased significantly with ctenophore volume ($F = 201.24$, $P < 0.01$) and average zooplankton density ($F = 34.87$, $P < 0.01$), and varied among sites ($F = 5.70$, $P < 0.01$), dates ($F = 13.82$, $P < 0.01$), and the interaction between sites and dates ($F = 3.39$, $P < 0.01$); the model r^2 was 0.80 ($P < 0.01$).

DISCUSSION

Temporal patterns of mesozooplankton, *M. leidyi*, and *C. quinquecirrha* in the Rhode River differed strongly between 2004 and 2005. In 2004 mesozooplankton abundances peaked in early summer and then declined as ctenophores gradually increased throughout the season. *C. quinquecirrha* medusae were rare, and their appearance did not result in a decline in ctenophore density or biomass. In contrast, in 2005, late spring through early summer mesozooplankton densities were low and ctenophore density and biomass were high. As *C. quinquecirrha* abundances increased in late summer, *M. leidyi* decreased and mesozooplankton densities increased. Peak densities of *M. leidyi* measured during this study in the Rhode River (approximately 200 individuals m^{-3} and nearly 300 mL m^{-3}) are higher than those reported in the Pamlico River, North Carolina (just over 60 mL m^{-3}; Miller, 1974) or the mid-Chesapeake Bay (Purcell et al. 2001), but similar to abundances reported for Narragansett Bay, Rhode Island (Deason, 1982; Sullivan et al., 2001). Peak Rhode River densities measured in this study were lower, however, than those reported for systems such as the Black and Caspian Seas to which *M. leidyi* has been introduced (Kideys and Romanova, 2001; Bilio and Niermann, 2004).

Interannual variation in salinity likely contributed to observed interannual differences in gelatinous zooplankton densities and food web interactions, but the effect of interannual variation in water temperatures is less clear. Low salinities in 2004 likely resulted in the low densities of *C. quinquecirrha* in that year. *Chrysaora quinquecirrha* polyps are generally not found in salinities less than 7 and become more abundant as salinities increase to between 7 and 10 (Cargo and King, 1990). During 2004, surface salinity did not reach 5 until mid-June, or 7 until July, and never reached 10. In contrast, surface salinity reached 7 by mid-June and 10 by early August in 2005. We suggest that salinities below 5 in May and early June also delayed or reduced early-season *M. leidyi* reproduction in Rhode River in 2004 (Purcell et al., 2001). We were unable to find published studies that report *M. leidyi* reproductive rates at salinities below 5. However, if this hypothesis is correct, there is a very narrow margin between salinities that prevent recruitment of *C. quinquecirrha* and allow *M. leidyi* populations to grow unchecked by predation and salinities that hinder *M. leidyi* populations by limiting reproduction. The combined effects of salinity on these two gelatinous species in Rhode River in 2004 appears to have resulted in a persistent *M. leidyi* population that did not become abundant until mid- to late July but then remained abundant at least through early September.

Although surface waters warmed earlier in the season during 2004 than during 2005, the effect of this warming on gelatinous zooplankton seasonal abundances is not clear and may have been overwhelmed by other factors. Spring temperatures were 5°C higher in 2004 than in 2005. By early May of both years, however, temperatures exceeded the 9°–13°C minimum temperature required for *M. leidyi* reproduction (P. Kremer, University of Connecticut, unpublished data), and by mid-May of both years, temperatures exceeded the 17°C threshold required for strobilation by *C. quinquecirrha* (Cargo and King, 1990; Purcell and Decker, 2005). In addition, there are no data to suggest that temperatures that occurred during the warmer 2004 spring should have reduced growth or reproduction of either gelatinous species. By late July 2005, surface water temperatures exceeded 30°C, the temperature at which *M. leidyi* suffers mortality in laboratory experiments (D. Breitburg, unpublished data). However, *M. leidyi* could have avoided high midday surface temperatures by moving lower in the water column, and the appearance of predatory *C. quinquecirrha* is a more parsimonious explanation as the major cause of the seasonal ctenophore decline during 2005, given the high percentage of *M. leidyi* with damage indicative of encounters with medusae (Purcell and Cowan, 1995; Kreps et al., 1997).

With a mean depth of 2 m, the shallow bathymetry of the Rhode River may limit the potential for coexistence of *M. leidyi* and *C. quinquecirrha*. In the Rhode River, densities of *M. leidyi* averaged less than 2 mL m^{-3} in August and September 2005 when *C. quinquecirrha* densities reached an average of 2–6 mL m^{-3}. In contrast, Keister et al. (2000) found 26.6 mL *M. leidyi* m^{-3} in the Patuxent River, Maryland, when *C. quinquecirrha* density averaged 11.8 mL m^{-3}. The deeper water column of the Patuxent, which includes a bottom layer with variable and sometimes severely hypoxic DO concentrations (Breitburg et al., 2003), may provide greater opportunity for spatial separation of *M. leidyi* and *C. quinquecirrha* and increase survival of *M. leidyi* at moderate *C. quinquecirrha* densities.

Prey availability could limit *M. leidyi* abundance and production, but our data do not suggest that low mesozooplankton densities were likely to have caused the large interannual variation in ctenophore abundances. Mesozooplankton densities were higher in 2004 than in 2005, and the temporal pattern of mesozooplankton and ctenophore abundances was more suggestive of ctenophore control of mesozooplankton than the reverse. An inverse relationship between copepod densities and ctenophore abundance has been noted previously in both Chesapeake Bay (Feigenbaum and Kelly, 1984; Purcell and Cowan, 1995) and Narragansett Bay (Sullivan et al., 2001). In both years of our sampling, high densities of *M. leidyi* recruits were found in the Rhode River during periods of lowest mesozooplankton densities. We did not sample microzooplankton, however, and cannot rule out their potential influence on ctenophore abundance.

The maximum egg production we measured in the Rhode River (9,000 eggs individual^{-1} *M. leidyi* day^{-1}) was lower than the maximum reported value of 14,000 eggs individual^{-1} day^{-1} (Kremer, 1976; Reeve et al., 1989) but well within the range of values reported elsewhere. *Mnemiopsis leidyi* egg production in the Rhode River was similar to that of field-collected ctenophores from elsewhere in Chesapeake Bay (Purcell et al., 2001), including the Patuxent River (D. Breitburg and R. Burrell, unpublished data). *Mnemiopsis leidyi* from the Patuxent produced a maximum of 610 eggs mL^{-1} of ctenophores at mesozooplankton abundance of 1 individual L^{-1}, which is very close to the rate found in this study of 668 eggs mL^{-1} at 2.2 mesozooplankton individuals L^{-1}. Variation among dates in the relationship between zooplankton density and egg production suggests an interesting pattern of trade-offs in energy allocation to somatic growth versus reproduction, or nutritional constraints.

Predicted changes in sea-surface temperatures and rainfall throughout the world may lead to changes in the geographic ranges of many aquatic organisms. The Rhode River provides an interesting model that may aid predictions of climate change-related shifts in ranges and predator–prey dynamics because it is often near the threshold of salinity tolerances and the dynamics of the system can fluctuate markedly from year to year. These characteristics of the Rhode River allowed us to examine the gelatinous zooplankton food web within the river during two distinct years: one with, and one without, strong influence by a top predator. Differences in species abundances and food web interactions observed here may help to predict dynamics in other systems as environmental conditions, and the range of *C. quinquecirrha*, change. Although generally considered a nuisance species by swimmers and fishermen, *C. quinquecirrha* may benefit fisheries and habitat by controlling densities of *M. leidyi*, which is an important predator of oyster larvae—a prey not utilized by *C. quinquecirrha* (Purcell et al., 1991; Breitburg and Fulford, 2006).

ACKNOWLEDGMENTS

We thank Charles Gallegos and Sam Benson (SERC) for the chlorophyll, temperature, and salinity data from their cruises and monitoring station. We also thank the Smithsonian Environmental Research Center NSF-REU program, the Smithsonian Institution Women's Committee, and the Smithsonian Institution Marine Science Network for funding.

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Patterns of Water Quality and Movement in the Vicinity of Carrie Bow Cay, Belize

Karen H. Koltes and Thomas B. Opishinski

ABSTRACT. Meteorological and oceanographic conditions have been monitored at the Smithsonian Field Station at Carrie Bow Cay, Belize, since 1993 through the Caribbean Coastal Marine Productivity (CARICOMP) program, and since 1997 through an automated monitoring system operated by the Caribbean Coral Reef Ecosystems Program (CCRE). Collectively, the two datasets represent a unique resource that provides a mechanism to improve our understanding of changing environmental conditions on the Mesoamerican Barrier Reef and, particularly, the conditions governing water quality and movement around Carrie Bow Cay. Especially evident is the broad influence on water quality of seasonal climate patterns as well as short-term events such as cold fronts and major storms. Among several variables examined, wind direction appears to be a good indicator of water quality conditions. From March to June, prevailing northeasterly airflow and limited rainfall result in higher water quality along this portion of the Belize Barrier Reef. Under decreased trade or increasing westerly winds, especially during periods of higher rainfall from October to January, turbid coastal water moves (drifts or is pushed) out onto the reef from the lagoon. The most significant finding, however, has been a dramatic loss of water quality along this portion of the Belize Barrier Reef since monitoring began at Carrie Bow Cay in 1993.

INTRODUCTION

Carrie Bow Cay, Belize, has been the site of extensive biological, geological, and ecological study as part of the Smithsonian Institution's Caribbean Coral Reef Ecosystem (CCRE) program (Rützler and Macintyre, 1982). Despite more than three decades of multidisciplinary research, however, relatively little is known about the complex interaction of physical factors that influence the reef environment, including winds, tides, temperature, and rainfall. These physical parameters provide the context for understanding and predicting relationships between reef organisms and their environment, but such parameters require accurate and consistent measurement over long time periods to establish a reliable description of baselines and trends. This is particularly true of water quality and movement, as the constant mixing and motion of water masses, bathymetry, and proximity to sediment inputs lead to significant spatial and temporal variability.

Establishing baselines and trends for environmental conditions has also become increasingly important as Belize, as well as neighboring countries, experience rapid

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urban and economic growth from the recent expansion of agriculture, aquaculture, and tourism. As the coastline and mangrove cays of Belize have experienced accelerated development over the past few decades, the barrier reef environment has been subjected increasingly to chronic and acute disturbances from terrigenous inputs. Poorly managed exploitation of coastal and offshore natural resources, extensive land modifications from dredging, land reclamation, deforestation, and conversion, and effluents from sewage and agriculture/aquaculture are delivering increased loads of sediments, nutrients, pesticides, herbicides, and other man-made chemicals to the central lagoon (Gibson and Carter, 2003). Eroded sediments and the residues of fertilizers and pesticides are also entering Belize's coastal waters from the more than 300,000 hectares of banana, oil palm, sugar cane, citrus, and pineapple crops cultivated across the wider Mesoamerican region (Burke and Sugg, 2006).

Early qualitative observations suggested that a period of heavy rainfall in the central portion of Belize was followed within 1 to 2 days by the appearance of a plume of low-salinity, turbid water over the fore-reef at Carrie Bow Cay (CBC). For major storms, the lens could be significant in duration and thickness. Rainfall from Hurricane Mitch, a Category 5 storm, approached 2 m over Central America between 29 October and 1 November 1998, causing severe flooding, landslides, and mudflows. Much of the storm discharge entered the Gulf of Honduras, where it flowed north as a highly turbid, plankton-enriched water mass, reaching the Belize shelf on 3 November 1998 (Andréfouët et al., 2002; Sheng et al., 2007). On 15 November 1998, K. Koltes observed this surface lens to be about 15–20 m in thickness in the waters adjacent to CBC. Further in situ characterization of the lens was not possible because of the closure of the field station, but recent numerical modeling of satellite images of terrestrial runoff plumes in the Gulf of Honduras confirms that influxes of sediments and nutrients are reaching the central reefs from local and more distant origins (Andréfouët et al., 2002; Tang et al., 2006; Chérubin et al., 2008; Paris and Chérubin, 2008).

Consistent monitoring of environmental variables began at Carrie Bow Cay in 1993 as part of the Caribbean Coastal Marine Productivity Program (CARICOMP). CARICOMP is a regional scientific effort to study land–sea interaction processes, to monitor for change on a local and regional scale, and to provide appropriate scientific information for management (Kjerfve et al., 1999; http://www.ccdc.org.jm/frontpage.html). In 1997, an automated environmental monitoring system (EMS) was installed at Carrie Bow Cay that provides an independent set of weather and water quality measurements. It was one of the earliest monitoring systems to process and transfer real-time data from a remote geographic location to a website for public access (http://nmnhmp.riocean.com). To our knowledge it is still the only automated system continuously monitoring oceanographic and meteorological conditions on the outer Mesoamerican Barrier Reef. In December 1997, a catastrophic fire destroyed the field station, suspending all monitoring except the automated water temperature measurements under the CARICOMP program. The full complement of CARICOMP measurements resumed after the station reopened in late 1999, and the automated measurements resumed after a new EMS was installed in September 2000.

Together, the CARICOMP and EMS datasets have provided a nearly continuous record of climatic and oceanographic conditions along the central portion of the Belize Barrier Reef. The 15 years of water temperature and Secchi disk measurements likely now constitute the longest continuous records for the Belize Barrier Reef and are among the longest for the entire Mesoamerican region. The data serve as an important resource for researchers to examine long-term trends, episodic events, and short-term and seasonal cycles (McField and Kramer, 2004). The data also allow comparative studies with other reef ecosystems to assess biodiversity and correlate environmental factors with biological phenomena. Data have been used to characterize prevailing conditions (Koltes et al., 1998) as well as the anomalous conditions that occur during extreme climatic events such as the El Niño–Southern Oscillation (ENSO) of 1997–1998 (Aronson et al., 2002) and powerful storms such as the Category 5 hurricanes Mitch, Keith, Iris, Dean, and Wilma.

These long-term datasets are beginning to yield reliable descriptions of meteorological and oceanographic conditions around Carrie Bow Cay. We report here on preliminary analyses of the patterns, trends, and relationships that are emerging from these long-term records, with special reference to factors that control water quality and movement around Carrie Bow Cay.

METHODS

Carrie Bow Cay is a small island (0.7 acres) located in the central province of the Belize Barrier Reef (Burke, 1982) about 18 km from the mainland (16°48′N and 88°05′W; Figure 1). Carrie Bow Cay lies on the barrier reef proper between two tidal passes, a relatively rare occurrence along the otherwise nearly continuous barrier

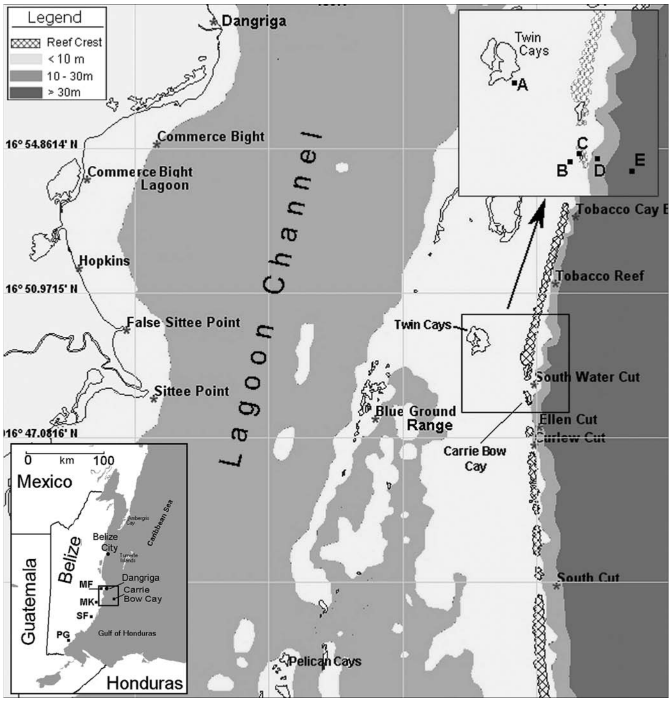


FIGURE 1. Map of the central province of Belize showing the location of the Smithsonian Institution's Field Station (16°48′N and 88°05′W) at Carrie Bow Cay. Note the Lagoon Channel that separates the outer lagoon platform from the mainland. Inset upper right: Location of the CARICOMP permanent monitoring sites in the seagrass beds near Twin Cays (A = "lagoon") and Carrie Bow Cay (B), on the inner fore-reef slope (D) and seaward of the barrier reef (E = "drop-off"), and (C) the Environmental Monitoring System on Carrie Bow Cay. Inset lower left: The Belize National Meteorological Service stations at Melinda Forest (MF), Maya King (MK), Savannah Forest (SF), and Punta Gorda (PG).

reef. It is in close proximity to deep ocean water (>300 m) to the east. A line of cays to the west that includes Twin Cays is part of a fault-block ridge that separates the shallower back-reef lagoon from the deeper Lagoon Channel that parallels Belize's shoreline. Although shoal formations are the outcome of a variety of factors such as currents and sea level changes, the present-day patterns of parallel shoals, reefs, and mangrove islands in this area resulted principally from faulting along a NNE trend during the Pliocene era (Dillon and Vedder, 1973; Macintyre and Aronson, 1997).

CARICOMP MEASUREMENTS

Scientific monitoring of meteorological and oceanographic conditions under the CARICOMP program has included daily measurement of precipitation (mm) and air temperature (°C) at Carrie Bow Cay ("C" in Figure 1) and weekly measurement of surface water temperature (°C) and salinity (‰) at a permanent monitoring station in the seagrass beds adjacent to Twin Cays ("lagoon"; "A" in Figure 1; water depth ≈1.2 m) and in the ocean seaward of the drop-off ("drop-off"; "E" in Figure 1; water depth >300 m). Bottom water temperatures have been recorded continuously at intervals of 15–48 min at the permanent CARICOMP monitoring sites in the lagoon ("A" in Figure 1), in the seagrass beds adjacent to Carrie Bow Cay ("B" in Figure 1; water depth ≈2m), and on the inner fore-reef ("D" in Figure 1; water depth ≈13.5m) using Onset Corporation's model HOBO, StowAway, and TidbiT data loggers (±0.2°C).

Water quality characteristics that are associated with water transparency have been measured by Secchi disk as horizontal distance (m) taken 0.5 m below the surface in the lagoon ("A" in Figure 1) and vertical distance (m) at the drop-off ("E" in Figure 1). From 1993 to 1997, water transparency was measured once a week between 1000 and 1200 using a 30 cm diameter disk with black and white quadrants. In 1999, the CARICOMP protocol was modified to take advantage of the 20 cm diameter black and white disk that is more available commercially. The difference in the diameters of the two Secchi disks has little effect on the measurements, particularly compared to other sources of error such as sun angle, cloud cover, sea state, wind, currents, and observer difference (Steel and Neuhausser, 2002; Hou et al., 2007). In 2002, the Secchi disk measurements were increased to two times per week to more accurately characterize water quality trends. No water transparency measurements were made during adverse weather conditions, particularly over the drop-off, during closure of the station in the fall of 1993 and 1994, and for approximately two years following destruction of the field station from the fire in 1997.

To better characterize water quality, especially during storm events, light intensity loggers were mounted on a cinder block (water depth ≈13.5 m) at the permanent CARICOMP monitoring site on the inner fore-reef (note "D" in Figure 1). Onset Corp.'s model StowAway LI was used from 2002 until 2005 when Onset ceased manufacturing this model; Onset's model HOBO UA-002-64 Pendant Temp/Light has been used since 2005. Light intensity (lumens/ft^2) was recorded at intervals from 5 s to 15 min over periods ranging from days to weeks from 2002 to 2008. While deployed, the light logger was kept free of sediment and epibionts by periodically wiping the surface of the housing. The StowAway LI was designed to measure relative light levels (e.g., sun versus shade) and was calibrated for incandescent sources (spectral response, ≈200–1,100 nm; range, ≈0.001–1,000 lumens/ft^2). The

HOBO UA-002-64 Pendant Temp/Light was designed to measure relative light levels indoors or outdoors (spectral response, ≈200–1,200 nm; range, ≈0–30,000 lumens/ft^2). Our objective was to establish patterns in relative light levels, and hence water transparency, by comparing in situ irradiance on the inner fore-reef ("reef irradiance") to that at the surface ("incident irradiance"). No attempt was made to relate these measurements to biologically active wavelengths.

Environmental Monitoring System

The EMS continuously records meteorological and oceanographic conditions at Carrie Bow Cay. A marine-grade wind monitor (RM Young model 05106), LI-COR model LI-200 pyranometer, temperature/relative humidity sensor (Vaisala model HMP50), and barometric pressure sensors monitor meteorological conditions. The weather sensors, mounted on an aluminum tower above the main laboratory, are approximately 13 m above ground level ("C" in Figure 1). Rain is measured with a Texas Electronics solid-state tipping bucket rain gauge (model 525USW). The pyranometer features a silicon photovoltaic detector designed to measure solar radiation under conditions of unobstructed natural daylight. Measurements of wind speed (mph) and direction (0°–360°), solar radiation (W/m^2), rain accumulation (mm) and rate (cm/h), barometric pressure (mbar), air temperature (°C), and relative humidity (%) are recorded every 10 min.

Oceanographic conditions are monitored via a YSI model 6600EDS multiparameter water quality sonde, mounted inside a stilling tube. The sonde is mounted on the dock on the west side of Carrie Bow Cay about 0.6 m below the surface of the water ("C" in Figure 1). Every 10 min, measurements are taken of water level (m), water temperature (°C), salinity (‰), dissolved oxygen (% saturation), pH, and turbidity (NTU).

Data acquisition of both oceanographic and meteorological systems is managed automatically by a datalogger and control system and transmitted by radio to a server on the mainland. A regular program of maintenance, including calibration of sensors to manufacturer's standards (Eaton et al., 2005) and minimization of fouling, is followed to maintain the best possible data quality. Data are subjected to a quality assurance/quality control (QA/QC) process to remove outliers and invalid and suspect data before they are included in the historical archives. The QA/QC process also incorporates established criteria and procedures to correct for sensor and fouling drift (Wagner et al., 2006).

The data have contributed to new and existing research studies, publications, and management programs for both Smithsonian researchers and an increasing number of organizations from the region (e.g., Renken and Mumby, 2009).

Analysis

The annual means and standard deviation of Secchi disk measurements from 1993 to 2008 for the lagoon (n = 787) and drop-off (n = 727) were calculated, and the 15-year trend in water quality was determined by least-squares regression analysis. To evaluate seasonal patterns in water quality, monthly means were calculated for the Secchi measurements from the lagoon because horizontal measurements are generally more reliable than vertical measurements (Steel and Neuhausser, 2002) and were more often taken during adverse weather conditions.

To examine annual variation in wind patterns, monthly wind rose plots were generated for Carrie Bow Cay using approximately 350,000 wind measurements collected between 2003 and 2008. A wind rose plot is a combination of a polar plot and a histogram that depicts the distribution of wind speed and the frequency of occurrences that wind blows from 1 of 16 cardinal directions (N, NNE, NE, etc.). Seasonal and geographic patterns of rainfall were derived by calculating monthly mean precipitation for Carrie Bow Cay and four coastal stations (Melinda Forest, Mayaking, Savannah Forest, and Punta Gorda; see Figure 1, lower inset) maintained by the Belize National Meteorological Service (2003–2008).

Previous oceanographic studies at Carrie Bow Cay suggested that tides play a major role in controlling water movement, and hence water quality, around Carrie Bow Cay (Greer and Kjerfve, 1982; Kjerfve et al., 1982). To examine the role of tides, reef irradiance was compared to meteorological and oceanographic variables using a harmonic regression analysis model based on linear regression algorithms to compute constituents. Specifically, we compared reef irradiance to incident irradiance and then wind direction and intensity, tidal stage, and precipitation from all stations. The objective of the analyses was to extract harmonic constituents to judge the relative strength of the tidal forcing on the light patterns. The analyses were inconclusive because tidal components were small relative to the strong solar forcing inherent to the measurements of light and from the lack of a strong diurnal or semidiurnal signal in the "microtides" of Belize (Kjerfve et al., 1982).

To establish annual changes in light, monthly means were computed for reef and incident irradiance from 2003 to 2008. The analyses included more than a half million reef irradiance samples and approximately 350,000 measurements of incident irradiance. The monthly means were normalized with respect to the maximum monthly mean observed in each set of light measurements; this established a common datum reference and allowed comparisons of monthly and seasonal variations and patterns. Additional qualitative analyses of the various time series suggested that a consistent correlation existed between patterns of reef irradiance and both seasonal and short-term changes in wind direction. A comparative analysis of conditions during periods of normal weather conditions and specific weather "events" was undertaken to further define the localized influence of wind direction and other parameters on water quality over the fore-reef and to identify external (regional) events that are observed in the Carrie Bow Cay measurements.

To establish annual changes in light, monthly means were computed for reef ($n \approx 500{,}000$) and incident irradiance ($n \approx 350{,}000$) from 2003 to 2008. The monthly means were normalized with respect to the maximum monthly mean computed for each set of light measurements; this established the maximum mean for each set as a common reference point and allowed comparisons of monthly and seasonal variations and patterns. Additional qualitative analyses of the various time series suggested that a consistent correlation existed between patterns of reef irradiance and both seasonal and short-term changes in wind direction. A comparative analysis of conditions during periods of normal weather conditions and specific weather "events" was undertaken to further define the localized influence of wind direction and other parameters on water quality over the fore-reef and to identify external (regional) events that are observed in the Carrie Bow measurements.

RESULTS

Significant temporal and spatial variability exists in the records of the meteorological and oceanographic variables. Particularly evident are longer-term seasonal patterns as well as signatures of short-term events such as cold fronts and major storms. The most significant finding, however, has been a dramatic decline in water clarity along this portion of the Belize Barrier Reef since monitoring began at Carrie Bow Cay in 1993 (Figure 2). Mean annual Secchi distance (horizontal) declined from 12.8 m in the lagoon in 1993 to 8.7 m by 2008, a loss of almost 0.3 m/year. During the same period, mean annual Secchi distance (vertical) declined from 23.8 m to 15.6 m over the drop-off or by about 0.5 m/year.

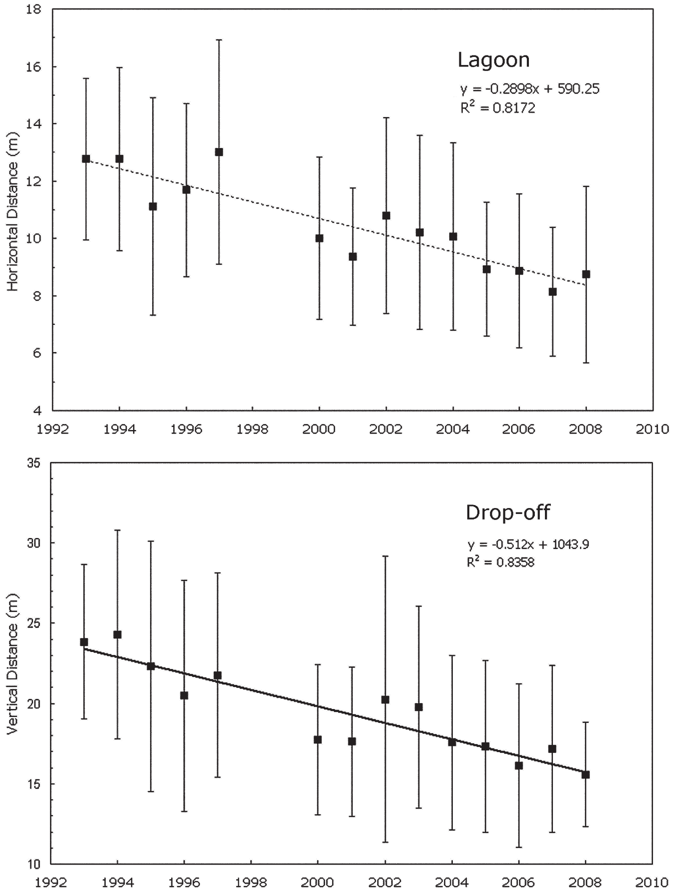
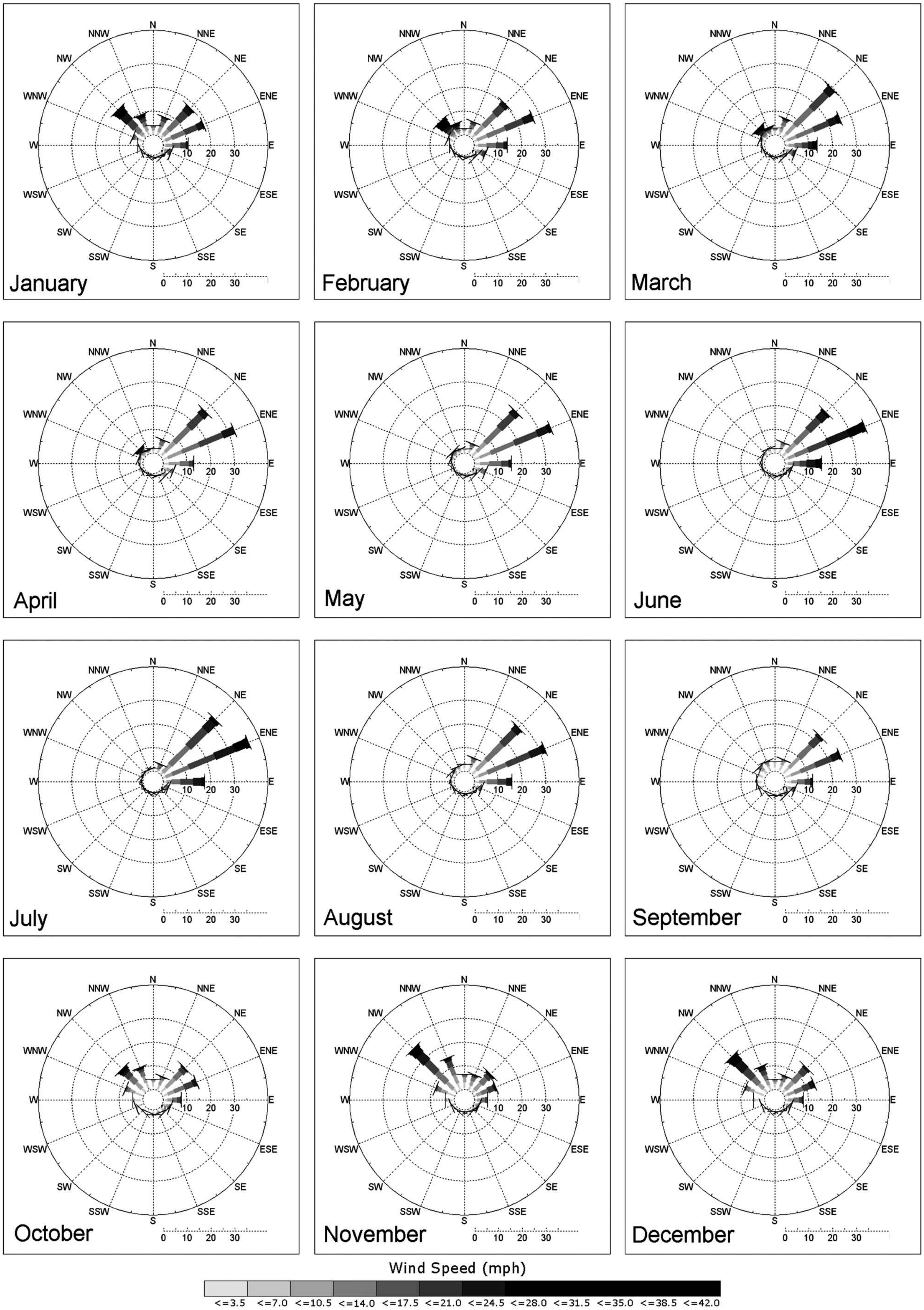


FIGURE 2. Annual mean and standard deviation of Secchi disk distance (horizontal, m) in the lagoon (top) and over the drop-off seaward of Carrie Bow Cay (vertical, m; bottom) from 1993 to 2008. There has been a dramatic and significant ($P < 0.001$) loss of transparency in the waters around Carrie Bow Cay during the past 15 years.

Comparisons of monthly means of water transparency, wind direction, and precipitation show that seasonal weather patterns strongly influence water quality (Figure 3). From February through May, the prevailing northeasterly airflow (Figure 3, left) is associated with a uniformly dry pattern across all stations (Figure 3, right). Monthly rainfall amounts average less than 75 mm. By June, a divergence can be seen among the stations, with those to the south receiving increasingly greater amounts of rain relative to the stations to the north, including Carrie Bow Cay. The sharp onset of the rainy season in the south is partly the result of the intrusion of the Inter-Tropical Convergence Zone as it migrates northward (http://hydromet.gov.bz/Climate_Summary.htm).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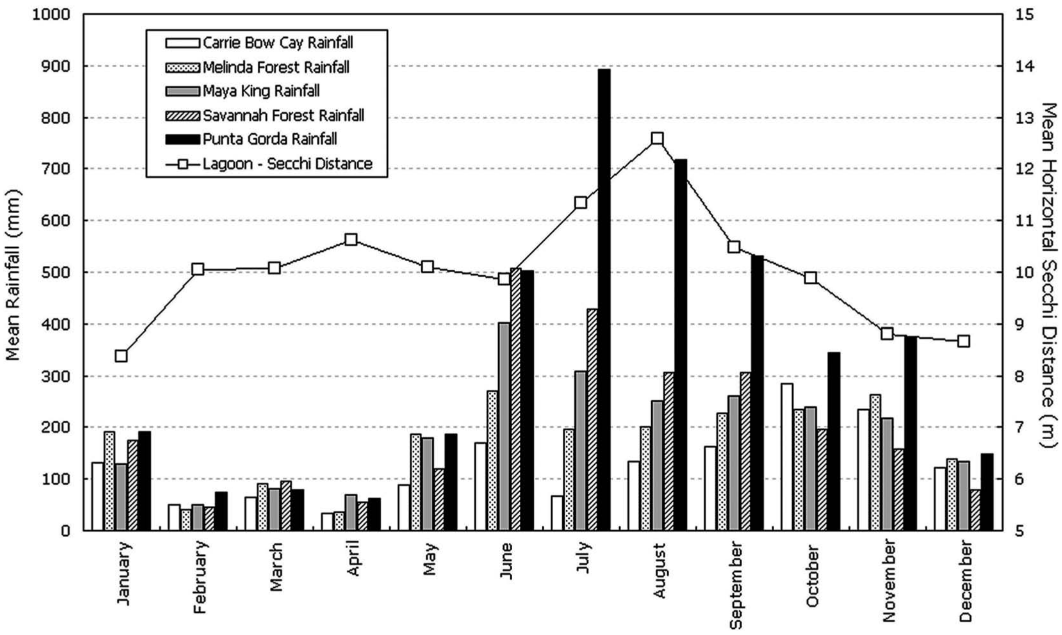

FIGURE 3. **Left** (*facing page*), Monthly means of wind speed and direction at Carrie Bow Cay for 2003–2008. The wind rose depicts the distribution of wind speed and direction: the length of each "spoke" indicates the percentage of time that winds blow from 1 of 16 cardinal directions (N, NNE, NE, etc.); the categories within the spoke represent the speed. Trade winds are the dominant pattern from March to September. Wind patterns are most variable during the transitional months of October/January/February. **Right** (*above*), Monthly means of rainfall at Carrie Bow Cay and the four Belize National Meteorological Service stations (left axis), and water transparency in the lagoon (horizontal Secchi disk distance [m], right axis) from 2003 to 2008.

Rainfall maxima also diverge in terms of timing. Mean monthly rainfall peaks in June–July in southern Belize, with approximately 900 mm at Punta Gorda; the maximum at Carrie Bow Cay (about 290 mm) occurs in October. The marked shift in rainfall patterns beginning in June is accompanied by consistent northeasterly winds and tropical waves moving westward from June to November (http://hydromet.gov.bz/Climate_Summary.htm). Cold fronts, or "northers," occur frequently from December to February and are associated with the southerly extension of the North American high-pressure system. During the peak season of December and January, cold fronts pass through Belize approximately every 10 days, the signatures of which appear in the temperature profiles on the fore-reef (Figure 4).

Monthly Secchi disk measurements in the lagoon (see Figure 3, right) correlate with the seasonal shift in climate patterns. Water transparency peaks in August (12.6 m), while incident irradiance is high (Figure 5) and the winds are still predominantly from the NE (see Figure 3, left). This peak also corresponds to a break in the rainy season on the mainland known as the "Mauga" (http://hydromet.gov.bz/Climate_Summary.htm). In contrast, the break in the rainy season occurs in July at Carrie Bow Cay (see Figure 3, right). Water transparency reaches a minimum in January (8.4 m) around the winter solstice and the period when cold fronts, characterized by strong NW winds, reach a peak (Figure 3, left). This period of increased storm activity and resulting high sea states also interrupts routine Secchi disk measurements such that the winter means may be biased upward.

The seasonal pattern of reef irradiance is similar to that observed for water transparency measured by Secchi disk (see Figure 5) and is largely governed by changes in incident irradiance. Maximum irradiance occurs around the solstice, with reef irradiance showing a peak in June compared to August for Secchi disk distance (see Figure 2) and July for incident irradiance. However, reef irradiance attenuates more rapidly toward the winter solstice relative to incident irradiance. By December, reef irradiance has fallen to less than 40% of its summer peak whereas incident irradiance has fallen only to 60% of its summer

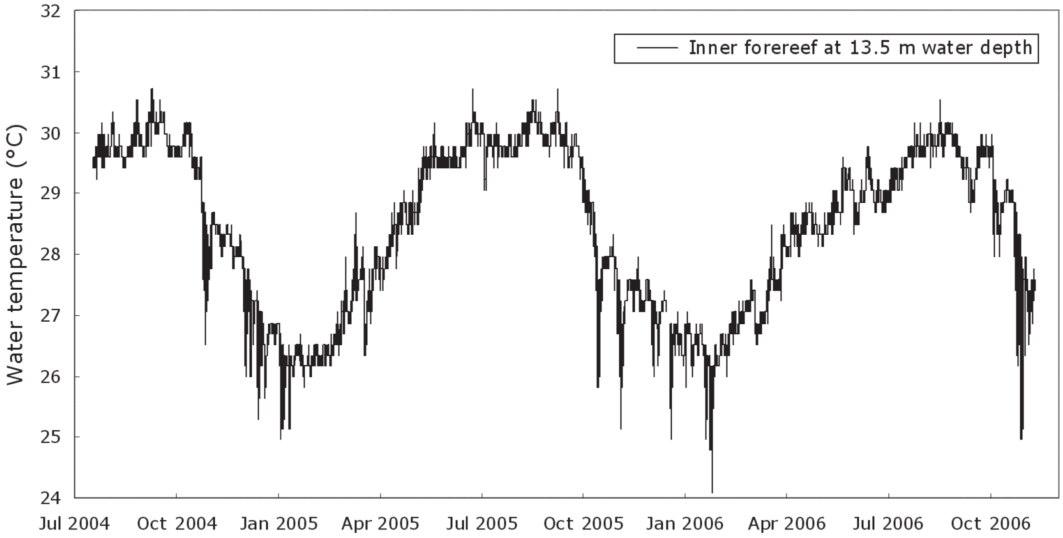

FIGURE 4. Water temperature on the inner fore-reef at 13.5 m from 29 July 2004 to 11 December 2006. Note the signatures of cold fronts in the temperature profile between October and January and a late season cold front that passed 1–3 April 2005.

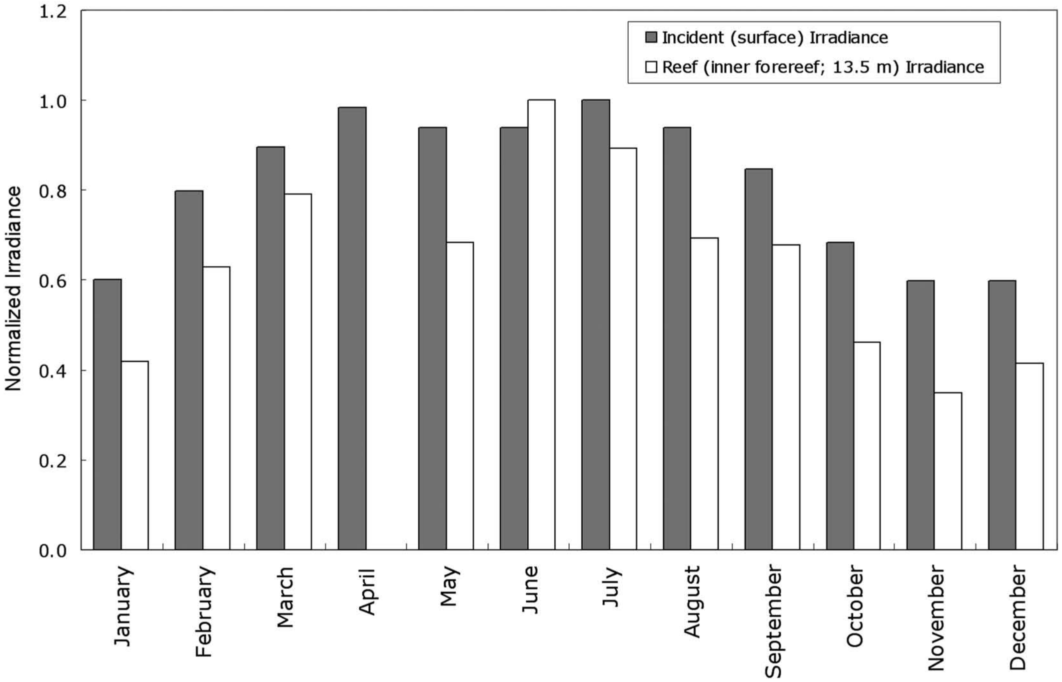

FIGURE 5. Monthly mean of reef irradiance (inner fore-reef, 13.5 m) and incident (surface) irradiance (2003–2008), normalized to allow comparisons among the light recording instruments. Reef irradiance attenuates at an accelerated rate relative to incident irradiance approaching the winter solstice.

peak. Decreased light levels around the winter solstice may be caused by lower sun angle, increased turbidity and/or higher sea states associated with the winter climate pattern.

Flow of turbid water into the area can also be seen in finer-scale comparisons of reef and incident irradiance (Figure 6) that suggest turbidity is transported from more distant locations. Following two days of light winds that had shifted from NNE first to the south and eventually to the NW, turbid water flowed on to the fore-reef, driving light levels down by about 50% despite nearly full incident irradiance. At least some of the flow may be related to tides (Figure 7), but as previously mentioned, the mixed, semidiurnal microtide of this region has made it difficult to analyze the role of tides.

DISCUSSION

The constant mixing and motion of water masses, localized inputs of sediments, and changing meteorological conditions produce strong spatial and temporal variations in conditions along the Belize Barrier Reef. These factors present a challenging analysis, especially when combined with Carrie Bow Cay's complex geomorphology that includes cuts in the reef to the north and south where disparate bodies of water mix together. Nevertheless, initial analyses have shown significant correlations between certain weather conditions, both episodic and seasonal, and water properties. Particularly evident are longer-term seasonal patterns, as well as signatures of discrete events such as the passage of cold fronts and other changes from

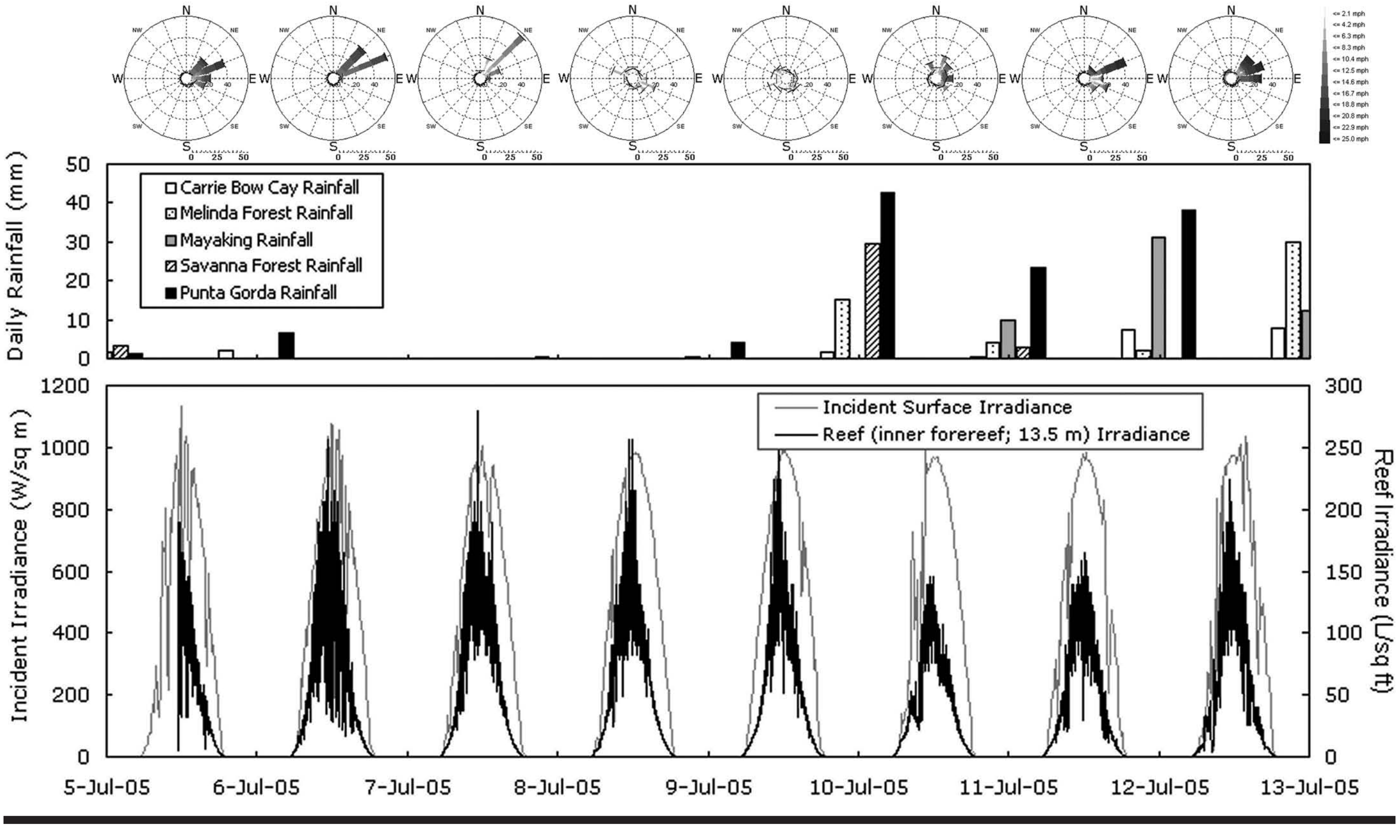

FIGURE 6. Progression of a turbidity event: Early in July 2005, light levels on the reef were among the highest recorded for reef irradiance (bottom, right axis). Beginning on 7 July, winds that had been blowing from the northeast at 15 mph began to taper off and remained calm through 9 July, as shown in the daily wind rose (top; see Figure 3 for description of wind rose). On 10 July, the winds increased at Carrie Bow Cay and heavy rainfall occurred on the mainland, particularly to the south (middle; stations as in Figure 3, right). Incident irradiance (lumens[L]/ft^2; bottom, left axis) remained high, but light levels on the reef dropped by nearly 50%. The drop in reef irradiance is attributed to a sediment plume, possibly from the south, that drifted over the fore-reef under conditions of little or no wind. Winds shifted around again to the northeast by 11 July, and subsequent mixing of water returned light levels over the reef to near maximum by 13 July.

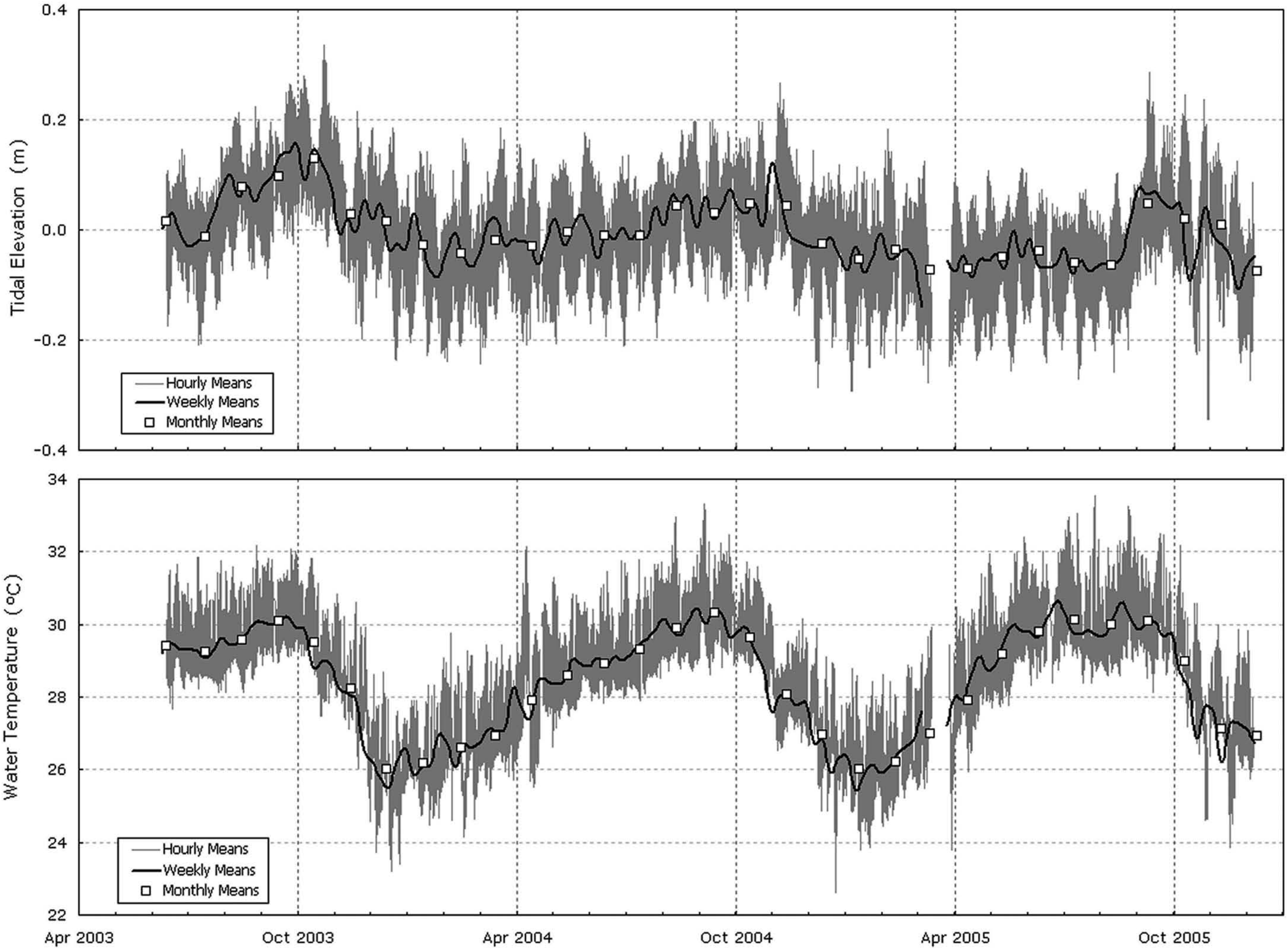

FIGURE 7. Hourly, weekly, and monthly means of tidal elevation (m) and water temperature (°C) measured at the dock at Carrie Bow Cay. Tidal elevation (top) reveals a complex pattern with a seasonal increase in elevation in October, when water temperature (bottom) reaches a maximum, that is typical of the Caribbean.

the typical weather patterns. Strong correlations are also apparent during less prominent variations in weather and particularly changes in wind direction such as those observed in July 2005. We found several other instances in which light levels on the reef dropped significantly when winds simply tapered off completely during the 24 to 48 hour "calm" period that often preceded a cold front. We also document a substantial decline of water quality around Carrie Bow Cay over the past 15 years.

Patterns of water transparency are driven largely by incident solar radiation, reflecting the strong seasonal cycle of solar radiation. However, variations in those patterns are useful at tracking short- and long-term changes in water transparency. The pattern of decreased light intensity on the fore-reef as a function of incident solar radiation in December versus June likely reflects the higher rainfall, consistent northwesterly winds, and frequent "northers" of the winter months and is consistent with recent simulation models showing locally higher turbidity during the winter months (Paris and Chérubin, 2008) from increased precipitation. This seasonal cycle is also apparent in the record of Secchi disk measurements. The difference observed between the timing of the maximum quality measured by Secchi disk and those measured by light logger may reflect the differences in the sampling period (1993–1998 versus 2002–2008). The disparity may also reflect the fact that the light logger data have not been collected as often during the spring–summer months as they have been during fall–winter months.

Although additional modeling and analysis are required, particularly of tidal currents, preliminary results suggest a strong link between climate patterns and water quality and movement along the barrier reef in the central province of Belize. We propose that, under the typical pattern of prevailing trade winds, sediment-laden riverine input is pushed shoreward and held along the coast where it flows south in the Lagoon Channel. A southerly flow of water immediately adjacent to the shoreline is consistent with circulation models that have been developed for the Gulf of Honduras (Ezer et al., 2005). We also suggest that the fault-block ridge along the eastern boundary of the Lagoon Channel forms a natural “sill” or “dam,” facilitating the segregation of turbid coastal water driven shoreward by wind forcing. Under the influence of “oceanic” water, turbidity over the fore-reef at Carrie Bow Cay is generally lower.

Localized turbidity events are triggered when the northeasterly flow of the trade winds changes in either speed or direction. Turbid water that is normally contained along the coast spills over the submarine ridge of the Lagoon Channel and drifts or is pushed out across the outer (back-reef) lagoon and onto the fore-reef. Changes in the prevailing weather patterns are also frequently accompanied by periods of rain on the mainland that discharge additional sediment and freshwater into the lagoon, increasing the volume and degree of turbid coastal water and spillover onto the reef platform.

The dramatic loss of water quality at Carrie Bow Cay over the past 15 years also suggests longer-term effects of increasing sediment and nutrient loads to the lagoon from the rapid modifications of the Belizean coastline and that of neighboring countries. Recent hydrological models of the Mesoamerican Barrier Reef estimated that runoff and associated river discharge have doubled and sediment delivery has increased 20 fold under present-day land use changes compared to a hypothetical “natural” (unaltered) state (Burke and Sugg, 2006). Although the modeling suggested that Belize contributed only about 10%–15% of the sediment load to the region, the Belize River was identified as a significant contributor of sediments and nutrients to the Mesoamerican Barrier Reef. In the central and southern portions of Belize, large amounts of fertilizers used to cultivate citrus and bananas and the direct discharges of domestic sewage produce high nutrient levels in several areas along the coast (Gibson and Carter, 2003). Shrimp and other aquaculture operations are also discharging effluents directly to the lagoon. These sediments appear to become entrained in the Gulf of Honduras gyre and, over the long term, are driving down water quality across the region.

Increasing turbidity also appears to be related to a wider regional increase in sedimentation and nutrient enrichment in the Gulf of Honduras (Burke and Sugg, 2006). Hydrological models indicate that sediment delivery increases southward along the coastline of Central America with Honduras contributing an estimated 80% of the sediment and half of the nutrients to the region. Circulation models of the Gulf of Honduras suggest that these sediments and nutrients are carried north along the Mesoamerican Barrier Reef by the Caribbean Current (Thattai et al., 2003). Recent modeling of satellite images indicate that runoff from watersheds in northern Honduras can extend as far north as Glovers Reef atoll (Andréfouët, 2002; Paris and Chérubin, 2008). Based on modeling of satellite images and the hydrological models of Burke and Sugg (2006), Chérubin et al. (2008) concluded that concentrations of buoyant matter from terrestrial runoff into the Gulf of Honduras were high from October to January. Plumes were transported by a cyclonic gyre toward the Yucatan, creating seasonal variation in the concentration of runoff loads along the Mesoamerican Barrier Reef. The influence of terrestrial runoff was maximal from October to January and minimal from March to April.

Long-term in situ measurements of the sort presented here are relatively rare. Although the results of our analyses are preliminary, they already demonstrate the value of these measurements for advancing our understanding of the range and complexity of interactions of natural and human-induced variables governing the conditions around Carrie Bow Cay and across the region. These in situ data are also critical to ground-truthing remotely sensed data such as the satellite-generated sea-surface temperature (SST) records used to calculate bleaching thresholds during the 1998 ENSO (Aronson et al., 2002). Finally, our data are beginning to yield reliable descriptions of water quality conditions in the central portion of the Belize Barrier Reef, including those conditions that have accompanied the rapid modifications of the Belizean coastal zone during the past few decades. Most significantly, the dramatic loss of water quality documented by these long-term records has significant biological, management, and economic implications for Belize and the other countries of the Mesoamerican Barrier Reef.

ACKNOWLEDGMENTS

This research was funded by grants from the Smithsonian Institution’s Caribbean Coral Reef Ecosystems Program. We thank Dr. Klaus Ruetzler for his support and encouragement of the monitoring programs and Mike

Carpenter for exceptional support to the field effort. We thank the many station managers who have assisted with data collection, especially noting the dedicated efforts of Dan Miller and Claudette DeCourley over many years. Dan has been largely responsible for maintaining the light meters on the reef. Dr. Randi Rotjan also generously assisted with the light loggers. We thank John Tschirky who has been part of the CARICOMP program since its inception. We thank two reviewers for helpful criticisms that improved the manuscript. This is contribution number 846 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, supported in part by the Hunterdon Oceanographic Research Fund.

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Global Change and Marsh Elevation Dynamics: Experimenting Where Land Meets Sea and Biology Meets Geology

J. Adam Langley, Marc V. Sigrist, James Duls, Donald R. Cahoon, James C. Lynch, and J. Patrick Megonigal

ABSTRACT. Coastal marshes must accumulate soil to keep up with rising sea levels. It is unknown how the response of these ecosystems to global change will influence their ability to continue to keep up with sea-level rise. Here, we describe an in situ experimental chamber approach for manipulating key environmental variables, such as atmospheric CO_2 and soil N availability, in a brackish marsh. We outfitted each chamber with surface elevation tables (SETs) to closely monitor soil elevation change, a sensitive indicator of marsh vulnerability to sea-level rise. Further, the design facilitates measurements of ecosystem exchange of CO_2, plant productivity, porewater chemistry, and other environmental parameters.

INTRODUCTION

Projecting the impacts of climate change, eutrophication, and other perturbations on ecosystems requires experimental manipulations. Large experimental facilities have been built and operated in all types of ecosystems over the past decades to provide such data. There are at least six characteristics that complicate experimental manipulations in tidal wetlands. First, such ecosystems can be quickly and irreversibly damaged by heavy foot traffic, so boardwalks must be built to minimize long-term impacts on vegetation and soils. Second, because many wetlands have deep, low-density, peaty soils, the permanent infrastructure, such as boardwalks and chambers, must be well anchored for stability. Third, tidal wetlands are often inundated by tides and can be under more than a meter of water during storm surges, which dictates that all buoyant equipment must be soundly fixed in place. All electrical service and sensitive equipment must be positioned high and be easy to remove during extreme flooding events. Further, emergency shutoff systems must be in place to cut off the electrical supply and gas exchange equipment during flood events. Fourth, the water that floods brackish marshes is saline and corrodes most metals. Fifth, the lack of shade means that UV-sensitive materials will degrade. Care must be taken to select UV-resistant materials, and even those must be monitored and frequently replaced. Sixth, high-latitude marshes may experience cold winters. Ice formation can severely damage even rigid and well-anchored infrastructure. Here we

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describe a global change experiment in a brackish marsh that was designed to overcome these substantial technical challenges.

SITE DESCRIPTION

This study took place at Kirkpatrick Marsh, which is located on the Rhode River, a subestuary of Chesapeake Bay at the Smithsonian Environmental Research Center in Edgewater, Maryland. The site is dominated by the C_3 sedge, *Schoenoplectus americanus* (formerly *Scirpus olneyi*), and less so by two C_4 grasses, *Spartina patens* and *Distichlis spicata*. The soils at this site are organic (80% organic matter) to a depth of approximately 5 m. Mean tidal range is 30 cm. The high marsh zone is 40–60 cm above mean low water level and is inundated by 2% of high tides. Salinity averages 10 parts per thousand (ppt) and ranges from 4 to 15 ppt seasonally. Average daily low air temperature is −4°C in January, and the average daily high is 31°C in July.

To examine the interactive effects of elevated CO_2 and nitrogen addition, we identified 20 plots of similar plant composition in summer 2005. Each plot consisted of one octagon (2 m across) that would be enclosed in an experimental chamber to allow for atmosphere manipulation and an adjacent rectangular portion (2 × 1 m) that served as a reference plot to account for spatial variation and to gauge potential chamber effects.

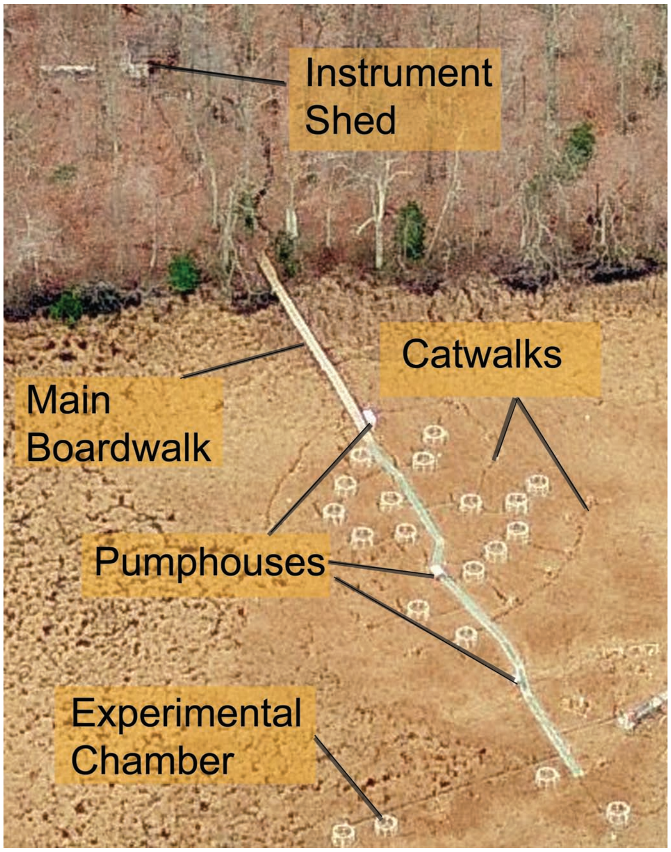

FIGURE 1. An overhead image of the entire CO_2 site. The main boardwalk connects to 20 experimental plots by smaller catwalks, the paths of which are visible. Gas samples are pumped via the pump houses to the analytical shed on the bank.

CONSTRUCTION

Walkways and Equipment Housing

A main boardwalk and a series of thinner, lighter "catwalks" were built to access each plot without continually walking on the marsh (Figure 1; see also Figures 4, 5). The main boardwalk, built perpendicular to shore, roughly bisected the experimental plots. Most of the horizontal surfaces of the boardwalks were fiberglass grating (50% open), which allowed light to penetrate through the boardwalks, sustaining plant life and providing excellent traction. The supports for the main boardwalk were built of 10 × 10 cm posts sunk 2 m into the ground. The catwalks departed from the main boardwalk, forming a perimeter around each experimental chamber (Figure 2). These catwalks were less than 30 cm above the ground to avoid shading the plots. They were built of fiberglass grating (30 cm wide planks) laid flat on supports built of 2.5 cm polyvinyl chloride (PVC) that were anchored more than 1 m into the marsh using segments of 2.5 cm PVC pipe. After all walks were in place, the marsh surface was rarely stepped upon directly.

Three small pump houses, which housed air sample pumps and remote datalogging equipment, were built alongside the main boardwalk. An analytical shed was constructed on the bank 5 m above sea level to house sensitive analytical equipment.

Open-Top Chambers

The chamber design followed that of a previous open-top chamber study in the same marsh (Drake et al., 1989), but with several major innovations to enhance durability and plot accessibility (Figures 2–5). In 2006, the chambers consisted of four major components: base, manifold, chamber skeleton, and chamber panels. The octagonal shape of the chamber was a compromise between two design goals. It approximated a cylinder, which was ideal for uniform air mixing inside the chamber and minimizing dead spots. The flat surface of each side allowed us to enclose the chamber with eight flat panels that can be removed easily for access to the inside of the chamber.

The base of the chamber was an aluminum octagon (0.5 cm thick, with an L-shaped cross section) implanted 10 cm into the marsh surface. In the portion of the base that was implanted into the soil, 2 cm holes were cut to allow root growth to further stabilize the base. A hollow octagonal manifold (cross section, 30 cm high × 6.35 cm wide) was attached to the base to distribute inflowing air equally around the chamber (see Figure 2). Manifolds were built from welded aluminum (grade 6061-T5) covered with transparent acrylic panels that allowed light transmittance.

Mounted to the top of the manifold was the "skeleton," consisting of eight vertical legs supporting an octagonal ring oriented horizontally at the top. The skeleton was built from 2.5 cm diameter PVC pipe. The only custom pieces in the skeleton were three-way fittings on the octagonal ring that join two PVC pipes in the ring with one leg. The joint was made by tapping female thread into the side of a 45° elbow. The legs of the skeleton sat in welded supports on the top of the manifold.

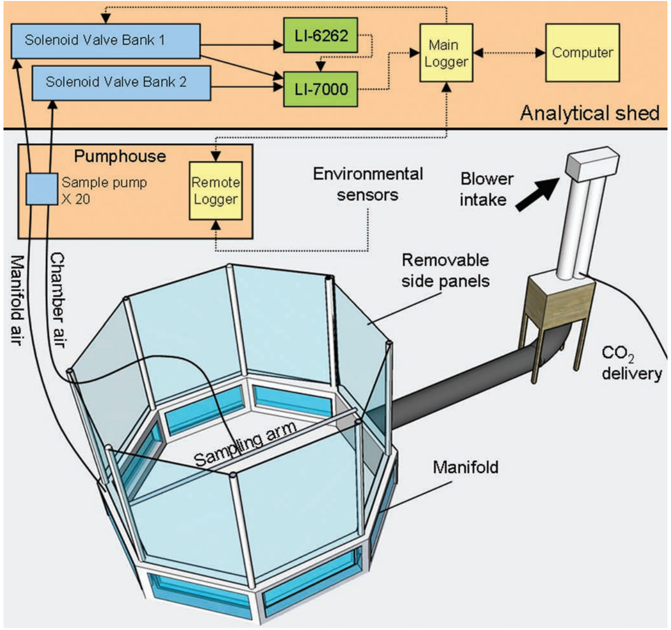

FIGURE 2. Schematic of an experimental chamber and gas sampling system. The ambient CO_2 chambers are the same except there is no CO_2 delivered into the blower stream. Solid (black) arrows represent air flow; dotted arrows (appearing light gray) represent information flow.

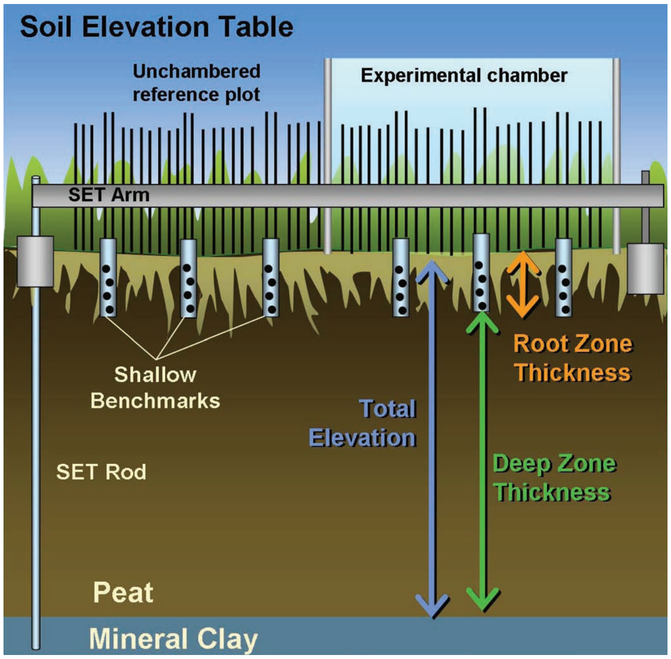

FIGURE 3. Schematic of the surface elevation table (SET) design. The SET arm is periodically connected to the SET rod benchmark, which has been anchored into the mineral clay underlying the peat profile. Pins are placed through holes in the SET arm to the soil surface to measure changes in elevation occurring over the entire profile. Any change in elevation of the shallow benchmarks must occur as a result of processes occurring beneath the root zone. Root zone changes are calculated by subtracting deep zone elevation change from total elevation change.

Removable rectangular panels were made from aluminum (grade 6063-T52), covered with infrared (IR)-transparent film (Aclar 22A, Honeywell) that was taped on using transparent UV-resistant tape (3M, 851). The film does not absorb IR radiation as do other films and therefore heat is not allowed to accumulate. The panels were attached to the PVC frame with custom-fitted PVC snaps so that any of the eight panels could be removed to access any portion of the plot. Further, panels were removed in the winter to prevent damage while CO_2 fumigation was terminated.

Finally, after the 2006 growing season, to conserve CO_2 and achieve a more stable CO_2 concentration by reducing wind incursions, an octagonal frustum, or wind foil, was added to the chamber design (see Figure 5). The frustum was constructed of 1.9 cm PVC, angled inward at 45°, and covered with the same film to reduce wind incursions. The final dimensions of the chamber were 1.5 m in height, 2 m in diameter, and with 1 m sides; the volume is 6.5 m^3.

FIGURE 4. Photograph of SET measurements being made in summer 2006. Each pin is gently lowered to the soil surface, while applying minimal pressure so that the pin does not depress the soil surface. (Photograph by M. V. Sigrist.)

To move ambient air through the open-top chamber, a blower (Dayton, 5C095) was mounted on a stand 1.5 m above the marsh surface to avoid high tides. The blowers were placed at least 6 m away from each chamber and oriented to avoid shading the study area (see Figures 1, 2, 4). PVC chimneys (two 15 cm pipes per blower) were affixed vertically to the top of the blower intake so that the blowers would take in air from 4 m above the ground that was not influenced by biological activity on the ground and thus had relatively stable [CO_2]. The chimneys were capped to prevent rainwater from entering the blower. A 20 cm diameter duct fed air from the blower to the chamber manifold. Two hundred fifty-two 1 cm diameter holes (the same total area as the intact pipes) were drilled on the inside of the manifold, so that air would flow in the chambers equally from each side of the octagon. The blowers forced 12.5 m^3 per minute through the chambers, resulting in an approximate chamber air turnover rate of 2 min^{-1}.

Surface Elevation Tables

To take repeatable measurements of soil elevation, each plot was outfitted with a rod surface elevation table (SET; see Figures 3, 4) (Cahoon et al., 2002) modified to accommodate plot dimensions. Outside each experimental chamber, a posthole was dug roughly 15 cm in diameter and 20 cm deep. A 30 cm long PVC pipe (15 cm diameter) was placed vertically into the hole. In the center of the PVC pipe, a series of attachable stainless steel rods was driven with an electric hammer through the entire profile of organic matter (4–5 m depth) and anchored to the point of refusal (6–7 m) into the subsurface mineral clay underlying the marsh. Concrete was poured into the PVC pipe to secure the top of the SET rod.

To isolate the influence of root zone processes on elevation, we implanted “shallow benchmarks” to a depth of 30 cm. The vertical movement of these benchmarks results from processes that occur below the top 30 cm of soil. The benchmarks were made of aluminum pipe (5 cm diameter by 40 cm long). Several 1 cm diameter holes were drilled into the sides of the lower 10 cm of the pipe to allow roots to grow through and anchor the benchmarks in place. Six benchmarks were implanted to a depth of 30 cm under the path of the SET arm in each chamber, three inside the chamber and three outside. After

FIGURE 5. Photograph showing a chamber with a frustum that was added to all chambers before the 2007 growing season. The tubing leading to one set of porewater wells, the gas sampling tube, and the catwalk is also visible. (Photograph courtesy J. A. Langley.)

placement, solid caps were placed on the top of each pipe. All these perturbations, as well as boardwalks to service each plot, were completed in the summer of 2005, at least 9 months before the beginning of the experiment.

At intervals ranging from 1 to 3 months, the modified horizontal aluminum SET arm (4 m long compared to less than 0.5 m long for the original rod SET design) was attached to the top of the SET rod benchmark, leveled precisely, and affixed to an aluminum post at the other end. The arm provided a horizontal reference of known elevation across the soil surface; changes in the distance from this reference surface to the soil surface were a sensitive measure of changes in soil elevation. Fiberglass pins (3 mm in diameter), all exactly 91.0 cm in length, were placed through precision-drilled holes in the SET arm at 1 cm increments. Approximately 40 individual measurements were made in each chamber and 40 in each adjacent, unchambered reference plot. Each pin was carefully lowered to the soil surface and gently placed so that no litter or live plant obstructed the pin. The height from the SET arm to the top of each pin was measured to the nearest millimeter (mm), providing a measurement of total elevation. Changes in absolute soil elevation were partitioned into either the root zone (top 30 cm of soil) or the deep zone (below 30 cm). To measure elevation changes occurring in the deep zone, we lowered 2 to 4 pins to the surface of each of the six shallow benchmarks (three inside and three outside each chamber) and measured in the same manner. We calculated the change in elevation resulting from processes occurring in the root zone, ΔE_R, from the two measured variables following the equation $\Delta E_R = \Delta E_T - \Delta E_D$, where ΔE_T represented the change in total elevation and ΔE_D represented elevation change attributable to change in thickness of the deep zone. Surface accretion was also measured using feldspar marker horizons in each plot (Cahoon et al., 1995). To eliminate compaction during coring, the deposition rate was estimated by taking cryocores (Cahoon et al., 1996) and measuring the amount of soil deposited on top of the marker horizon.

Total soil elevation was strongly related to innate spatial and temporal variability of deep zone dynamics. Specifically, changes in the thickness of the deep zone followed mean monthly sea level through time, and distance from the bank predicted the amplitude of that oscillation. To isolate treatment effects on various soil elevation parameters, we accounted for variation by referencing SET measurements in experimental chambers to those in the adjacent, unchambered reference plots, so that relativized ΔE = experimental plot ΔE − reference plot ΔE, where E = the elevation parameter of interest. We used a repeated-measures multivariate analysis of variance (MANOVA) to test for changes in elevation through time; we used *t* tests to liberally detect chamber effects on elevation parameters at individual dates and a two-way analysis of variance (ANOVA) to test for treatment differences in surface accretion.

TREATMENT APPLICATION

CO_2 Delivery and Sampling System

Carbon dioxide was delivered to each of the 10 elevated CO_2 chambers at a rate of approximately 6 L min^{-1} to achieve a target concentration of 720 ppm, which is nearly double the current ambient concentration of 380 ppm. Each CO_2 delivery line was controlled with metered valves and fed into the intake chimney on the blower for each respective elevated chamber. Adding the CO_2 upstream of the blower ensured sufficient mixing before air entered the chamber through the manifold.

Two sample lines continuously pumped air from each of 20 chambers to instruments located in a nearby shed: one line sampled manifold air and the other sampled the chamber atmosphere. To achieve a representative sample of the chamber atmosphere, air was sampled with a 2 m long pipe oriented horizontally across each chamber. The pipe was 1.3 cm diameter PVC with caps on both ends and a series of 2 mm diameter holes at geometrically increasing intervals away from the center of the pipe. The geometry allowed air drawn from the center of the pipe to be a composite sample representing each point on a transect through the chamber equally. The sampling pipe was positioned horizontally and adjusted to roughly half the green canopy height to best represent the air that photosynthetic tissue experienced.

Air was pulled under negative pressure from each chamber a short distance to a Teflon-coated double diaphragm pump (Thomas Industries, 2107-CA14-TFE), from which it was pushed under positive pressure to the analytical shed (see Figure 1). To avoid drawing water into the pumps, they were plugged into normally closed float switches (Dayton 3BY75) that cut the power supply when the water level approached the height of the gas sampling lines. Each of the 40 lines entered a bank of solenoid valves (model 3V1, Sizto Tech Corporation), then flowed into a common line, one for manifold lines and one for chamber lines. The two solenoid valves controlling each chamber opened simultaneously, one with manifold air and the other with chamber air; the other solenoid valves remained closed so that the contents of only one chamber at a time passed through the common lines to the gas analyzers. Each chamber was sampled for 2 min to allow ample time for air in the common portion of the system to be flushed out before measurements were logged, which meant that each chamber was sampled at least once every 40 min.

One infrared gas analyzer (IRGA) measured the difference between a chamber's manifold air (i.e., incoming air) and a dry, zero-CO_2 reference gas. A second IRGA measured the difference between manifold air and chamber air. This configuration maximized our ability to precisely measure absolute CO_2 concentration and to accurately measure the CO_2 concentration difference between two locations. A LI-6262 (Licor, Lincoln, NE) had dry, zero-CO_2 air cycling through the reference cell and the manifold air passing through the sample cell. A Li-7000 (Licor) had the manifold air passing through the reference cell and chamber air passing through the sample cell. Cell A of the LI-7000 was referenced to an analog signal from the LI-6262 as the absolute concentration of CO_2 and H_2O in the manifold air.

We monitored the manifold line to determine how much CO_2 was being delivered to each manifold. The chamber air sampling line allowed us to monitor the actual chamber atmosphere and to fine tune the CO_2 delivery rate to achieve our target concentration in the chamber atmosphere, accounting for photosynthetic drawdown and wind incursions.

NITROGEN FERTILIZATION

A total of 25 g N year^{-1} was applied to each high-N plot. Ammonium chloride was dissolved in 5 L brackish water from the nearby Rhode River, the subestuary adjacent to the site. At five dates (approximately monthly, avoiding high tides) throughout the growing season we used backpack sprayers to deliver the fertilizer (equivalent to 5 g N) solution to 10 plots. Then, the fertilizer solution was rinsed from standing vegetation with another 5 L unamended river water applied with backpack sprayers. Each fertilization treatment simulated 5 g N m^{-2} in the equivalent of 0.5 cm river water. The 10 unfertilized chambers received 10 L unamended river water applied in the same manner. The river water was taken from the tidal fetch area adjacent to the marsh. Mean annual [NH_4^+] in that water ranges from 32 to 82 μg L^{-1}, with a mean of 52, and salinity has ranged from 4.0 to 10.6 ppt, with a mean of 6.7, over the past 20 years (growing season means from biweekly sampling; Thomas Jordan, unpublished data). Assuming the added NH_4Cl integrated into the top 40 cm of porewater (as our sampling indicates), and excluding losses from the ecosystem or plant uptake, we estimated that this fertilization would have increased porewater salinity by a maximum of 0.05 ppt, less than 1% of normal salinity.

MEASUREMENTS

The chambered experimental plots consisted of two halves, one-half geological and one-half biogeochemical. All sampling that involved disturbance of soil was performed on the biogeochemical half. All elevation measurements, which were considered to be more sensitive to soil disturbance, were performed on the geological half.

ABOVEGROUND BIOMASS

We estimated peak aboveground biomass with a combination of allometry and harvested subplots (Erickson et al., 2007). At the end of July of each year, eight 30 × 30 cm quadrats were placed in prescribed locations in each plot, six inside the chamber and two in an adjacent unchambered control plot. In the quadrats, each *Schoenoplectus americanus* stem was counted and nondestructively measured for total height, green height, and width at half-height. In the corner of each quadrat, we clipped and removed all vegetation and litter in a 5 × 5 cm area. Vegetation was sorted according to species. We measured the clipped *S. americanus* stems for total height and width. Clippings were dried for 72 h at 60°C and weighed. We measured length and width on a subset of freshly clipped stems. We used the calculated relationship between linear dimensions and dry mass ($r^2 > 0.9$) to estimate the mass of each live *S. americanus* stem. To estimate *Spartina patens* and *Distichlis spicata* mass, we scaled up from mass in the clipped areas to total chamber area.

ROOT PRODUCTIVITY

Three soil cores (30 cm depth × 5 cm diameter) were taken from each plot and replaced with cylindrical ingrowth bags (30 cm height × 5 cm diameter). The bags were constructed from 1 cm mesh and filled with milled, moistened peat so as to achieve the bulk density of in situ peat, 0.12 g cm^{-3}. Bags were implanted in winter and removed in November the following year. Contents were washed over a 1 mm sieve. Large organic fragments were picked out by hand. Root mass was separated into fine (<2 mm diameter) and coarse (>2 mm) categories, dried for 72 h at 60°C, and weighed.

POREWATER WELLS

We implanted nine porewater wells (three replicates at each of three depths: 20, 40 and 80 cm) in each experimental plot. We built wells from 0.6 cm internal diameter rigid Teflon tubing (GE Polymershapes) plugged at the bottom with silicon caulk and open at the top, which extended 10 cm above ground. Sixteen holes (1 mm diameter) were drilled into the bottom 10 cm of the Teflon tube to allow ample conductance of porewater into the well. A vinyl hose (6 mm [OD], 3 mm inner diameter [ID]) was fastened to the top of each well and draped over the chamber for easy access from outside the chamber. Wells were flushed with 60 mL, equivalent to more than total well volume, and sampled monthly for a suite of chemical parameters using syringes.

NET ECOSYSTEM EXCHANGE (NEE)

The chambers were also designed to allow for measurement of net ecosystem exchange (NEE) of CO_2 between the atmosphere and the enclosed ecosystem (Figure 6). Periodically throughout the growing season, octagonal caps were placed on a subset of chambers. The purpose of the caps was not to render the chamber airtight, but to eliminate wind incursions and generate a consistent, predictable pattern of air flow through the chambers. The caps were octagons with a crossbeam built from 1.9 cm PVC pipe covered with the same IR-transparent film for the chamber panels. The film was perforated with 2 cm diameter holes. The gas sampling pipe, described above, was raised to a height roughly 30 cm below the cap and aligned with the cap perforations. This arrangement allowed us to measure the [CO_2] of air exiting each chamber after it had been influenced by soil and vegetation.

To estimate flow rate of air through the chamber, we cut a slit in the air delivery ducts from each blower and measured air velocity using a handheld anemometer (AM 4822, Mastech; www.p-mastech.com). We initially measured the velocity at a range of distances from the duct wall and determined that the mean of two measurements (centered at 4 cm and 9 cm from the duct wall) adequately estimated the average velocity for the entire cross section. Multiplying velocity (cm s^{-1}) and cross-sectional area (cm^2)

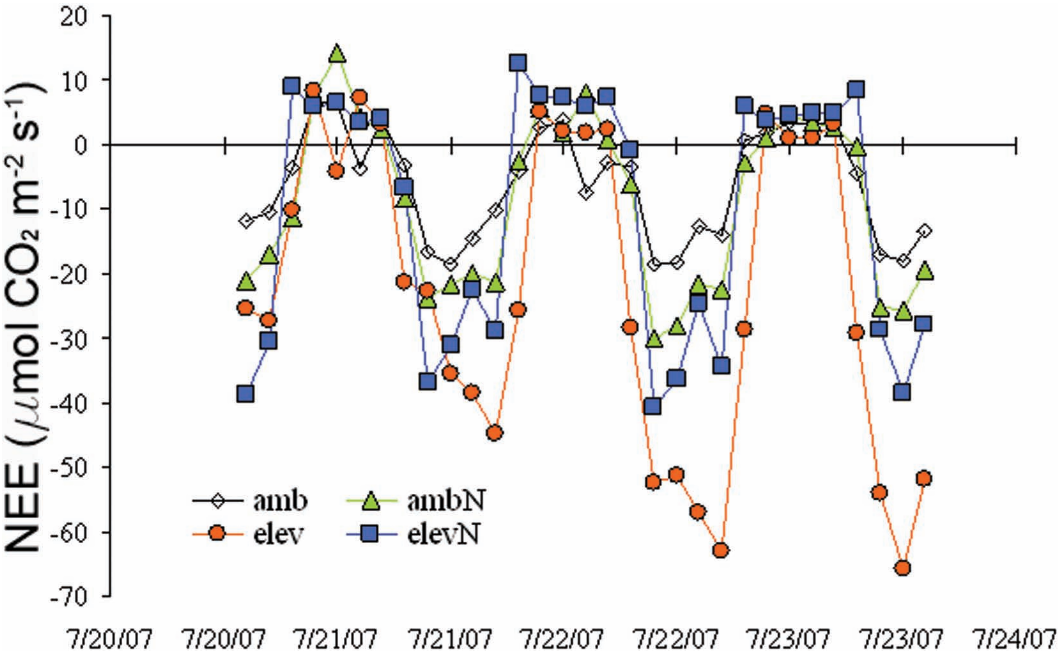

FIGURE 6. Net ecosystem exchange (NEE) of CO_2 over three days in July 2007. Negative values represent net uptake by the ecosystem. Generally, values are negative in summer daytimes when photosynthetic rate surpasses respiration rate. Each point represents the means of approximately 12 individual measurements from each of two replicate chambers binned into 2.4-h intervals. amb = ambient; elev = elevated; ambN = ambient N; elevN = elevated N.

yielded volumetric flow rate (cm^3 s^{-1}). The volumetric flow rate was converted to mass flow using air temperatures from the site. We calculated NEE as ($[CO_2]_{in} - [CO_2]_{out}$) × flow rate.

Because we did not want to incur chamber effects such as warming or rain exclusion, we measured NEE on a rotating subset of chambers balanced by treatment, for variable intervals from 3 to 7 days. These data will be used to calculate NEE light-response curves for net CO_2 uptake during the day and NEE temperature-response curves for net CO_2 release during the night. The response curve models will be driven with continuous measurements of soil temperature and photosynthetically active radiation to extrapolate up to integrated NEE for a complete growing season (Rasse et al., 2003). The gas sampling program was adjusted to increase the frequency with which NEE chambers were sampled to increase resolution for these low signal-to-noise NEE measurements, compared to the relatively stable absolute atmospheric [CO_2] data when all chambers are sampled equally.

Environmental Variables

Soil temperature was measured at 5 and 15 cm depth using type-T thermocouples. Wind speed was monitored with an anemometer (O14A-L, Campbell Scientific, Logan, UT). Water level was recorded using a differential pressure transducer (PS-9805, Northwest Technologies) placed at the bottom of a 0.5 m well. All environmental data were logged on a combination of a multiplexor (AM32T, Campbell Scientific) for temperature and a datalogger (CR10X, Campbell Scientific), which were positioned remotely in the marsh to minimize analog signal degradation. Information was then relayed digitally between the marsh and main datalogger (CR1000, Campbell Scientific) using multidrop interfaces (MD485, Campbell Scientific).

RESULTS AND DISCUSSION

Treatment Application

Average daily mean CO_2 ± SE was 394 ± 1.2 ppm in ambient and 707 ± 6.0 ppm in elevated chamber atmosphere in 2007, a treatment difference of 313 ppm. The standard deviation among daily means for individual chambers averaged 21.9 and 59.0 ppm for individual ambient and elevated chambers. The variation in means between days was driven by differences in wind speed (Figure 7). High winds resulted in incursions of ambient air into elevated chambers, thereby diluting the elevated [CO_2]. On the other hand, stillness allowed respired CO_2 to accumulate overnight, which increased background [CO_2] in ambient and elevated chambers. Because this buildup affects each treatment equally, the difference between ambient and elevated chambers persisted. However, wind incursions drove down concentrations in elevated chambers only, which decreased the difference between ambient and elevated [CO_2].

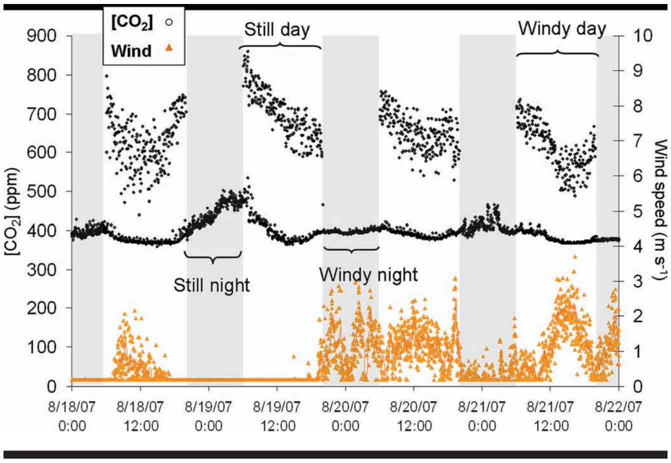

FIGURE 7. The CO_2 treatment and wind speed from four varying days in August 2007. The shaded areas represent hours of darkness when the CO_2 delivery was shut down. During those off hours, all chambers were at ambient [CO_2]. During still nights, ambient [CO_2] approached concentrations much higher than well-mixed atmospheric [CO_2] as respired CO_2 accumulated relatively near the ground.

In 2006, before chambers were equipped with frusta, ambient and elevated chambers [CO_2] were 395 and 669, a difference of 274 ppm. Although the mean [CO_2] could have been elevated in the chamber without adding frusta, the fluctuations with wind would have been extreme, and the expense of the additional CO_2 was deemed prohibitive.

The [NH_4] in porewater was successfully increased by the N addition by a factor of 2.9, from 17 to 64 µmol L^{-1} averaged over the growing season in 2006. The factor by which N addition increased porewater [NH_4] was much higher early in the season and declined as growing plants took up N.

Measurement Validation: Chamber Effects

Elevation

To examine the possibility of chamber effects on elevation, we examined the measurements in the ambient CO_2, low-N (no added N) treatment (Figure 8). The in-chamber measurements were very similar to those in the reference plots. Both sets of data revealed significant changes in elevation through time (repeated-measures MANOVA, $P < 0.05$). Most notably, all plots experienced a dip of roughly 0.8 cm in total elevation during March 2007, followed by a strong recovery. This dip was driven entirely by dynamics in the thickness of the deep zone. Compared to absolute changes in elevation (range, >1.2 cm), the differences between in-chamber and reference elevation were relatively small (range, <0.2 cm). There was a trend of a chamber effect on total elevation driven by deep zone dynamics. This effect was significant in summer 2007 but has vanished since then. The relativized root zone thickness in ambient CO_2, low-N chambers never differed from zero (*t* test, $P > 0.40$ for all dates), which indicated that there was not a detectable chamber effect in this stratum where we expected treatment effects to be manifested.

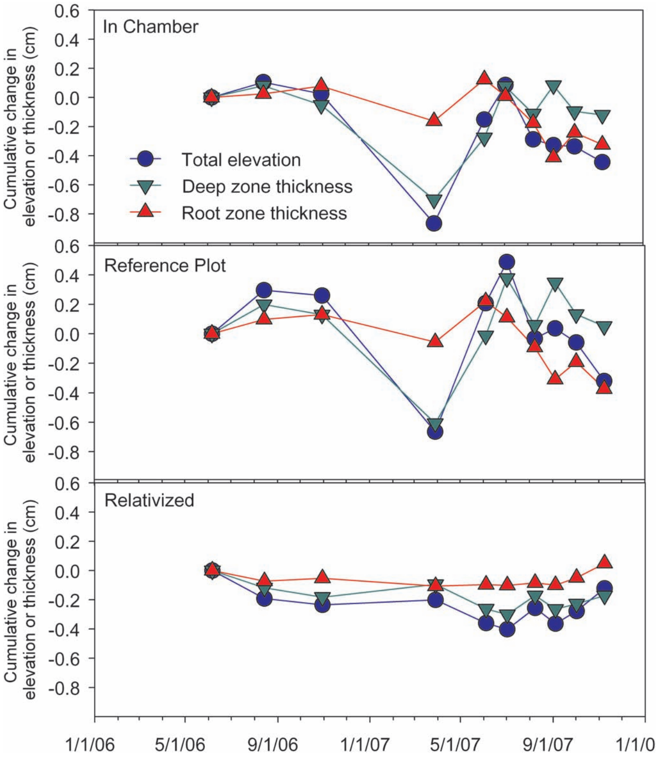

FIGURE 8. Elevation data from the five ambient CO_2, low-nitrogen (N) plots. Change in total elevation is partitioned between changes in thickness of either the deep zone or root zone. Top panel: elevation and thicknesses from inside the experimental chambers; middle panel: from the adjacent reference plots; bottom panel: difference between the in-chamber and reference measurements (relativized). There was a slight chamber effect on total elevation, driven by contraction of deep zone thickness. Root zone did not differ from zero.

Surface Accretion

One criticism of the design was that the chambers, by enclosing plots, may have excluded sediments from being deposited on the marsh surface. The difference between in-chamber and reference accretion measured with cryocores in November 2007 was small (0.058 cm) and did not differ significantly from zero (95% confidence interval: −0.18 to 0.07, $n = 20$). The treatment means also did not differ from each other (two-way ANOVA: CO_2, $P > 0.10$; N, $P > 0.10$) or from the reference plots (chamber effect: $P > 0.10$; Figure 9).

CONCLUSIONS

The design of our field experiment proved robust to a number of challenges unique to tidal salt marsh environments, including saltwater corrosion and deep tides. More importantly the chamber design allowed us to consistently elevate atmospheric CO_2. The frustum was a key feature of the chamber because it average-stabilized and raised the $[CO_2]$ in the elevated treatment, likely resulting in saved

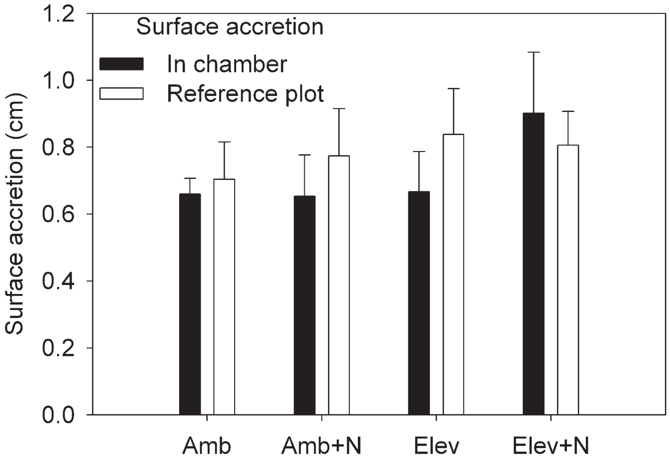

FIGURE 9. Surface accretion measured as the accumulation of matter on top of the marker horizon inside the chamber versus that outside the chamber. It was thought the chambers may exclude exogenous sediment, but there was no difference between in-chamber (black bars) and outside-chamber (reference plot, white bars) accretion rates. Amb = ambient; Elev = elevation.

CO_2. N addition yielded higher porewater N concentrations as expected, but further chemical analyses are needed for a more precise estimate of the magnitude of the N treatment. The SET design allowed for sensitive measures of soil elevation change. The chambers, perhaps by virtue of their mass, appeared to slightly depress soil elevation. However, there was no chamber effect in the root zone where the most important treatment effects are expected to occur. Further, the size of the chamber effect on elevation was small (0.2 cm; Figure 8, bottom panel) relative to the natural range of variation in those elevation parameters (1.2 cm; Figure 8, middle panel).

ACKNOWLEDGMENTS

We thank J. Keller, G. Peresta, B. Drake, E. Sage, A. Martin, D. McKinley, S. Chapman, K. White, and N. Mudd from the Smithsonian Environmental Research Center for construction and maintenance of the field experiment. The field study was supported by the U.S. Geological Survey Global Change Research Program, U.S. Department of Energy (grant DE-FG02-97ER62458), the U.S. Department of Energy's Office of Biological and Environmental Research through the Coastal Center of the National Institutes for Climatic Change Research at Tulane University, and the Smithsonian Institution.

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Herbivory, Nutrients, Stochastic Events, and Relative Dominances of Benthic Indicator Groups on Coral Reefs: A Review and Recommendations

Mark M. Littler, Diane S. Littler, and Barrett L. Brooks

ABSTRACT. Threshold levels (i.e., tipping points where the probability of community phase shifts is increased and the potential for recoverability is reduced) for critical bottom-up interactions of productivity (e.g., nutrients) and those for top-down disturbances (e.g., herbivory) must be known to manage the competitive interactions determining the health of coral-dominated reefs. We further posit that latent trajectories (reduced resiliencies/recoverability from phase shifts) are often activated or accelerated by large-scale stochastic disturbances such as tropical storms, cold fronts, warming events, diseases, and predator outbreaks. In highly diverse and productive reef ecosystems, much of the overall diversity at the benthic primary producer level is afforded by the interaction of opposing nutrient-limiting/nutrient-enhancing and herbivory controls with the local physical and spatial variability, such that a mosaic of environmental conditions typically occur in close proximity. Although the relative dominance model (RDM) appears straightforwardly simple, because of the nature of direct/indirect and stimulating/limiting factors and their interactions it is extremely complex. For example, insufficient nutrients may act directly to limit fleshy algal domination (via physiological stress); conversely, abundant nutrients enhance fleshy algal growth, with the opposite effect on reef-building corals (via toxic inhibition or increased diseases). Furthermore, the effects of controls can be indirect, by influencing competition. Even this seemingly indirect control can have further levels of complexity because competition between algae and corals can be direct (e.g., overgrowth) or indirect (e.g., preemption of substrate). High herbivory (via physical removal) also acts indirectly on fleshy algae through reduced competitive ability, whereas lowered herbivory and elevated nutrients also indirectly inhibit or control corals and coralline algae by enhancing fleshy algal competition. Other ecologically important bottom-up factors, such as reduced light, abrasion, allelopathy, disease vectoring, and sediment smothering, also result from indirect side effects of fleshy algal competition. These factors tend to selectively eliminate the long-lived organisms in favor of weedy fast-growing species, thereby reducing desirable complexity and biodiversity.

INTRODUCTION

There has been an exhaustive debate in the coral reef literature over the relative importance of forces that regulate community structure and resilience (i.e., the potential to resist stresses and to recover following disturbances). The expansion of the human population and associated increases in destructive fishing

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Manuscript received 13 May 2008; accepted 20 April 2009.

(Hughes, 1994) and nutrient loading (Lapointe, 1999), compounded with ocean warming (Hoegh-Guldberg, 1999) and stochastic environmental effects (Precht et al., 2005), have been broadly debated to explain the increasing degradation of coral reefs worldwide. Because human population growth is not expected to abate, discriminating among various stressors is critical to determine conservation strategies and to eventually ameliorate the accelerating degradation of coral reefs. What has been lacking is the ability to rigorously test and differentiate among the possible acute versus chronic stressors—leading to ongoing controversy. In an attempt to address this problem, several workers (Mora, 2008; Burkepile and Hay, 2006) have conducted broad correlative and statistical assessments of communities over large regional scales. These studies have suggested a clear interaction between eutrophication in conjunction with declining herbivorous organisms as direct causes for maintaining present undesirable phase shifts on coral reefs.

Such phase shifts have been devastating to the many uniquely specialized benthic photosynthetic symbionts dominating tropical reefs, which are responsible for some of the most productive natural ecosystems known. Four major space-occupying groups of benthic primary producers combine to create high coral-reef primary productivity: reef-building corals (containing symbiotic algae), crustose coralline algae, algal turfs (fleshy filamentous and low-growing prostrate forms, and frondose macroalgae. Of these, photosynthetic corals create much of the structural heterogeneity and complexity and, with coralline algae, are primarily responsible for accretion of $CaCO_3$ into the reef matrix—making them the most desirable functional groups from a management perspective.

A basic objective in management ecology is to determine the mechanisms by which natural and anthropogenic factors maintain or alter structure and interactions in biotic communities. Anthropogenic eutrophication and destructive overfishing (i.e., herbivore removal by trapping, netting, poisoning, blasting) are the most tractable factors correlated with the marked global decline in tropical reef communities over the past two decades (see reviews in Ginsburg, 1994; Birkeland, 1997; papers in Szmant, 2001). The theoretical framework involving "top-down" regulation by predators and "bottom-up" control by resource availability in terrestrial systems was first proposed by Hairston et al. (1960), concepts that were later used (Atkinson and Grigg, 1984) to describe mechanisms that regulate the structure of coral-reef communities. These factors provide a valuable perspective (Figure 1) to assess and manage the human activities that affect the interactive mechanisms controlling stable states, tipping points, phase shifts, and recovery among the dominant functional groups of primary producers on tropical reefs.

In healthy coral-dominated reefs, nutrient concentrations are extremely low and attachment space is occupied by a broad diversity of three-dimensional overgrowing organisms. Given these conditions, the major tenets of the management model proposed by Littler and Littler (2006: fig. 1, relative dominance model [RDM]) are (1) that competition for space and light is crucial in determining the relative abundances of major benthic photosynthetic organisms, and (2) that the outcome of competition for these resources is most often, but not exclusively, controlled by the complex interactions of biological factors (top-down controls such as grazing) and environmental factors (bottom-up controls such as nutrient levels). As suggested by Grime (1979) for terrestrial plants and expanded for marine macroalgae (Littler and Littler, 1984; Steneck and Dethier, 1994), primary producer abundance and evolutionary strategies are controlled by physical disturbances (i.e., factors that remove biomass) coupled with physiological stresses (i.e., factors that limit metabolic production). In the conceptual relative dominance model (RDM; see Figure 1), grazing physically reduces biomass (top-down) and nutrients control production (bottom-up). The complex natural interactions between herbivory and nutrients are most dramatically impacted by large-scale catastrophic disturbances such as tropical storms (Done, 1992), warming events (Macintyre and Glynn, 1990; Lough, 1994), cold fronts (Precht and Miller, 2007), diseases (Santavy and Peters, 1997), and predator outbreaks (Cameron, 1977). These events serve to trigger or accelerate the ultimate long-term phase shifts postulated in the RDM. Such stochastic events selectively eliminate the longer-lived organisms in favor of faster-growing fleshy macroalgae, which are often competitively superior (Birkeland, 1977). However, nutrients and herbivory, in the absence of large-scale disturbances, are both sufficient to maintain phase shifts independently or in concert (Smith et al., 2001; Armitage and Fong, 2004; Littler et al., 2006a).

On undisturbed oligotrophic coral-reef habitats, the effects of well-documented top-down physical controls via intense herbivory prevail, where changes in grazing intensity often show acutely rapid effects. Conversely, bottom-up stimulatory controls are more chronic, the result of lack of nutrient availability, overcompensation by grazers, and a slower growth response, compared with acute physical destruction by herbivory. However, under persistent elevated nutrient conditions (relative to low [near-undetectable] concentrations), consistent coral declines can occur, con-

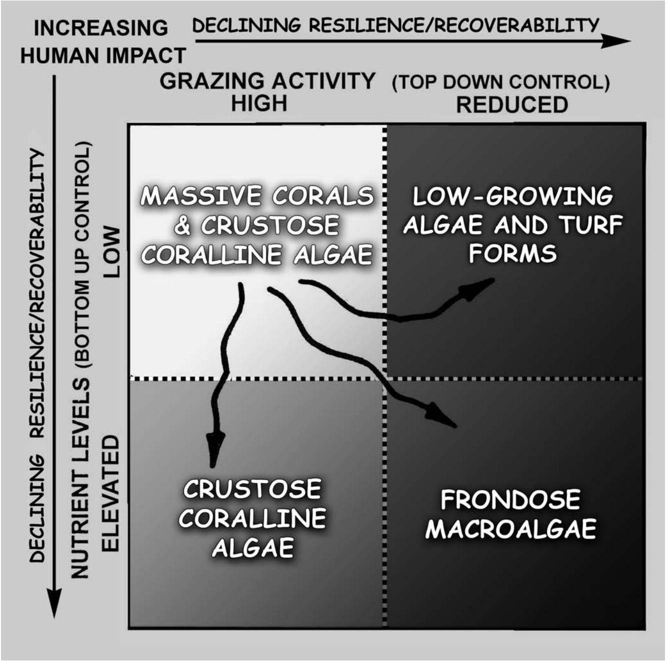

FIGURE 1. The competition-based relative dominance model (RDM). All the functional indicator groups occur under the conditions of every compartment of the model; however, the RDM predicts which group will most often *dominate*. Light to dark shading indicates declining desirability of each functional group from a management perspective. Crustose coralline algae are posited to be competitively inferior and dominate mainly by default, that is, where fleshy algae are removed by herbivores and some corals are inhibited by nutrients. The dashed lines approximate tipping points where declining herbivory and increasing nutrients reach critical levels that begin to reduce resilience to and recoverability from phase shifts. One vector can partially offset the other; for example, high herbivory can delay the impact of elevated nutrients, or low nutrients may offset the impact of reduced herbivory. As a baseline for healthy coral-reef habitats, herbivore population abundances and diversity should be high and palatable test plants should show at least greater than 50% loss $6\ h^{-1}$ (i.e., <6 h half-life) during a replicated series of midday in situ exposures. Hypothetical nutrient tipping points (i.e., thresholds that sustain algal growth) are thus far indicated to be quite low (i.e., ~0.1 μM soluble reactive phosphorus [SRP], ~1.0 μM dissolved inorganic nitrogen [DIN]), as suggested by laboratory growth experiments, case studies for macroalgal overgrowth of coral reef communities, and in situ experimental nutrient enrichment research (Bell, 1992; Bell and Elmetri, 1995; Lapointe et al., 1993, Bell et al., 2007). We further posit that latent trajectories (reduced resilience/recoverability from phase shifts) are often triggered or accelerated by large-scale stochastic disturbances such as tropical storms, cold fronts, warming events, diseases, and predator outbreaks. Although these are events from which coral reefs have recovered for millions of years in the absence of humans, when tipping points remain surpassed, less-desirable stable states can persist.

comitant with algal increases that may lead to enduring states throughout all combinations of herbivory (Littler et al., 2006a). Changes in bottom-up controls and their interactions not only alter the dominance patterns of the major benthic functional groups on coral reefs but, hypothetically, could have profound long-term consequences mediated through structural transformations and chemical modifications to reef systems and their herbivorous fish populations. In other words, excessive nutrient enrichment not only increases the productivity and biomass of weedy macroalgae via bottom-up controls that alter patterns of competitive dominance (Littler et al., 1993) but, over the long term, may lead to coral habitat degradation through (1) reduced spatial heterogeneity by overgrowth (Johannes, 1975; Pastorok and Bilyard, 1985; Szmant, 1997) and (2) nighttime anoxic conditions (tolerated by macroalgae, but not by coral competitors and herbivorous predators; Lapointe and Matzie, 1996) that could indirectly reduce top-down grazer effects. Furthermore, fleshy macroalgal blooms, irrespective of how they are induced, decrease the growth and reproductive capacity of the more structurally complex reef-building corals (Tanner, 1995; Miller and Hay, 1996; Bellwood et al., 2006; Hughes et al., 2007), as well as inhibit coral larval recruitment (Birkeland, 1977; Tomascik, 1991; Ward and Harrison, 1997) and survival (Lewis, 1986; Hughes et al., 1987; Hughes, 1989; Wittenberg and Hunte, 1992). Such complicated feedback loops following eutrophication (e.g., anoxia) are known to occur in seagrass meadows (Sand-Jensen and Borum, 1991; Duarte, 1995) and could also explain decreases in fish populations on coral reefs with long-term histories of eutrophication.

CORAL-REEF MANAGEMENT

The data relevant for long-term reef management consist of (1) many important short-term caging and feeding experiments (in the case of exceedingly well-documented top-down herbivory effects), (2) circumstantial evidence (Hallock et al., 1993), (3) correlative biogeographic surveys contrasting oligotrophic versus eutrophic systems (Littler et al., 1991; Verheij, 1993; Mora, 2008), (4) comparative experiments on systems containing natural nutrient gradients (Lapointe et al., 2004, 2005b; Vroom et al., 2005), (5) physiological assays (Littler and Littler, 1990; Lapointe et al., 1997), and (6) logistically complicated, in situ, long-term, experimental/causality studies, in the case of bottom-up nutrient controls (Smith et al., 2001; Littler et al., 2006a). Top-down control by abundant populations of large mobile herbivores is particularly well studied for coral reefs, beginning nearly five decades ago with the caging study of Stephenson and Searles (1960 As examples, Sammarco et al. (1974), Ogden and Lobel (1978), Sammarco (1980), Carpenter (1986), Lewis (1986), Morrisson (1988), and numerous other workers (see review by McCook et al., 2001) have demonstrated that lowering herbivory in low-nutrient habitats (usually assumed) often results in rapid increases in low-growing stages of fleshy macrophytes.

In the study of Lewis (1986) on the same reef flat studied by Littler et al. (2006a, 2006b), increases in a dominant vegetative algal turf form (*Vaughaniella* stage) with its upright fertile *Padina* blades, *not* blooms of mixed macroalgae, followed short-term (11 week) reductions of herbivorous fish grazing under conditions of low nutrient levels. Lewis' (1986) table 4 (although pseudoreplicated) shows statistically significant, but relatively small, increases (26%) in the above *Vaughaniella*-turf stage and its reproductive *Padina* blades; however, in contrast to several literature citations, no significant increases occurred in any of the abundant upright macroalgal dominants such as *Turbinaria turbinata* and *Halimeda* spp. Such low mats are unique in containing an abundance of nitrogen-fixing blue-green algae that can enrich other members within the low-growing algal community (Adey and Goertmiller, 1987; Adey, 1998). In presumably higher-nutrient environments, herbivore removals usually result in dramatic blooms of larger frondose macroalgae (Bellwood et al., 2006: fig. 4; Hughes et al., 2007).

Throughout the past decade, many biologists and managers have not recognized the importance of chronic nutrient enrichment and associated eutrophication problems facing coral reefs. A recent study (Littler et al., 2006b) provided a detailed review and discussion of the misinterpretations, misunderstandings, and suboptimal experimental designs that pervade the literature in regard to nutrient enrichment and the health of coral reefs. Overgrown 0.5 L porous clay-pot diffusers ("mini-reefs," following a decade of recruitment, colonization, and competition) were utilized (Littler et al., 2006b) to evaluate protocols for studies of controlled nutrient enrichment on coral reefs. A commonly used nutrient source, Tree Food Stakes containing up to 6% chlorine, resulted in a significant 11-fold and 20-fold decrease of fleshy algae and calcareous coralline algae, respectively, relative to the control treatments, while blue-green algae (Cyanobacteria) became significantly (6 fold) more abundant. Osmocote-filled mini-reefs showed no significant differences from the controls for any of the indicator groups. By avoiding the pitfalls of suboptimal study areas, insufficient duration of colonization/competition studies, inadequate nutrient detection limits, and inappropriate sources of enrichment in future research, the potential to provide new insights into the nutrient status of coral reefs will be greatly improved. Nutrient research is logistically difficult and, because the growth responses are relatively slow (i.e., chronic), requires more emphasis on multifaceted approaches carried out over sufficiently long time periods. Optimally, studies should include in situ enrichment experiments that test the long-term competitive interactions of functional indicator groups on healthy coral-dominated reefs, in addition to precisely monitoring water column nutrient levels, tissue C:N:P ratios, and algal physiological response assays.

Although nutrient data are typically lacking in coral-reef herbivory studies, natural background levels in conjunction with ample water motion are usually assumed to exceed levels that are limiting to macroalgal growth (Fong et al., 2003). As pointed out by Lewis (1986), large frondose macroalgae such as *Sargassum* and *Turbinaria* do occur in oligotrophic reef areas adjacent to coral colonies (see also Littler et al., 1986; McCook et al, 2001; Vroom at al., 2005); however, many of these frondose forms occupy microhabitats that generate increased current acceleration, such as the reef crest and tops of patch reef rocks, implicating higher nutrient fluxes (Atkinson et al., 2001). Also, large biomass/standing stocks of slow-growing perennial macroalgae (e.g., rockweeds) can develop over time under low inorganic nutrient concentrations; rainforests are good illustrations of this as well. Furthermore, *Sargassum* spp. can coexist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999); therefore, in this particular situation, large plant biomasses of low diversity do not necessarily indicate detrimentally abundant dissolved nutrients. Tissue analyses of mid-shelf S*argassum* transplants on the great barrier reef (McCook, 1999) revealed a C:N ratio of 32:1 and a C:P ratio of 1261:1, exceeding values for pelagic S*argassum* in the nutrient-impoverished Sargasso Sea (C:P = 877:1; Lapointe, 1995), which are compelling for substantial N limitation and severe P limitation. A further consideration is the now-ubiquitous presence of significant anthropogenic nitrogen sources (from burning fossil fuels) in rainfall worldwide (Vitousek et al., 1997), making the term "pristine" relative, at best. The demise of copious coral cover (Pollock, 1928) and concomitant rise in frondose algae (Doty, 1971) and coralline algae (Littler, 1971) on the reef flat at Waikiki, Hawaii, was the first phase shift from coral to macroalgal domination that was postulated (Littler, 1973) as caused by increases in eutrophication (bottom-up control).

Eutrophication affects coral reefs to different degrees and on varying scales. Several studies (Atkinson et al., 1995; Grigg, 1995; Steven and Broadbent, 1997; McCook, 1999; Bongiorni et al., 2003) indicated no substantial adverse responses of coral species to elevated nutrients. However, other laboratory and field experiments (Pastorok and Bilyard, 1985; Tomascik and Sander, 1987; Muscatine et al., 1989; Stambler et al., 1991; Jokiel et al., 1994; Koop et al., 2001) have concluded that corals are negatively affected by increased levels of nutrients and that diversity suffers. Numerous in situ observations exemplify the types of shifts from coral dominance to algal dominance that suggest linkages with chronic nutrient loading, including case studies in Hawaii (Littler, 1973; Banner, 1974; Smith et al., 1981; Maragos et al., 1985; Grigg, 1995), Venezuela (Weiss and Goddard, 1977), the Red Sea (Mergener, 1981; Walker and Ormond, 1982), Barbados (Tomascik and Sander, 1985, 1987), American Samoa (Green et al., 1997), Reunion Island (Cuet et al., 1988; Naim, 1993), Bermuda (Lapointe and O'Connell, 1989), the Great Barrier Reef (Bell, 1992), the Florida Keys (Lapointe et al., 1994), Martinique (Littler et al., 1993), and Jamaica (Goreau et al., 1997; Lapointe et al., 1997).

In a number of cases, herbivory patterns alone (similar to nutrient levels) do not explain the distribution and abundance of benthic algae on coral reefs (Adey et al., 1977; Hay, 1981; Hatcher, 1983; Hatcher and Larkum, 1983; Carpenter, 1986). Several studies (Hatcher, 1981; Schmitt, 1997; Lirman and Biber, 2000) found no significant correlation between grazing intensity and algal biomass. A dramatic increase in algal biomass resulting from eutrophication, without any simultaneous reduction in herbivore populations, was reported (Fishelson, 1973). The importance of the very low nutrient levels involved in eutrophication (i.e., nutrient threshold hypothesis, NTH), either natural or anthropogenic, has only recently come to light (Bell, 1992; Lapointe et al., 1997; Small and Adey, 2001; Bell et al., 2007) regarding the potential for phase shifts from corals toward macroalgal dominance. These kinds of biotic phase shifts also have been attributed to overfishing of herbivore stocks (see Hughes, 1994 on Jamaican reef trends), in concert with cultural eutrophication (Goreau et al., 1997; Lapointe et al., 1997). It is now clear (Burkepile and Hay, 2006; Mora, 2008) that both herbivory and nutrient levels interact on large scales as major factors in maintaining or degrading coral-reef health.

We hasten to point out that individuals of all the functional indicator groups can and do occur under the conditions of every compartment of the RDM (see Figure 1); however, the model predicts which group most often will *dominate* (as does the very similar fig. 2a in Bellwood et al., 2004). Such apparent presence/absence anomalies, on closer inspection, are often scientifically logical but have led to different perspectives. Following large coral bleaching events and die-offs in Belize, we have observed dramatic increases in chemically defended sponges (e.g., *Chondrilla*) and Cyanobacteria (blue-green algae) under high levels of grazing by sea urchins and fishes. Other observations that appear counterintuitive include some corals growing in high-nutrient habitats, some large fleshy macroalgae growing under low nutrients, certain turf algae exposed to high herbivory, and the frequent coexistence of crustose corallines and the other functional groups. We agree with these observations and have addressed such anomalies herein.

The general applicability as well as the limitations of the RDM can be demonstrated further in relationship to a number of recent studies. For example, nutrients and herbivory are not independent, and the positive effects of nutrients on marine plant productivity and growth can actually make plants more palatable and susceptible to grazers (McGlathery, 1995; Boyer et al., 2004). Furthermore, nutrient increases are sometimes associated with coral inhibition (Koop et al., 2001) as well as coral diseases (Harvell et al., 1999, 2002; Bruno et al., 2003), and algal blooms can serve as disease vectors (Nugues et al., 2004). The sophisticated enrichment study (ENCORE) on a large and carefully controlled scale (Larkum and Koop, 1997; Encore Group, 2001) did not produce supportive results because (1) ambient nutrient levels within the lagoon at One Tree Island are well above tipping-point concentrations that may be inhibitory to some corals, while being more than sufficient to support luxuriant frondose macroalgal growth (Bell, 1992; Larkum and Koop, 1997; Bell et al., 2007) and (2) the test organisms were isolated on raised grids to measure growth rates, precluding natural encroachment, overgrowth, or other competitive interactions crucial to testing the RDM. However, all increases in nutrient levels did adversely affect coral reproduction (Koop et al., 2001). Additionally, several short-term (<4 months) studies (Thacker et al., 2001; Belliveau and Paul, 2002; Miller et al., 1999; McClanahan et al., 2002) reported lack of algal stimulation following nutrient enrichment, further documenting the low ambient nutrient concentrations sustaining ample algal growth.

In contrast, two in situ experimental studies conducted over longer time scales in healthy coral-reef settings (Smith et al., 2001; Littler et al., 2006a), in conjunction with natural successional and competitive interactions, provided the most relevant causality data demonstrating the importance of both nutrient and herbivory influences; the present review builds on these findings. The paper by Lapointe (1997) was the first to put forth a convincing case for the effectiveness of the RDM in addressing harmful algal bloom issues on coral reefs. Additionally, highly diverse living model systems of coral-reef communities (i.e., mesocosms), operated for decades (Small and Adey, 2001), clearly have demonstrated that minute increases in nitrogen and phosphorus reduce coral growth (sometimes causing substantial die-backs). Such self-contained systems require continuous removal of nutrients by algal-turf scrubbers or protein skimmers in combination with an abundance of fish and invertebrate grazers to maintain a high coral and algal diversity. The burgeoning awareness of coral-reef degradation worldwide (see Ginsburg, 1994; chapters in Birkeland, 1997; Gardner et al., 2003), particularly from coastal eutrophication (Bell, 1992; Windom, 1992; Nixon, 1995; Lapointe, 1997, 1999) and destructive overfishing (Hughes, 1994; Jackson et al., 2001), makes this management perspective relevant and opportune (see Figure 1).

Although harmful macroalgal blooms on coral reefs have long been attributed to nutrient enrichment and eutrophication (Littler, 1973; Banner, 1974; Johannes, 1975; Smith et al., 1981; Lapointe, 1997; Lapointe et al., 2005a, 2005b), some reef biologists have countered that such changes in benthic community structure routinely result primarily from natural stochastic events (Precht et al., 2005), overfishing of herbivorous fish stocks (Hughes, 1994; Pandolfi et al., 2003; Lesser, 2004), or loss of keystone grazers, such as the long-spined sea urchin *Diadema antillarum* (Jackson et al., 2001). Although generally supported, these last observations are not typical of the majority of grazer reduction experiments in extreme oligotrophic environments (see Lapointe, 1999), most of which have reported an expansion of small low-growing algal forms rather than macroalgal blooms (as predicted in Figure 1). It is encouraging that the critical role of excess nutrients on coral reefs has begun to receive attention in recent review papers (Scheffer et al., 2001; Hughes et al. 2003; Bellwood et al., 2004; Pandolfi et al., 2005; Burkepile and Hay, 2006; Mora, 2008). Some scientists (e.g., Precht et al., 2005) downplay declining resilience issues, instead emphasizing fundamental stochastic factors such as upwellings, hurricanes, and cold fronts (see caption, Figure 1). These occurrences represent unmanageable events from which coral reefs have recovered for millions of years, but not in the presence of modern human influences such as destructive overfishing and nutrient pollution (see Mora, 2008). There are strong interactions between catastrophic stochastic factors and the roles of herbivores and nutrients that strongly impact reefs. For example, coral mortality following hurricanes and coral bleaching events opens up large amounts of new two-dimensional space readily colonized by fast-growing algae. Such increases in productivity and the area available for grazing hypothetically satiate the herbivore pressure over large areas, assuming that natural herbivore populations have an upper limit in the amount of reef area that they can graze effectively (Williams et al., 2001; Mumby, 2006). This diluted grazing pressure and reduction in suitable shelter could in turn lead to further increases in algal cover and a decline in the recovery capacity (i.e., resilience) of coral communities. Thus, stochastic processes are unquestionably important factors in determining the trajectories of reef health and interact with the processes discussed herein.

To establish the baseline conditions and detect subsequent changes, a combination of environmental, survey, inventory, and bioassay data are essential to characterize and monitor the ambient nutrient and herbivory environments and antecedent nutrient history of a given management area. Valid and reliable data are the cornerstone needed to prioritize among different management strategies and motivate the local populace and politicians/lawmakers to support and implement the goals necessary for responsible management. The RDM provides a clear visual depiction that is easily understood and, therefore, can serve as a convincing illustrative aid. It is essential that assessment and monitoring methods should be both simple and rapid to use. Chlorophyll *a* concentration (determined by fluorometric or spectrophotometric methods; see Bell and Elmetri, 1995) is an especially useful ancillary indicator of water column enrichment because phytoplankton blooms can rapidly attenuate critical light energy while buffering inorganic nutrient pulses. Along with nutrient levels, chlorophyll *a* serves as a valuable tipping-point indicator, where levels in excess of 0.2–0.3 $\mu g\ L^{-1}$ indicate approaching overabundances of nutrients (Bell et al., 2007).

Water column nutrient concentrations represent the net sum of internal cycling, algal assimilation, and external inputs, relative to macroalgal growth demands (Lapointe, 1997), and therefore offer the most direct method to assess nutrient excesses on any given coral reef. Consequently, a nutrient threshold model based on nutrient concentrations (rather than on nutrient fluxes) is not only valid but is likely the best index of nutrient status. Low-nutrient tipping points, where increasing nutrients reach hypothetically critical levels that begin to reduce recoverability from phase shifts (i.e., $\sim$1.0 μM dissolved inorganic nitrogen

[DIN] = nitrogen: 0.014 ppm N or 0.040 ppm NO_3 and ~0.10 μM soluble reactive phosphorus [SRP] = phosphorus: 0.003 ppm P or 0.007 ppm PO_4), have been broadly corroborated (in developing the nutrient threshold hypothesis [NTH]; Bell, 1992; Lapointe et al., 1993; Bell et al., 2007) for sustaining macroalgal overgrowth of seagrass beds and coral reefs. The physiological/kinetic basis for such low-nutrient tipping points is the hyperbolic Monod relation (Droop, 1985; Bell et al., 2007), which is also supported by controlled, high-flux, continuous-culture laboratory experiments (Caperon et al., 1971 DeBoer et al., 1978; Lapointe and Tenore, 1981). In our experience, if modern analytical instruments can detect measurable nutrient levels, so can growth-limited macroalgae.

Additionally, a wealth of in situ coral-reef studies carried out in areas characterized by nutrient levels only moderately above the putative 0.1 μM SRP and 1.0 μM DIN tipping points (Larkum and Koop, 1997; Miller et al., 1999; Thacker et al., 2001) have reported minimal algal stimulation following experimental nutrient enrichment, further documenting the low natural nutrient concentrations required for ample algal growth and their widespread applicability. Some corals can tolerate high levels of DIN and SRP; however, nutrient tipping points not much above the present analytical limits of detection represent levels of resource availability at which resilience begins to be reduced (Scheffer et al., 2001), such that stochastic or other disturbances and stresses can trigger coral-reef ecosystem shifts toward sustained dominance by macroalgal stable states. Moreover, the macroalgal overgrowth experimentally stimulated (Smith et al., 2001; Littler et al., 2006b) in reduced-grazing/elevated-nutrient treatments demonstrates that ambient nutrient concentrations inhibitory to growth under the natural turbulence levels found on coral reefs are similar to those reported above for other tropical marine algae. It should be noted that the remote reef in the northwestern Hawaiian Islands studied by Smith et al. (2001) had nutrient levels at or above the hypothetical levels needed to sustain macroalgal growth (i.e., 1.1 μM DIN and 0.2 μM SRP). This system, with its present lack of macroalgae and dominance by unbroken thickets of three branching and one massive coral species, may be the result of overcompensation by intense grazing and, consequently, could be susceptible to a future relative dominance reversal.

Littler et al. (2006a: tbl. 1) give typical baseline herbivorous fish assay and population density data contrasting natural Belize Barrier Reef sites of low and high herbivory. Based on similar experiments conducted worldwide on coral reefs by a range of workers (Hay, 1984; Lewis and Wainwright, 1985; Paul et al., 1987; Sluka and Miller, 2001; Littler et al., 2006a), Littler and Littler (2006 posited that less than a six hour half-life (>50% mean loss per 6 h for palatable algae) during a series of in situ, midday, assay periods is indicative of a healthy level of herbivory for the particular habitat(s) tested. Herbivore abundances also should be enumerated by counting numbers of individuals (by species), from midmorning to midafternoon throughout a typical day for weather (Littler et al., 2006a, see their table 1), at fixed distances on either side of random replicates of standardized transect lines. Video transects are quick; enumeration can be done later in the laboratory, and the videos provide a permanent record of the target species (Littler et al., 1986).

FUNCTIONAL INDICATOR GROUPS

The fast growth and turnover rates of fleshy algae compared to other reef organisms suggest their value as early-warning indicators of reef degradation. Representatives of ubiquitous algal form/function groups (from Littler and Littler, 2006) are increasingly encountered as dominants on reefs, particularly those subjected to human activities (see Littler and Littler, 2006: fig. 2).

Reef-Building Corals (Cnidaria)

A predominance of diverse corals and calcareous coralline algae are universally accepted as the most desirable components of biotic reefs because of (1) their three-dimensional architecture, which provides habitats for a myriad of other reef organisms (largely responsible for much of the heterogeneity/high biodiversity), (2) their roles in producing the massive carbonate structure of reefs, and (3) their aesthetic qualities. The vertical structure and horizontal canopies of branching forms allow abundant populations of shade-dwelling crustose coralline algae to co-occur. Reef-building corals, while preyed upon by a few omnivorous fishes and specialist invertebrates (e.g., crown-of-thorns sea star), generally achieve dominance under the top-down control of intense herbivory (Lewis, 1986; Lirman, 2001) and extremely low nutrient concentrations (Bell, 1992; Lapointe et al., 1993). Massive corals are resistant to grazing at the higher levels of herbivory (Littler et al., 1989). Hard mound-shaped forms show relatively little colony mortality under high grazing pressure, even though occasionally rasped by parrotfishes. Contrastingly, some delicately branched corals such as *Porites porites* are quite palatable and readily eaten by parrotfishes (e.g., *Sparisoma viride*; Littler et al., 1989; Miller and Hay, 1998). Nutrient increases are sometimes associated with coral diseases (Harvell et al., 1999, 2002; Bruno et al., 2003). As mentioned earlier, numerous corals tolerate elevated nutrient levels (Atkinson et al., 1995; Steven and Broadbent, 1997; Bongiorni et al., 2003), but their diversity suffers. Conversely, others are physiologically inhibited by increases in nitrate (e.g., *Montastrea annularis* and *Porites porites*: Marubini and Davies, 1996), ammonium (e.g., *Pocillopora damicornis*: Stambler et al., 1991; Muller-Parker et al., 1994), and orthophosphate (e.g., *Porites compressa*: Townsley, cited in Doty, 1969; *P. damicornis* and *Stylophora pistillata*: Høegh-Guldberg et al., 1997). Nutrient inhibition of coral larval settlement also has been shown for *Acropora longicyathis* (Ward and Harrison, 1997). During the extensive ENCORE program on Heron Island, all increases in nutrient levels adversely affected coral reproduction (Koop et al., 2001).

MACROALGAE

With an increase in nutrients, the growth of harmful fleshy algae is favored over that of the slower-growing but highly desirable corals (Genin et al., 1995; Miller and Hay, 1996; Lapointe et al., 1997), and the latter become inhibited by competition for space and light, increased diseases, and physiological inhibition. On healthy oligotrophic coral reefs, even very low nutrient increases may exceed critical levels that can shift relative dominances by stimulating macroalgal production while inhibiting corals. As indicated earlier, large biomass, or standing stocks, of slow-growing perennial macroalgae (e.g., rockweeds) can develop over time under low inorganic nutrient concentrations (McCook, 1999), and *Sargassum* spp. can coexist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999). Therefore, in this particular situation, large plant biomasses do not necessarily indicate detrimentally abundant dissolved nutrients. Filamentous and frondose algae can outcompete corals (Birkeland, 1977; but see McCook et al., 2001), many of which are inhibited under elevated nutrient levels (reviewed in Marubini and Davies, 1996). Fast-growing algae are not just opportunists that depend on disturbances to release space resources from established longer-lived populations but become the superior competitors (Birkeland, 1977) when provided with sufficient nutrients. As a result, frondose macroalgae as a group are now generally recognized as harmful to the longevity of coral reefs because of the linkage between excessive blooms and coastal eutrophication (ECOHAB, 1997). Potential competitive dominance of fast-growing macroalgae is inferred from their overshadowing canopy heights, as well as from inverse correlations in abundances between algae and the other benthic producer groups (Lewis, 1986), particularly at elevated nutrient concentrations (Littler et al., 1993; Lapointe et al., 1997). Macroalgae, such as *Halimeda* spp., also gain competitive advantage by serving as carriers of coral diseases (Nugues et al., 2004). The fleshy macroalgal form-group has proven to be particularly attractive to herbivores (see Hay, 1981; Littler et al., 1983a, 1983b) and only becomes abundant where grazing is decreased or swamped by excessive algal growth (chemically defended forms, e.g., Cyanobacteria, are exceptions). Such overcompensation by herbivory may explain some of the reported cases (Crossland et al., 1984; Szmant, 1997; Smith et al., 2001) of specific corals surviving high-nutrient reef environments.

CRUSTOSE CORALLINE ALGAE

The predominant members of this indicator group, the coralline algae, tend to be slow-growing, competitively inferior taxa abundant in most reef systems (Littler, 1972). However, they span a spectrum of morphotypes from thin sheet-like crusts to thick massive pavements to upright branched and columnar coral-like heads that contribute to both cementation and bulk. This functional group is highly resilient and is able to recover or restore the coral-reef system relatively more quickly, given that some crustose coralline algae chemically attract and facilitate the survival of coral larvae (Harrington et al., 2004) whereas the other two algal functional groups inhibit larval settlement. Because crustose corallines continually slough upper surface layers, they play a key role, as do filter-feeding corals, in physically preventing the settlement and colonization of many undesirable fleshy fouling organisms on coral reefs (Littler and Littler, 1997). Crustose corallines, because of their slow growth rates, tolerate low nutrient levels and generally are conspicuous, but not dominant, under low concentrations of nutrients and high levels of herbivory (Littler et al., 1991). Accordingly, they do well under both low and elevated nutrients; that is, most are not inhibited by nutrient stress and many are maintained competitor free by surface cell layer shedding (Johnson and Mann, 1986), even at lower levels of grazing (Littler and Littler, 1997). Therefore, crustose coralline algae do not require elevated nutrients, as might be inferred from the RDM (Figure 1); instead, their rise to dominance is largely controlled indirectly by the factors influencing the abundances of the other groups, primarily corals and fleshy macroalgae. The key point is that crustose corallines predominate mainly by default (i.e., under conditions of minimal competition), where either corals are inhibited by elevated nutrients or fleshy algae are removed by intense herbivory. In independent corroboration of the herbivory portion of the RDM, a gradient of frondose- to turf- to coralline algal groups was closely correlated with escalating herbivory on coral reefs (Steneck, 1989).

LOW-GROWING AND TURF ALGAE

The turf algae are mostly dense filamentous and low-growing frondose members of all four algal phyla and tend to become dominant under minimal inhibitory top-down and stimulatory bottom-up controls. Domination by low-growing algae suggests desirably low nutrient levels but an inadequate herbivory component. Their relatively small size and rapid perennation results in moderate losses to herbivory at low grazing pressures. They have opportunistic life history characteristics, including the ability to maintain substantial nutrient uptake and growth rates under low-nutrient conditions (Rosenberg and Ramus, 1984), and also contain an abundance of nitrogen-fixing Cyanobacteria (Adey and Goertemiller, 1987; Adey, 1998) that can enrich other low-growing members of the dense turf community. Algal turfs have been shown to be favored under reduced nutrient-loading rates (Fong et al., 1987) or infrequent nutrient pulses (Fujita et al., 1988) and can form extensive horizontal mats.

DISCUSSION

This paper directly addresses the goals of an imperative research agenda (ECOHAB, 1997) by providing a management perspective and assessment strategies for the mechanisms that initiate and sustain harmful blooms of algae that degrade coral-reef ecosystems. The complex interactions of herbivory and nutrients can change gradually with no apparent effects to induce subtle declines in resiliency and recoverability of coral/coralline-dominated reef systems (Scheffer et al., 2001). As mentioned, these systems then become vulnerable to catastrophic impacts by large-scale stochastic disturbances that typically trigger or accelerate such low-resilience reef systems (Scheffer et al., 2001; Bellwood et al., 2004). Most importantly, recovery to coral domination cannot occur unless tipping points are returned to healthy levels, and even then alternative stable states may persist. For example, when catastrophic events selectively eliminate the longer-lived organisms in favor of early-successional fleshy algae (Littler and Littler, 1984), the settlement of coral planulae is prevented and the algae persist as competitively superior states (Birkeland, 1977; Lewis, 1986). For completeness, we also point out the obvious devastating effects of toxic spills, carbonate mining, land-fill, and sediment inundation, some of which also are associated with nutrient pollution and algal blooms.

Because of global-scale degradation of coral-reef ecosystems (Ginsburg, 1994; Wilkinson, 1999), it is important to obtain relevant information on tipping points for both top-down herbivory (relatively fast acting, acute) and bottom-up nutrient controls (slower acting, chronic), both of which are reemphasized. As the first approximation, we posit that on a healthy reef system, herbivore abundances and diversity should be high, and palatable test plants should show at least a 50% mean loss per six hours (i.e., <6 h half-life) during a series of midday in situ assays. Table 1 in Littler and Littler (2006 summarizes baseline assay and critical fish population data of this sort for two natural coral-reef zones of low and high herbivory.

Nutrient threshold points (where increasing water column nutrients reach critical resilience levels such that they reduce recovery from phase shifts) have been widely postulated (as $\sim$1.0 μM DIN and $\sim$0.10 μM SRP [NTH]; Bell, 1992; Lapointe et al., 1993; Bell and Elmetri, 1995) for potential macroalgal overgrowth of coral-reef communities. As mentioned earlier, a further useful tipping-point indicator is water column chlorophyll *a*, where levels in excess of 0.2–0.3 μg L^{-1} also indicate detrimental overabundances of nutrients (Bell and Elmetri, 1995).

CONCLUSIONS

Assessment protocols for determining and monitoring the status of any given coral reef are suggested: these include (a) herbivore population assessments, (b) herbivory assays, (c) water column nutrient levels, and (d) standing stocks of functional indicator groups. These measurements can reveal quantitative tipping-point levels beyond which resilience to and recovery from undesirable phase shifts begin to become critically reduced. Tipping-point approximations are reviewed and posited both for inorganic nutrients and for herbivory.

This review specifically addresses the relatively acute top-down effects of herbivory and the more chronic bottom-up effects of nutrient enrichment on critical indicator groups of benthic primary producers: reef-building corals, crustose coralline algae, dense turf algae, frondose macroalgae, and herbivore associates.

A predominance of massive corals and calcareous coralline algae relative to frondose macroalgae and low-growing algae indicates a healthy spatially heterogeneous condition reflecting low nutrients and high herbivory. With a few exceptions, an abundance of frondose macroalgae illustrates the least desirable condition of elevated nutrient levels and reduced herbivory, possibly reflecting eutrophication in concert with destructive herbivore fishing practices. A high coverage of coralline algae suggests healthy high herbivory levels but also suggests problems with elevated nutrients that may be inhibitory to some corals. Domination by dense low-growing and turf algae indicates desirably low nutrient levels but also suggests an inadequate herbivory component.

From a management perspective, levels of herbivory and herbivore populations and of nutrients rank among the most useful quantitative indicators of coral-reef resilience and recoverability, whereas the degree of health, degradation, and mortality are inferred by the relative abundances of functional indicator groups.

The bioassay and indictor group monitoring approaches provide powerful perspectives and essential measurement criteria to enable resource managers to protect coral reefs and similar coastal systems from eutrophication, destructive overfishing, and initiation of harmful algal blooms. Human population growth has always been accompanied by changes in land and sea use and by increased exploitation of natural resources, attitudes that continue to cause broad alterations in the structure of coral-reef communities. Unless curbed, anthropogenically induced phase shifts will expand geographically at an accelerated pace. However, solutions are available, which include the use of Marine Protected Areas, banning of destructive fishing practices (e.g., trapping, poisoning, blasting, netting), and regulations protecting keystone herbivorous fish species (e.g., parrotfish, surgeonfish) from market exploitation. Fisheries controls must be backed up by strategies to regulate the effects of pollution along with an international commitment to reduce the emission of greenhouse gases and, finally, the implementation of long-term strategies to reduce or stabilize the ultimate cause of all these stressors, the world's human population growth.

ACKNOWLEDGMENTS

Support for this work came from a Scholarly Studies Grant (Smithsonian Institution, Office of Fellowships and Grants), the Caribbean Coral Reef Ecosystems (CCRE) Program (administered by Klaus Ruetzler, the Smithsonian Marine Station at Ft. Pierce (Valerie Paul, Head Scientist), and the National Museum of Natural History. This is CCRE contribution number 847, supported in part by the Hunterdon Oceanographic Research Fund, and SMSFP contribution number 763.

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Impacts of Human Disturbance on Soil Erosion Potential and Habitat Stability of Mangrove-Dominated Islands in the Pelican Cays and Twin Cays Ranges, Belize

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ABSTRACT. The Mesoamerican Barrier Reef System (MBRS) is the longest unbroken reef in the Western Hemisphere and contains hundreds of mangrove-dominated islands. These islands provide critical habitat supporting marine biodiversity and create a self-sustaining system that counterbalances sea-level rise. Undisturbed mangrove islands build vertically through accumulation of organic matter (peat), which forms a strong, erosion-resistant matrix. Clear-cutting and dredging activities for development of tourist resorts, fishing camps, and "improved land" for resale, however, threaten mangrove-dominated islands and adjacent seagrass and coral reef assemblages. Effects of mangrove disturbance were examined on four islands in the designated marine preserves of Twin Cays and the Pelican Cays, Belize. Mangroves were clear cut (1.0–6.2 ha), and marine sediment was dredged from nearby reef flats and seagrass beds to raise land elevations to support beach vegetation and buildings. Removal of mangroves and especially addition of dredged fill significantly altered soil characteristics and decreased shear strength and aggregate stability of soil surfaces. Deep cores collected at both island ranges also revealed underlying deposits of peat (1.5–10.8 m thick), which influence local land subsidence. Although infilling with dredged material temporarily raised elevations, the inexorable subsidence of peat through natural processes of compaction and decomposition and sea-level rise will ultimately submerge such areas. Our findings thus show that soil erosion potential is increased and that long-term stability of islands may be compromised by mangrove clearing and dredging activities. Degradation of key biophysical components and critical habitat will ultimately impact ecotourism activities that depend on a healthy, natural environment.

INTRODUCTION

Persistence of oceanic mangrove islands is dependent upon maintenance of soil elevations relative to sea level. Mangrove-dominated islands can counterbalance rising seas by accumulating organic matter (mangrove-derived peat), which gradually builds land vertically (McKee et al., 2007a). In addition, biodiversity of intertidal and subtidal ecosystems in the Caribbean Region is dependent upon the presence of mangroves because a number of marine species are exclusively associated with the mangrove habitat (Ellison and Farnsworth, 1992; Goodbody, 2000; Taylor, 2000; Rocha et al., 2005). Mangroves also serve as nurseries for many reef fish and other marine organisms (Mumby et al., 2004). Consequently,

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changes in mangrove extent may have a cascading effect on habitat stability and capacity to keep pace with sea-level rise, as well as on marine biodiversity, in regions with mangrove-dominated islands and adjacent seagrass and coral reef assemblages.

The Mesoamerican Barrier Reef System (MBRS) off the coast of Belize, Central America, contains hundreds of mangrove islands in association with extensive seagrass beds and coral reefs (www.mbrs.org.bz; accessed 11 June 2008). Unfortunately, clear-cutting of insular mangroves has greatly accelerated in Belize and other locations in recent years for development of tourist resorts, fishing camps, and "improved land" for resale (K. L. McKee, personal observation). Even if such areas are ultimately abandoned and allowed to recover, recolonization by mangroves may be extremely slow, if it occurs at all. For example, a site on Twin Cays, an island range that was clear cut in 1992, is slowly recovering, but regenerating mangroves are still sparse and have taken 15 years to reach sapling size (~1–2 m tall) (McKee et al., 2007b). In addition to removal of mangroves, bottom sediments are dredged from adjacent seagrass beds and reef flats and pumped onto cleared mangrove areas to raise elevations sufficiently to support beach vegetation and buildings. This type of disturbance thus destroys multiple ecosystems, which require many years for recovery. In the interim, there may be additional consequences from the loss of habitat stability and increased erosion.

The specific objectives of this study were to assess the potential for changes in soil erosion and habitat stability on mangrove islands subjected to clear-cutting and dredging activities. The work focused on the designated marine preserves of Twin Cays and the Pelican Cays ranges, which have been highlighted as critical habitat for marine biodiversity in the region (Macintyre and Rützler, 2000; Macintyre et al., 2004a).

STUDY SITE

The MBRS is the longest unbroken reef in the Western Hemisphere and extends 220 km from the southern part of the Yucatan Peninsula to the Bay Islands of Honduras. Two main areas where clear-cutting and filling of mangrove islands has occurred were studied: Twin Cays and the Pelican Cays. Twin Cays, which consists of two larger and two smaller islands, is located in the central part of the barrier reef system and about 2 km west of the reef crest (Figure 1). The Pelican Cays archipelago is located 21 km south of Twin Cays and contains multiple mangrove-dominated islands (Figure 1). Twin Cays and the Pelican Cays ranges have been a major focus of mangrove research by the Smithsonian Institution (Macintyre and Rützler, 2000; Macintyre et al., 2004a). These mangrove islands are far from the mainland, and peat cores contain no terrigenous sediment (Cameron and Palmer, 1995; McKee and Faulkner, 2000; Purdy and Gischler, 2003; Macintyre et al., 2004b). The only source of freshwater is rainfall, and the entire landform is intertidal (mean tide range [neap] = 0.2 m). The vegetation on undisturbed islands is dominated by *Rhizophora mangle* L. (red mangrove), which is the most common mangrove species in the Caribbean Region. The area has been impacted by numerous hurricanes and tropical storms.

Twin Cays occurs in the Central Province of the barrier reef (16°50′N, 88°06′W) (see Figure 1). Mangrove communities were established at Twin Cays about 8,000 years ago on the Pleistocene surface of the Belize Barrier Reef Platform when it was flooded during the Holocene Transgression (Macintyre et al., 2004b; Purdy and Gischler, 2003). Deep deposits of peat (as much as 11 m thick) have developed as Twin Cays accreted vertically with rising sea level (Macintyre et al., 2004b; McKee et al., 2007a). Cores collected through these deposits indicate that the primary means of vertical land movement is accumulation of mangrove organic matter (mostly root matter) (McKee et al., 2007a). At Twin Cays, five areas ranging in size from 0.1 to 6.2 ha have been cleared and elevations raised by infilling with dredged material, beginning in the early 1990s and continuing until the present; small fishing camps consisting of one or more buildings have been established. Our study targeted the largest site on East Island that was clear cut and filled in 1995.

The Pelican Cays occur in the south central lagoon of the reef system (16°39.8′N, 88°11.5′W). Here, mangroves have developed as part of a complex network of coral ridges that surround deep circular ponds (Macintyre et al., 2000). There are several mangrove cays, including Northeast Cay, Fisherman's Cay, Manatee Cay, Cat Cay, Ridge Cay, Avicennia Cay, Co Cat Cay, the Bird Cays, and several unnamed smaller cays. Mangroves established at the Pelican Cays only within the past 1,000 years (Macintyre et al., 2000; McKee et al., 2007a) but have accumulated deposits of peat as much as 1.5 m thick (McKee and Faulkner, 2000). Disturbance at the Pelican Cays began in the mid-1990s with mangrove clearing on Northeast Cay. Aerial surveys conducted in April 2006 showed disturbed areas on Northeast Cay, Co Cat Cay, and Ridge Cay, and a follow-up survey in April 2007 showed new areas of mangrove clearing and dredging at Manatee Cay and Fisherman's Cay (I. C. Feller, personal communication).