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Front Cover: The reef crest indicator species, *Acropora palmata*, on Gaulin's Reef, San Salvador Island. Gaulin's Reef is a classic bank-barrier reef that has shown remarkable resilience following two significant disturbances: El Niño-induced warming of the sea surface in 1998 and Hurricane Floyd in September, 1999 (see Peckol et al., this volume). Photo by Janet Lauroesch.

Back Cover: The oolite shoals of Joulter's Cay, north of Andros Island, Bahamas, site of the pre-meeting field trip. Photo by Ben Greenstein.

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RESILIENCE AND RECOVERY OF CORAL REEFS FROM LARGE-SCALE DISTURBANCES: CONTRASTING PATTERNS FOR SAN SALVADOR ISLAND, BAHAMAS AND BELIZE

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ABSTRACT

Coral cover and diversity are declining while macroalgal abundance is increasing in most Caribbean coral reef systems. Although a complex interaction of natural and anthropogenic disturbances is likely causal, the effects of a specific disturbance may vary dramatically for different reef systems. The coral reefs off the coasts of San Salvador Island, Bahamas and Belize, considered to be in relatively good condition, recently experienced near-direct hits by Hurricanes Floyd (1999) and Mitch (1998), respectively. In addition, NOAA scientists indicated that during 1998, tropical sea surface temperatures (SSTs) reached their highest levels above the normal annual maximum for this past century. With repeated monitoring of reefs off south-central Belize and San Salvador Island, Bahamas, we have been able to document the severity of effects from these large-scale natural disturbances. Our patch reef and bank-barrier reef sites off San Salvador showed minimal damage from Hurricane Floyd, while our study sites on the forereef region off Belize were more heavily impacted by the passage of Hurricane Mitch. Although *Agaricia* spp. was the coral most strongly affected by the 1998 elevated SSTs on patch reefs around San Salvador Island (McGrath and Smith, 1999), we found scant evidence of bleaching of any coral colonies by January and June 2000. However, three-fold increases in partial colony mortality for this species are likely related to the bleaching stress. On the coral-reef ridges off south-central Belize, *Agaricia tenuifolia* experienced >90% mortality associated with the 1998 warming event. The mound and boulder corals were also strongly affected by elevated SSTs; > 50% of the colonies of *Montastrea annularis* complex and *Diploria* spp. were severely bleached. A major reef-builder, *M. annularis* still showed widespread bleaching 9 months after the warming event, with ~55% of the corals showing >50% partial colony mortality. Mean partial colony mortality was 2 to 5 times higher for reef sites monitored off south-central Belize than San Salvador. For example, a major reef builder, *Acropora palmata*, showed a significant decline in partial colony mortality off San Salvador, while 75% of the colonies off Belize showed dramatic mortality. *M. annularis* experienced similar, elevated trends of colony degradation on the Belize reef; the condition of the San Salvador population remained relatively stable over the two-year period. A combination of large-scale disturbances, including two coral bleaching events (1995 and 1998) and the effects of Hurricane Mitch have thus taken a dramatic toll on the Belize reef complex. The reefs off San Salvador Island showed notable resistance and resilience to these large-scale disturbances. We hypothesize that escalating anthropogenic impacts on the Belize barrier reef have exacerbated the effects of Hurricane Mitch and elevated SSTs; thus, full recovery from these back-to-back natural disturbances may be difficult and lengthy for this reef system.

INTRODUCTION

Over the past two decades, there has been widespread deterioration of coral reefs worldwide (Buddemeier, 1992; Wilkinson, 1992). Reduction in coral cover and diversity with concomitant increases in macroalgal abundances have been related to the well documented mass mortality of the sea urchin herbivore, *Diadema antillarum* (Liddell and Ohlhorst, 1986; Lessios, 1988; Hughes et al., 1999), to the unprecedented increase in coral diseases (Bruckner and Bruckner, 1997; Santavy and Peters, 1997), and widespread elevated sea surface temperatures resulting in coral bleaching (Glynn, 1993; Goreau and Hayes, 1994; Brown, 1997; Strong et al., 1997; Wilkinson et al., 1999). While the greatest degradation of Caribbean reefs is documented for areas associated with large human populations (Hughes, 1994), fewer studies have evaluated the condition of coral reefs in areas experiencing less human disturbance, as is the case off San Salvador Island, Bahamas, and the Belize barrier reef system (Peckol et al., 1999).

Although the reef systems of San Salvador, Bahamas and Belize have not been strongly affected by human disturbances, large-scale natural disturbances such as episodic warming events and hurricanes can take a heavy toll on coral reefs. The 1998 global sea-surface thermal anomaly related to the 1997-98 El Niño/Southern Oscillation (ENSO) event affected the corals off San Salvador Island, Bahamas (McGrath and Smith, 1999), and the island experienced a near-direct hit by Hurricane Floyd at very close to the time of its highest intensity, top end of category 4 on the Saffir/Simpson Hurricane Scale, on September 13-14, 1999 (Pasch et al., 1999).

Until recently, the Belize barrier reef system had escaped the impact of coral bleaching events reported in many other areas of the Caribbean (Macintyre and Aronson, 1997; McField, 1999); however, several major disturbances, including two major warming events that occurred during 1995/1996 (Burke et al., 1996; McField, 1999) and 1998/1999 (Mumby, 1999; Aronson et al., 2000), and a near-direct hit by Hurricane Mitch (Fall 1998) have had important effects on this reef system.

The 1998 bleaching event began in September following a month of calm weather and increasing water temperatures. The eye of Hurricane Mitch, a category 5 storm, passed ~200 km SE of Glovers Reef in late October 1998 (Mumby, 1999).

These events provided us with the unique opportunity to examine the impacts of these large-scale natural disturbances on the coral reefs off San Salvador, Bahamas and Belize. We have been investigating these two reef systems as part of a larger effort, the Atlantic and Gulf Rapid Reef Assessment (AGRRA) Program (Ginsburg and Kramer, et al., 1999), which seeks to establish a regional baseline of coral reef condition in the Western Atlantic and Gulf of Mexico. In the present study, we present the varying responses of coral populations in both areas to the similar, large-scale disturbances.

STUDY SITES AND METHODS

Study Sites

San Salvador Island is located about 600 km ESE of Miami (24°N, 74°30'W) on an isolated carbonate platform, well east of the Great Bahamas Bank (Fig. 1). The island is bordered by a narrow shelf with an abrupt shelf-edge break leading to a very steep slope. The eastern and southeastern coasts of the island typically are windward to the prevailing trade winds. A well-developed *Acropora palmata*-dominated bank-barrier reef lies off the north coast of the island, and smaller bank-barrier reefs occur along the southeast and southern coasts. Hundreds of small patch reefs dot the island's eastern shelf, and on the leeward western shelf larger patch reefs occur in the broad embayments of the coast.

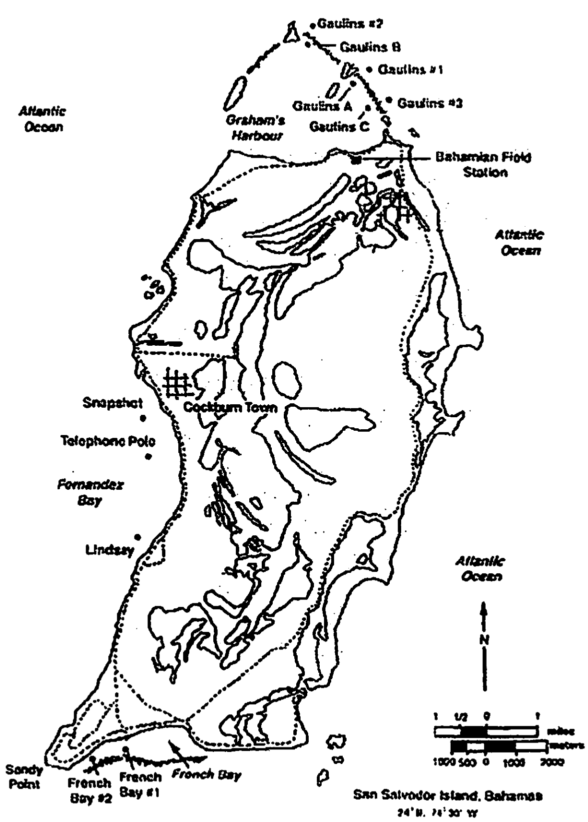

Figure 1. Index map of San Salvador Island, Bahamas, showing location of study areas.

Our study off San Salvador Island, Bahamas focused on 11 sites (Fig. 1), including 6 sites on the bank-barrier reef (Gaulin's Reef) off the north coast, three sites in the leeward Fernandez Bay and two sites in French Bay off the southern coast. The three forereef areas (depth 1-4 m) of Gaulin's Reef have a shallow (<3 m) spur formation, that extends out from the reef crest to a low relief carbonate pavement dominated by sea fans and *Millepora* spp. *Acropora palmata* is the dominant coral of the reef crest region. The backreef region (2-8 m depth) at Gaulin's Reef is characterized by large colonies (height 1-4 m) of *Montastraea annularis* complex. *Millepora* spp. and *A. palmata* are also important coral components of this site.

The leeward patch reefs (Snapshot, Telephone Pole, and Lindsay reefs) are relatively close to shore in water depths of 3-7 m. Snapshot Reef (~200 m offshore) consists of an aggregation of individual coral colonies dominated by *M. annularis* complex; Telephone Pole Reef (~ 250 m offshore) covers a larger area than Snapshot Reef and is dominated by large *M. annularis* complex colonies interspersed with colonies of *Porites porites* growing on layers of dead *A. cervicornis*. Lindsay Reef extends out from a sandy beach, and because it is closest to shore, this reef has a relatively high sediment load compared to the other two patch reefs.

The two windward patch reefs are located on the southern end of the island in French Bay. These sites are behind a well-developed reef crest area in approximately 3-5 m water depth. This area is dominated by dead *A. palmata* with large heads of the encrusting coral *Agaricia tenuifolia*. The 11 sites off San Salvador Island were sampled prior to (June 1998) and after (January and June 2000) the occurrence of the warming episode (early autumn 1998) and passage of Hurricane Floyd (September 1999).

The Belize barrier reef complex is the largest continuous reef system in the western North Atlantic, extending a distance of 250 km south from the northern end of Ambergris Caye. A major NNE-trending fault system is clearly reflected in the alignment of the coastline, barrier reef, and three oceanic atolls (Rützler and Macintyre, 1982; Macintyre and Aronson, 1997). At its northern-most end, the reef is fringing, but as it extends southward, the reef becomes a nearly continuous barrier with a well-developed forereef, reef crest, and an extensive backreef (lagoonal) area. In the shallower portions of the forereef zone, interdigitating coral buttresses and sandy troughs form a sometimes massive spur and groove system. The reef crest is a high energy zone consisting of a shallow rampart built of coral rubble and dominated by the coral species *Acropora palmata* (James and Ginsburg, 1978). The backreef area has a large number of cayes (islands), many with associated patch reefs. The south-central portion of the backreef region also contains a complex network of coral-reef ridges supporting spectacular coral growth (Macintyre and Aronson, 1997; Macintyre et al., 2000).

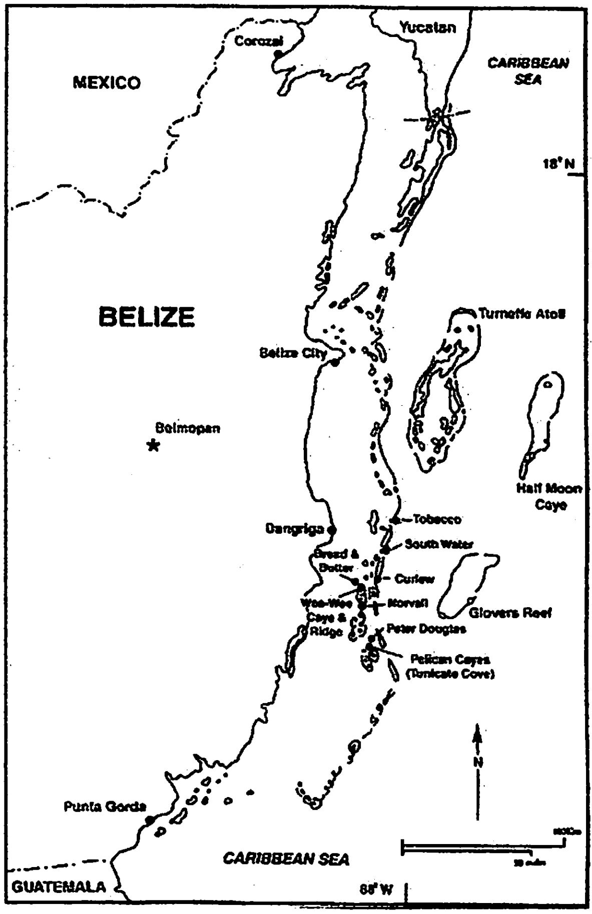

Figure 2. Index map of Belize showing location of study areas.

This study focused on 9 sites on the south-central portion of the Belize barrier reef (Fig. 2). We completed surveys on 3 backreef patch reefs associated with cayes, selecting reefs on the windward sides of Wee-Wee, Bread & Butter, and Norvall Cayes. The dominant coral species is *Montastraea annularis* complex, with all reefs at ~2-5 m depth. We censused 3 forereef sites; our most northerly site, Tobacco Reef (depth ~12-13 m), has a low-relief spur and groove formation. This site had large, healthy *M. annularis* colonies; *Agaricia tenuifolia* was growing on top of substrates consisting largely of dead *Millepora complanata*. Also in this area is a large coral-rubble ridge that runs southward from Tobacco Caye to near South Water Caye and northward for a considerable distance. The forereef site off South Water

Caye (up to 14 m depth) has high-relief (3-5 m) spur and groove development with much *Siderastrea siderea* and some large *Montastraea* colonies. *M. complanata* and *Agaricia* spp. were abundant on the spurs. Curlew Bank (reef), located just south of Carrie Bow Caye, is characterized by low-relief spur and groove formation; the majority of corals observed were *M. annularis* complex, *S. siderea, Diploria* spp., and *Acropora palmata*..

We also conducted surveys on unique features located in the backreef (lagoonal) region of south-central Belize: rhombohedral-shaped shoals and reefs. These steep-sided reef ridges likely were formed by the growth and accumulation of corals on the ridges of polygonal karst topography formed by the dissolution of underlying Pleistocene limestone (Macintyre et al., 2000). These areas show greatest coral development at depths of 3-8 m; at greater depth, living coral becomes sparse. Prior to the warming event of autumn 1998, the dominant coral on these reef ridges was *Agaricia tenuifolia,* which originally had colonized and overgrown *Acropora cervicornis* rubble (Aronson and Precht 1997). The reef ridges we studied were off Wee-Wee Caye, Peter Douglas Caye, and an area locally known as "Tunicate Cove" within the Pelican Cayes. These sites were sampled directly after the warming event and passage and Hurricane Mitch (January 1999) and re-censused five months later (June 1999).

Methods

We used the AGRRA protocol (Steneck et al., 1997) with subsequent modifications to assess the coral populations. At each site, 12-18 ten-meter long transect lines spaced at least 5 m apart were haphazardly arranged parallel to the long axis of the reef. Along each transect, SCUBA divers determined the following for all coral colonies larger than 10 cm: genus and species, colony diameter and height (measured to nearest cm), percent of the colony that is dead (recently or long dead), and evidence and proportion of disease and bleaching in the living colony. Corals were considered recently dead if the non-living parts of the coral were white and intact or corroded with a fine layer of sediment; a coral was assessed as long dead if the corallites were covered by algae or invertebrates (Steneck et al., 1997).

RESULTS

Hurricane Effects

The eye of Hurricane Floyd passed within 20-30 nautical miles NE and N of San Salvador Island, Bahamas September 1999 with winds reaching 131 mph and a storm surge reaching 6 m above normal (Pasch et al., 1999). Because this storm had the greatest impact on the leeward side of the island, which experienced substantial coastal erosion and damage to buildings and infrastructure, we focused our January 2000 assessment on sites in Fernandez Bay and Gaulin's Reef (Fig. 1). We found negligible impact from Hurricane Floyd; we observed a few colonies of *Montastraea annularis* complex toppled at Snapshot Reef but very little breakage of the branching corals. Local dive shop operators reported that the only hurricane impact they had observed was a scouring and removal of macroalgae from the reef. By January 2000 when we censused the reef, macroalgae were again abundant on the patch reefs, reaching 62% and 41% cover at Telephone Pole and Snapshot Reefs, respectively. During our June 1998 monitoring, macroalgal cover averaged ~50% on these patch reefs (Peckol et al., in press).

On the Belize Barrier Reef the greatest impact of Hurricane Mitch (September 1998) was felt on the forereef and outer reef regions (Fig. 2, also see Mumby 1999). We assessed reef condition along the forereef in January

species	Bahamas June 1998	 June 2000	Belize January 1999	 June 1999
Agaricia spp.	9% (117)	28% (145)	62% (118)	67% (424)
Montastraea annularis	40 (217)	46 (418)	31 (416)	54 (473)
Acropora palmata	61 (143)	44 (193)	57 (7)	75 (36)

Table 1. Percent of corals showing greater than 50% partial colony mortality, San Salvador Island, Bahamas and Belize. Number of coral colonies sampled shown in parentheses after each percentage.

1999 and found that the shallow forereef zone exhibited a fair amount of damage from this hurricane, with much coral rubble and relatively little living *Acropora palmata.* We observed numerous examples of large boulder/mound corals transported from the forereef region across the reef crest. At our forereef sites, we documented that 3% of the *Montastraea* colonies were toppled (87 colonies censused), 33% of branching species, *Millepora alcicornis* and *Porites porites*, were broken (20 colonies censused), and 10% of the *M. complanata* colonies were broken (19 colonies censused). We also observed a great deal of scouring and removal of gorgonian corals and macroalgae from the forereef sites.

Effects of Elevated SST

Our June 1998 survey off San Salvador Island, Bahamas occurred prior to the 1998 warming episode associated with a major ENSO event; at that time we measured negligible occurrence (2% of >1000 coral colonies censused) of coral bleaching (Peckol et al., in press). However, McGrath and Smith (1999) reported that *Agaricia* spp. was the species most affected by both the 1995 and 1998 thermal anomalies. During our June 2000 census, we found negligible signs of bleaching (<1% of all colonies censused), and no evidence of bleaching for *Agaricia* colonies. This species did show a three-fold increase in partial colony mortality during the two-year interval (Table 1). It is likely that this high partial mortality is directly related to stress from bleaching. Although the *Agaricia* spp. category includes two species, their relative proportion is similar (dominated by *A. tenuifolia*, which represents 95% and 70% of the genus encountered in the Bahamas and Belize, respectively) allowing for interregional comparison. The response of each taxon was not similar within each region, and is discussed below.

On the Belize barrier reef, the coral species most strongly affected by the warming anomaly were *Agaricia tenuifolia* (Aronson et al., 2000) and *Montastraea annularis* complex. At our reef ridge sites, 90% of the censused colonies of the dominant coral, *A. tenuifolia*, had already died by January 1999

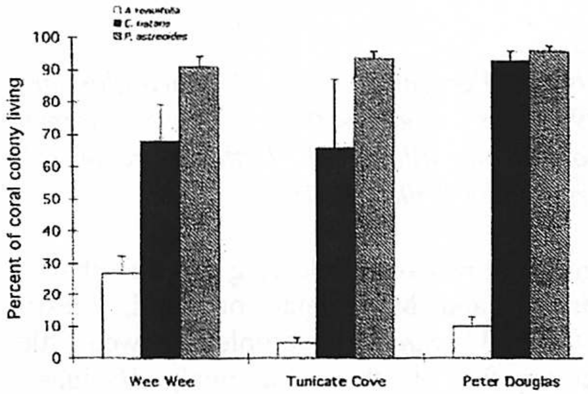

Figure 3. Mean (±SE) percent of living coral colony for Agaricia tenuifolia, Colpophyllia natans, and Porites astreoides at the coral-reef ridges of south-central Belize, June 1999.

following the bleaching stress of autumn 1998. By June 1999, this coral substratum was largely covered by encrusting sponges (*Chondrilla* cf. *nucula* Schmidt; K. Rützler, pers. comm.) and macroalgae. In contrast, relatively small, low-relief coral colonies like *Colpophyllia natans* and *Porities astreoides*, showed low partial mortality at these reef ridges, with percent colony living usually exceeding 70% (Fig. 3). A congeneric of *A. tenuifolia, A. agaricites,*, showed lower percentage colony bleaching, and forereef populations of *A. tenuifolia* showed markedly lower percentages of colony bleaching (~10% of censused colonies) and mortality (mean partial colony mortality=15%) associated with the warming event. However, considered together, nearly 70% of the censused *Agaricia* spp. had partial colony mortalities exceeding 50% by the June 1999 census (Table 1).

During our January 1999 census, we found that 50% of the *Montastraea* colonies showed evidence of bleaching; the other major mound corals, *Diploria* spp. and *Siderastrea siderea*, were also severely bleached (Table 2). Although these latter two species showed significant recovery following this disturbance (January and May data compared, *t*-tests, $P<0.05$), *M. annularis* complex showed little recovery from the thermal anomaly. By June 1999, 44% of the colonies of this major reef builder still showed bleaching effects. A further consequence of the thermal stress was a 2-3 fold increase from January to May 1999 in the incidence of coral diseases at patch reef and forereef sites off Belize (Table 3).

	January	-	June
Montastraea annularis	50%		44%
Siderastrea siderea	35		15
Diploria spp.	32		15
Porites porites	15		26

Table 2. Percent of corals bleached (January 1999) associated with the 1998 thermal anomaly and still bleached after a "recovery" period (June 1000), Belize.

Reef type	n	Percent diseased
Patch reefs		
January	704	1%
May	766	2%
Forereefs		
January	312	1%
May	823	3%

Table 3. Percent of coral colonies with disease during January and May, 1999, at patch reefs and forereef areas, Belize.

Coral Condition

As a measure of degradation or recovery of the reefs off San Salvador Island, Bahamas, we documented coral colony mortality at each reef type during June 1998 and June 2000 (Fig. 4). We found no change (windward patch reefs) or slight declines (all other sites) in partial colony mortality over the two-year interval. Most notably, while the leeward patch reefs, including Lindsay, Telephone Pole and Snapshot Reefs, experienced the greatest impacts from the thermal anomaly (McGrath and Smith 1999) and Hurricane Floyd, these areas showed overall stability ($t< 1.0$) in mean partial colony mortality (for June 1998=32%; for June 2000=27%). The major reef builders,

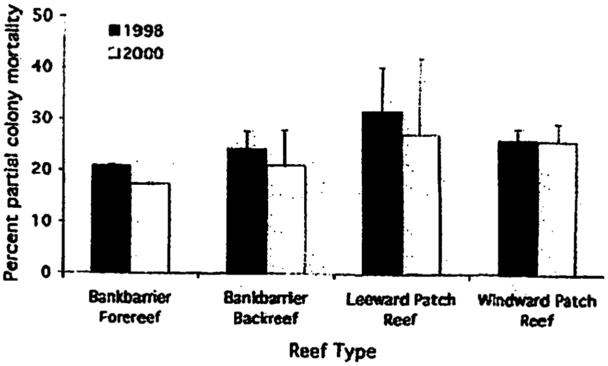

Figure 4. Mean (±SE) percent partial coral colony mortality (all species combined) for the four reef types off San Salvador Island, Bahamas, June 1998 and June 2000.

Montastraea annularis complex and *Acropora palmata*, displayed contrasting patterns of partial mortality over this period (Table 1). *A. palmata* showed a reduction while *M. annularis* experienced a slight increase in the percent of corals with greater than 50% partial colony mortality. Overall, mean percent of coral colonies living ranged from ~70% to >80% for all reef types, indicative of a relatively healthy reef system (Fig. 4).

The large-scale disturbances had a greater impact on coral mortality on the Belize barrier beef. Partial colony mortality at the three reef types ranged from 18% (forereefs) to 60% (reef ridge sites) during our January 1999 census, shortly after the thermal anomaly and passage of Hurricane Mitch (Fig. 5).

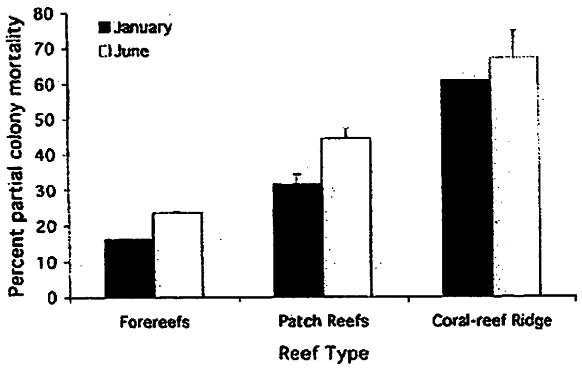

Figure 5. Mean (±SE) percent partial coral colony mortality (all species combined) for the three reef types off south-central Belize, January and June 1999.

Coral mortality continued to rise in our June 1999 assessment for the forereef and patch reef sites. *Montastraea annularis* complex and *Acropora palmata* experienced large increases in the number of coral colonies with >50% partial mortality (Table 1). The impact of such high mortality was particularly noticeable for patch reefs, dominated by *M. annularis*. Here, we documented a significant (t=3.23, P=0.01) increase in partial colony mortality between January and May 1999 (Fig. 5). Because the dominant coral species on the reef ridges, *Agaricia tenuifolia*, experienced mass mortality with the January census, we documented little change at these sites during May (Figs. 3, 5).

DISCUSSION

This study evaluated the responses of coral populations to similar large-scale natural disturbances, hurricanes and a widespread ENSO-driven thermal anomaly, on reefs off San Salvador Island, Bahamas and south-central Belize. The history of perturbations and responses of each reef system is summarized in Table 4. Overall, neither reef system showed much long-term damage from near-direct hits of hurricanes: Hurricane Floyd off San Salvador Island and Hurricane Mitch off Belize. Although corals on the forereef and outer reefs of Belize showed substantial damage associated with the passage of this major storm, by June 1999 we measured negligible lingering effects. Similarly, Mumby (1999) reported limited impact of this hurricane on coral recruit densities on the forereef of Glovers Reef. Our findings would seem to confirm those of Smith and Buddemeier (1992) regarding the resilience and rapid recovery of coral reefs to large-scale hurricane disturbances.

In contrast, the thermal anomaly of 1998 had dramatically different effects on these reef systems. Although *Agaricia* spp. was most strongly affected by the warming event in both reef areas (McGrath and Smith, 1999; this study), this coral group experienced nearly 100% mortality on the coral-reef ridges of south-central Belize, a phenomenon unprecedented in recent geologic history (Aronson et al., 2000). In the aftermath of this disturbance, more than twice as many colonies of *Agaricia* spp. showed partial mortality exceeding 50% off Belize compared with those measured off San Salvador Island, Bahamas. Further, the dead *A. tenuifolia* colonies at the reef ridge sites are now

Reef System	Disturbance	Response (2000)
Belize	1995 ENSO-related thermal anomaly. 1998 ENSO-related thermal anomaly. Hurricane Mitch (1998). Increasing anthropogenic stress.	Nearly 100% mortality of *Agaricia spp.* (reef ridges, south-central Belize. Long-term bleaching of *M. annularis* complex, consequent increased incidence of disease. Overall increase in partial colony mortality
San Salvador, Bahamas	1998 ENSO-related thermal anomaly. Hurricane Floyd (1999).	Increase in partial mortality following bleaching of *Agaricia spp.* Improvement or stability in live coverage of major reef builders.

Table 4. Summary of disturbances to reef systems of Belize and San Salvador, Bahamas.

covered in sponges and macroalgae, making recruitment of corals onto this substrate difficult.

In the south-central portion of the Belize barrier reef, the mound and boulder corals, dominant reef builders, were also strongly affected by the warming event. In particular, we found that nearly 50% of the censused colonies of *Montastraea annularis* complex were still bleached 9 months after the thermal anomaly. This species also showed high colony mortality, particularly at patch reef sites. In contrast, following a 1995 warming event along the Belize barrier reef, McField (1999) found that most coral colonies regained their coloration, and only ~10% of all corals experienced partial mortality as a direct result of the bleaching stress. We think it likely that the 1995 thermal anomaly, in which 75% of *M. annularis* colonies were bleached (McField, 1999), exacerbated the impact of the 1998 warming event and contributed to slower coral recovery from bleaching. The consequent increased incidence of disease and colony mortality of this dominant reef builder on the Belize barrier reef further reduces the potential for recovery.

Overall, the coral colonies off San Salvador Island, Bahamas had high (~75%) percent live cover following the large-scale disturbances. In fact, two major reef builders, *Acropora palmata* and *Montastraea annularis* complex, showed marked improvement or remained relatively stable during the two-year period (June 1998 to June 2000), respectively. Similarly, over a period of 8 years (1984-1992), Curran et al. (1993) did not measure significant change in the percent live coral on Snapshot Reef, one of the patch reefs evaluated in the present study, concluding that this reef was in steady state and relatively good condition. Meyer et al. (1991) reported that the population densities of two species of the crinoid *Davidaster* (formerly *Nemaster*) that resided in the large *Montastraea annularis* complex heads were increasing, also suggestive of an essentially healthy reef. The San Salvador Island reef system seems characterized by notable resilience and rapid recovery from natural disturbances, perhaps due to relatively low impact from human activities, such as fishing and coastal development.

In contrast, the Belize barrier reef has experienced escalating anthropogenic impacts over the past two decades and has undergone noticeable decline (Carter et al., 1994). Tourism in Belize has been expanding rapidly, from less than 100,000 visitors in 1985 to over 250,000 by 1990. Ambergris Caye, on the northern portion of the reef (Fig. 2), had borne the brunt of the effects of coastal tourism, including degradation of the reef, dwindling fish stocks, and surface runoff.

Our observation of the differing responses of these systems suggests multiple disturbances may be required before some "threshold" is reached and degradation occurs. Results from San Salvador indicate that reefs in environments with distinct wave energy regimes essentially survived a combination of two distinct disturbances: a 1998 ENSO event followed by Hurricane Floyd. However, in Belize, the 1998 ENSO event and Hurricane Mitch were augmented by an earlier (1995) ENSO event and background conditions of a variety of anthropogenic disturbances (Table 4). The response has been an overall degradation of reefs in north and south-central portions of the reef tract, and near total loss of *Agaricia* spp. Against the background stress of higher sea surface temperatures induced by global warming (Wilkinson, 2000) our results suggest that fewer short-term disturbances will be required to push reef systems past a "threshold" from which they cannot readily recover.

In 1987, the government of Belize established the Hol Chan Marine Reserve off Ambergris Caye; this reserve was zoned with a multi-use management scheme that has achieved some success. Notably, we documented significantly lower partial mortality of coral colonies, greater robustness of reef fish populations, and overall greater coral health on the patch reefs within the Hol Chan Marine Reserve compared with similar reefs of south-central Belize (Peckol et al., in press). We believe that such improvements in the formerly degraded reef (Carter et al., 1994) are related to the establishment of the Reserve. Our data on coral populations from the south-central portion of the Belize barrier reef suggest a troubling degradation of this once pristine reef environment (Perkins and Carr, 1985; Cortes, 1997). Such deterioration may stem from a combination of the effects of recent large-scale disturbances, including two coral bleaching events (1995 and 1998) and Hurricane Mitch, as well as from increased fishing pressures in the region. The successful Hol Chan Marine Reserve admirably serves as a model for future reef conservation of the Belize barrier reef system, and might well serve as an appropriate model for marine reserves in the Bahamas.

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