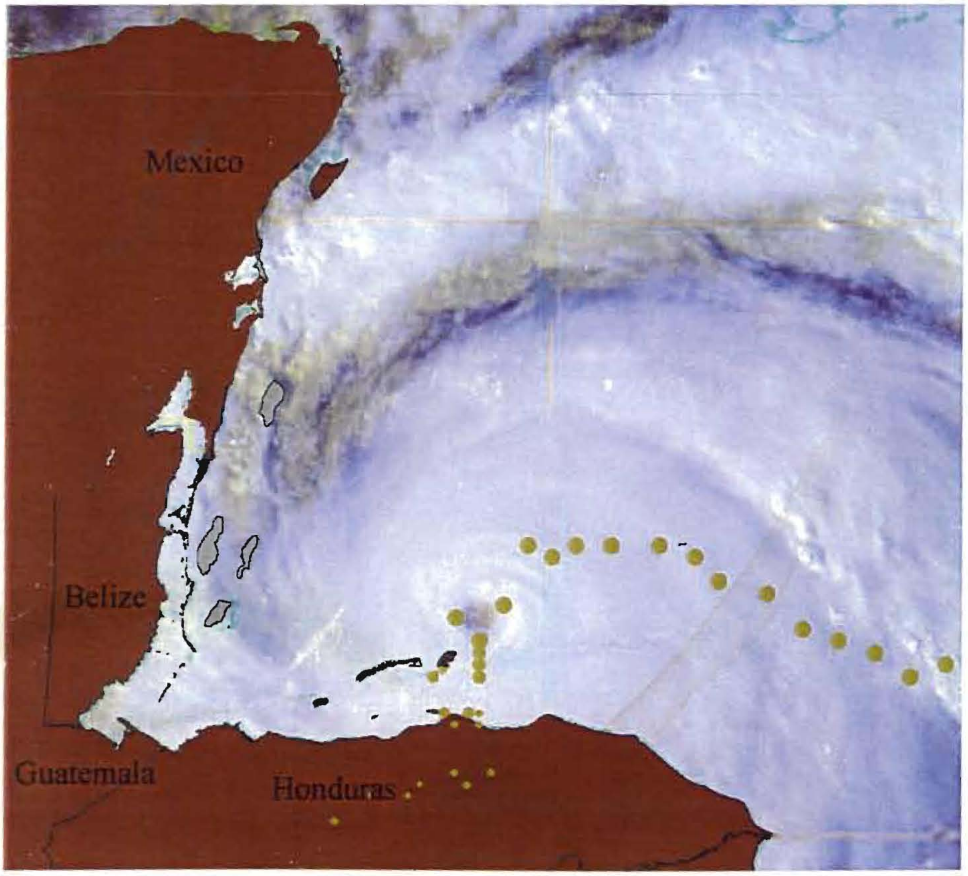
ECOLOGICAL STATUS OF THE MESOAMERICAN BARRIER REEF SYSTEM

Impacts of Hurricane Mitch and 1998 coral bleaching



Philip A. Kramer
Patricia R. Kramer

This report is dedicated to
Robert N. Ginsburg **for his guidance and**
insightful discussions on this project.

ECOLOGICAL STATUS
OF THE
MESOAMERICAN BARRIER REEF SYSTEM

IMPACTS OF HURRICANE MITCH AND 1998 CORAL BLEACHING

Final Report to the World Bank

Philip A. Kramer and Patricia R. Kramer[1]

January 2000

Front cover: Large photo: The track of Hurricane Mitch (Category V) superimposed on a satellite image of the hurricane near the island of Guanaja, Honduras (Satellite image from USGS, CINDI-CDROM, 1998). Bottom left photo: Colony of *Diploria strigosa* (center) and other reef debris transported from fore reef to shallow reef crest during Hurricane Mitch. Middle photo: *Siderastrea siderea* colony still partly bleached from the 1998 bleaching event and suffering high recent mortality partial mortality. Right photo: Shallow water gorgonians suffered high mortality from Hurricane Mitch. Photos by K. Marks and P.A. Kramer.

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Executive Summary

The Mesoamerican Barrier Reef System (MBRS) is a unique and extensive coral reef system extending from the northern most part of the Yucatan, Mexico through Belize and east to the Bay Islands of Honduras. In 1998, a sequence of catastrophic disturbance events impacted the region. In August 1998, high sea-surface temperatures appeared first in the Yucatan, then spread south to Belize and Honduras in the ensuing weeks. This timing coincides with numerous reports of severe coral bleaching. In late October 1998, Hurricane Mitch a category 5 storm passed through the Honduran Bay Islands causing massive wind and flood damage. With support from the World Bank, we conducted a large-scale survey between March and June 1999 to specifically assess bleaching and hurricane damage of over 150 shallow and fore reef sites. The survey results revealed widespread impacts that ranged from minor to severe with a large degree of variability between sites and across different spatial scales.

The 1998 bleaching event effected the entire MBRS region, and was possibly more severe than the 1995 mass bleaching event (the only other mass bleaching event in recent history reported for this region). There was significant spatial variability in the magnitude of remnant bleaching and recent mortality explained primarily by the geographical differences in the temperature stress, interspecific patterns of susceptibility to temperature stress, and accompanying secondary effects. The magnitude of the bleaching was evident in deep fore reef sites where significant remnant bleaching was observed up to 10 months after the initial bleaching (up to 44% of corals exhibited tissue discoloration). Accompanying high levels of remnant bleaching were high incidences of coral disease (mainly white disease and black band disease), especially on shallow reefs in Belize and fore reefs in the Bay Islands where 10% of colonies were infected. Localized shallow sites experienced catastrophic losses due to the initial bleaching event, especially in southern Belize (54% average recent mortality). The most affected species were *Agaricia tenuifolia*, *Diploria labyrinthiformis*, *Millepora complanata*, and *Montastraea annularis* complex.

Hurricane Mitch caused widespread damage across much of the MBRS region. Across larger spatial scales (between countries), the greatest degree of damage was observed in Belize (up to 29% of colonies damaged), particularly along central east-northeast exposed shallow sites, although sites in Honduras and Mexico were affected as well. At smaller spatial scales (within countries), the amount of hurricane damage depended primarily on a reef's location, species present, and existing architectural complexity. In general, Hurricane Mitch resulted in localized coral mortality at prone sites, however the main impact of the storm was the reduction of reef structure since bleaching mortality was already widespread by the time the storm passed through. Besides the immediate physical destruction caused by wave energy, there were also numerous secondary effects, like sediment run-off, that were much more difficult to quantify or separate from synergistic bleaching impacts. Anecdotal evidence suggests that the passage of the hurricane may have benefited some areas by decreasing water temperatures thus alleviating some of the temperature stresses on corals.

The cumulative effects of the 1998 impacts are expected to have long-term ecological consequences for the entire MBRS region. Many reefs from southern Yucatan through Belize and the Bay Islands are in moderate to severe disturbed state. Recent coral mortality averages 18% for shallow and 13% for deep sites, with localized shallow sites reaching up to 70%. Existing old coral mortality from other recent disturbances (white band disease and 1995 bleaching) has compounded the situation such that total coral mortality (recent and old) is presently high for the entire region (49% for shallow reefs and 33% for deep reefs). The extensive loss of certain coral species to the region (e.g., *Agaricia tenuifolia*, *Millepora complanata*, *Acropora palmata*, *Montastraea annularis* complex) is of particular concern given their important roles as major reef builders. A complete understanding of the synergistic and secondary effects from the 1998 impacts, as well as the potential for recovery, may take years or even decades to fully elucidate and understand.

Introduction

The Mesoamerican Barrier Reef System (MBRS) is one of the most significant ecosystems in the tropical western Atlantic extending more than 1000 km along Mexico, Belize, Guatemala, and Honduras (Fig. 1). In 1997, the Presidents of these four countries signed the "Declaration of Tulum" which recognized the shared resources and connections between each of the four country's coastal areas and agreed to work towards a regional conservation strategy to ensure the integrity and future management of this system. However, the widespread occurrence of coral bleaching beginning in August 1998 and the passage of Hurricane Mitch in October 1998 left many questions regarding the condition of the reef system. To help guide the development and implementation of long-term monitoring and management programs in the region, there was an urgent need to understand the extent of damage and overall condition of the reef system. To address this need, we conducted a large-scale field survey of coral reefs in the MBRS region to evaluate the lethal and transient effects from the 1998 bleaching event and physical destruction caused by Hurricane Mitch. We focused mainly on hard-coral species that are responsible for reef building and that are vital to the overall integrity of the reef system. The specific objectives were:

1. Develop an overview of the range of damage to major reef-building corals following the 1998 bleaching event and Hurricane Mitch.
2. Identify priority areas for monitoring programs or marine protected areas.
3. Establish baseline data on reef condition and region-wide comparable data.
4. Map spatial patterns of reef condition

Determining the status of coral reefs over large areas, particularly after catastrophic events, is challenging given the lack of widespread pre-existing or historical information and the lack of consensus among experts as to which parameters constitute "normal" or healthy reefs. Like many biological systems, reefs are now understood to be fairly dynamic undergoing both long-term and short-term changes associated with the degree and duration of stress events. The role of both temporal and spatial scale is important in understanding the trends observed in how disturbances control reef communities and processes. Over longer time scales (k-yrs), we know that reefs are fairly robust, able to withstand massive changes associated with sea level and climate changes by shifting to more favorable growing areas. Over shorter time scales (decadal), storms and other disturbances often lead to dramatic changes that may be followed either by recovery to pre-disturbance conditions (e.g., Done, 1988; 1992; 1997) or continued degradation (Hughes, 1994). Since coral reefs are frequently subjected to different levels of perturbations they are continually fluctuating through various stages of recovery in response to these disturbances. The ability for a reef to recover from severe disturbance depends on numerous factors including the availability of new recruitment, water quality, and the presence of other stresses.

Over the past 25 years, coral reefs in the Caribbean appear to have experienced an increase in the frequency and intensity of disturbances, with a few areas experiencing several repeat and/or coinciding events. Large-scale disturbances often affect coral cover, size frequency distributions, abundance, and fitness of corals and potentially lead to the reduction of reef structure and architectural complexity. Up until 1998, the principal disturbances affecting the MBRS region were hurricanes, coral diseases, and just recently (1995) mass coral bleaching, although the 1983-4 regional die-off of the herbivorous sea urchin *Diadema antillarum* undoubtedly had serious implications. A series of moderate to severe hurricanes have impacted localized areas in Mexico and Belize (e.g., Jordán-Dahlgren and Rodríguez-Martínez, 1998; Stoddart, 1962a; 1963; 1974) and recovery from these storms have been variable. White band disease is suspected to have devastated acroporid populations beginning in the early 1980's (e.g., Aronson and Precht, 1997), including many areas in Belize where they were once a primary shallow reef builder (Rützler and Macintyre, 1982). Mass bleaching was first reported in the MBRS in 1995 and differentially affected reefs (Burke, 1996; McField, 1999; Guzman and Guevara, 1998). Despite these disturbances, many reports routinely describe the reefs of the MBRS region as being in good to excellent condition into 1998 (Gutiérrez et al., 1993; Fenner, 1993; Wilkinson, 1988).

1998?

This report presents the results from our survey, discusses their implications, and concludes with a list of recommendations to assist in the management of the MBRS system. In addition, we collaborated with in-country reef specialists and other regional experts to incorporate and synthesize existing information. It is hoped that the information will be used to help identify priority areas for future monitoring and to promote regional coordination of research and conservation efforts in the MBRS region over the next five years.

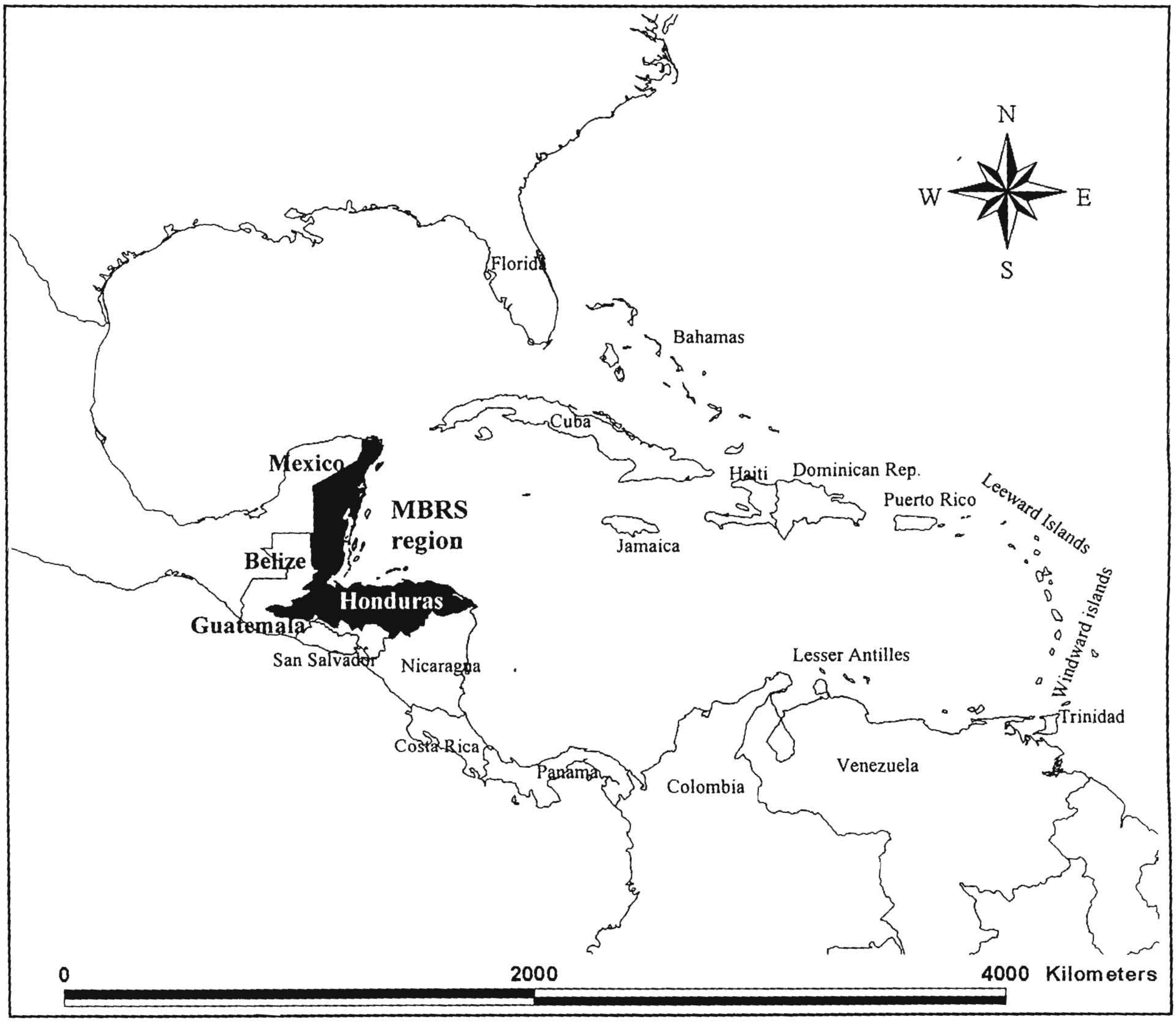


Figure 1. Map showing the location of the Mesoamerican Barrier Reef System (MBRS), shared by the countries of Mexico, Belize, Guatemala, and Honduras, in relation to the Caribbean.

Setting

The Mesoamerican Barrier Reef System (MBRS) extends over 1000 km from the northern tip of Yucatan in Mexico south along the Belize coastline and east through the Bay Islands of Honduras (Fig. 1). The region's terrestrial topography shows distinct differences from north to south (Fig. 2). Northern Belize and Yucatan are composed of flat and low-lying karst. In contrast, the rest of the region is influenced by coastal mountains (e.g., Maya mountains central/southern Belize, the Sierra de Chama in Guatemala, and the Cordillera Nombre de Dios in Honduras). Weather patterns are driven by the seasonal easterly tradewinds that define the dry and wet seasons. The wet season is bimodal, with the majority of the rain (>100 cm) falling from October to January. Southern Belize, Guatemala, and Honduras receive more rainfall than northern Belize or Yucatan. Most significant rivers occur from southern Belize to Honduras and empty into the Gulf of Honduras (Fig. 2). The degree of reef development varies both on local and regional scales (Fig. 3). At least 41 scleractinian coral species have been reported for Mexico, 49 for Belize, and between 44-66 species[1] in Honduras. A brief description of reefs within each of the principal countries of the MBRS is given below. Since there is relatively little or no reef development in Guatemala (e.g., Bortone et al., 1988), we limit our discussion to Mexico, Belize and Honduras.

Mexico: The eastern side of the Mexican Yucatan region contains an extensive fringing reef system along the nearly 350 km of coastline from the tip near Isla Contoy south to Tulum, including offshore islands and the Banco Chinchorro atoll (Fig 3a, Photo 1a). The Yucatan coastline is characterized by flat Eocene-Holocene limestone terrain with alternating sandy beaches and rocky outcrops. The shelf margin is very narrow and typically drops abruptly within several kilometers of the coastline to depths greater than 400m. A dry climate coupled with the highly permeable limestone terrain results in very few rivers throughout the Yucatan Peninsula. However, runoff and underground seepage may provide fresh and brackish water to nearby fringing reefs in some areas. Overall the degree of reef development along Quintana Roo varies both on a local and regional scale and is often very discontinuous. In general, three broad geomorphic zones are recognized: north, central, and southern. The reefs in the north area are characterized by overall low biotic cover (17%) and mostly denuded hard grounds, with a small amount of high biotic cover areas dominated by stands of dead *Acropora palmata*. The central and southern areas contain more continuous shallow reefs and better developed platform reefs. Banco Chinchorro is a large (46 km x 14 km) atoll located 27 km off the southeastern coast between Xcalak and el Ubero and separated by a 1000m deep channel (Chavez and Hidalgo (1984). More detailed overviews of various parts of the Yucatan reef system can be found in Jordán-Dahlgren et al., 1981; Chavez and Hidalgo, 1988; Fenner, 1988; Jordán-Dahlgren and Martin, 1991; Padilla et al., 1992; and Gutiérrez et al., 1993.

Belize: The Belize reef complex is the longest continuous barrier reef in the western Atlantic extending more than 250 km and contains a diverse assemblage of lagoonal patch reefs, fringing reefs, and offshore atolls (Fig. 3b, Photo 1b). Three landward tilting, block fault ridges that dip to the south provide the foundation for the Belize barrier platform (Purdy, 1974a). The most landward ridge serves as the foundation for the reefs in the northern region; the next ridge seaward, Chinchorro Bank – Turneffe Island ridge, provides the base for the central region reefs; and the Glover's Reef-Lighthouse Reef ridge provides the structure for the southern reefs. The northern Shelf (north of Belize City) is characterized by a shallow, flat platform, with very little relief except that associated with relict drowned drainage and karst topography. Water depths typically average of 2.5 to 3 m. In contrast, the southern Shelf has much higher bathymetric relief, and progressively deepens to the south to more than 65 m in the Gulf of Honduras. In general, four broad biogeomorphographic reef provinces are recognized in Belize: northern, central, southern, and the atolls. Northern and southern reefs are typically discontinuous, while the central region has the best-developed and most continuous reefs due to its elevation, good water quality, and modified wave regime (Burke, 1993). Good descriptions of Belizian reefs can be found in Stoddart, 1962a, b; Purdy, 1974; Miller and Macintyre, 1977; Wallace and Schafersmann, 1977; Burke, 1979; Rützler and Macintyre, 1982; Perkins, 1983; Macintyre and Aronson, 1997.

[1]44 species were reported in Roatan (Fenner 1993), 66 species in Cayos Cochinos (Guzman 1998).

Honduras: Along much of the mainland coast of Honduras, reef growth is inhibited due to high runoff, the result of high rainfall and the mainland's mountainous terrain. Only a few scattered, poorly developed coral communities exist along the coast (Mills et al., 1967; Donnelly et al., 1990). The predominant reef development in Honduras is associated with the offshore Bay Islands. The Cayman Trench separates the coastal areas of Honduras from Belize and reaches depths > 6km (Pinet, 1976). The Bay Islands are located in an east-west orientation along the southern margin of the Trench, and consist of more than 60 minor islands and several relatively large islands forming four main island groups: Roatan, Utila, Guanaja, and Cayos Cochinos. The principal reefs of the Bay Islands are fringing escarpment reefs that extend seaward to 30-40 ft (9.1-12.2 m) depth than sharply dropping off to depths up to 250 ft (76.2 m) or greater (Fig. 3c). Well-developed reef buttresses are found discontinuously on nearly all of the Bay Islands dominated by rich coral growth of *Montastraea annularis*. In addition, a poorly developed and discontinuous shallow fringing barrier reef of *Acropora palmata* and *Agaricia tenuifolia* exists around the northern coastlines of Roatan, Guanaja, and portions of Cayos Cochinos and southeastern Utila. These shallow ramparts are sometimes exposed at low tides and much of the coral is dead and covered with dense turf algae (Fenner, 1993). The shallow reef platform is dissected by numerous channels (>126ft deep) formed by erosion during glacial times (Wells, 1988).

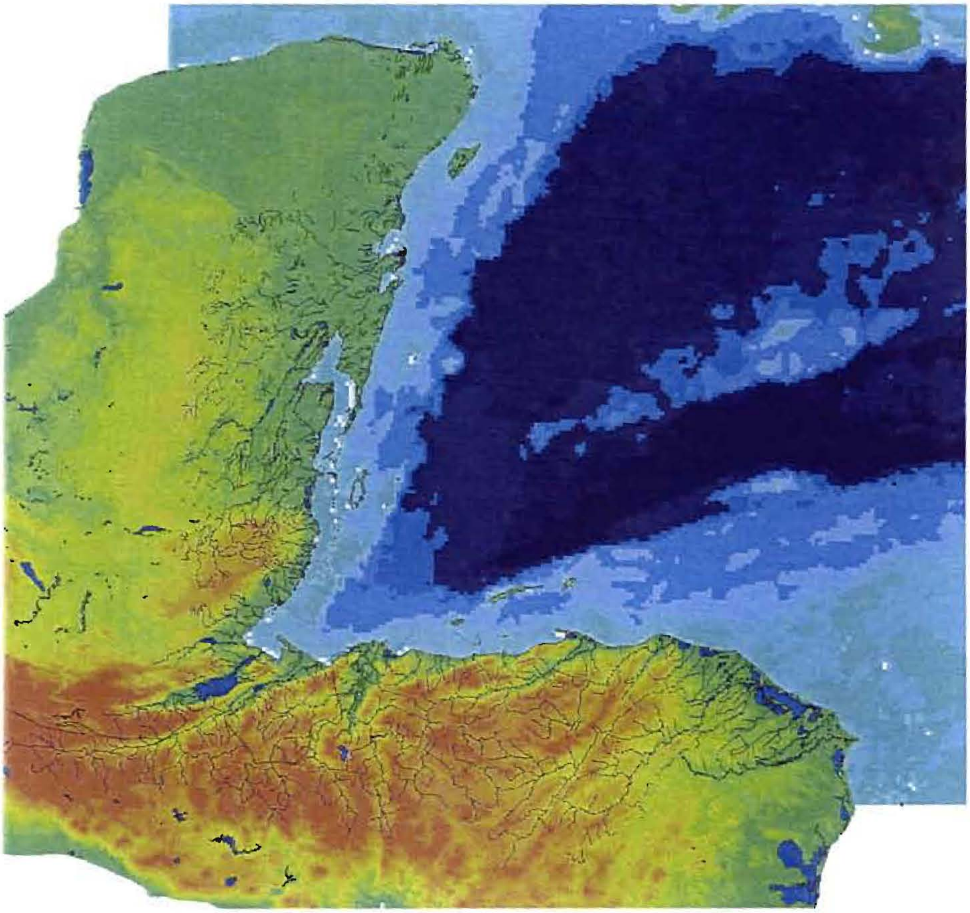


Figure 2. Map of the MBRS region showing elevation, bathymetry, and rivers. For elevation, dark brown indicates higher elevation, green indicates low elevation. For bathymetry, darker blues indicate deeper water. Most rivers occur in the southern part of the region.

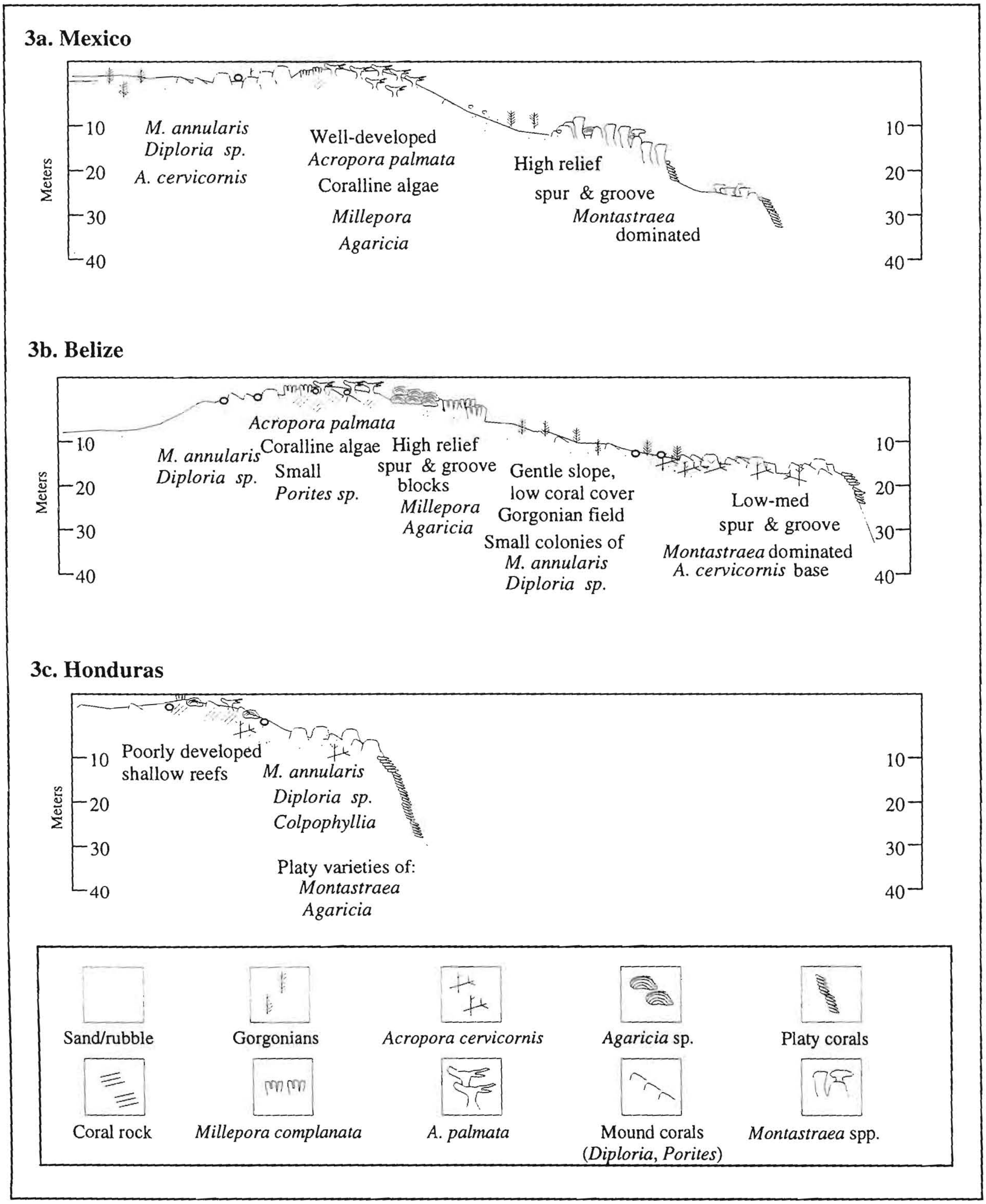


Figure 3a-c. Schematic cross sections of typical reefs in the MBRS. a). Reefs in the southern part of the Yucatan, Mexico normally have a well-developed shallow *A. palmata* reef crest and well-developed spur and groove system on the deeper fore reef. Northern Yucatan deep fore reefs are not as well-developed as shown here. b). Along the shallow barrier in Belize, the reef crest has well developed spurs capped with *Agaricia* and *Millepora*. The fore reef has a gentle sloping low relief spur and groove system dominated by *M. annularis*. c). In Honduras, the shelf is narrow and the reef crest is normally poorly developed. The fore reef is also narrow with a steep wall.

1a. Central Yucatan fringing barrier

1b. Belize barrier

Photo 1a-b. Aerial photographs of shallow reefs of a). Central Yucatan and b). Central Belize.

Background

1998 Mass Bleaching Event

Historically, the MBRS region experienced few large-scale bleaching events compared to other areas in the Western Atlantic and Eastern Pacific (Coffroth et al., 1990; Glynn, 1991; 1993; 1996). The scarcity of severe bleaching events in this area may be due to fewer high temperature stresses and/or the lack of other environmental stresses compared to other areas in Caribbean (McField, 1999). While coral bleaching was reported for much of the Caribbean during 1983 and 1987, the first well-documented mass bleaching event in Belize occurred in 1995 where 52% of coral colonies surveyed were affected by bleaching (McField, 1999). By May 1996, most corals had recovered although about 10% of the corals suffered some partial mortality. Impacts of the 1995 bleaching event were also documented in Cayos Cochinos, Honduras, where sea surface temperatures increased more than 3.5°C (a high of 32°C) affecting 73% of scleractinian corals and 92% of hydrocorals (Guzman and Guevara, 1998). Higher coral mortality rates were reported for this area than Belize, although species specific responses to the bleaching event were observed in both Belize and Honduras.

From mid-1997 to late-1998, unprecedented bleaching of hard corals was documented globally coinciding with a large El Niño event, followed by a strong La Nina. The maps in figure 4 depict typical monthly sea-surface temperature anomalies for the Caribbean from June through October 1998. Based on high resolution satellite derived sea surface temperatures, these maps show areas where coral reef bleaching activity was most likely occurring during this time (Gleason and Strong, 1995). During 1998, high sea-surface temperatures in the MBRS region first appeared during August and intensified during September as indicated by NOAA's "hot-spot" sea-surface temperature anomaly maps shown in figure 4. Coral bleaching coincided with these temperature anomalies. The timing of bleaching varied throughout the region and appeared to have started in the Yucatan, Mexico and then in Belize and Honduras. Water temperatures along the Yucatan coast were reported to be 29.5-30.5°C in August and September (Appendix 1, Jordán-Dahlgren) and up to 31.1 °C in early October (Appendix 1, Hernandez). This is nearly a full degree higher than normally recorded for this region. Bleaching along the Yucatan coast, particularly the southern area, was first observed in mid-August (Appendix 1, Jordán-Dahlgren) and reached a peak in late October (Appendix 1, Land, Sale). In Belize, intense bleaching was observed by mid-September (Appendix 1, Bright, McField). Recent coral tissue mortality was first reported in early October, particularly in *Agaricia tenuifolia* (Appendix 1, McField, Aronson & Precht, Bright). Reports of massive bleaching and mortality of *A. tenuifolia* and *Millepora* spp. in the central lagoon and southern region followed (Appendix 1, Bertness & Bruno, Aronson & Precht). In Honduras, bleaching was reported in September in both shallow and deep reefs. By mid-September up to 50% of live coral cover was estimated to be bleached around Roatan affecting primarily *A. tenuifolia*, *Montastraea* spp., and *Diploria* spp., while *Acropora* spp. and *Millepora* spp. were less affected (Appendix 1, Hatziolos). Following the passage of Mitch in late October, sea surface temperatures decreased and recovery of some branching corals was reported while massive corals continued to remain bleached into 1999.

2a. **2b.**

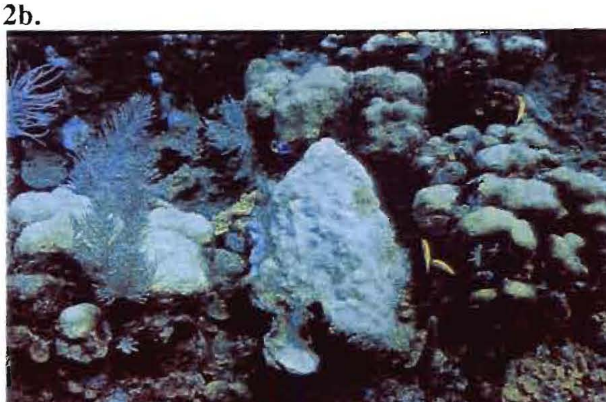


Photo 2a-b. a). Bleached *Acropora palmata* and *Agaricia tenuifolia* (center foreground) on shallow reefs at Basil Jones Cut, Belize. (Photo courtesy of G. Smith, Sept 1, 1998). b). Bleached *Montastraea franksi* on deep fore reefs in Cayos Cochinos, Honduras. (Photo courtesy of C. Garcia-Saez, early Oct. 1998).

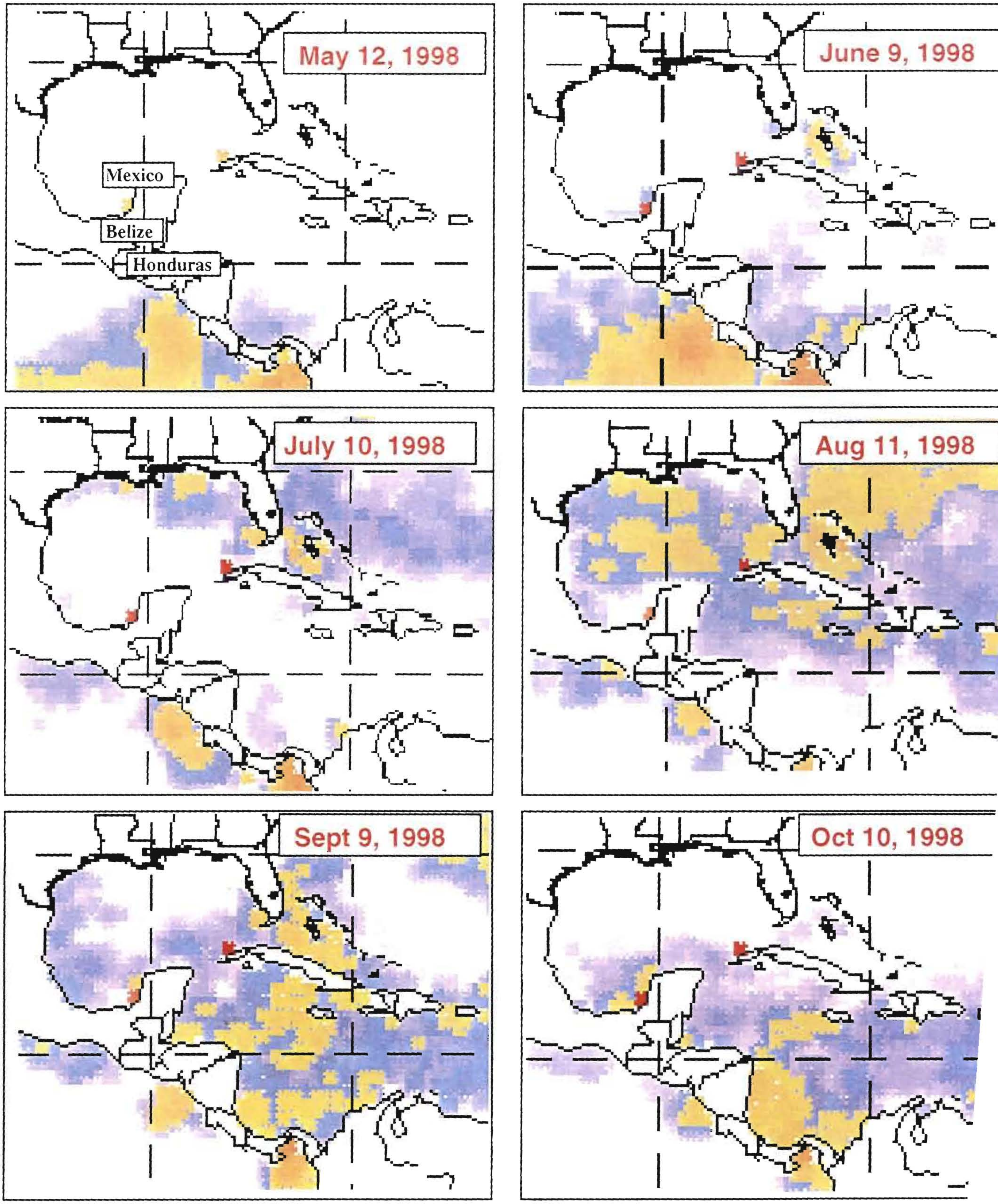


Figure 4. Sea surface temperature anomaly maps for the Caribbean during summer months of 1998 from NOAA's "hot spot" bleaching program. White colors represent "normal" SST, while progressively hotter colors indicate warmer water. Yellow indicate roughly 1 °C above normal SST. The MBRS was enveloped in abnormally warmer waters beginning in August and extended through October, after which temperatures decreased back to normal.

Hurricane Mitch

The MBRS region lies within the principal trajectories of late-season (October/November) hurricanes and over the years numerous large storms have affected the area. Eight notable storms passed through the Yucatan Peninsula near Puerto Morelos between 1915-1993 (Neumand et al.. 1978: Jordán-Dahlgren and Rodríguez-Martínez. 1998). Three most recent were Hurricane Allen (Class V) in 1980. Gilbert in Sept. 1988 (Class V), and Keith (tropical storm) in November 1988. Each had different paths, intensities and impacts on the shallow *A. palmata* reefs. Jordán-Dahlgren and Rodríguez-Martínez (1998) documented a shift in coral size from large colonies to smaller colonies after hurricane Gilbert. In 1995, Hurricane Roxanne passed over southern Yucatan, although little damage was reported (Ruiz-Renteria et al., 1998). In Belize, it has been estimated that storms and hurricanes hit the coast an average of 112 times in 100 years (Gentry, 1971). Hurricane Greta (1978) was one of the most significant storms to hit the central coast of Belize impacting the reefs in central Belize, including Carrie Bow Cay (Still et al., 1982: Rützler and Macintyre, 1982). Stoddart had documented impacts of earlier hurricane in Belize (1963, 1965, and 1969 and 1974). One of the most significant hurricanes to hit Honduras was Hurricane "Fifi" in 1974, which killed at least 2,000 people and up until Mitch, was considered the most devastating hurricane of Honduras in recent history. It is unclear what impacts Fifi had on the marine environment.

Hurricane Mitch was a late in the season Category 5 hurricane that turned into one of the largest and deadliest tropical cyclones of this century (Fig. 5). First documented as a hurricane in the early hours of Oct. 24, Mitch formed from a tropical depression in the southern Caribbean off the coast of Columbia. For the next three days the storm grew in strength and size as it proceeded slowly to the northwest missing the islands Hispaniola and Jamaica. Driven by unusually warm late October surface waters, the storm quickly achieved astonishing windspeeds in excess of 180+ mph as it moved into the MBRS region. Near the Honduran Bay Island of Guanaja, the storm slowed and stalled suddenly from late October 27 until the evening of October 29. .Strong winds and waves slammed Guanaja (Photo 3a-b) and the adjacent Bay Islands, while large storm waves battered coastlines throughout Belize and Yucatan, Mexico destroying docks and piling up sand and debris. The storm gradually turned to the southwest towards mainland Honduras and intense and widespread rainfall began to reach catastrophic proportions in both Honduras and Nicaragua. The floodwaters in the Honduran capital of Tegucigalpa rose to unprecedented levels as the Choluteca River overflowed its banks. Mudslides and continued flooding over the next three days left over 11,000 people dead and 2,000,000 people homeless. The storm also destroyed greater than 50% of the infrastructure in Honduras and Nicaragua. Numerous large trees, mud, and debris washed up onto beaches and reefs during the weeks following the storm. On Nov. 3, Mitch's ghostly remains entered the southern Gulf of Mexico and warm waters rejuvenated the system into a tropical storm which affected parts of south Florida before heading out into the Atlantic.

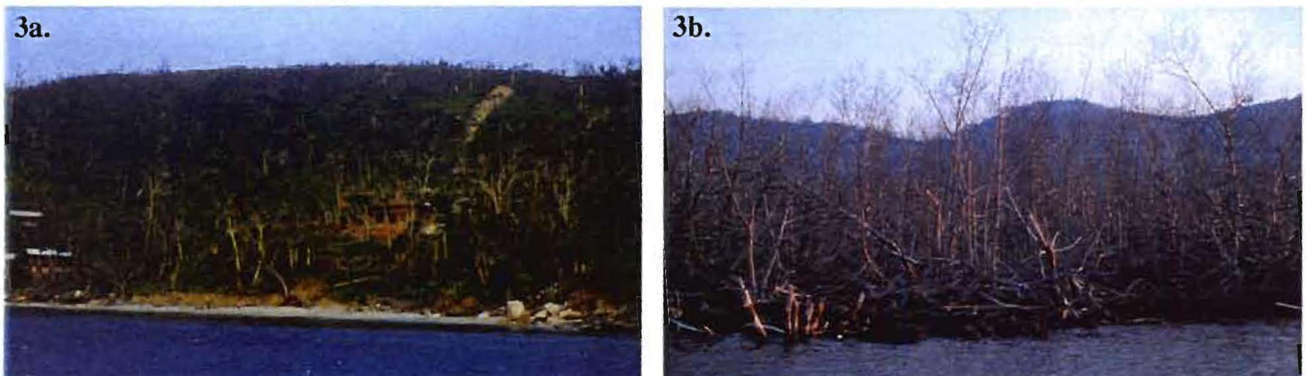


Photo 3a-b. a).Strong winds from Hurricane Mitch defoliated the majority of native forests on the east side of Guanaja. Revegetation of the understory was visible 8 months after the storm. b). Mangrove forests along the west cut of Guanaja were killed by salt spray mobilized during the storm. Both photos taken May 1998, courtesy of K. Marks.

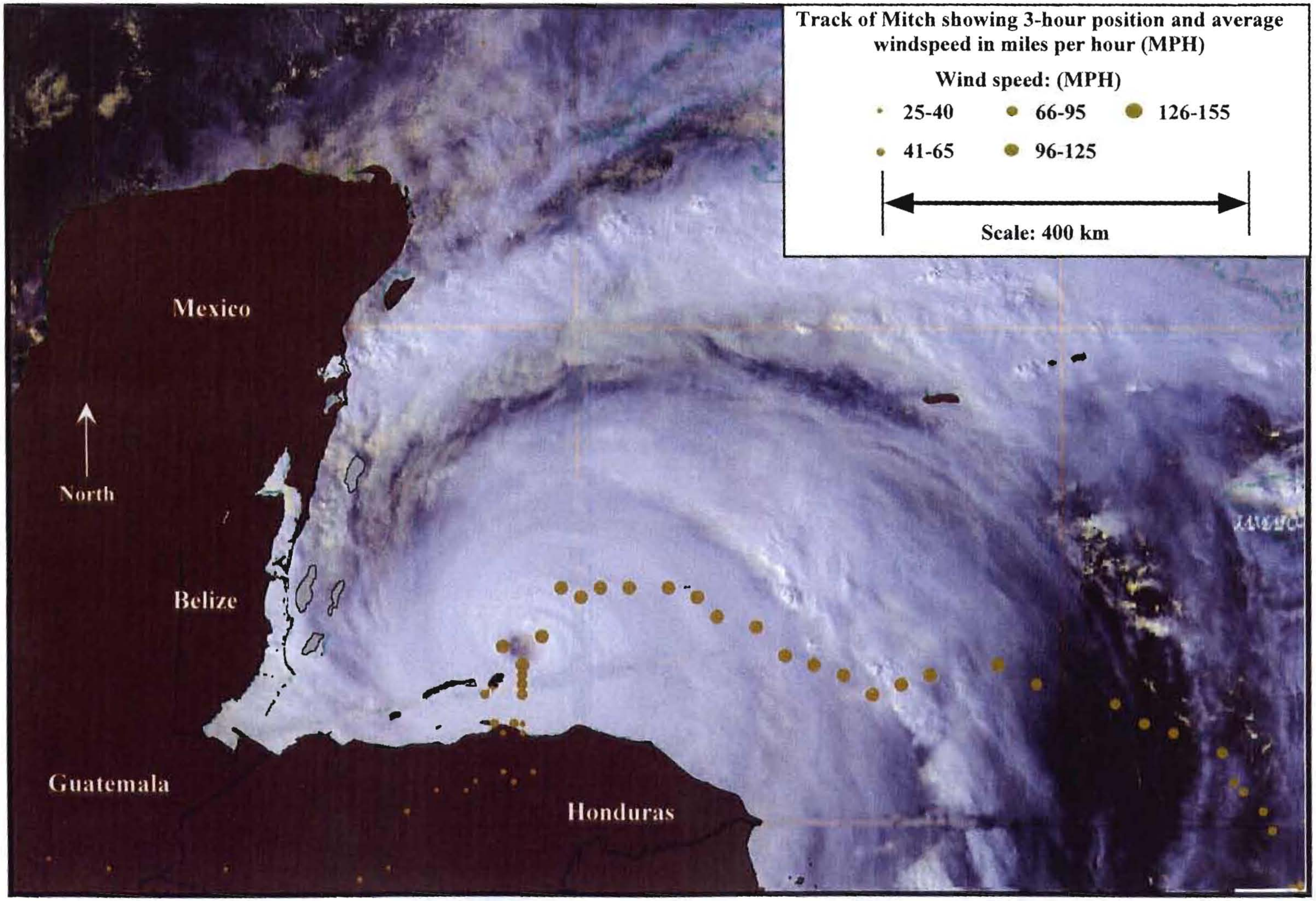


Figure 5. Storm track of hurricane Mitch from 10/26/98 through 10/31/98 superimposed on a satellite image taken of Mitch on 10/29/98 when the storm stalled just north of the island of Guanaja, Bay Islands. Satellite image adapted from Digital Atlas of Central America CINDI, USGS, 1998.

Methods

The principal methods for the field survey included rapid assessments of coral colonies at selected sites supplemented with broad-scale tow boarding over larger areas. These methods provided an efficient way to collect baseline data over large spatial scales. We divided the MBRS region into different categories (Fig. 6): **COUNTRY** (Mexico, Belize, Honduras) was defined as the coarsest scale category (~100-500 km scale); **AREA** (10-100 km scale) was based on similar geomorphology within a country (e.g., north, central, south, atolls); REEF (~1-10 km scale), and **SITE** (0.1-km scale) was defined as an area of habitat that was more or less homogeneous and accessible from an anchored boat. To take into account natural variability normally observed within and among reefs, we stratified study **SITES** into similar shallow (1-3m) and deep fore reef (8-17-m) types. The shallow reefs, including shallow reef crests, back reefs, and patch reefs, were characteristically dominated by *Acropora* spp., *Millepora* spp., *Agaricia* spp. and/or *Porites astreoides*. The fore reef sites were typically fringing fore-reef dominated by *Montastraea* spp. We used several sources of information (benthic maps, charts, local knowledge, reconnaissance by Manta tow-board, size, depth, and position relative to land) to select survey sites. Site descriptions were prepared for each site surveyed and included location (GPS coordinates), approximate size and shape, relief features (e.g., spur and groove), and depth. For each REEF that was chosen, we surveyed at least one SITE within each chosen depth interval. A total of 151 sites were surveyed along the MBRS system and over 9,000 corals were assessed (Fig. 7-9 and Tables 1-2). Twenty seven sites were surveyed in Mexico between March 7-21, 1999, 80 sites in Belize between June 6-24, 1999, and 44 sites in Honduras between April 26-May 5, 1999.

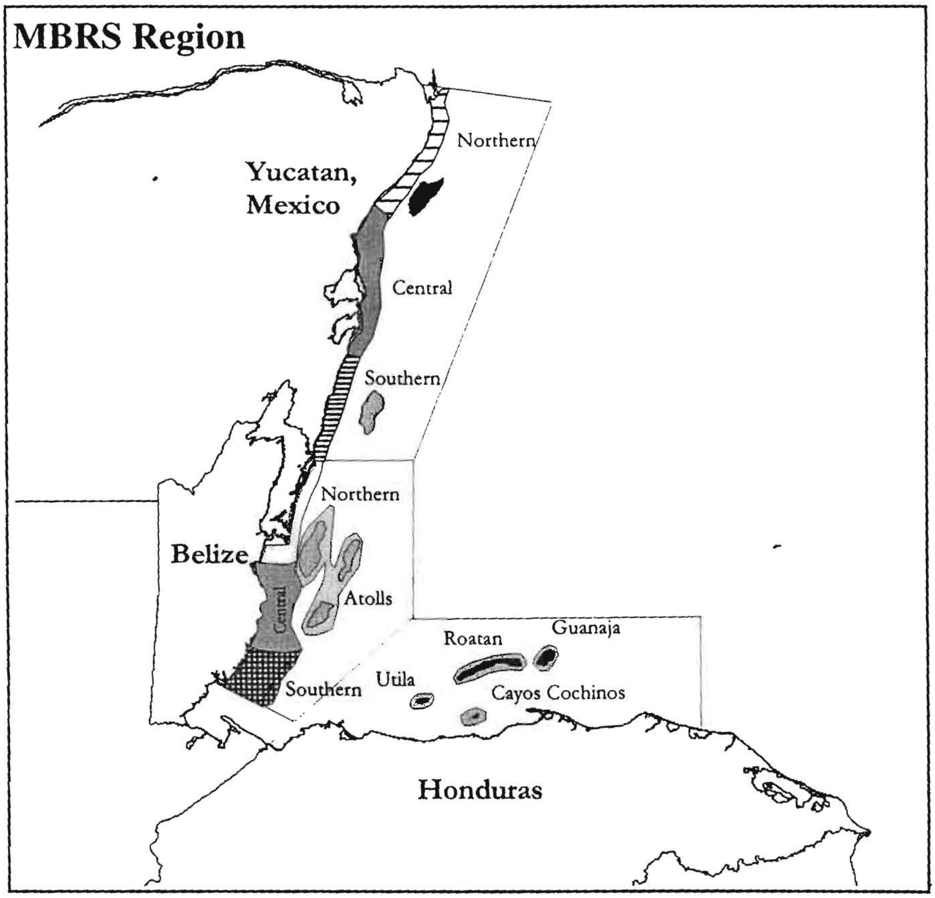


Figure 6. Map of Mesoamerican Barrier Reef System showing sampling area. Shaded areas delineate the geographic areas (e.g., north, central) within each country used to group sampling sites.

Yucatan, Mexico

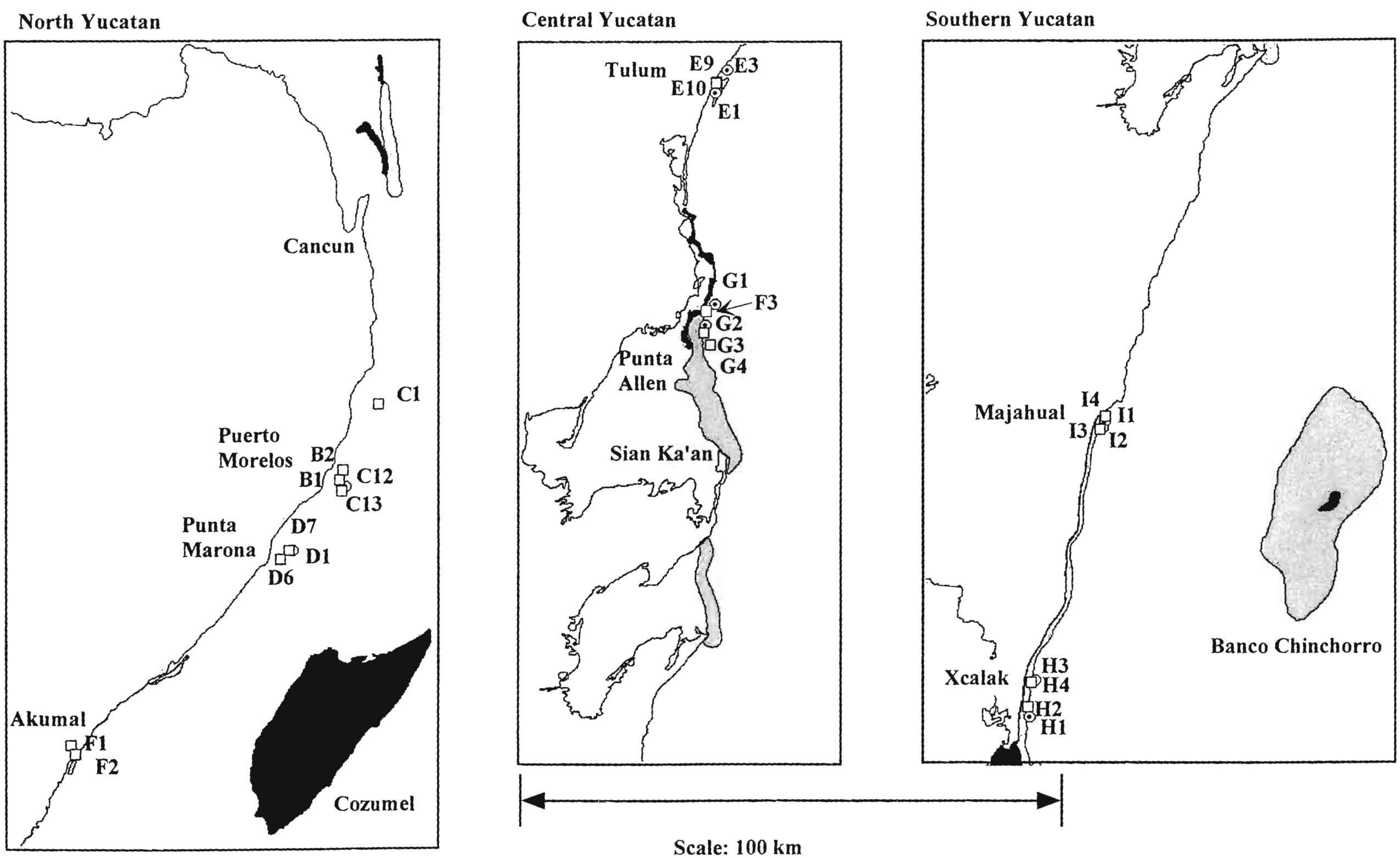


Figure 7. Study site locations in Yucatan, Mexico. Twenty-seven shallow (squares) and deep fore reef (circles) sites were surveyed between March 7-21, 1999. The GPS positions of some shallow and deep sites overlap, thus only one symbol may appear.

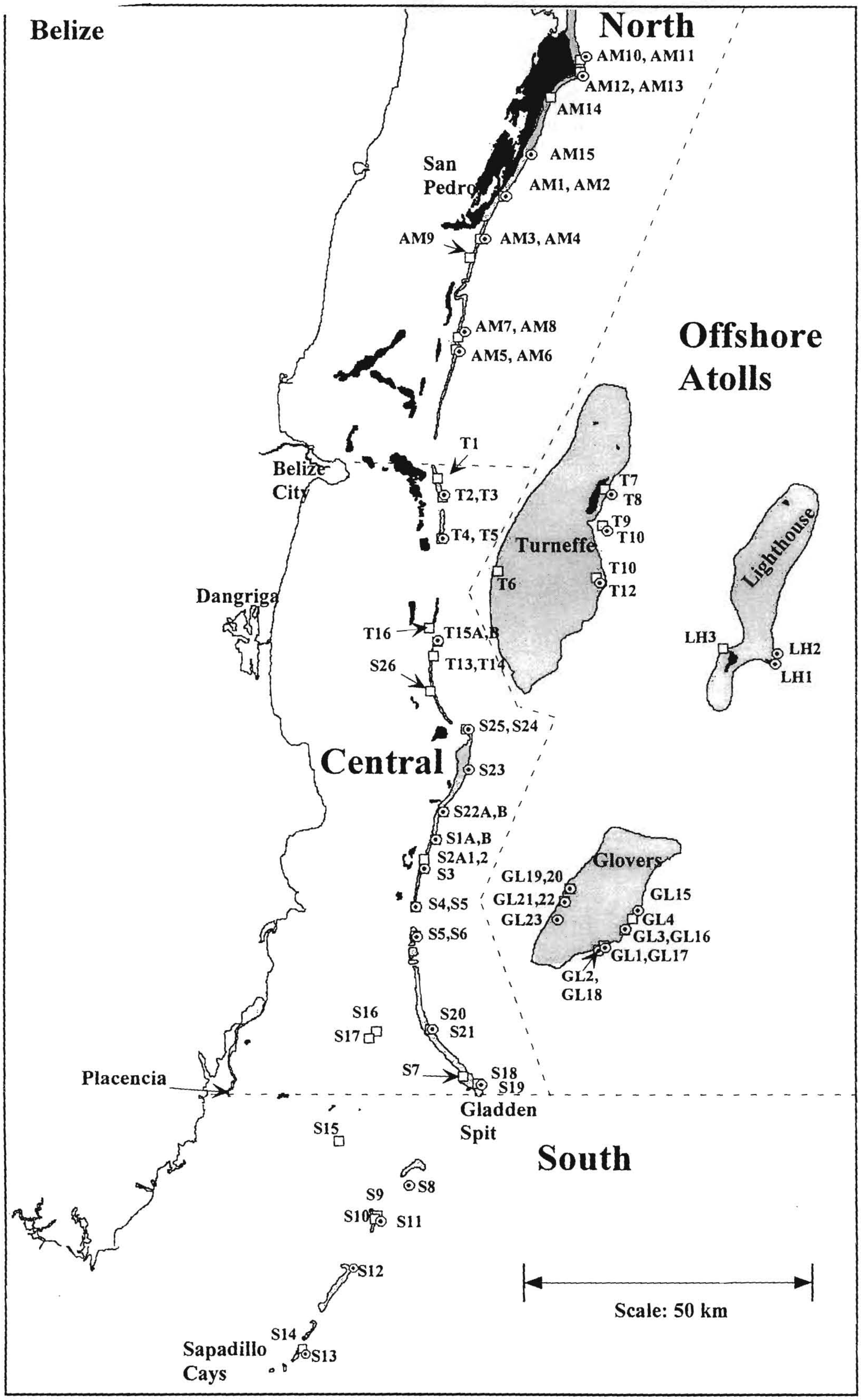


Figure 8. Study site locations in Belize. Eighty shallow (squares) and deep fore reef (circles) sites were surveyed between June 6-24, 1999. The GPS positions of some shallow and deep sites overlap, thus only one symbol may appear.

Bay Islands, Honduras

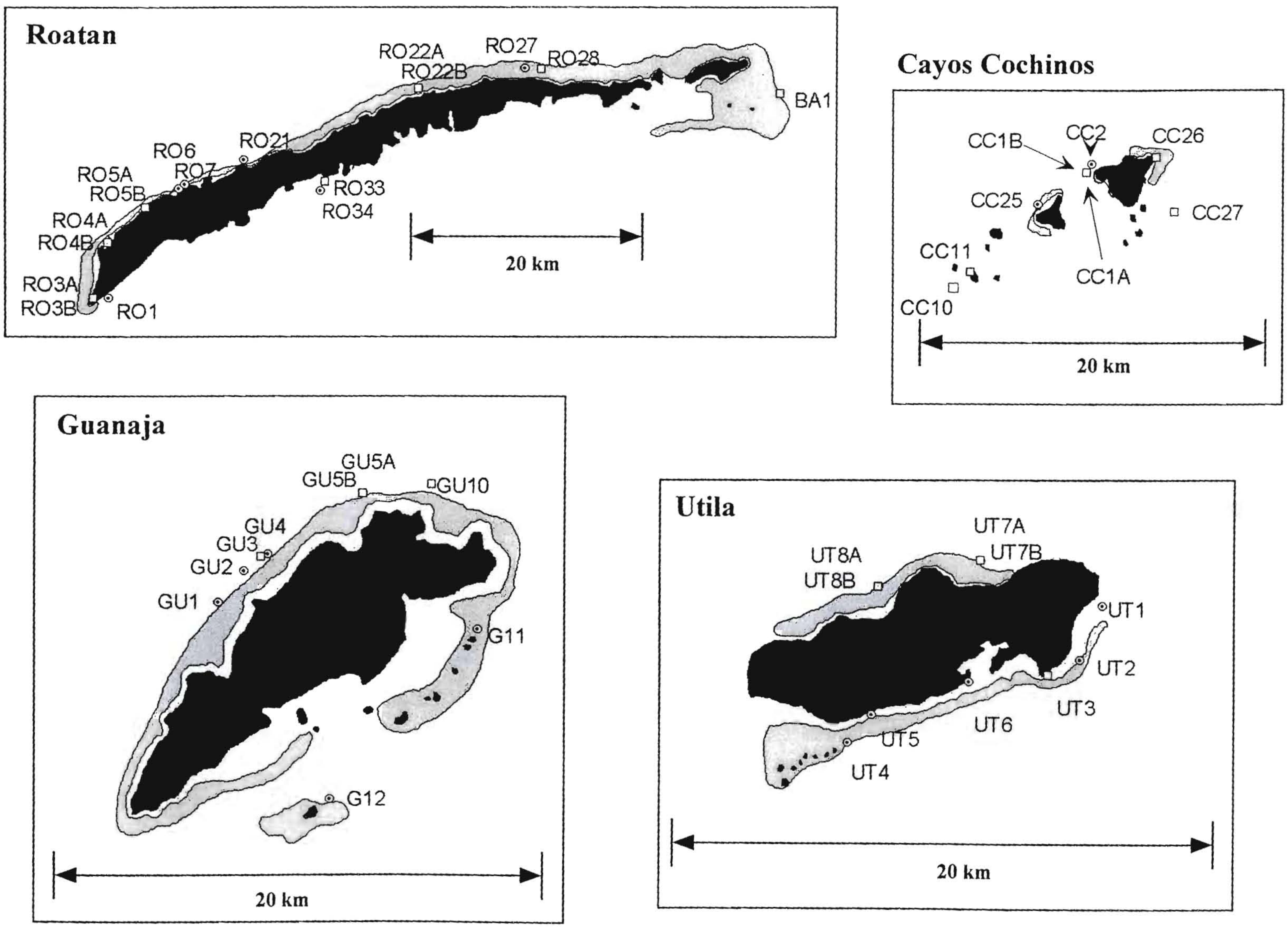


Figure 9. Study site locations in Bay Islands, Honduras. Forty-four shallow (squares) and deep fore reef (circles) sites were surveyed between April 25- May 5, 1999. The GPS positions of some shallow and deep sites overlap, thus only one symbol may appear.

... Country codes are M=Mexico, B=Belize, H=Honduras. Region codes are N=north, C=central, S=south, CC= CayosCochinos, UT=Utila, RO=Roatan, GU=Guanaja, A=atolls. Reef Type codes are E=east facing, BR= back reef, NW=northwest facing, N=north facing, NE= northeast facing, S=south facing, P=patch reef, SE= southeast facing, W=west.

Site code	Site name	Country	Region	Reef type	Depth (m)	Total # corals	Latitude	Longitude
C1	La Bonanza	M	N	E	1	68	20.96482167	86.81482333
B2	Bocana	M	N	E		32	20.85833333	86.87333333
B1	P. Morelos-F	M	N	E	1	45	20.84166667	86.88
C13	S. Puerto Moreles	M	N	E	3	62	20.82396817	86.87646583
D7	Punta Moroma	M	N	E	1	54	20.727489	86.96375567
D6	S. Punta Moroma	M	N	E	1	55	20.71383117	86.97770317
F2	S. Akumal	M	C	E	1	51	20.41333333	87.31666667
F3	Chenchomac	M	C	E	2	41	20.4	87.30833333
E9	La Caburn	M	C	BR	2	36	20.20634117	87.4263455
E10	S. Pescadors	M	C	BR	1	45	20.20420083	87.428105
F1	N. Akumal	M	C	E	1	60	20.20420083	87.428105
G3	Punta Allen-N	M	C	E	2	21	19.7991925	87.4480875
G4	Punta Allen-S	M	C	E	1	46	19.78094283	87.43806683
I4	N. Majahual	M	S	E	1	38	18.720435	87.7026935
I3	S. Majahual	M	S	E	1	46	18.6998355	87.7104505
H4	N. Xcalak	M	S	E	1	46	18.28860467	87.8238275
H2	S. Xcalak	M	S	E	1	47	18.25010417	87.82898267
AM10	Bacalar Chico	B	N	BR	3	39	18.1468285	87.82373617
AM12	Rocky Point	B	N	E	3	64	18.126095	87.82404733
AM14	Basil Jones	B	N	E	3	51	18.085878	87.86947867
AM1	Tres Cocos	B	N	E	3	54	17.92919933	87.94350217
AM3	Hol Chan	B	N	E	3	87	17.86317417	87.97878933
AM9	Coral Gardens-Patch	B	N	P	3	65	17.83382533	87.99466267
AM7-1	Caye Caulker	B	N	E	3	88	17.70842133	88.0130305
AM7-2	Caye Caulker back	B	N	E	3	55	17.70842133	88.0130305
AM5	Caye Chappel	B	N	E	3	96	17.68868567	88.0158575
T1	Gallows-N	B	C	E	3	50	17.48748783	88.0441065
T2	Gallows-S	B	C	E	3	51	17.45736667	88.03515867
T4	Sergeant's	B	C	E	3	58	17.392484	88.0373045
T16	Rendezvous-patch	B	C	P	3	54	17.25301983	88.05680417
T15A	Rendezvous	B	C	E	3	61	17.23273167	88.04335017
T13	Alligator	B	C	E	3	64	17.20942317	88.04989467
S26	Pelican patch	B	C	P	3	57	17.15327383	88.055935
S25	N. S. Long Rock	B	C	E	3	38	17.09371817	87.99950133
S22A	S. Cross Cay	B	C	E	3	78	16.96292283	88.036489
S1A	Tobacco	B	C	E	3	23	16.91908483	88.04736267
S2A1	Tobacco Cut-front	B	C	E	3	44	16.88915667	88.06447517
s2A2	Tobacco Cut-back	B	C	BR	3	49	16.88915667	88.06447517
S3A	S. Tobacco	B	C	E	3	56	16.87347117	88.065355
S4A	S. Water	B	C	E	3	99	16.81367933	88.07865333
S5	Curlew Cut	B	C	E	3	64	16.76749167	88.07825633
S21	Central Gladden	B	C	E	3	67	16.62036183	88.05604233
S17	E. Tarpon	B	C	P	3	65	16.61627417	88.137737
S16	W. Tarpon	B	C	P	3	83	16.60590467	88.1497855
S7	Swab Patch	B	C	P	3	55	16.54602167	88.00545583
S19	Gladden Spit	B	C	E	3	73	16.53345833	87.98237283
S15	Laughing Bird	B	C	P	3	78	16.442864	88.19636483
S9	Ranguana #1	B	S	NE	3	69	16.32513117	88.13898167
S10	Ranguana #2	B	S	SE	3	34	16.320169	88.14160483
S14	Nicholas	B	S	E	3	39	16.11731883	88.25945567
LH3	Long Cay	B	A	BR	2	27	17.22265	87.60405
T6	W. Turneffe	B	A	W	3	58	17.342906	87.9518815
T7	Grassy Key	B	A	E	3	59	17.47166667	87.78666667
T9	Pelican	B	A	E	3	65	17.40833333	87.77833333
T11	Soldier	B	A	E	3	43	17.33333333	87.8
GL1	East Cut- Glovers	B	A	E	3	48	16.75418267	87.78800917
GL2	Middle Cay	B	A	SE	3	39	16.74764333	87.79603433
GL3	Carmen	B	A	E	3	45	16.77821517	87.75662733
GL4	NE Glovers	B	A	NE	3	56	16.7962075	87.74399417
GL19	NW Glovers	B	A	W	3	94	16.84359133	87.84006017
GL21	CW Glovers	B	A	W	3	65	16.8231315	87.84897583
CC1A	Cayos-channel	H	CC	NW	3	34	15.97379933	86.4890475
CC10	Cayos- south	H	CC	N	3	36	15.93601767	86.533186
CC11	Cayos- edge	H	CC	NE	4	29	15.94128017	86.52745683
CC26	Cayos- east end	H	CC	NE	5	64	15.97880433	86.46617367
CC27	Cayos- stadium	H	CC	SE	3	26	15.960855	86.45997783
UT3	Light Tower	H	UT	SE	3	21	16.08487483	86.89233383
UT7A	Lagoon -1	H	UT	NW	3	62	16.12195917	86.91474633
UT8A	Lagoon-2	H	UT	NW	3	91	16.11362817	86.94836517
RO3A	West End	H	RO	N	3	23	16.27281733	86.60219383
RO4A	Cut	H	RO	N	2	21	16.31345817	86.59197467
RO5A	NC Roatan	H	RO	N	3	36	16.33868167	86.56429967
RO22A	UK cut	H	RO	N	2	46	16.424877	86.36490417
RO28	NE Roatan	H	RO	N	3	13	16.4388085	86.2745835
BA1	Barbaretta	H	RO	E	2	31	16.42150283	86.09903833
RO33	Fantasy Island	H	RO	S	4	63	16.35755367	86.433263
GU4	North side	H	GU	N	3	58	16.49577867	85.90520583
GU5A	Volcano tubes	H	GU	NE	2	18	16.5191835	85.86648533
GU10	Guanaja- east	H	GU	S	2	40	16.52256317	85.84083817

Table 2. Deep survey site information. Country codes are M=Mexico, B=Belize, H=Honduras. Region codes are N=north, C=central, S=south, CC= Cayos Cochinos, UT=Utila, RO=Roatan, GU=Guanaja, A=atolls. Reef Type codes are FR= fore reef, E=east facing, N= north facing, S=south facing, W=west facing.

Site code	Site name	Country	Region	Reef type	Total # corals	Depth	Latitude	Longitude
C12	S. Puerto Morelos	M	N	FR-E	74	9	20.83123683	86.87079033
D1	Punta Marona	M	N	FR-E	109	9	20.727666	86.9578065
E1	The Whale	M	C	FR-E	45	11	20.188145	87.43106617
E3	La Picina	M	C	FR-E	70	10	20.22665617	87.411293
G1	Sian Ka'an-N	M	C	FR-E	81	13	19.84553583	87.43092667
G2	Punta Allen	M	C	FR-E	60	10	19.81224417	87.44673567
I1	Majahual	M	S	FR-E	78	11	18.71187867	87.70373417
I2	Majahual-S	M	S	FR-E	71	13	18.70020033	87.70725867
H3	Xcalak-N	M	S	FR-E	73	15	18.291877	87.81803917
H1	Xcalak-S	M	S	FR-E	60	15	18.2344615	87.82687433
AM11	Bacalar Chico	B	N	FR-E	68	17	18.15185483	87.81597933
AM13	Rocky Point	B	N	FR-E	69	13	18.12058567	87.820936
AM15	Mexican Rocks	B	N	FR-E	70	18	17.99502617	87.90047417
AM2	Tres Cocos	B	N	FR-E	113	14	17.92979483	87.939157
AM4	Hol Chan	B	N	FR-E	100	13	17.86385	87.97233067
AM8	Cay Caulker	B	N	FR-E	106	17	17.71711717	88.00362133
AM6	Caye Chaple	B	N	FR-E	97	15	17.685703	88.0112065
T3	Gallow-S	B	C	FR-E	88	10	17.462082	88.03373717
T5	Sergeant's	B	C	FR-E	92	8	17.39275217	88.03512117
T15B	Rendezvous	B	C	FR-E	82	12	17.23273167	88.04335017
T14	Alligator	B	C	FR-E	79	12	17.233386	88.04390267
S24	N. S. Long Rock	B	C	FR-E	100	16	17.093541	87.99748433
S23	N. Columbus	B	C	FR-E	90	18	17.03014433	87.99627733
S22B	S. Cross	B	C	FR-E	83	17	16.96292283	88.036489
S1B	Tobacco	B	C	FR-E	36	14	16.91908483	88.04736267
S3B	S. Tobacco	B	C	FR-E	42	13	16.87347117	88.065355
S4B	S. Water	B	C	FR-E	90	14	16.81367933	88.07865333
S6	Curlew	B	C	FR-E	105	13	16.76612917	88.0758585
S20	Central Gladden	B	C	FR-E	97	16	16.62046383	88.05147717
S18	Gladden Spit	B	C	FR-E	97	20	16.53179533	87.97683133
S8	Pompion	B	S	FR-E	83	15	16.37314267	88.08945733
S11	Ranguana	B	S	FR-E	46	10	16.31811983	88.13364933
S12	N. Spot	B	S	FR-E	57	10	16.241532	88.18008383
S13	Nicholas	B	S	FR-E	13	13	16.10899333	88.255604
LH2	Odd-Wreck	B	A	FR-E	38	18	17.21418333	87.52188333
LH1	Halfmoon Cay	B	A	FR-E	40	18	17.19803333	87.52506667
T8	Grassy	B	A	FR-E	64	18	17.46333333	87.77666667
T10	Pelican	B	A	FR-E	69	11	17.4	87.7725
T12	Soldier	B	A	FR-E	72	14	17.325	87.795
GL15	North East	B	A	FR-E	68	12	16.80817017	87.73692383
GL16	Carmen	B	A	FR-E	61	10	16.77932033	87.75542567
GL17	Middle	B	A	FR-E	79	10	16.74468767	87.79668883
GL18	East	B	A	FR-E	70	10	16.75060983	87.78741383
GL20	North West	B	A	FR-W	76	10	16.84326417	87.839792
GL22	Central West	B	A	FR-W	83	10	16.82203717	87.8494265
GL23	West cut	B	A	FR-W	82	13	16.79459283	87.860268
CC1B	Cayos channel	H	CC	FR-N	50	10	15.97379933	86.4890475
CC2	Cayos wall	H	CC	FR-N	47	14	15.976562	86.48739533
CC25	Cayos north	H	CC	FR-N	63	14	15.96346733	86.50522133
UT1	Utila-SE1	H	UT	FR-S	71	13	16.10730883	86.87458833
UT2	Utila-SE2	H	UT	FR-S	85	10	16.0897995	86.88194833
UT4	Utila- SW1	H	UT	FR-S	79	9	16.0627145	86.958461
UT5	Utila-SW2	H	UT	FR-S	62	8	16.0718125	86.95053767
UT6	Utila-bl. coral wall	H	UT	FR-S	46	6	16.08267017	86.91860333
UT7B	Utila-NC	H	UT	FR-N	62	11	16.12195917	86.91474633
UT8B	Utila-NC-2	H	UT	FR-N	85	10	16.11362817	86.94836517
RO34	Fantasy Island	H	RO	FR-S	98	13	16.3512075	86.43735067
RO1	SW Roatan-1	H	RO	FR-S	67	10	16.2728655	86.59097683
RO3B	West End	H	RO	FR-N	37	8	16.27281733	86.60219383
RO4B	Anthony's	H	RO	FR-N	47	10	16.31345817	86.59197467
RO5B	North Central 1	H	RO	FR-N	38	10	16.33868167	86.56429967
RO6	North Central 2	H	RO	FR-N	40	10	16.352672	86.5409
RO7	Roatan-Central	H	RO	FR-N	53	10	16.3557565	86.5364315
RO21	Roatan-NE1	H	RO	FR-N	67	13	16.373604	86.49352683
RO22B	Roatan-NE2	H	RO	FR-N	40	15	16.424877	86.36490417
RO27	Roatan-NE3	H	RO	FR-N	46	11	16.43923233	86.28634767
GU1	Guanaja-NC1	H	GU	FR-N	85	14	16.47895033	85.92145467
GU2	Guanaja-NC2	H	GU	FR-N	76	11	16.4906395	85.911702
GU3	Guanaja-NC3	H	GU	FR-N	46	11	16.4968085	85.9025825
GU5B	Guanaja-VolcanoTubes	H	GU	FR-N	50	11	16.5191835	85.86648533
G11	Guanaja-south side	H	GU	FR-S	52	6	16.46896183	85.8235915
G12	Guanaja-SE	H	GU	FR-S	66	8	16.40591383	85.87866267

Coral condition assessments- For stony coral (scleractinian and *Millepora* spp.) assessments, 2-4 observers swam transects using the "weighted bar swimming transect method" (McField, 1999). In this method, a one meter ¾" diameter PVC tube filled with sand with 5 markings spaced 25 cm apart was used to randomly census corals. Each observer swam in a straight line parallel to the reef axis with the bar held horizontally perpendicular out in front. Every 10 cycle kicks the bar was dropped on the substrate (= 1 bar-drop) and the species and condition of the coral (=>10 cm) nearest each mark was assessed. The five marks demarcated five adjacent non-overlapping circles and the closest coral within 12.5 cm of each mark was assessed. If no coral was within a given circle, it was recorded as zero. If a large coral was under the bar, each mark the coral occupied was scored similarly. This provided a measure of the relative importance of corals species and their condition as a function of coverage in each reef area. For each "bar-drop", anywhere from zero to five corals were assessed. The total number of "bar drops" and corals assessed was recorded for each site. A minimum of 12 bar drops was done at each site.

Each colony less than or equal to 10 cm was assessed for species, % recent and old mortality (plan view), bleaching (pale, partly bleached, bleached), diseases, and hurricane damage (knocked over, broken, abraded). A coral colony was defined as any autonomous, freestanding coral skeleton that was still identifiable to genus level (preferably to species level) based on the presence of living tissue or identifiable corallites. Colonies that were 100% dead and knocked over or dislodged were also assessed. We considered corals with living tissues distributed among several physiologically separate units as the same colony. For example, species like the columnar *Montastraea annularis* that grow as clusters of basally interconnected lobes having live tissues only at their summits were assessed as one colony. We considered corals like *Acropora cervicornis*, that grow as thickets, as one colony unless we could distinguish the boundaries of the constituent colonies. Although we did not specifically survey for species diversity or richness, our survey method did provide a good indication of species abundance of major reef building corals (those corals that contribute most to the three dimensional architecture).

We distinguished partial coral mortality to include both "recent" dead and "old" dead as used in the Atlantic and Gulf Rapid Reef Assessment (AGRRA) method (see http://coral.aoml.noaa.gov/agra/methods.html). The amount of "recent dead" approximates coral mortality that occurred within the previous days-months, while the amount of "long dead" represents an integration of disturbances influencing coral mortality over longer time scales. "Recently dead" is defined as any non-living parts of the coral in which the corallite structures are white and either still intact or covered over by a thin layer of filamentous algae or mud. In contrast, "old dead" is defined as any non-living parts of the coral in which the corallite structures are either gone or covered over by organisms that are not easily removed (e.g., certain algae and invertebrates). The use of coral mortality as an indicator of coral condition is well established (e.g., Dustan, 1977; Garzon-Ferreira and Kielman, 1994; Ginsburg, 1994; Bak and Nieuwland, 1995; Lewis, 1996).

Causes of recent coral mortality were recorded (but only with positive identification) focusing primarily on bleaching or hurricane damage, although diseases, predation by fish or invertebrates, or other condition (algal or invertebrate overgrowth, sedimentation, and coral aggression) were also recorded. For this report, bleaching refers to the remnant bleaching observed due to the 1998 event. Tissue that was bleached was distinguished by white (translucent) or pale coloration, although the color patterns differed between species and intensity of bleaching. Bleached tissue was recorded as pale (discoloration of coral tissue), partly bleached (patches of fully bleached or white tissue not due to other coral diseases), or wholly bleached (tissue is totally white, no zooxanthellae visible and over 90% of colony tissue was bleached). Since our surveys spanned a four month window during which corals continued to recover their zooxanthellae, the results are somewhat influenced by when the surveys took place.

Hurricane damage was classified as knocked over (whole colony dislodged from original growth position), broken (part of colony or branches are broken off), or abraded (tissue damage or loss due to chafing). Areas of recent mortality and adjacent coral tissue were examined closely to determine if calices were disrupted or damaged (fish bites), if corallivores were present (e.g. gastropods or polychaetes), if polipary structures were abnormally large or tumorous (hyperplasm or neoplasm), or if a disease condition existed. Coral disease conditions were recorded based on color, including black (black-band disease), white (white-band or other white-type diseases in acroporids, white plague in massive corals), other (including yellow-blotch disease or red-band disease and unknown) (Appendix 2).

Since this was mainly a visual census, it was important to have consistent and comparable visual estimates and to minimize individual bias among different observers. Therefore, we carefully standardized methods prior to data collection. All surveyors were trained and consistency exercises were conducted regularly to minimize differences in visual estimates and build consistency between observer estimates.

Data analysis- The data for bleaching, hurricane damage, and disease are presented as the percentage of individual corals exhibiting a particular condition (incidence). All corals assessed are weighted equally, independent of their size or how much of the bar they occupy. For mortality estimates, we wanted to take into account the spatial significance of corals contributing to the existing cover. Therefore, the data are presented as number of bar tics with a particular value of recent/total mortality. The main difference is that larger corals that occupy more bar tics are given more weight than smaller corals.

One of the objectives of the survey was to identify any patterns in response to the hurricane and 1998 bleaching event. To do this we examined the data on two different spatial scales, regional (between countries) and reefal (within country). We also examined differences between reef types and differences between coral species. To identify regional differences, we compared sites between countries, Mexico Belize, and Honduras. For reefal scale patterns, we compared data between similar areas within a country. For Mexico, we divided the areas into north, central, and south. For Belize, we divided survey sites into north, central, south, and atolls, based on similar geomorphological classifications by Miller and Macintyre (1977). For Honduras, we divided sites based on individual islands surveyed - Cayos Cochinos, Utila, Roatan, and Guanaja. We examined differences between reef types (e.g., patch reef, fringing), although no patch reefs or back reefs were surveyed in Honduras. We also investigated patterns between reefs that had different exposure levels to prevailing oceanic currents. Exposure levels were defined as exposed, partially protected, and protected (although no protected shallow sites were surveyed in Mexico). To identify interspecific differences, we looked at how individual coral species responded to and were affected by the two events. A more detailed statistical analysis of the data is currently underway

Limitations- While we believe our surveys provided a good indication of the relative condition of MBRS reefs and the extent of impact from Hurricane Mitch and bleaching, we also recognize several limitations of the data. The most important of these were 1) lack of pre-existing data from the majority of sites; 2) surveys took place 5-9 months after the peak events; 3) evidence of on-going lingering effects; 4) focus on scleractinian reef building corals.

The lack of preexisting information at the majority of sites prevents translating our data on percentages of mortality and physical destruction into more quantifiable terms such as loss of coral cover or loss of rogosity. The recent mortality percentages do provide an indication of what the loss of coral cover has been, however the relationship needs to be better established with a comparative study. The fact that our surveys took place 5-9 months after the peak hurricane and bleaching events rather than immediately after also introduces a number of factors which complicates associating damage at a particular site to one of the two disturbances. In the case of hurricane damage, it is possible that winter storms contributed to or altered some of the physical damage results during the interim period (November-March/June). For bleaching damage, the main factor was that during the interim time, the appearance of recently dead corals continued to change so that associating them with the bleaching disturbance (as opposed so an earlier disturbance) became more difficult. Recent mortality for some species (*Millepora complanata*) was more difficult to identify than others because distinct corallite structures are less evident. We overcame this limitation by visiting monitoring sites early on where the recent disturbance history was known so that a clear "search image" of characteristic bleaching mortality for each species could be developed. The fact that ongoing lingering effects such as diseases were evident at many sites suggests that our surveys may have been conducted before the full consequences of bleaching and hurricane damage have become evident. We believe that the bulk of change has taken place, but that there will likely be smaller amounts of change attributable to one of the two events that may well continue for several more years. Finally, our survey only examined scleractinian corals and Millepora spp. > 10 cm and do not reflect damage (especially hurricane) to other benthic invertebrates (sponges, gorgonians, soft corals, etc.) or fish populations. For the most part, damage to these other invertebrates was reflected by damage to hard corals, but this was not always the case. In several instances we observed piles of accumulated soft corals within reef cavities and on adjacent beaches but a lack of damage to hard corals. This was particularly true for sites lacking significant scleractinian coral development.

Cumulative Impacts - Since there was considerable variability in the level of disturbance from the 1998 disturbance events, we developed a ranking system based on the cumulative amount of disturbance due to recent mortality, bleaching, disease, and hurricane impacts to help determine the condition of reefs. The level of disturbance is divided into three categories: "Low", "Moderate", and "Severe" for each country (see end of Result section for results). Each reef was placed in a category by ranking the main disturbance factors (recent mortality, bleached, diseased, and hurricane damage). Recent mortality had a heavier weight in the ranking process, while bleached, diseased, and hurricane damage had equal weights. In some cases, old mortality may have been high, but is not included in the ranking since it could not be attributed to the 1998 events. "Low" disturbance reefs experienced only minor damage although some transient (often non-lethal) or localized effects may have been present. Recent mortality was below 10% and the other disturbance impacts (bleach, hurricane, disease) were lower than the average for the region "Moderate" disturbance reefs experienced moderate to severe levels of damage, usually with recent mortality between 10-20%, and a moderate to high amount of bleaching, disease, or hurricane damage. "Severe" disturbance reefs experienced serious damage, with recent mortality greater than 20% and usually high disturbance.

Results

The following section summarizes results of the field surveys including community composition, remnant coral bleaching, incidence of coral diseases, physical hurricane damage, and coral mortality. Within each subsection, regional, in-country, and interspecific patterns are discussed. This section concludes with a synthesis of cumulative damage for each country.

Community composition

The MBRS region contains a diverse variety of stony coral species (scleractinian and *Millepora* spp.). Much of the variation in the community composition was due to the variety of reef types found on local and regional spatial scales along the MBRS. For shallow sites in the MBRS region, at least 26 species were observed during survey transects (Fig 10a, b). *Acropora palmata* was the most abundant species, comprising 33% of all corals assessed (although many of these colonies were standing dead – 100% dead tissue, but still in growth position). Other important reef building species included *Millepora complanata* (13%), *Agaricia tenuifolia* (10%), *Montastraea annularis* (10%), *Diploria* strigosa (7%), and *Porites astreoides* (7%). *Acropora palmata* was more abundant in Mexico (>50% of all species surveyed), Belize and Honduras had similar amounts (~30%) of *A. palmata. Porites astreoides*, *M. complanata*, and *D. strigosa* were the next three abundant species in Mexico. In Belize, *Millepora complanata*, *M. annularis*, and *A. tenuifolia* were the other three abundant species. In Honduras, *Diploria strigosa*, *Agaricia* sp., *P. astreoides* and *M. annularis* were also abundant. More species were observed at deep fore reef sites (> 29 species). *Montastraea annularis* was the most dominant species in the region, comprising 20% of the total. *Montastraea franksi*, *Agaricia agaricites*, *M. faveolata* were also abundant (14%, 11%, 10%, respectively) in the region. Other important reef building species included *M. cavernosa* (6%), *Porites astreoides* (6%), and *Diploria strigosa* (5%). *Montastraea annularis*, *M. franksi*, *M. faveolata* and *Agaricia agaricites* were the most common species in both Mexico and Belize, whereas, *P. astreoides* and *D. strigosa* replaced *M. franksi* and *M. faveolata* in abundance. *Montastraea annularis* was slightly more abundant in Belize than Mexico or Honduras. The spatial variation in the region is explained by a combination of physiochemical, geological, and environmental variables (e.g., light, topographic features, currents, winds, temperature), as well as biotic processes or interactions (e.g., life history strategies, predation, competition).

Sequence of events

A good illustration of the impacts, especially synergistic effects, on the MBRS region from the bleaching and hurricane events comes from two sets of time series photographs taken by naturalist Greg Smith in 1998-1999 near Basil Jones Cut, Ambergris, Belize (Photo 4). In the first series of photos, the initial photos taken in July 1998 show a fairly healthy thicket of *Acropora cervicornis* suffering from white band disease (WBD). By September 1, nearly 50% of the thicket had died from WBD and was covered by a thin layer of turf algae while the remainder of the thicket had bleached because of temperature stress. By October 1, the remainder of the thicket died from bleaching and turf algae was beginning to colonize it. The last photograph was taken on November 3 following the passage of Hurricane Mitch and shows the majority of the thicket was reduced to rubble by large storm waves and transported out of the frame. The second series of photos, of the massive coral *Montastraea annularis* located in the back reef near Basil Jones Cut, shows a slightly different sequence of bleaching disturbance. The first photograph taken October 1, 1998 shows the entire colony in a bleached state. Eight months later in June 1999, the colony showed signs of recovery although large patches of pale tissue were still evident. There was also evidence of recent mortality and the presence of white plague disease. By September 15, four months later and almost one year after the initial bleaching event, the colony still had not recovered full pigmentation and was in a stressed condition with both disease and recent mortality damage evident. Both of these sets of photographs illustrate the significant impact of bleaching on both branching and massive corals.

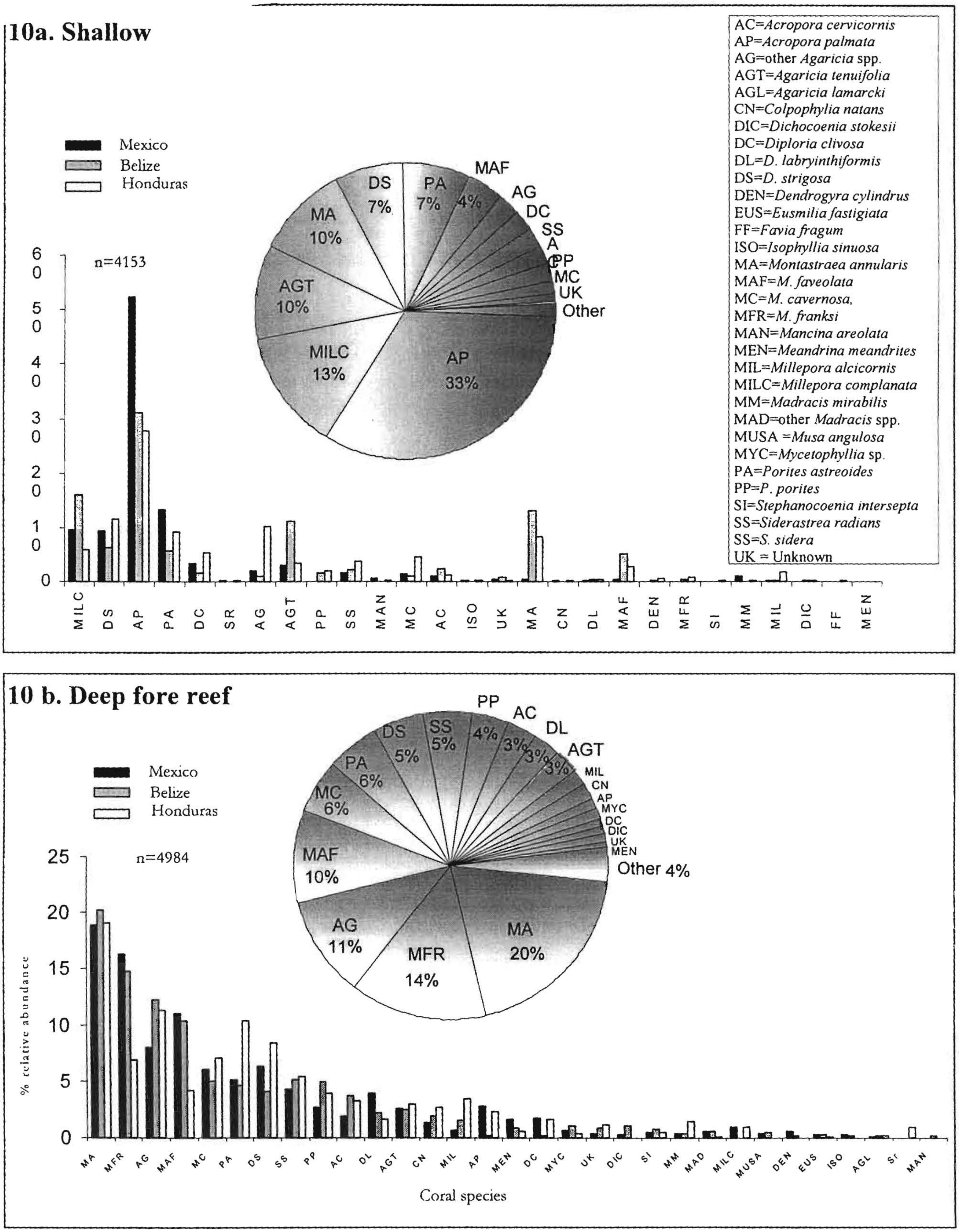
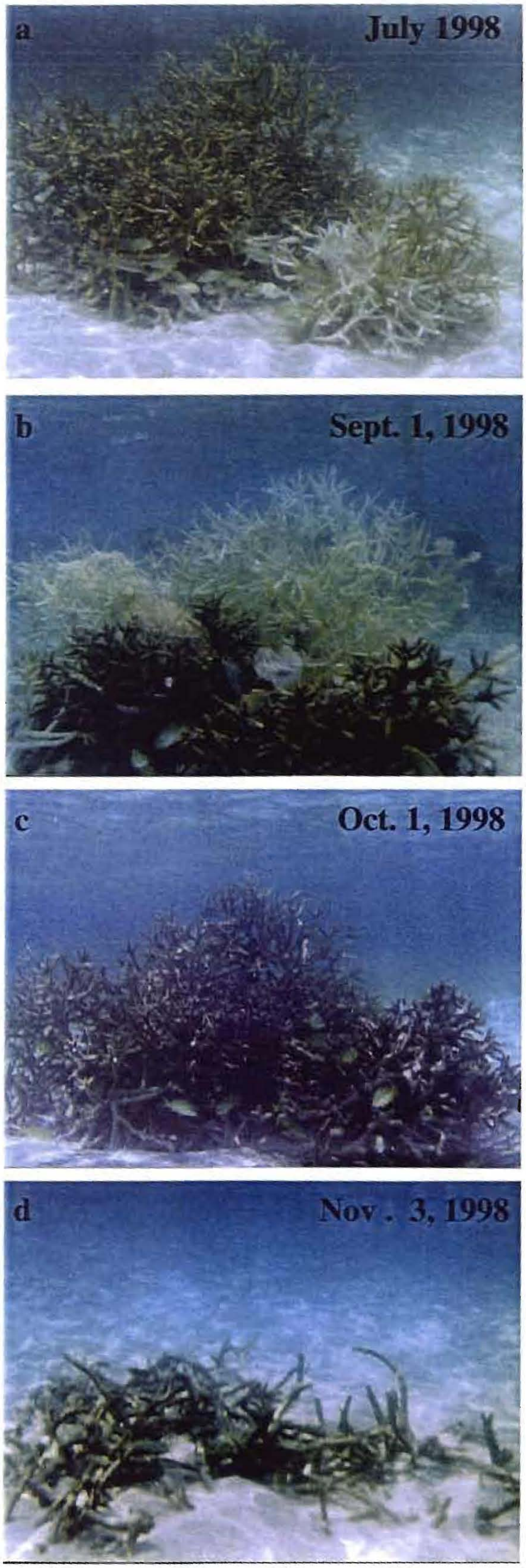


Figure 15. a) Coral community composition on shallow sites in the MBRS(top pie chart). Lower graph shows breakdown of coral species for each country. b). Coral community composition on fore reef sites in the MBRS (top pie chart). Lower graph shows breakdown of coral species for each country. Species abbreviations are given in 10a.



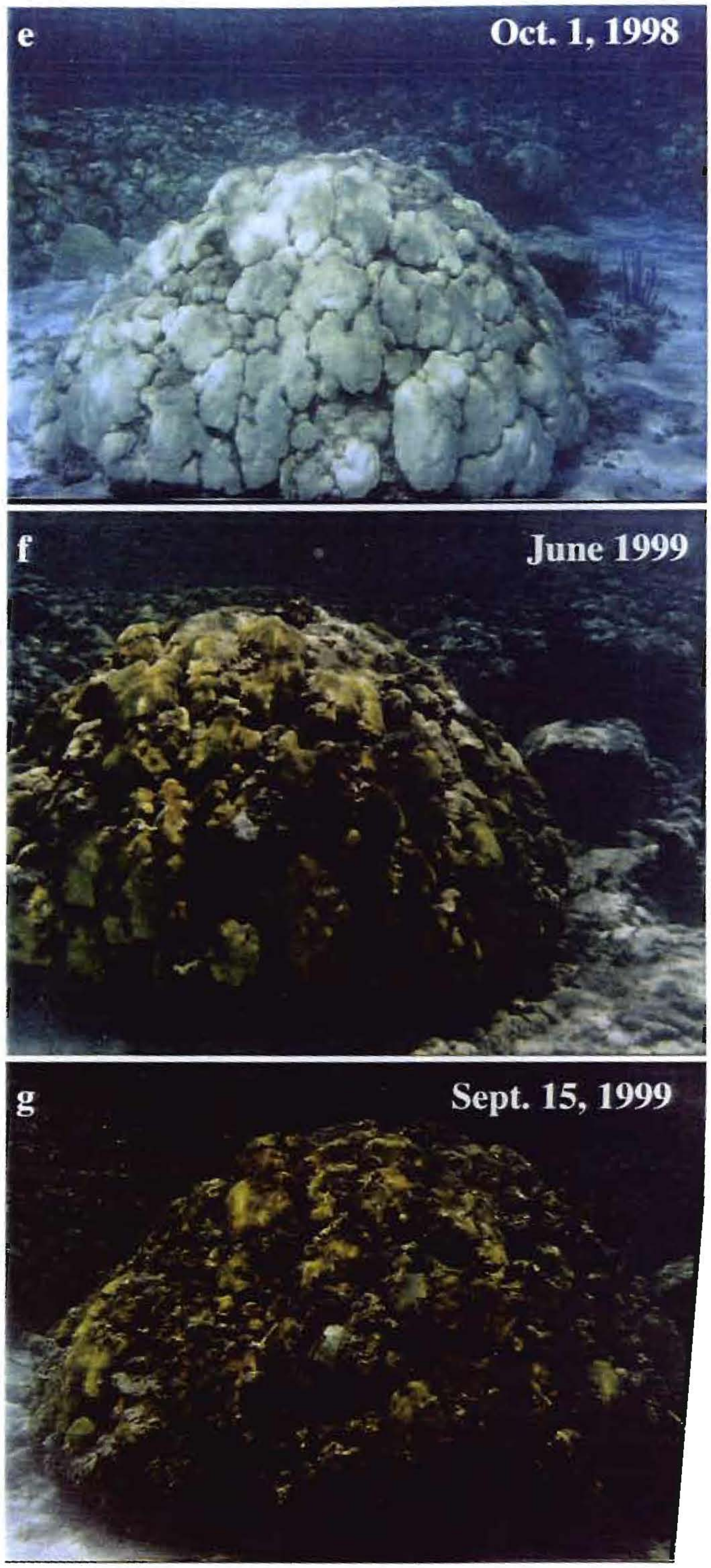


Photo 4. a-d). Time series of *Acropora cervicronis* at Basil Jone Ambergris, Belize. a). Most of thicket was alive, although smal portion was recently dead due to white band disease. t September, most of the colony was bleached. c). By Octob entire thicket was dead and covered with fine turf algae. d). Hu Mitch destroyed and removed a large portion of the dead thicke

e-f). Time series photos of large *Montastraea annularis* co back reef of Basil Jones Cut. e). Colony first began bleachir 26, 1998. f). By June 1999, colony was still pale and white pla ease was present. g). Incidence of disease continued to incre cause mortality.

Remnant Coral Bleaching

Prolonged coral bleaching was still present over much of the MBRS region up to 10 months after the initial event. Comparisons between different sites reveal significant patterns in bleaching that varied with spatial scale, reef type and depth, and coral species. For the entire MBRS region, remnant bleaching was highest on deep fore reef sites (23% of corals still exhibited tissue discoloration) whereas shallow sites had fairly low remnant bleaching (6%) (Fig. 11). The most prevalent type of remnant bleaching for the entire region was the category "pale" (19% deep, 5% shallow), followed by "partly bleached"(4%, 1%) and only a few cases of "bleached"(0.2%, 0.1%).

On a regional scale (between and within country differences), remnant bleaching was on average highest in Mexico (both shallow and deep), surveyed 7 months after the event, followed by Honduras and Belize surveyed 8.5 and 10 months after the event, respectively (Fig. 12). Within Mexico, there was significantly higher remnant bleaching on deep fore reefs in the southern area, whereas levels between shallow reef areas were more uniform. No colonies on Mexico's deep fore reefs were fully bleached and only <0.1% of shallow colonies were fully bleached. Between areas in Belize (for both shallow and deep fore reef sites), remnant bleaching was fairly uniform (except southern shallow reefs had much lower values). Shallow sites with the most remnant bleaching were typically more protected west facing reefs, patch reefs and back reefs which were often dominated by *Montastraea annularis*. Only 15 of 44 shallow sites showed no signs of bleaching, while the remaining sites displayed low incidence of mostly pale bleaching (4.6%). Within Honduras, there was low variation on shallow sites between the islands although there was high site to site variability within an area (=island). Cayos Cochinos deep fore reefs had the highest levels of bleaching (43%-significantly higher on average than all other islands), although more uniform patterns of bleaching were observed on all deep fore reef sites in the Bay Islands. It should be stressed that the levels of bleaching presented here represent the extent of remnant or prolonged bleaching evident in corals assessed at the time of the surveys and do not reflect lethal effects of bleaching, particularly for shallow sites. The lethal effects from the bleaching event are better represented in the recent mortality data discussed latter in this section.

Fourteen species in the shallow and 21 species in the fore reef displayed remnant bleaching (Fig. 13). *Montastraea faveolata*, *Millepora complanata*, and *Montastraea annularis* displayed the highest levels, with about 20-30% of all colonies of these species still pale bleached. The massive, major reef-building corals like *Diploria* spp., *Siderastrea siderea*, and *Stephanocoenia intersepta* also displayed high levels of remnant bleaching (Photo 5). Similarly on the fore reef sites the *Montastraea* complex had the most prolonged bleaching, *M. faveolata*, in particular showed the highest levels of pale bleaching – almost 50% of colonies. In some cases, colonies of *Montastraea annularis* complex, *Siderastrea siderea*, and *D. labyrinthiformis* had pale areas that were in the process of dying or infected by disease (see following sections).

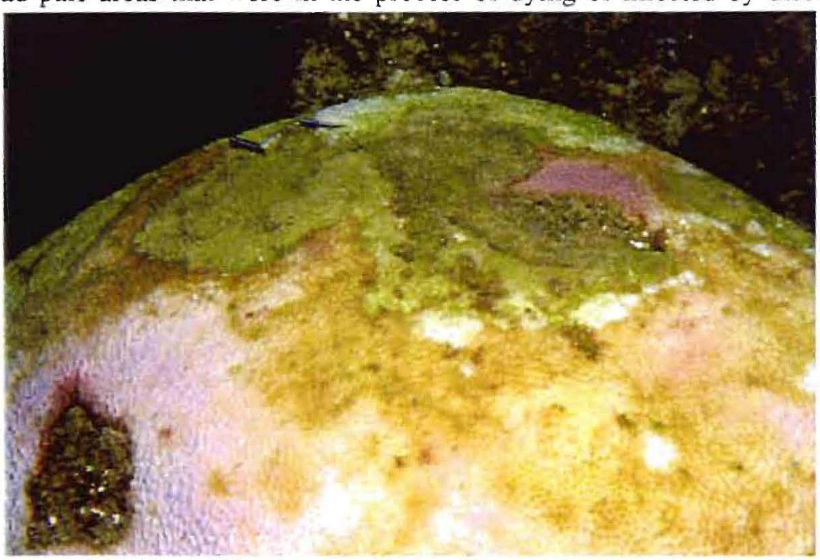


Photo 5a. Remnant bleaching in *Siderastrea siderea* in Hoduras, 9 months after initial 1998 bleaching event in Honduras. Photo courtesy of K. Marks, May 1999.

Remnant Coral Bleaching

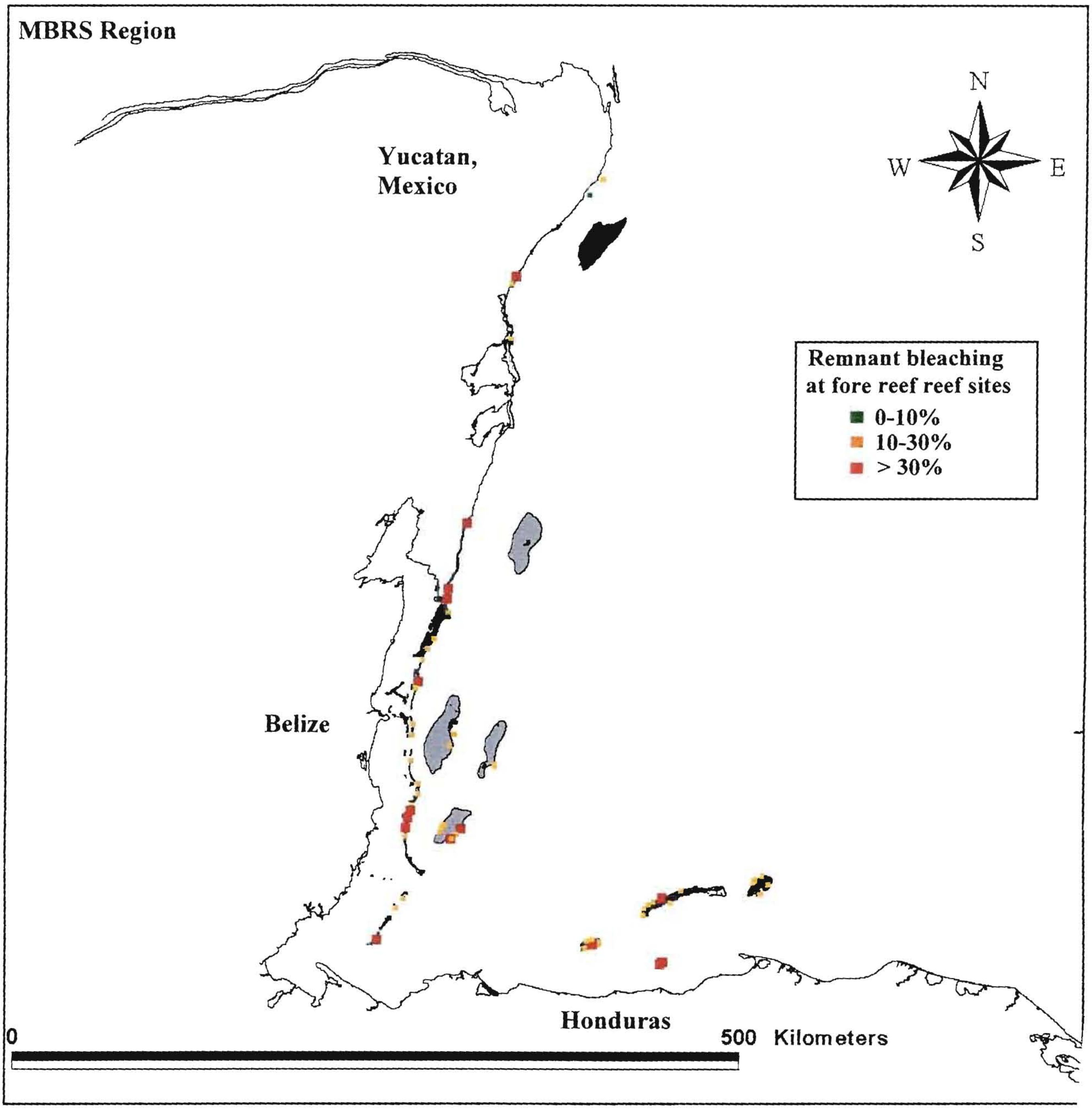


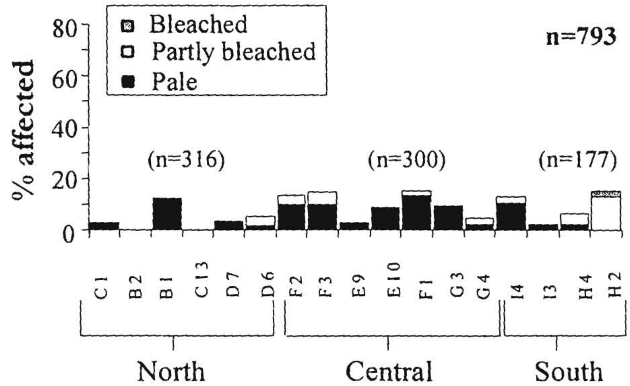
Figure 11. Spatial variation in remnant coral bleaching on fore reef sites recorded at the time of our surveys as the percent of colonies showing pale, patchy bleaching, or bleached tissue.

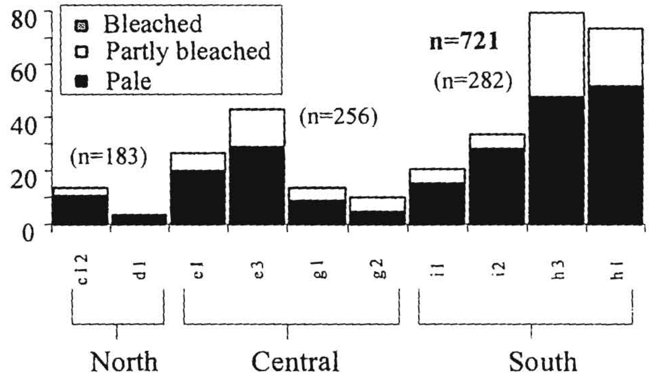
Bleaching

Shallow Reefs

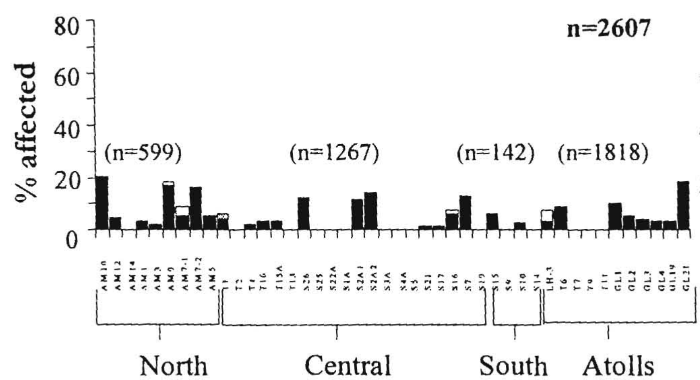
Fore reefs

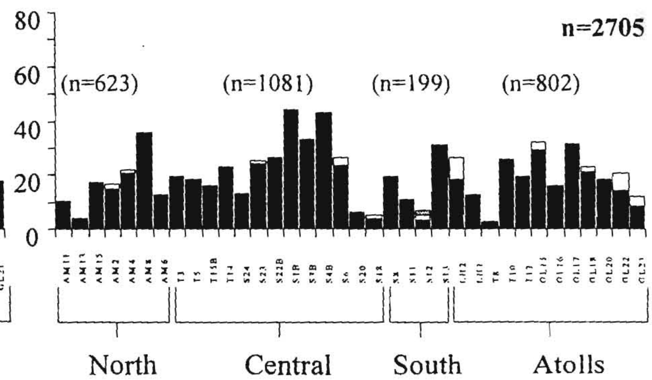
Mexico



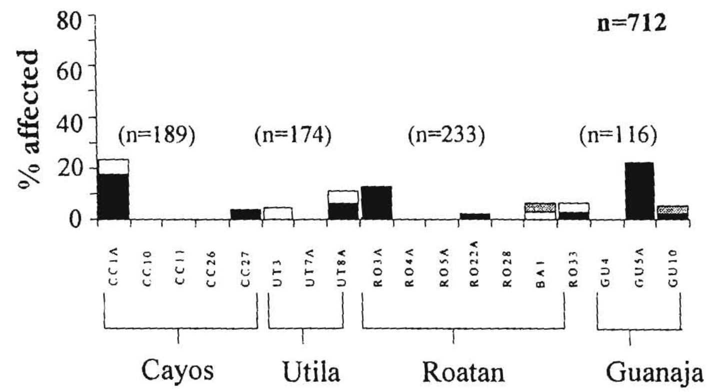


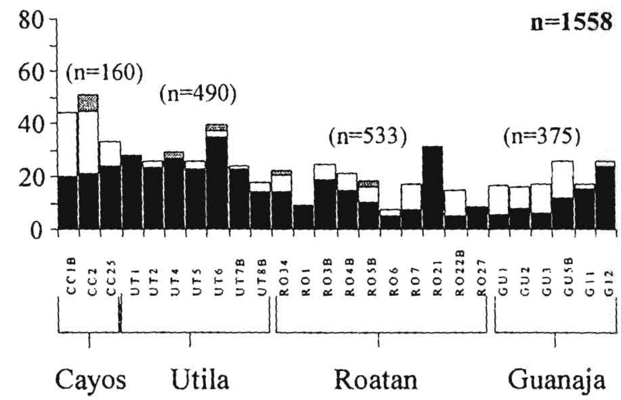
Belize





Honduras





Site Locations

Figure 12. Degree of coral bleaching in shallow and fore reef sites in Mexico, Belize, and Honduras. Total number of corals (n) surveyed is given for each country and each region within a country.

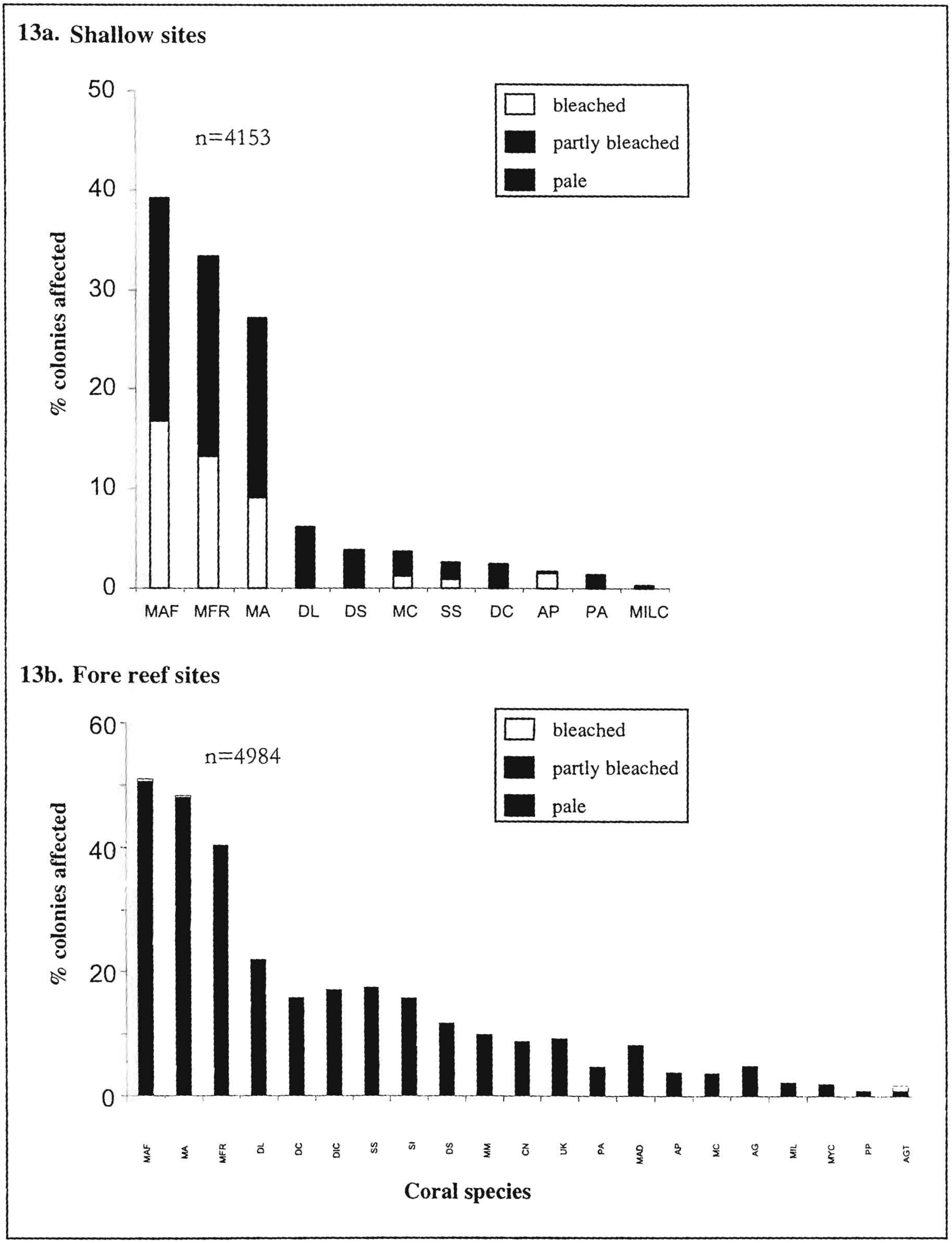


Figure 13a-b. Species in the MBRS region exhibiting remnant bleached condition at time of survey for shallow sites (a. top graph) and fore reef sites (b. bottom graph). See figure 10a for species abbreviations. Note different scales for each graph.

Coral Diseases

Coral diseases were evident at many of the sites we assessed in the MBRS region, particularly deep fore reef sites (7%) which had higher averages of total incidence of disease (all sites combined) than shallow sites (4%) (Fig. 14). There was a surprising amount of disease at fore reef sites in Honduras (10%), more so than what we observed at Belize (5%) and Mexico (3%). The shallow sites in Belize (6%) had more disease than Mexico (3%) or Honduras (2%). The most predominant diseased condition observed in both shallow and fore reef sites was "white", usually corresponding to white plague described by Dustan (1977) and Santavy and Peters (1997), and was often higher (by site averages) at deep fore reef sites than shallow sites, particularly in Honduras (8%).

Within-country comparisons showed several patterns between areas and reef types. Within areas in Mexico, the incidence of diseases observed at both shallow and deep fore reef sites was similar at northern (5% shallow, 3% deep) and southern (7%, 4%) areas, whereas the central area displayed a significantly lower incidence (0%, 1%). Within Belize, the total disease incidence was higher on shallow reefs in northern areas (12%) than any of the other areas. Protected shallow reefs (west-facing barriers, back reefs, patch reefs) in particular tended to have more infected colonies than exposed higher energy reefs (e.g., Bacalar Chico- AM10, Cay Caulker backreef-AM7, and Swab Patch- S7). For deeper fore reef sites, there was no significant difference between areas, although the incidence of disease at Glover's fore reefs was consistently high. Honduras' fore reef sites had similar high values between islands, although there was high variability on the site to site scale.

Intraspecific differences in the infection rate of diseases were large and help explain some of the site to site variance. Twelve species in the shallow sites and 11 in the deep sites were infected with disease (Fig. 15). The *Montastraea annularis* complex was the most affected genus for both shallow and deep sites in the region (Photo 6a-b). At fore reef sites, the *Montastraea* complex (*M. franksi* (22%), *M. faveolata* (17%), *M. annularis* (10%)) had significantly higher infection rates than other species, although *Diploria labyrinthiformis* (7%) also had high levels (Fig. 15a). A similar pattern was evident at shallow sites, although the infection rates for black-band disease in the *Montastraea* complex (~20%) was nearly 10 times higher than deeper sites (Fig. 15b). It is noteworthy to mention that very few acroporids were observed with active diseases (white band) during our surveys.

6a

Photo 6a-b. White plague disease on a). *Montastraea annularis* on shallow reef in Belize and b). *M. faveolata* on deep fore reef in Honduras.

6b

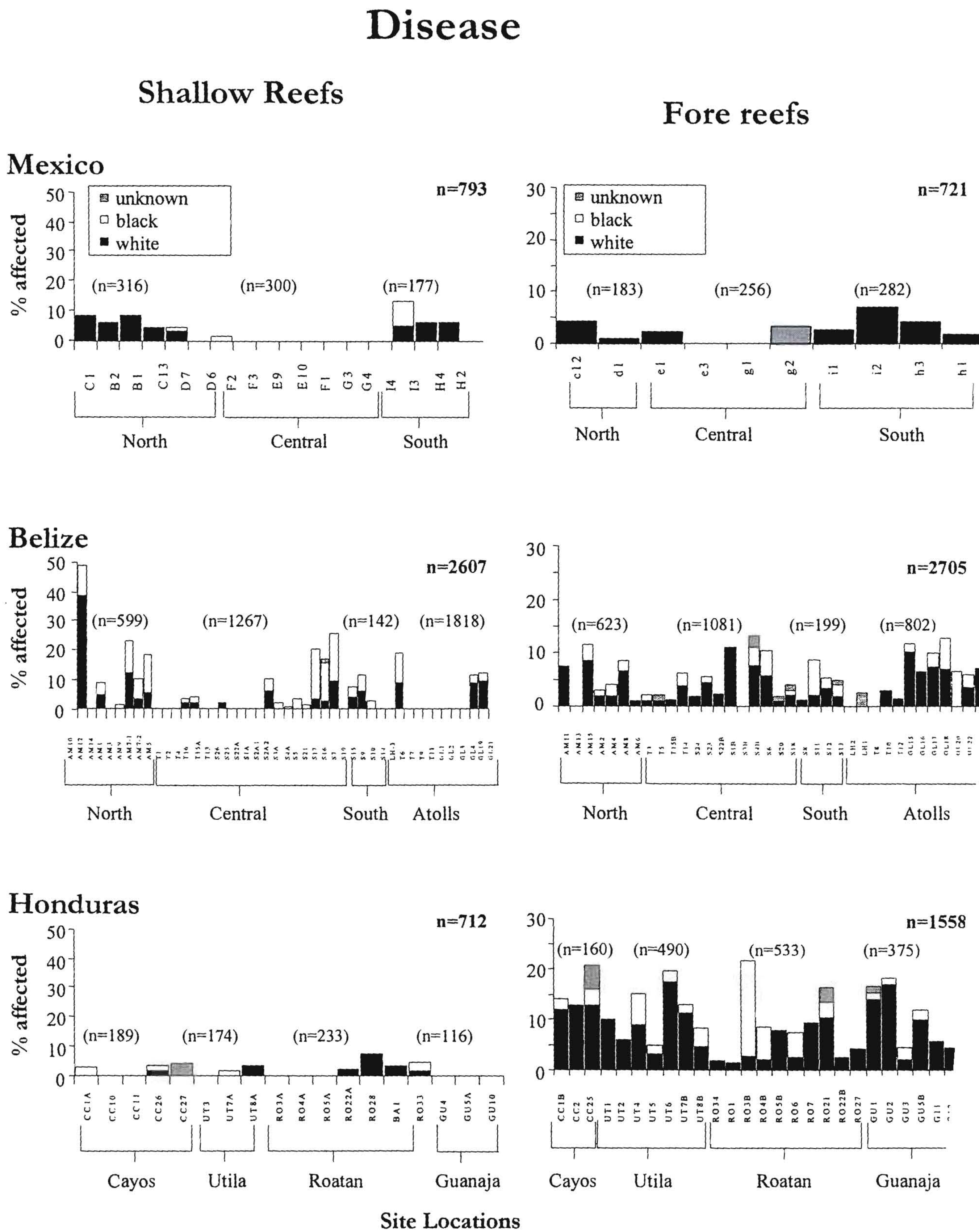


Figure 14. Incidence of coral disease observed in Mexico, Belize and Honduras. Total number of corals (n) surveyed is given for each country and each region within a country. (Note differences in scales for shallow and fore reef sites).

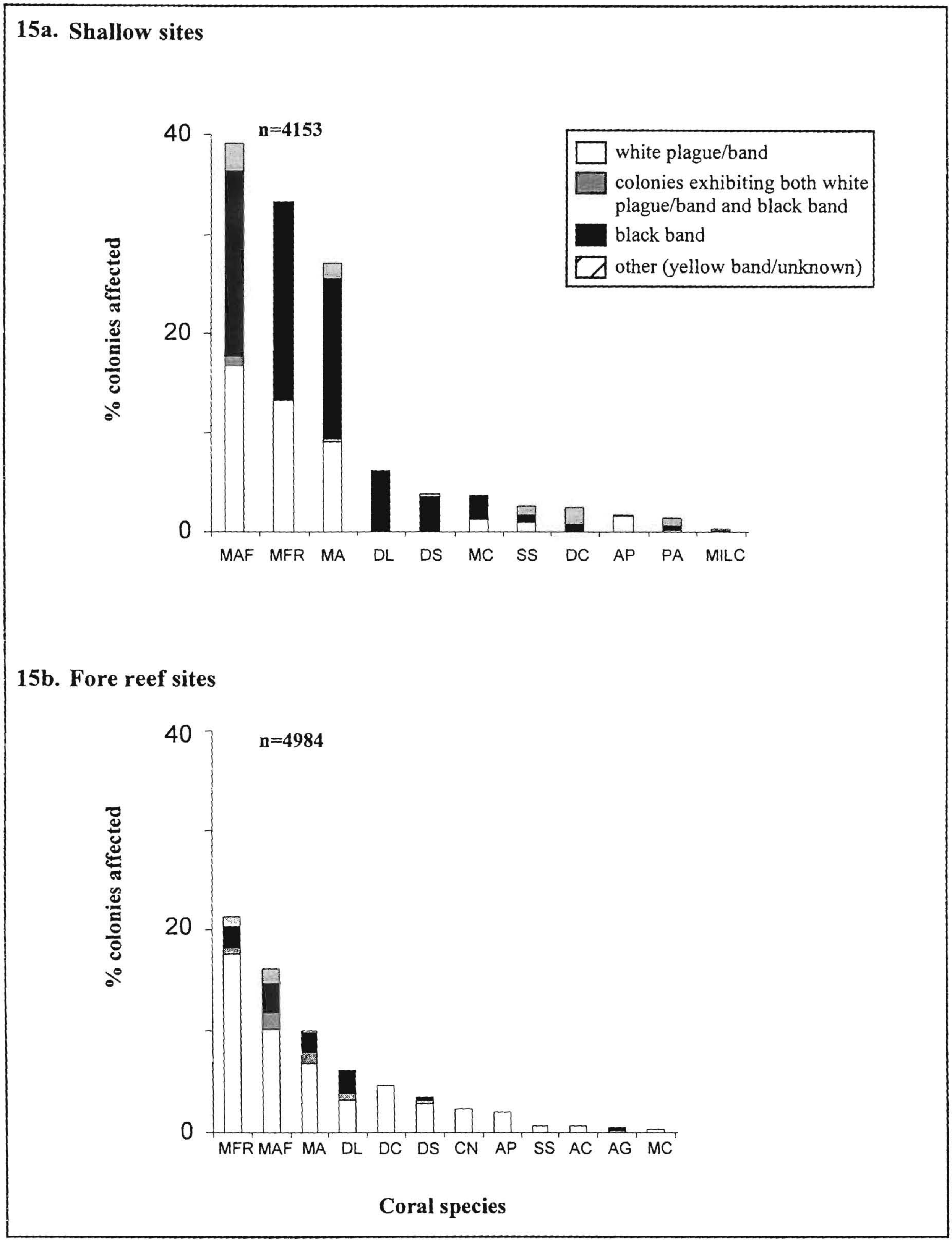


Figure 15a-b. Percentage of each species with diseased condition for the entire MBRS region. See figure 10a for species abbreviations.

Hurricane Mitch Damage

The extent of physical damage to reef corals observed in our field surveys was highly variable and often unpredictable (Fig. 16, Photo 8). Across larger spatial scales (between countries), the greatest degree of damage was observed in Belize, with 29% of colonies displaying signs of damage on shallow reefs while only 11% of colonies were affected in Honduras and Mexico. For deep fore reef sites, 5% of colonies were affected in Belize while Honduras and Mexico the percentage of colonies affected was 2% and 0.4%, respectively. The most prevalent type of hurricane damage recorded in all shallow sites combined was broken colonies (~8%), followed by knocked over corals (~ 6.7%) and abraded corals (~ 3.7 %). For deep fore reef sites, damage most commonly consisted of knocked over corals (2%) and only a few abraded colonies and broken colonies (0.4% each).

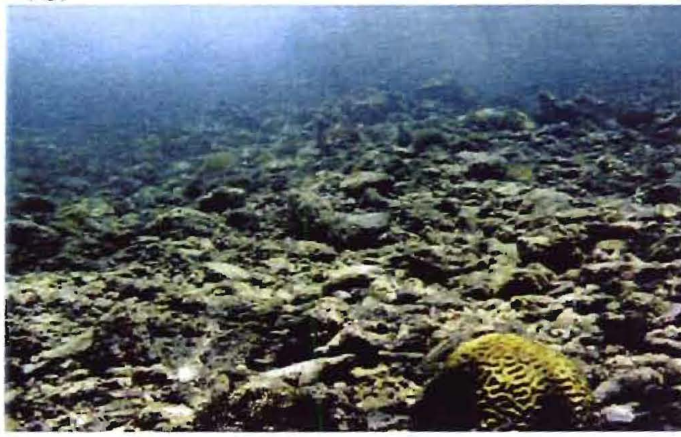
Across smaller spatial scales (between areas within a country), there was also significant variability in the degree of hurricane damage (Fig. 17). In Mexico, there was fairly low hurricane damage on shallow reefs (practically none on deep), although shallow sites in the southern and central areas had more damage than the northern Yucatan (Fig. 17). Most of the damage observed on shallow sites was abraded or broken corals with no knocked over colonies.

In Belize, shallow sites were impacted by storm damage significantly more than deep fore reef sites (Fig. 17). The total damage at shallow sites was similar between regions, although southern Belize (33% colonies affected) had slightly more than northern Belize (25% of colonies affected). The greatest distinctions were seen between sites with different exposure levels. In general, exposed east facing shallow sites experienced the highest degree of hurricane damage. East facing exposed shallow sites on Glover's and Turneffe atolls had considerable damage; NE Glover's (GL4) had the highest in region. Uniformly high damage was also seen on shallow exposed sites in the central barrier region (e.g., Tobacco-S1A, Tobacco Cut-S2A1). Other localized shallow sites were also heavily impacted (e.g., Chapel Cay-AM5 and Hol Chan-AM3 in the north, Ranguna-S9-Nicholas-S14 in the south). Protected shallow sites, particularly back reefs, patch reefs, reefs on the west (leeward) side of the atolls, and sections of the Belize barrier behind the shadow of the atolls experienced low to moderate hurricane damage. Damage to deep fore reef sites consisted mainly of knocked over or broken corals. In several cases, when high damage was seen on exposed shallow sites along the barrier, adjacent deep fore reef sites also had high amounts. Low damage was observed in the north area near Ambergris (T3-S24) and higher amounts occurred in the central area between N. Columbus (S23) south to S. Water (S4B). Exposed deep fore reef sites on Turneffe and Glovers had higher than average damage.

In Honduras, hurricane effects were highly variable in both shallow and deep fore reef sites (Fig. 17). Mean hurricane damage on shallow sites was greatest on islands closest to the storm when it was at its peak strength (Guanaja = 22% of colonies affected, Roatan = 13%, Utila = 8%, and Cayos Cochinos = 5%). Sites with the highest damage occurred on the north, northeast sides of the shallow reefs of Barbaretta (BA1), Guanaja (GU4, GU5A), Roatan (RO4A) and Utila (UT7A). The most common types of hurricane damage on shallow reefs were knocked over or abraded (20% highest for each). Overall, most deep fore reef sites in Honduras had low to moderate hurricane damage, usually either abraded or knocked over. A surprising result was the low amount of damage observed on deep fore reefs on the north side in Guanaja, (except for GU3) and south side. Localized damage was observed at sites on the northeastern part of Roatan (e.g., Barbaretta-BA1) and southeastern Utila. Overall, Cayos Cochinos had fairly low damage in shallow sites and no visible physical damage was observed on deep fore reef sites.

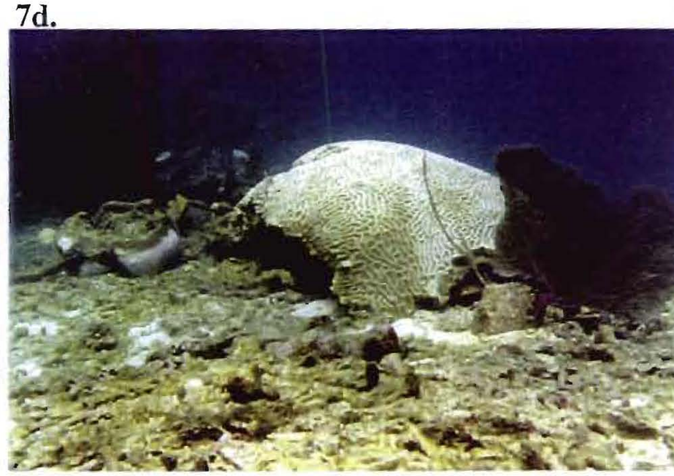
7a.

7b.

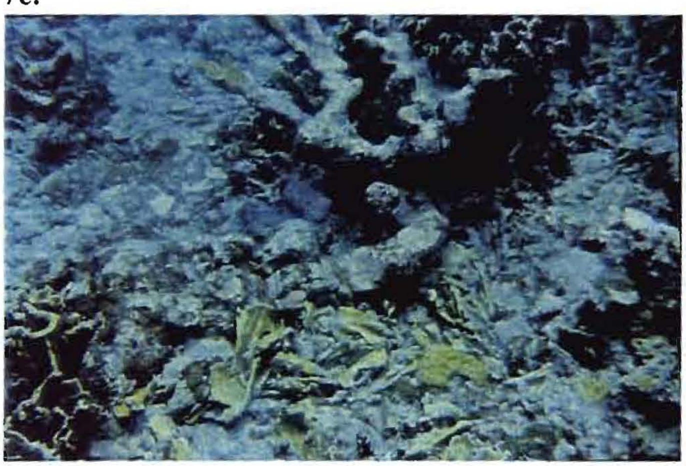


7c.

7d.



7e.



7f.

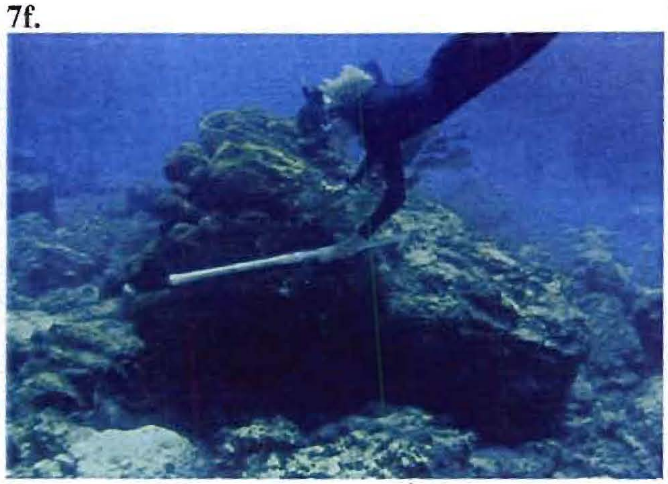


Photo 7. Hurricane Mitch damage in Belize. a). Recently accumulated storm rubble on central barrier b). Coral debris (live and dead) piled up at Chapel Cay. c). Recently dead gorgonians. d). Fore reef corals transported to shallow barrier, near Ranguna. e-f). Both fragile (*Millepora complanata*) and massive (*Montastraea annularis*) corals were affected by storm damage.

Hurricane Mitch damage

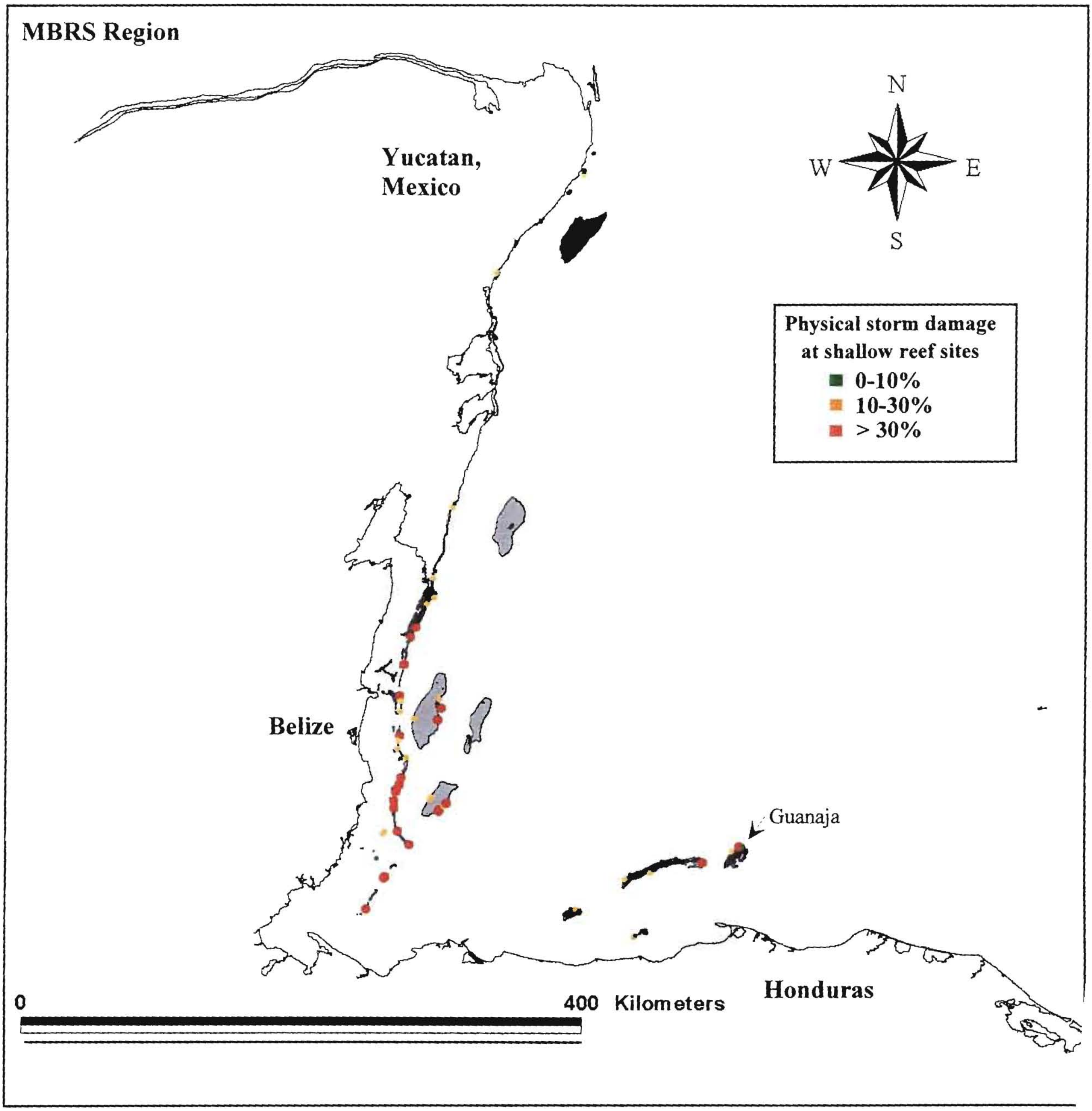


Figure 16. Spatial variation in hurricane Mitch storm damage recorded as the percent of colonies at each of the shallow (1-3 m) sites in the MBRS region showing broken, knocked over, or abraded condition. The greatest impacts occurred in central and southern Belize from large storm waves generated when the storm eye was near Guanaja.

Hurricane damage

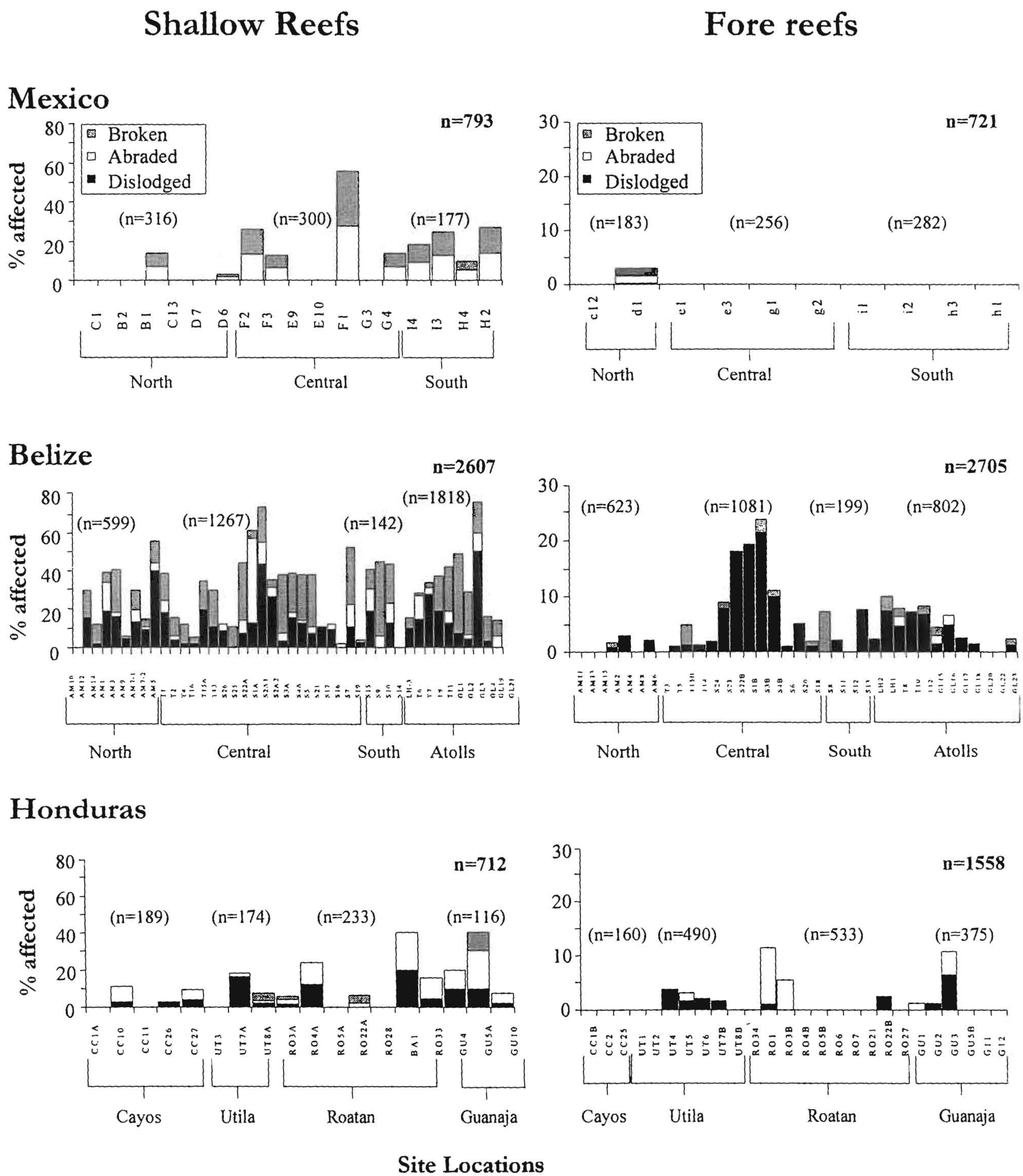


Figure 17. Frequency of physical hurricane damage to coral colonies. Total number of corals (n) surveyed are given for each country and each region within a country. (Note differences in scales for shallow and fore reef sites).

Coral Mortality

Recent mortality in the MBRS region was slightly higher on shallow sites (18%) than deep fore reef sites (13%), although the high variability suggests significant localized differences (Fig. 18, 19). Belize (24%) shallow sites had higher mean recent mortality values than Honduras (16%) or Mexico (7%). Deep fore reef sites in Honduras (17%) had more recent mortality than Belize (12%) or Mexico (11%) (Fig. 20a). Recent mortality was consistently higher on shallow sites than deep fore reef sites in both Honduras and Belize, but not for Mexico. The 1998 bleaching event caused the majority of recent mortality observed on shallow sites (particularly in Belize), although Hurricane Mitch was responsible for a lower proportion of the recent mortality. Extensive recent mortality occurred at many deep fore reefs due to the combination of lethal bleaching and extensive disease outbreaks. The amount of storm damage related mortality was generally lower at deep fore reef sites (except isolated areas). Recent mortality due to other factors are not separated in the findings below.

Within-country patterns of recent mortality displayed several trends. In Mexico, shallow sites in the southern area (18%) had significantly higher recent mortality than those sites either in the northern (5%) or central (3%) areas (Fig. 19). The same pattern was evident at deep fore reef sites, with more in the southern area (23%) than the north (3%) and central (2%). In Belize, recent mortality for shallow sites was significantly higher in the south (54%) than in the other areas. Back reefs, lagoonal patch reefs, and protected west facing barrier sites generally had higher recent mortality than exposed reef crest sites (Fig. 20b). Glovers' Reef atoll (particularly GL18-East Glovers) exhibited higher levels of recent mortality than the other two atolls. In Honduras, recent mortality levels were moderately high on all fore reef sites, although Roatan (19%) and Guanaja (18%) had higher levels than Cayos Cochinos (14%) or Utila (13%). For shallow sites, Utila (23%) and Guanaja (22%) displayed slightly higher mortality averages than either Roatan (15%) or Cayos Cochinos (9%).

The species susceptibility to bleaching and disease impacts presented earlier is clearly evident in the recent mortality percentages. Eighteen of the 26 species observed in shallow sites displayed recent mortality averages greater than 5% (Fig. 21a). Several major shallow water reef building species had severely high levels (>20%) of mortality including *A. tenuifolia*, *Millepora complanata*, *Diploria* spp., and *Montastraea* spp. *Dichocoenia stokesii* had the highest mortality (>50%), although this species was not observed frequently (n<10). *Acropora palmata*, the most abundant species in shallow sites had very low levels of recent mortality often because colonies were either 100% old dead or completely alive. Recently dead colonies of *Agaricia tenuifolia* and *M. complanata* were common at many shallow sites and are thought to reflect impacts from last year's bleaching event (Photo 7). Larger mound coral species like *Montastraea annularis* and *Diploria* spp. typically displayed partial mortality and rarely were completely dead. In deep fore reef sites, 22 of the 29 species observed had recent mortality, 13 of which had >5% recent mortality (Fig. 21b). *Montastraea franksi* had the most recent mortality (>20%), and seven other major reef building species had >10%, including *D. labyrinthiformis*, *M. faveolata*, *M. annularis*, *C. natans*, *D. clivosa*, *M. complanata*, and *D. strigosa*. All of these species suffered more partial mortality than 100% mortality. *Agaricia agaricites*, another important and abundant reef builder on the fore reef had very low recent mortality. Driving factors of mortality in these massive species was due to the synergistic effects of bleaching (as evident by the presence of pale tissue) stress and disease. The prevalence of white plague disease, in particular, observed at many deep fore reef sites most likely contributed to much of the recent mortality of *Montastraea franksi*. A summary of the weighted species contribution to recent mortality estimates for the entire MBRS region is shown in figure 22.

Visual estimates of old coral mortality, estimated to have occurred sometime during the past 10-20 years, was consistently high throughout the MBRS region, particularly on shallow reefs. Here we present total mortality percentages which simply represent the sum of old and recent values recorded at each site. Total mortality in the region was consistently higher on average in shallow (49%) than deep fore reefs (33%) (Fig. 23). Belize shallow sites (58%) had greater total mortality than Honduras (40%) or Mexico (38%). Within Belize, shallow sites in the southern area (85%) had significantly higher averages than the other area (54-57%) (Fig. 24). Of concern is several shallow reefs in Belize had 50-80% total mortality. The central and southern shallow areas of Mexico also had higher total mortality than the north (Fig. 24).

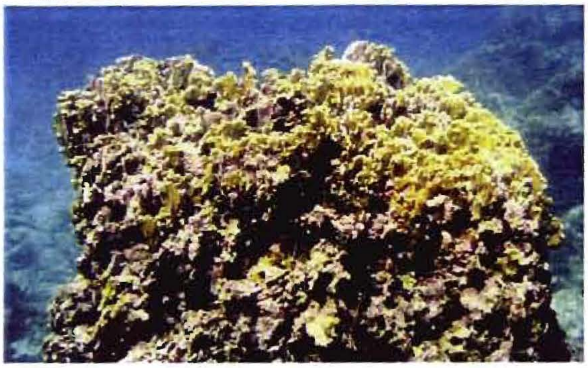
Utila (59%). Guanaja (46%) and Cayos (40%) had higher levels than Roatan (29%). For deep fore reefs in the region. Honduras (35%) had slightly greater total mortality than Belize (33%) or Mexico (26%). Within Honduras. deep fore reefs of Roatan. Guanaja. and Utila had similar amounts of total mortality (35-37%) which were slightly higher than Cayos (29%). Within Belize. there was no significant difference between areas (North 36%. Central 29%. South 35%. and Atolls 34%). although within Mexico. there was a significant difference between the high levels of total mortality observed in the south (39%) from those in the north (20%) and central areas (15%).

8a.

8b.

8c.

8d.



8e.

Photo 8. *Agaricia tenuifolia* (a-b) and *Millepora complanata* suffered high recent mortality from the 1998 bleaching event.

Recent Coral Mortality

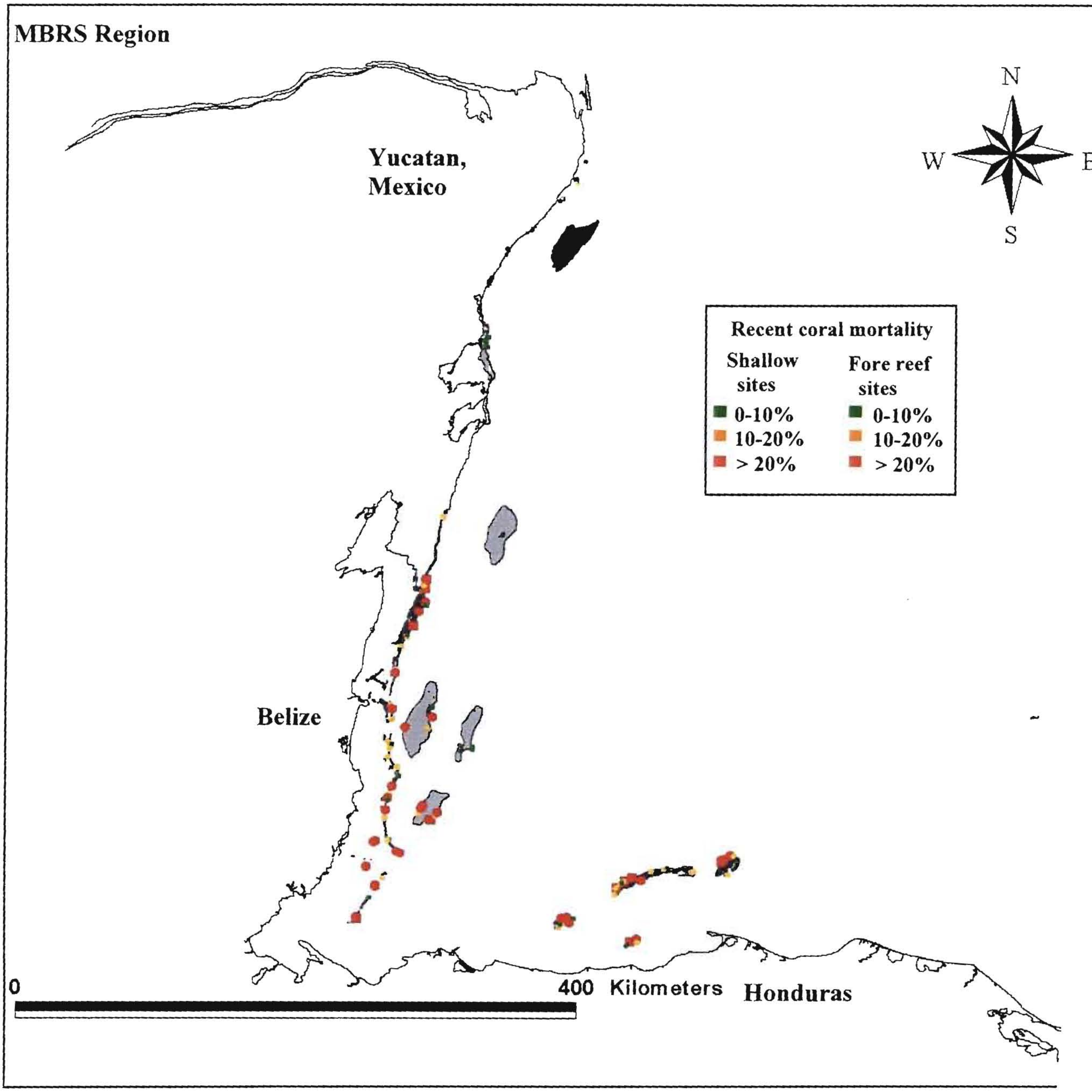


Figure 18. Spatial variability in recent mortality for both shallow (circles) and deep (squares) sites. Note some sites have overlapping positions and thus only the shallow sites values are displayed.

Recent mortality

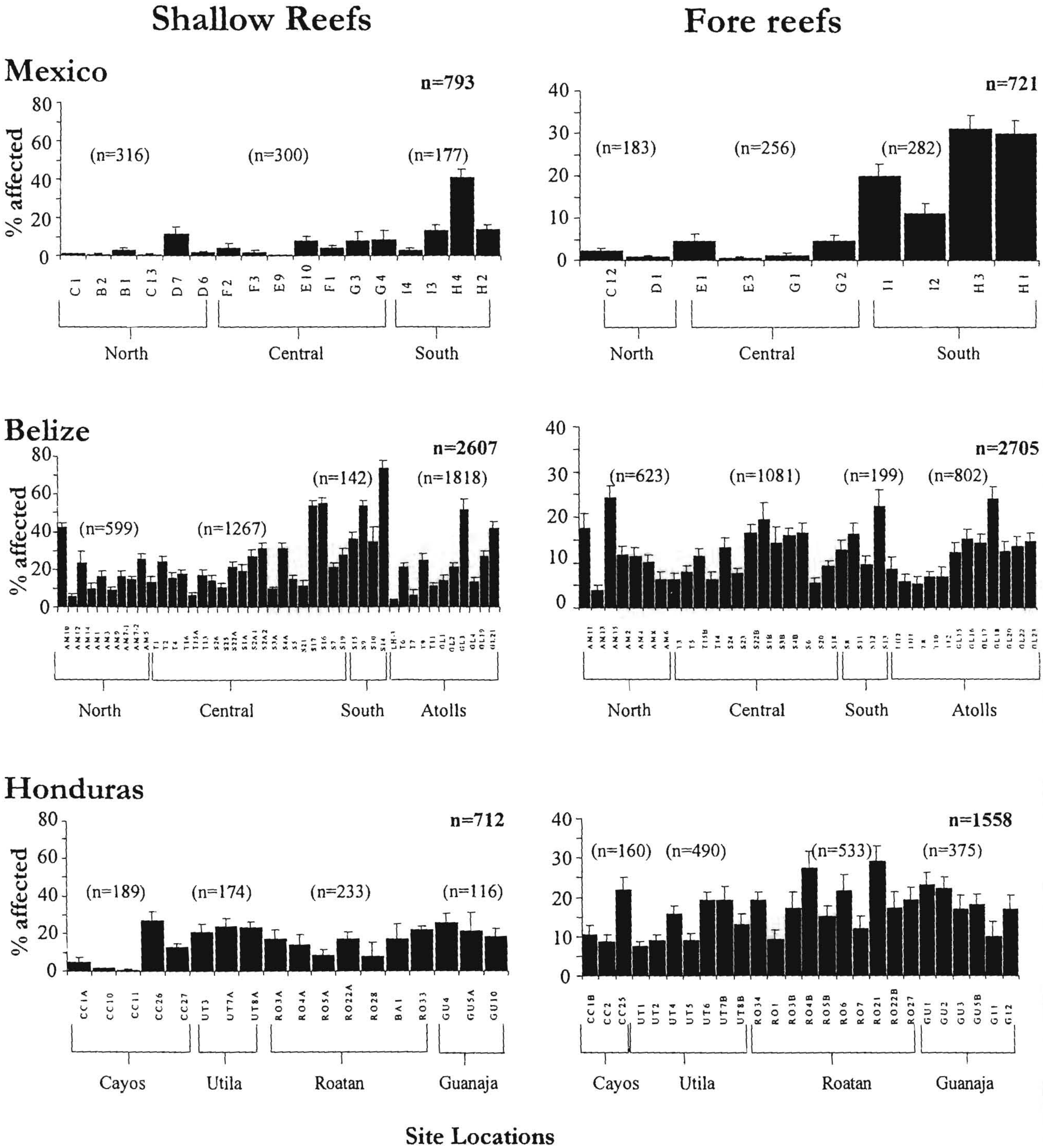


Figure 19. Amount of recent coral mortality by country for the MBRS region. Total number of corals (n) surveyed are given for each country and each region within a country. (Note differences in scales for shallow and fore reef sites).

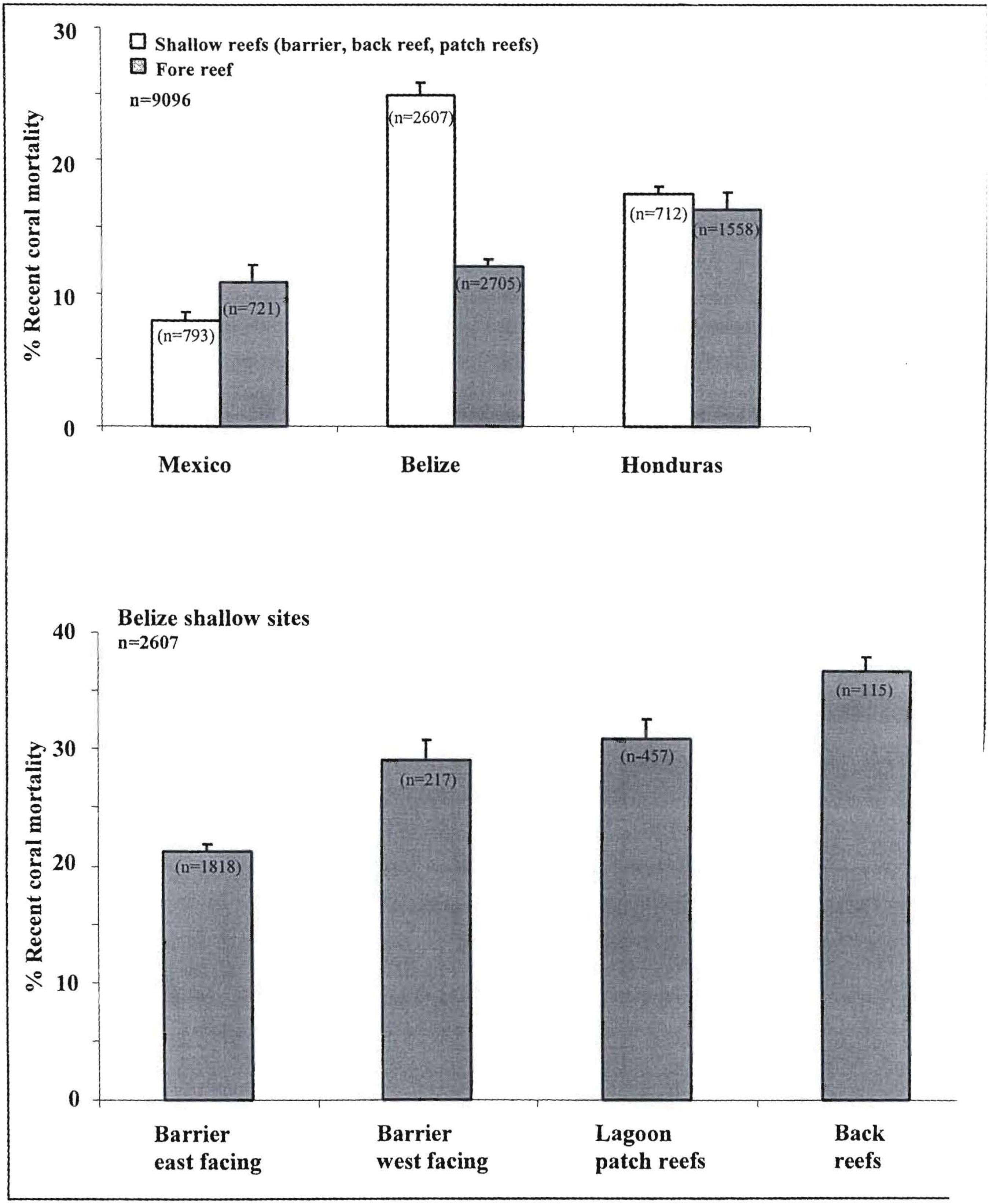


Figure 30a-b. a). Recent coral mortality by country for shallow and deep fore reef sites. b). Recent coral mortality on shallow sites in Belize by reef type.

Recent mortality by species

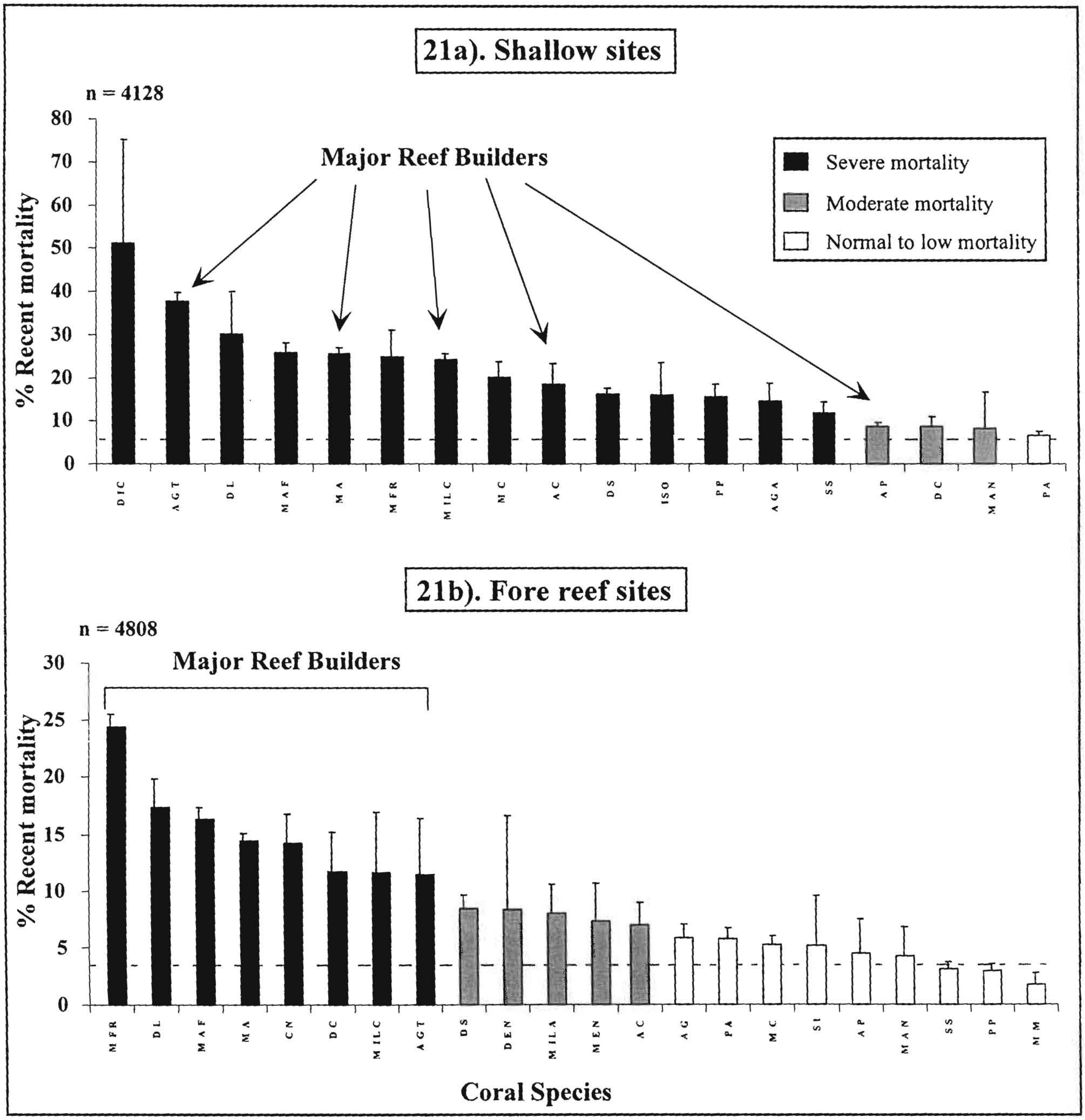


Figure 21a-b. Recent coral mortality by species for shallow (a-top graph) and fore reef sites (b-bottom graph). Data from Lighthouse Atoll not included. Error bars = 1 standard error.

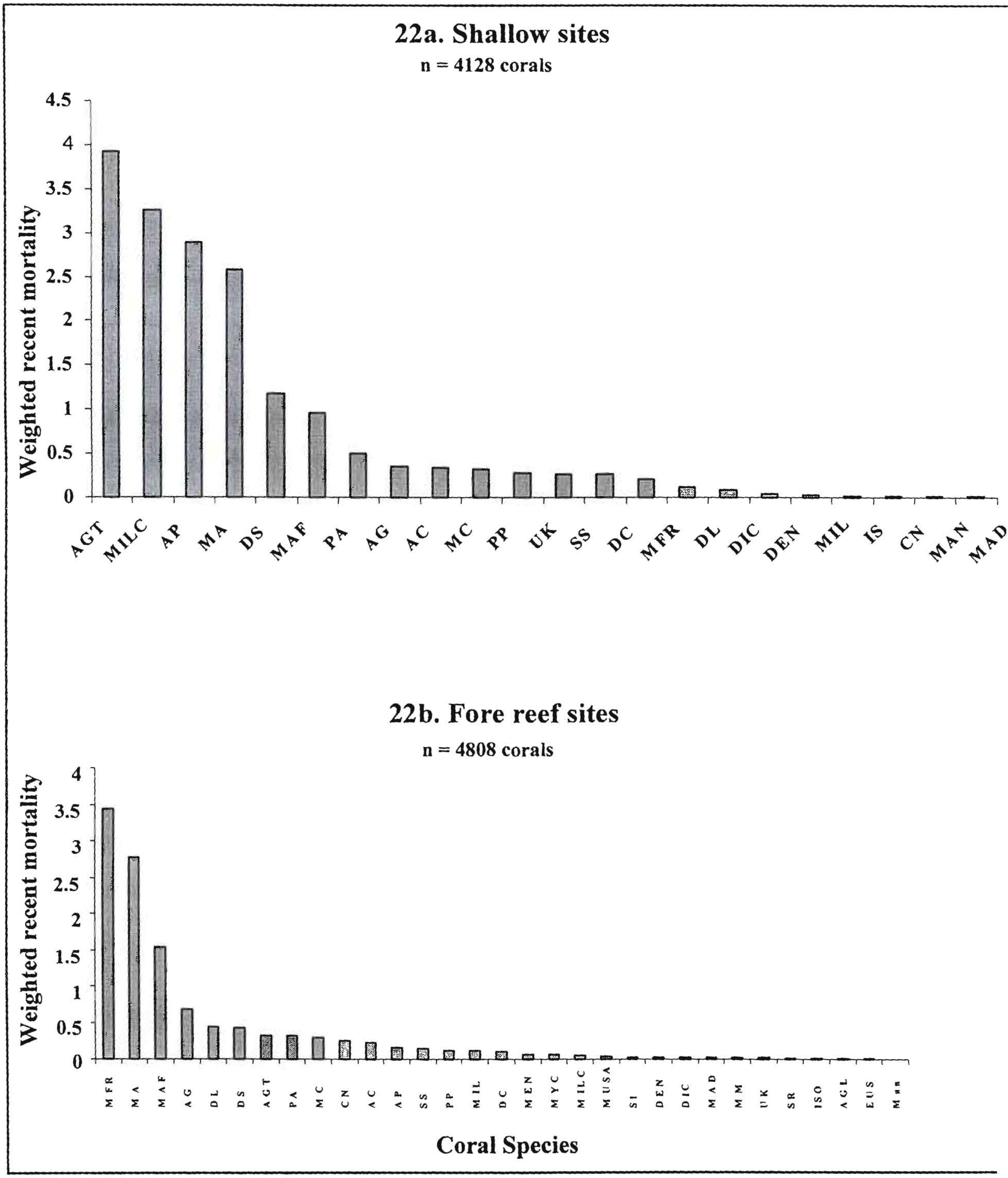


Figure22a-b. Recent mortality by species weighted by species abundance for shallow (a-top graph) and deep fore reef (b-bottom graph) sites. See figure 10a for species abbreviations.

Total Coral Mortality at shallow sites

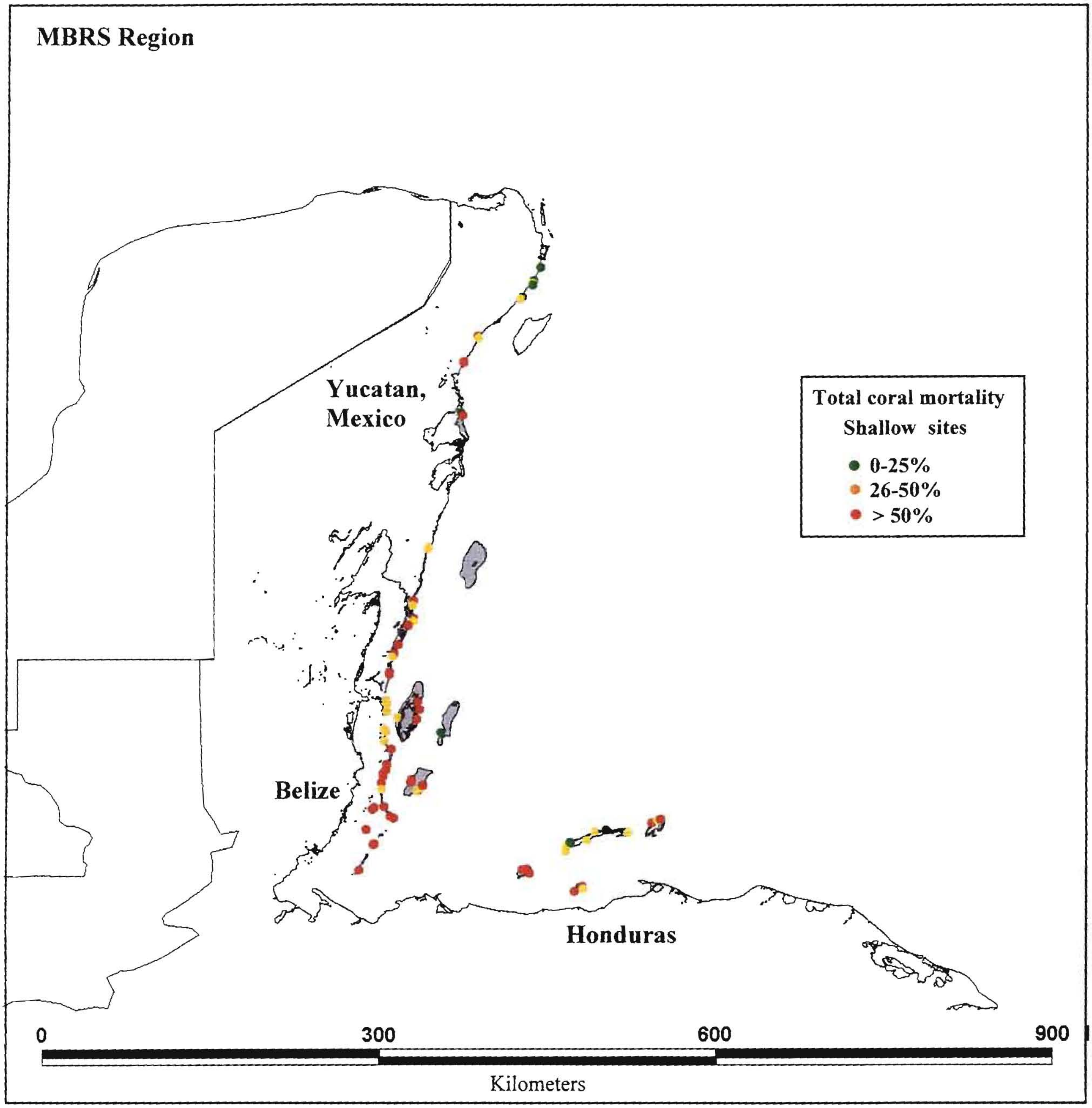


Figure 23. Map showing total (recent and old) coral mortality for shallow sites of the MBRS region. Previous disturbances like the 1995 bleaching event and 1980's white band episodes has dramatically compounded the effects of the 1998 bleaching and hurricane leaving many shallow reefs with little live coral.

Total coral mortality

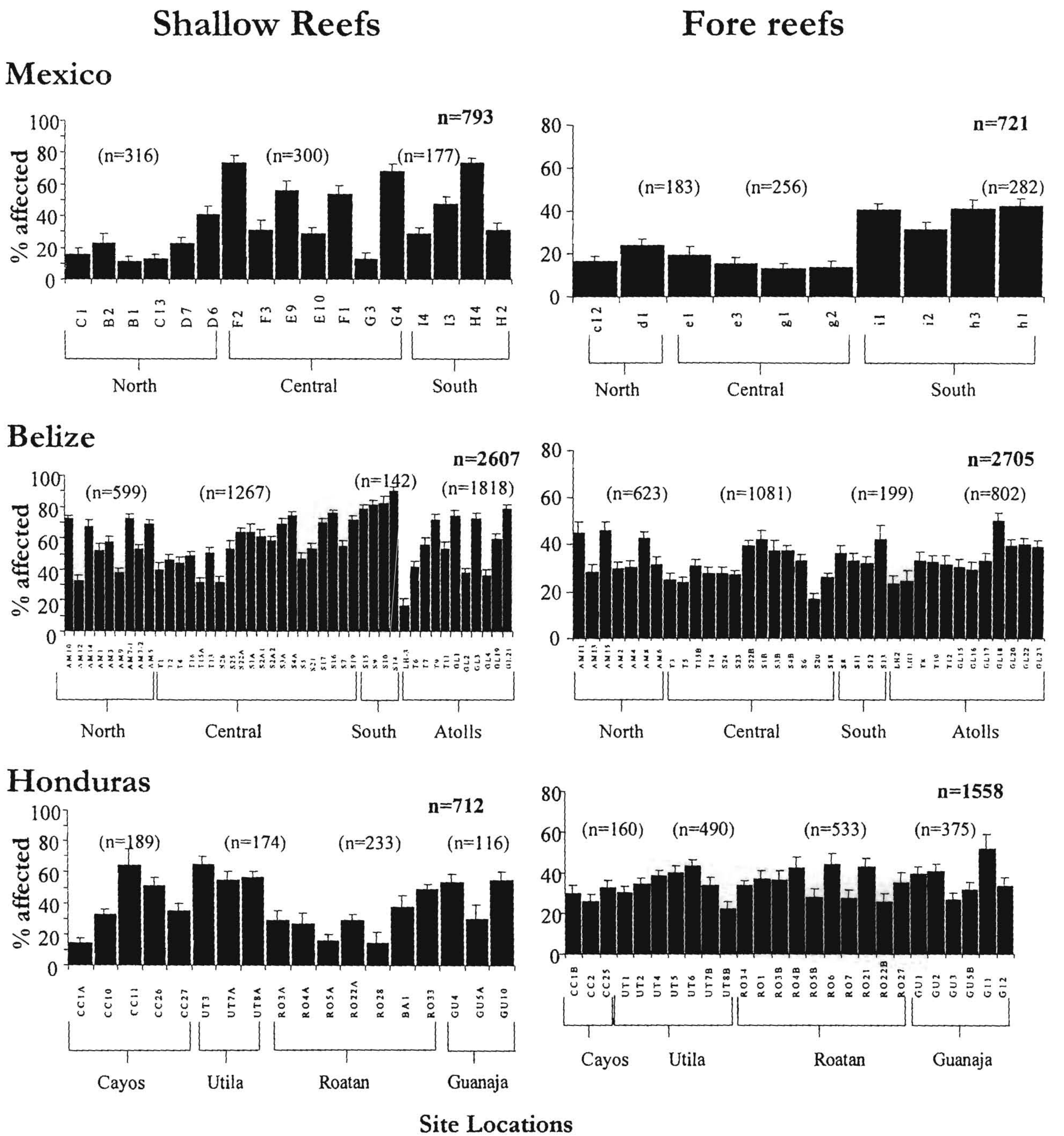


Figure 24. Total coral mortality in shallow and fore reef sites in Mexico, Belize, and Honduras. Total number of corals(n) surveyed are given for each country and each region within a country. (Note differences in scales for shallow and fore reef sites).

Synthesis and Condition of reefs

In this section we discuss the condition of reefs in each region based on the ranking results, including significant differences between countries, areas, and sites (Fig. 25). The level of disturbance is divided into three categories: "*Low*", "*Moderate*", and "*Severe*" for each country (see Method section for definitions).

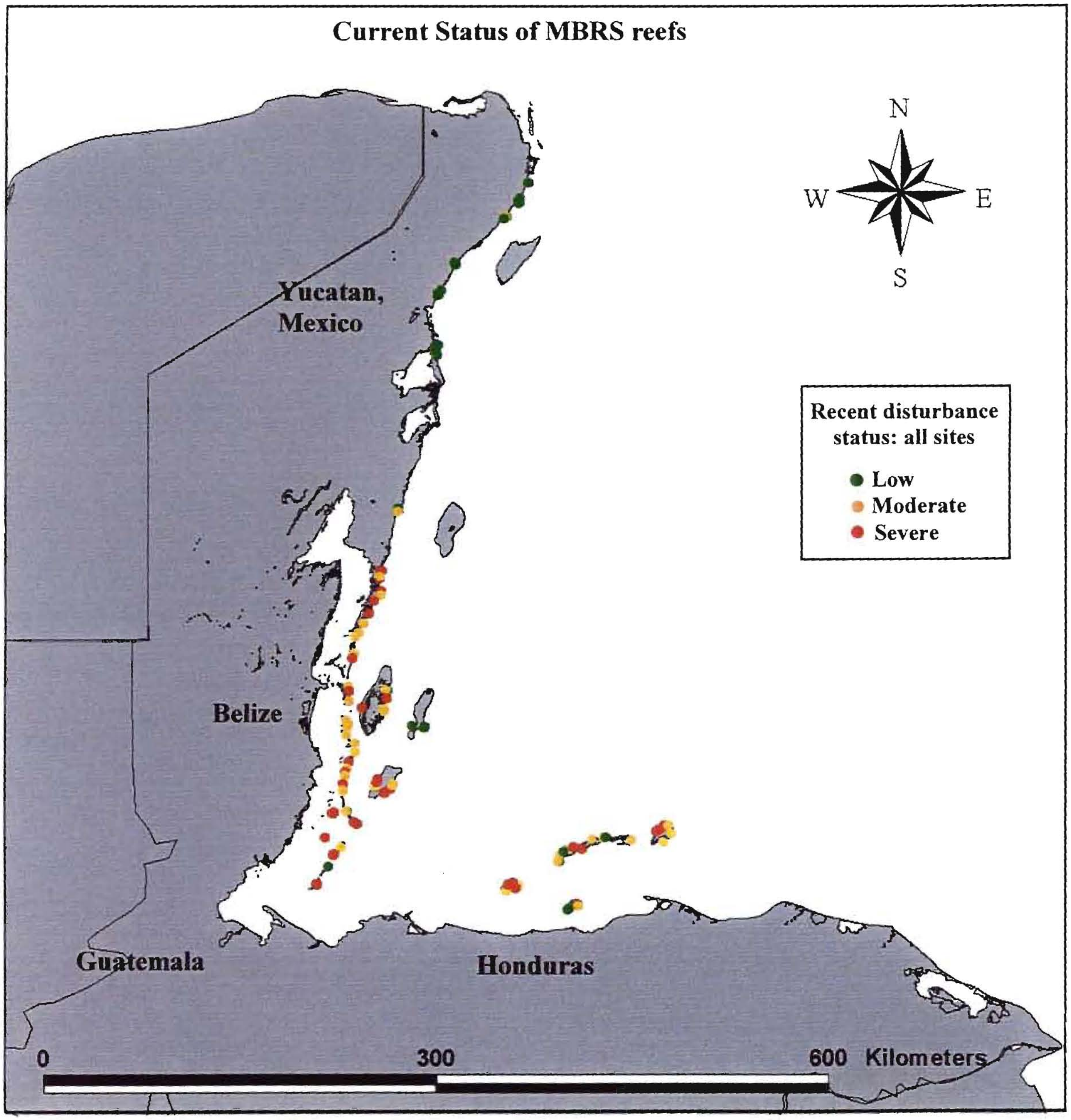


Figure 25. Qualitative ranking of the condition of shallow and deep fore reefs of MBRS region based on the extent of total recent (1998-99) disturbance (e.g., bleaching, disease, hurricane, other).

Mexico - Reefs in Mexico were affected far less than Belize or Honduras; of the 27 reefs surveyed in Mexico, 19 experienced low disturbance, four experienced moderate disturbance, and four experienced severe disturbance (Table 3). The southern area had the most disturbance (moderate to severe) due mainly to bleaching and disease and higher levels of recent mortality while the north and central had only low disturbance (except d7). Only one shallow site (N. Xcalak-H4) had severe disturbance because of recent mortality, bleaching, and disease, whereas three deep fore reef sites (Majahual-I1, N. Xcalak-H3, S. Xcalak-H1) had severe recent mortality and bleaching. At these deep fore reef sites, it is likely that the remnant bleaching resulted in additional recent mortality in the following months. Our mortality, bleaching and disease data are similar to AGRRA data collected at Akumal and Xcalak during the same time period (B. Steneck, unpublished data).

Low disturbance

	Shallow
C1	La Bonanza (disease)
B2	Bocana (some disease)
B1	P. Morelos (bleach, disease)
C13	S. Puerto Morelos
D6	S. Punta Moroma (bleach)
F2	S. Akumal (old, bleach)
F3	Chenchomac (bleach)
E9	La Caburn (old)
E10	S. Pescadors (RM, bleach)
F1	N. Akumal (old, bleach)
G3	Punta Allen-N (RM, bleach)
G4	Punta Allen-S (old)
I4	N. Majahual (bleach, disease)
	Deep
C12	S. Puerto Morelos (disease)
D1	Punta Marona
E1	The Whale (mod-high bleach)
E3	La Picina (low RM, high bleach)
G1	Sian Ka'an-N (low bleach)
G2	Punta Allen (low bleach)

Moderate disturbance

	Shallow
D7	Punta Moroma (RM)
I3	S. Majahual
H2	S. Xcalak (mod bleach)
	Deep
I2	Majajual-S

Severe disturbance

	Shallow
H4	N. Xcalak (RM, disease)
	Deep
I1	Majajual
H3	Xcalac-N
H1	Xcalac-S

Table 3. Qualitative condition of shallow and fore reef sites in Mexico (site number and names). Notable observations are given in parentheses. (RM= recent mortality, old=old mortality, bl=bleaching, dis=disease, hurri=hurricane)

Belize - The most severe disturbance was observed in Belize where the majority of reefs (72 of 80) had significant negative impacts; 46 reefs suffered moderate disturbance, 26 had severe damage, and only 8 of the reefs showed signs of low damage (Table 4). Generally, the greatest impacts on shallow sites occurred south of S. Cross Cay (S22A), including Glover's, caused usually by a combination of bleaching, disease and hurricane. Shallow sites also tended to have high old mortality, suggesting these sites had experienced other major disturbances in the past 10 years. The majority of deep fore reef reefs throughout Belize had low to moderate recent mortality and moderately high bleaching.

The northern area of the Belize had primarily "moderate" disturbance; several shallow sites were severely impacted by the hurricane while deep fore reef sites were less affected, primarily disturbed only by bleaching. The central area of Belize experienced moderate to severe disturbance with the most exposed shallow sites often having more hurricane damage; while protected sites tended to have higher incidences of disease (particularly in the southern part of this central area). Sites in the southern region of Belize were moderately to severely disturbed; shallow sites had some of the highest recent and total mortality in the entire MBRS region.

Glovers Reef Atoll experienced the most disturbances of the three Belize atolls; shallow windward reefs of Glovers suffered severe hurricane damage and recent mortality, while bleaching and diseases impacted leeward reefs more. Deep fore reef reefs had similar levels of moderate to high recent mortality between sites and higher than average levels of bleaching and disease. Disturbance on Turneffe was highly variable on shallow reefs and more uniform on deep fore reef reefs. Shallow reefs on the eastern (windward) side suffered mostly from the hurricane and no bleaching or disease although there was low live coral cover due to high old mortality. Deep fore reef sites had moderately high bleaching (except T8), although very low recent mortality. Only one deep fore reef site (Pelican - T9) had severe disturbance most likely due to hurricane impacts. West Turneffe (T6) shallow had high recent and old mortality and severe disturbance due to bleaching and disease. Lighthouse Cay, the far-eastern atoll, had low recent mortality with few signs of disturbance, except for some low to moderate hurricane damage and low bleaching at deep fore reef sites on the eastern side of the atoll.

Honduras - The majority of sites in Honduras (38 of 44) also exhibited extensive signs of significant damage; 25 had moderate disturbance, 13 had severe disturbance, and 6 had low disturbance (Table 5). Recent mortality was highly variable on shallow sites, but overall low disturbance levels, except localized areas of hurricane damage in Guanaja. Deep fore reef sites consistently had similar levels of moderate to severe recent mortality, bleaching, and disease, with relatively few impacts from the hurricane.

In Utila, all shallow sites were severely disturbed, while all deep fore reef sites were moderately disturbed. Shallow sites also had high old mortality (resulting in very low live coral cover) and only localized effects of bleaching or hurricane. Deep fore reef sites tended to have moderate to high bleaching and disease and negligible effects from the hurricane. In Roatan, shallow site had low to moderate disturbance (low bleaching, disease, and mortality), while deeper fore reef site had more severe disturbance often because of high recent mortality, bleaching and disease. West End (RO3B) deep fore reef site, which was recently designated within a protected area, had high disease, recent mortality and bleaching. In Guanaja, both shallow and deep fore reef sites were moderately to severely disturbed, particularly on the northern side of the island. Live coral cover was low on most shallow sites, as was the incidence of disease. Shallow sites were affected more by hurricane, while deep fore reef sites were more impacted by bleaching and disease. Impacts to shallow reefs on Cayos Cochinos was highly variable (low to severe), while deep fore reef reefs had either moderate or severe disturbance. Bleaching, disease, and hurricane impacts on shallow reefs were generally low, except for a few localized areas. The reefs on the far-eastern and western edge of the archipelago had high total mortality. Deep fore reef reefs had severely high bleaching and disease, and no signs of hurricane damage.

Belize

Low Disturbance

Shallow	
LH-3	Long Cay
Deep	
North	
AM13	Rocky point
Central	
S20	Central Gladden
S18	Gladden Spit
South	
S12	N. Spot
Atolls	
LH2	Odd-Wreck
LH1	Halfmoon Cay
T8	Grassy

Moderate Disturbance

Shallow	
North	
AM12	Rocky-point (hurricane)
AM1	Tres Cocos (old, hurricane)
AM3	Hol Chan (old, hurricane)
AM9	Coral Patch (disease, bleach)
AM7-1	Caye-Caulker(old, hurricane)
AM7-2	Caye-Caulker bk (all, old)
Central	
T1	Gallows-N
T4	Sergeant's
T16	Rendezvous-patch (RM)
T15A	Rendezvous(hurricane)
T13	Alligator (hurricane, RM)
S26	Pelican patch (hurricane, bleach)
S25	N. S. Long Rock (old, hurricane)
S1A	Tobacco(old, hurricane)
S3A	S. Tobacco(old, hurricane)
S5	Curlew Cut
S21	Central Gladden(old, hurricane)
Atolls	
T7	Grassy Key(old, hurricane)
T11	Soldier (old, hurricane)
GL1	East Cut-GL(total, hurricane)
GL4	NE Glovers
Deep	
North	
AM11	Bacalar Chic
AM2	Tres Cocos
AM4	Hol Chan
AM8	Cay Cauker
AM6	Caye Chapple
Central	
T3	Gallow-S
T5	Sergent's
T15B	Rendezvous
T14	Alligator
S24	N. S. Long Rock
S23	N. Columbus
S22B	S. Cross
S3B	S. Tobacco
S4B	S. Water
S6	Curlew
South	
S8	Pompion
S11	Ranguana
Atolls	
T10	Pelican
T12	Soldier
GL15	NE
GL16	Carmen
GL17	Middle
GL20	NW
GL22	CW
GL23	*West cut*

Severe Disturbance

Shallow	
North	
AM10	Bacalar Chico (disease)
AM14	Basil Jones (old)
AM5	Caye Chapel (hurricane, old)
Central	
T2	Gallows-S
S22A	S. Cross Cay (old, hurricane)
S2A2	Tobacco Cut-back (bl, dis, hurri)
S2A1	Tobacco Cut-front (bl, old, hurri)
S4A	S. Water(old, hurricane)
S17	E. Tarpon (disease)
S16	W. Tarpon (disease)
S7	Swab Patch (bleach, old, disease)
S19	Gladden Spit (old, hurricane)
S15	Laughing bird (old)
South	
S9	Ranguana #1 (disease)
S10	Ranguana #2
S14	Nicholas
Atolls	
T6	W. Turneffe (disease)
T9	Pelican (old)
GL2	Middle Cay
GL3	Carmen (hurricane)
GL19	NW Glovers (bleach, dis., old)
GL21	CW Glovers (bleach, dis., old)
Deep	
North	
AM15	Mexican Rocks
Central	
S1B	Tobacco
S13	Nicholas
Atolls	
GL18	East

Table 4. Qualitative condition of shallow and fore reef sites in Belize (site number and names). Notable observations a given in parentheses. (RM= recent mortality, old=old mortality, bl=bleaching, dis=disease, hurri=hurricane)

Honduras

Low Disturbance		Moderate Disturbance		Severe Disturbance	
	Shallow		***Shallow***		***Shallow***
CC1A	Cayos-channel (bleach)	CC27	Cayos-stadium (hurricane)	CC26	Cayos east end (old)
CC10	Cayos- south (hurr.)	RO3A	West End (bleach)	UT3	Light Tower
CC11	Cayos- edge (old)	RO4A	Cut (hurricane)	UT7A	Lagoon–1 (hurricane)
RO5A	NC Roatan	RO22A	UK cut (hurricane)	UT8A	Lagoon-2 (bleach, hurri.)
RO28	NE Roatan (disease)	BA1	Barbaretta (hurricane)	RO33	Fantasy Island (hurricane)
		GU10	Guanaja-east (old, hurricane)	GU4	North side (hurricane)
				GU5A	Volcano tubes (hurri., bl.)
					Deep
	Deep		***Deep***	CC25	Cayos north (bl., dis.)
SW Roatan-1(hurricane)		CC1B	Cayos channel (bl., dis.)	RO4B	Anthony's (bl., dis.)
		CC2	Cayos wall (bleach, disease)	RO6	North Central (disease)
		UT1	Utila-SE1 (bleach, disease)	RO21	Roatan-NE1 (bl., dis.)
		UT2	Utila-SE2 (bleach, disease)	GU1	Guanaja-NC1 (bl., dis.)
		UT4	Utila-SW1 (bleach, disease)	GU2	Guanaja-NC2 (bl., dis.)
		UT5	Utila-SW2 (old, bleach)		
		UT6	Utila-black coral (bl,dis, old)		
		UT7B	Utila-NC (bleach, disease)		
		UT8B	Utila-NC-2 (bleach, disease)		
		RO34	Fantasy Island (bleach)		
		RO3B	West End (bleach, disease)		
		RO5B	North Central 1(bl., dis.)		
		RO7	Roatan Central (bl., dis.)		
		RO22B	Roatan-NE2 (bleach)		
		RO27	Roatan-NE3 (old)		
		GU3	Guanaja-NC3 (bl., hurri.)		
		GU5B	Gua Vol Tubes(hurri, bl, dis		
		G11	Guanaja-south (bl., dis.)		
		G12	Guanaja-SE (bleach)		

Table 5. Qualitative condition of shallow and fore reef sites in Honduras (site number and names). Notable observations are given in parentheses. (RM= recent mortality, old=old mortality, bl=bleaching, dis=disease, hurri=hurricane)

DISCUSSION

1998 Bleaching impacts

Our field data are consistent with initial reports suggesting that the 1998 bleaching event was widespread and probably the most severe to effect the MBRS region. The best measures to gauge the extent and magnitude of bleaching come from the remnant bleaching and recent mortality data. Remnant bleaching was widespread across the entire MBRS region but most evident at deeper fore reef sites. The fact that some of our deep fore reef sites in Belize had up to 20% of the colonies exhibiting pale discoloration 8 months after the event is further indication of the magnitude of the 1998 event. These temporal "recoveries" are similar to the 8-12 months reported by other studies (Goenaga et al., 1980; Porter et al., 1989; Bunkley-Williams et al., 1991; Lang et al., 1992; McField, 1999). Shallow reefs experienced catastrophic losses due to the initial bleaching and had fewer corals showing signs of remnant bleaching at the time of our survey. Shallow reef corals tended to either die or recover more rapidly compared to deeper depths where recovery from bleaching proceeds more slowly. This is consistent with earlier observations made by Lang et al., 1988, 1992; Williams and Bunkley-Williams, 1990; and Bunkley-Williams et al., 1991.

Recent mortality data offer the best measure for evaluating the impact and spatial extent of *lethal* bleaching that the region experienced, particularly for shallow sites. Partial mortality rates were generally higher on shallow than adjacent fore reefs sites, but considerable variability on both large and small spatial scales was evident. A small amount of this variance is probably attributable to temporal influences since our surveys took place over a four-month window during which some partial coral mortality was taking place. In addition, at hurricane prone sites, storm effects may have contributed to recent mortality percentages by damaging corals and/or sweeping away corals from the site. However, most of the variance in our bleaching and recent mortality data set is probably the result of 1) Geographic variability of the temperature stress (=magnitude and duration of temperatures above maximum mean summer temperatures) within the MBRS region; 2) Interspecific patterns of susceptibility to temperature stress; and 3) Secondary effects of bleaching stress.

Temperature Stress

Geographical differences in temperature stress explain some of the larger scale variability in recent mortality trends within the MBRS (Fig. 4, 26). One of the most significant trends which emerged from the field survey data was the low amount of recent mortality (~<5%) documented for both shallow and deep fore reef sites in central and northern Yucatan compared to southern Yucatan and the rest of the MBRS region. The high remnant bleaching observed on fore reef sites from Sian Ka'an north to Puerto Morelos taken together with local reports suggest that extensive bleaching did take place throughout the Yucatan, but the impacts were primarily transient rather than lethal in the central and northern areas. The most likely explanation for this pattern is that the central and northern Yucatan areas experienced a lower degree of temperature stress during late summer/early fall 1998. This theory is supported by NOAA temperature anomaly maps for the region which show that cumulative temperature stress from August through October 1998 was significantly lower in central and northern Yucatan compared to further south (Fig. 26). Unfortunately, the coarse resolution of existing temperature anomaly maps prevent finer correlation to site-site differences.

In Belize, some of the most severe bleaching damage (22-56% mortality) was found on patch reefs, particularly in the southern lagoon. Temperature maps do show that this region was experiencing severe temperature stresses during much of September and October. An interesting observation was that patch reefs close to openings or "cuts" through the barrier had less bleaching damage than more restricted sites far from openings in the barrier. This would suggest that tidal flushing of offshore waters may have reduced temperature stress and/or influenced the ability of the corals to recover from bleaching. Temperature and solar radiation stress are usually greater during periods of calm weather (Wilkinson, 1998) and agitated water produced by flushing may allow corals to better cope with temperature stress.

Pilot charts (Clarke, 1997) indicate the presence of strong currents in central and northern Yucatan which also may help explain the lower temperature stress and ability to recover in this area (Fig. 27).

The southern extent of the warm water temperature event appears to have extended through the Gulf of Honduras all the way east to the Bay Islands (Fig. 4, 26). The consistently high recent mortality (~17%) and incidence of remnant bleaching (~24%) encountered at fore reef sites suggest that temperature stress was high throughout the Bay Islands, although it is possible that runoff from hurricane Mitch may have contributed to this stress (see following section). Shallow sites usually only displayed moderately high recent mortality (~16%) compared to other parts of the MBRS (e.g., 24% in Belize), although considerable variability existed between sites. This mortality is perhaps lower than expected given the extent of bleaching and recent mortality of deeper fore reef sites. This can be explained in part by the fringing nature of many of the shallow reefs around the Bay Islands and absence of shallow lagoonal patch reefs and back reef settings most susceptible to bleaching mortality. In addition, during the 1995 bleaching event, shallow sites suffered significant mortality (e.g., ~83% mortality at two sites in Cayos - Guzman and Guevara (1998)). Thus, the lower recent mortality percentages recorded for shallow sites around Cayos (and some of the other sites in the MBRS) is partially a reflection of past disturbances which left few living corals on the reefs prone to the 1998 bleaching event.

Interspecific Patterns

A portion of the spatial variability in recent mortality is probably a factor of interspecific differences and spatial variability in community structure. The remnant bleaching results show patterns reflective of a species' tolerance to prolonged temperature stress, while the recent mortality data is more reflective of the lethal effects. Previous studies have shown that differences in interspecific responses to bleaching is common, with individual taxa showing different degrees of discoloration and recovery times (e.g., Glynn, 1984; Brown and Suharsono, 1990; Coffroth et al., 1990; Glynn, 1990; Williams and Bunkley-Williams, 1988, 1990; Lang et al., 1992). For example, branching and platy species often have a higher likelihood of bleaching earlier and with more intensity than massive mound species. Of particular concern is the combination of high remnant bleaching and recent mortality observed for several major reef-building species, especially in areas that have already experienced other severe disturbances.

Local observations made during the 1998 MBRS bleaching event (Appendix 1) indicate that *Millepora complanata* and *Agaricia tenuifolia* on shallow reefs bleached first and also suffered greater tissue mortality before many other species. Our survey indicated high recent mortality (attributed primarily to bleaching) for both *Agaricia tenuifolia* (>35%) and *Millepora complanata* (~28%) in shallow sites. Our results compare to high levels of mortality (43%) reported for *A. tenuifolia* in Belize after the 1995 bleaching event, although *Millepora* spp. was only minimally affected (McField, 1999). The concomitant loss from the 1995 and 1998 bleaching events raises concerns for the potential of local extinction of *Agaricia tenuifolia*, especially considering the susceptibility of this species to bleaching and the high likelihood for future bleaching events and/or other catastrophic disturbances. Massive corals, such as *Montastraea annularis* sensu lato, bleached gradually in a patchy pattern, and often had the highest levels of remnant bleaching in both shallow (~25-40%) and deep fore reef sites (~40-50%). Although these species are known to be "prolonged" bleachers (e.g., Lang et al., 1992; McField, 1999), the amount of recent mortality observed at shallow (~27%) and deep fore reef (~15-25%) sites raises question on the long-term impact of these synergistic stresses and the ability of these species to recover. Guzman and Guevara (1998) found *Millepora* suffered the highest mortality (74% of colonies) and *Montastraea* and *Agaricia* had extensive partial mortality in Cayos Cochinos after the 1995 bleaching event. Our data suggested other dominant shallow water species such as *Acropora palmata* were more differentially affected, and in many cases did not bleach or suffer large losses due to the 1998 event.

These interspecific patterns may result from inherent physiological differences between and within scleractinian species, but are also influenced by a species' adaptation to a particular habitat zone (especially depth) and that zone's susceptibility to temperature stress. For example, deeper fore reef zones probably did not experience as severe temperature stress as shallow sites, yet corals may have been more susceptible to bleaching because they were not as well adapted to temperature fluctuations. Thus, while

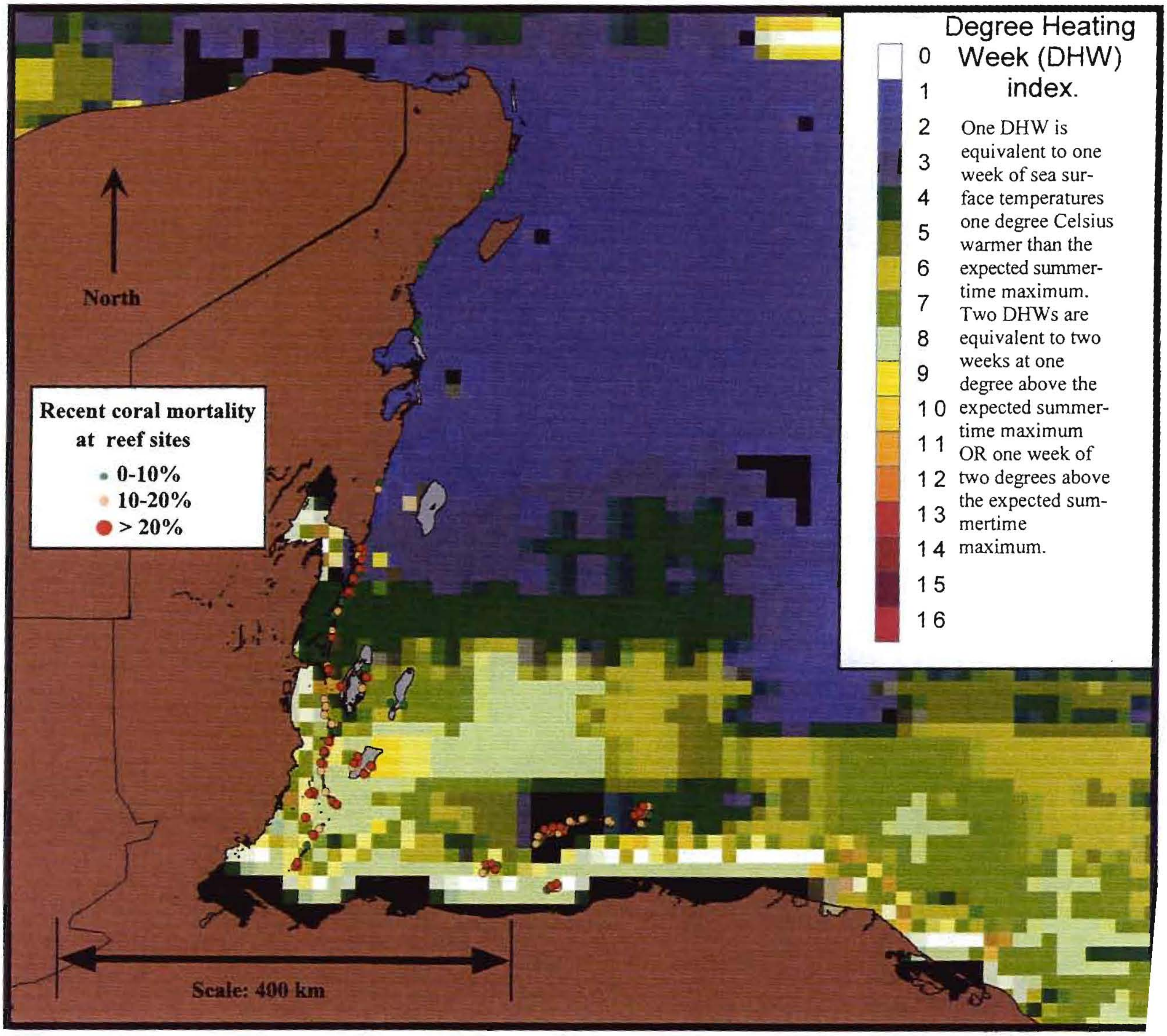


Figure 26. Cumulative Degree Heating Weeks (DHW) for August 1-October 31, 1998 from NOAA's coral bleaching hot-spot program. The amount of recent coral mortality recorded at sites (circles) shows a good correlation with DHW over large spatial scales, particularly along Yucatan, Mexico.

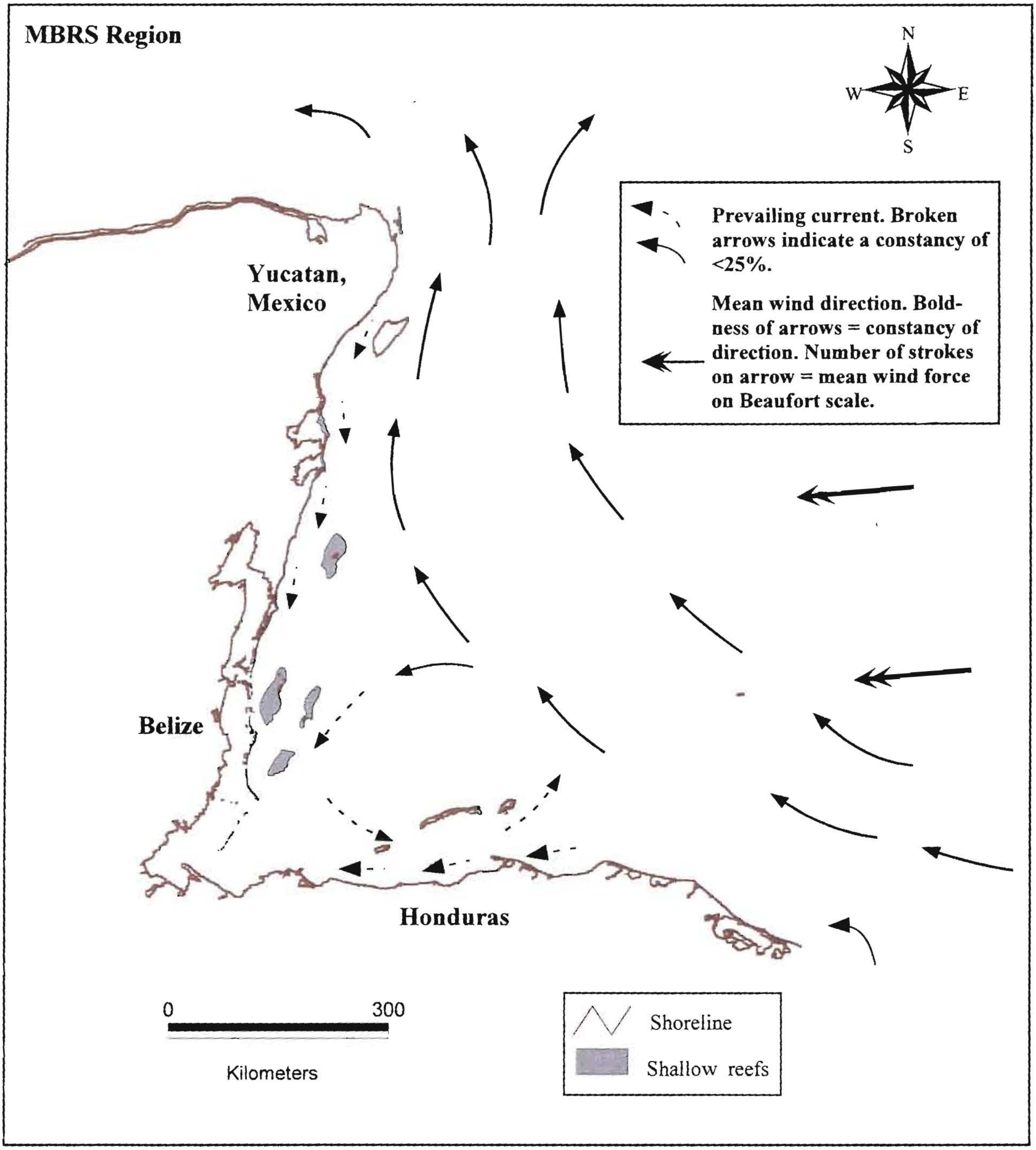


Figure 27. Prevailing currents in the MBRS region. Data adapted by Clarke 1997 and D'Croz et al., 1998.

temperature stress was probably lower at deeper depths, corals often showed high levels of bleaching. A better understanding of other factors that influence temperature stress (flushing for example) and on how these factors vary across small (<100 m) spatial scales is needed. There is increasing evidence that interspecific patterns in bleaching and mottled or patch bleaching within individuals may be influenced by the type of symbiotic algal found in the tissue (Rowan et al., 1997; Baker and Rowan, 1997). Three distinct algal genotypes have been identified (clads A, B, and C) and which genotype a coral hosts appears to depend on numerous factors including geographic local, coral species, and water depth. In the Caribbean, Rowan et al. (1997) suggested that some strains of zooxanthellae are more temperature tolerant than others - corals hosting clad C may be more prone to bleaching than those with clads A or B. In support of this hypothesis, McField (1999) found that during the 1995 bleaching event in Belize, corals hosting mainly clad C symbionts were more prone to bleaching than corals hosting clade B symbionts. However, during our surveys, we did not find substantial evidence for correlations between symbiotic algal genotypes and remnant bleaching or recent mortality. For example in shallow sites, *Agaricia tenuifolia* (clade C) suffered high recent mortality from the bleaching, but other species with clade C symbionts (e.g., *Siderastrea siderea* and *D. clivosa*) did not suffer high bleaching or mortality. The highest mortalities occurred in species capable of hosting multiple clads of zooxanthellae (e.g., *M. annularis* complex, *D. labyrinthiformis*). Our data is somewhat limited because we did not look at all species (only those >10cm) and we did not survey during the peak bleaching event.

Secondary effects

Apart from the initial impacts of large-scale bleaching, mainly recent mortality occurring during or immediately after peak bleaching, there are also lingering secondary effects that continue in the ensuing months and possibly years. Several studies have shown that bleaching inhibits a corals ability to recover from small tissue damage and increases the likelihood of damage from other stressors (e.g., Meesters et al., 1993; Mascarelli and Bunkley-Williams, 1999). Secondary effects of bleaching can include reduced skeletal growth (Leder et al., 1991), decline in reproductive fitness or failure (Glynn, 1990; Szmant and Gassman, 1990; Guzman and Cortes, 1992), and reduced ability to resist invasion by pathogens and/or bioeroders (Glynn, 1997). At the time of our surveys (5-8 months after peak bleaching), we noted on-going recent partial mortality of numerous massive corals which were probably secondary effects of the initial bleaching and probably were exacerbated by the passage of Hurricane Mitch (see following section).

The most evident secondary effect was the high number of corals infected with white plague and black band diseases documented over much of the MBRS. Remnant bleaching, partial recent mortality, and white plague and/or black band disease were commonly observed on the same colonies (mainly *Montastraea annularis* sensu lato and *Diploria* spp). The reason for the disease outbreaks is not well understood, but for the MBRS, it is likely that the cumulative effects of bleaching, Hurricane Mitch, and recent mortality made many species more susceptible to pathogens and possibly triggered activity of infectious microorganisms (bacteria, cyanobacteria, fungi, protozoans). The unusually warm waters just before and after Mitch were ideal environmental conditions for many marine pathogens (Rützler et al., 1983; Edmunds, 1991; Peters, 1997). Hurricane disturbance may have acted as a disease vector to spread disease and increase the number of infected colonies by either 1) mobilizing sediment with dormant microbes in it or by transmitting the disease (especially black band) in the water column from infected colonies to nearby colonies (e.g., Edmunds, 1991; Kuta and Richardson, 1996). The number of corals we observed that were injured or weakened by these events may explain the high number of colonies inflicted with disease.

Past information on the extent of disease incidence in the MBRS is patchy and incomplete. Some of the best documentation comes from studies that found the extensive mortality in the early 1980s of *Acropora cervicornis* was attributed to white band disease in Belize (e.g., Aronson and Precht, 1997) as well as much of the Caribbean (e.g., Williams and Bunkley-Williams, 1990). The occurrence of white band disease was reported in Roatan although the extent was not determined (Rogers, 1985), whereas Fenner (1987) found no signs of coral disease in his study of Roatan. Guzman and Guevara (1998) found black band disease increased in Cayos Cochinos after the 1995 bleaching event, with 34% of *M. faveolata* colonies infected. McField (1999) found many bleached corals (particularly *M. annularis* sensu lato) also became infected with black band disease. In general, background levels of black band disease at any given time have been estimated to be ~0.5-1% in other areas (Edmunds, 1991). The incidence of disease we observed in some areas was higher than reported for other areas of the Caribbean, for example Bruckner and Bruckner (1997) found about 6% of coral populations in St. Ann's Bay, Jamaica were infected with black band, resulting in significant mortality. Of interest was the finding that the amount of disease in shallow sites tended to be either very low at a site or extremely high, particularly in Belize. In addition to high rates of prolonged bleaching, the large proportion of *Montastraea annularis* sensu lato colonies infected and dying from disease is of particular concern, especially in Belize shallow reefs and deep fore reefs in the Bay Islands. Many of these sites surveyed were continuing to experience high rates of disease infection and subsequent partial mortality into the fall of 1999. Other secondary effects of 1998 bleaching may take many years to fully elucidate.

In summary, our surveys suggest that recent mortality rates on a regional scale averaged 18% for shallow sites and 14% for deep fore reef sites which approximately equates to the amount of coral cover that has been lost. The majority of this mortality is attributed to bleaching and to a lesser degree disease and hurricane. After the 1995 bleaching event in Belize, McField (1999) reported mortality of approximately 10%, and Burke (1996) documented a 13% loss in coral cover on shallow lagoonal patch reefs. But on a local scale, our surveys reveal there has been a much more dramatic change, with some reefs experiencing up to 74% recent mortality which has led to a significant reduction in species diversity and coral cover. Species specific extinction has occurred at the site and reef scale, but not at the country or regional scale. In Belize, the loss of significant amounts of *Agaricia tenuifolia* and *Millepora complanata* are particularly significant because of their dominant reef building role on many reef (Rützler and Macintyre, 1982; Lasker, 1984). On a Caribbean-wide basis, the impact from the 1998 bleaching event is only beginning to emerge. The Atlantic and Gulf Rapid Reef Assessment program has found that on a Caribbean-wide scale, most areas recovered from bleaching with only minor amounts of mortality, with the exception of the northern Bahamas where bleaching mortality was high (Fig. 28). On a global scale, there appears to have been higher levels of bleaching mortality in other parts of the world, especially in the Indian Ocean (Wilkinson, 1999).

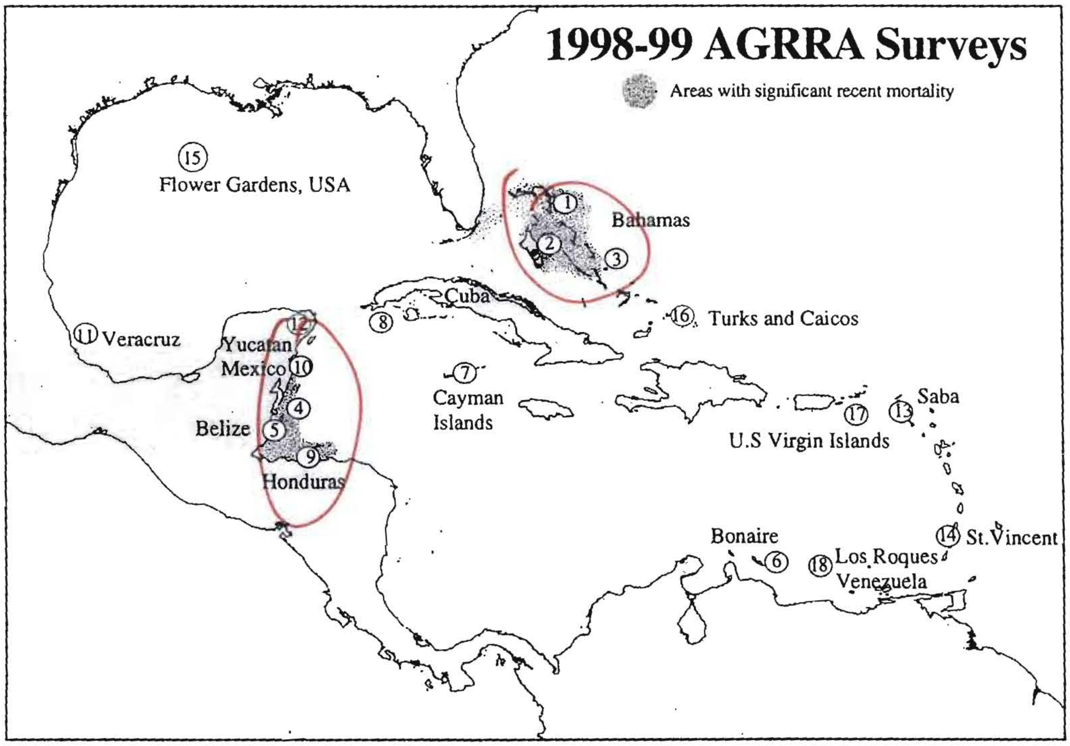


Figure 28. AGGRA results from 1998. Stipled areas show reefs where significant recent mortality was observed

Hurricane Mitch Impacts

The percentages of physically damaged corals (both in place and displaced) recorded during our surveys are most useful as a relative scale to characterize spatial variability of damage caused by Hurricane Mitch. Translating the percentages into what this means in terms of loss of structure or coral cover would require "before-storm" data, which is lacking for nearly all of the sites. These percentages are probably a minimum estimate of what was actually affected, since we only could evaluate corals that remained in the site vicinity. The hurricane survey data displayed pronounced spatial variability suggesting the importance of a reef's susceptibility to damage based on the individual characteristics of the hurricane and reef type.

Impacts from Mitch ranged from minor to severe and extended from Honduras to as far north as the northern Yucatan. The spatial variability in the extent and type of damage observed in the region is due partly to the characteristics of the hurricane. Hurricane Mitch's most notable effects originated from its extended stationary position and its intensity. An interesting result of our survey was that sites in Belize often showed more severe storm damage than sites in the Bay Islands closer to Mitch's track. The most likely explanation is that the combination of a long fetch (100-300 km) and large radius of hurricane-tropical force winds (~100 km) around Mitch's center set up sea level and created huge storm waves in the northern sector of the storm. The majority of Mitch's wave power was generated when the storm was stationary for nearly 48 hours near the island of Guanaja. During that time period, the Bay Islands experienced strong hurricane-force winds, although wave heights were limited to less than 5 m by the short fetch (100-km) between the Bay Islands and Mitch's center. In addition, the position of the Bay Islands on the less severe southwest side of the storm probably spared reefs from more severe damage. In contrast, the brunt of Mitch's storm waves impacted windward east-northeast facing sites in Belize and southern Mexico. According to local reports from Belize City and San Pedro, sea level was observed to rise by several meters during the height of the storm. In exposed areas, huge storm waves reported in the 5-15 m range crashed on north and east facing beaches and reef crests. Many of the unprotected small cays located along Belize's barrier reefs experienced substantial wave damage and erosion on their northeast sides, thus also supporting this scenario (T. Bright and personal observation).

Sites in the lee of offshore atolls or protected behind barrier reef structures to the east were spared from this kind of severe damage. Although there was evidence of knocked over and broken colonies (up to 20%), particularly of *A. palmata*, on a few more protected leeward sites (for example, west sides of Glovers and Turneffe). Despite this damage, it does not appear that the hurricane significantly reduced the reef's structural complexity of these reefs. Had Mitch's track gone through the Belize lagoon, the extent of damage on well-developed back and protected reefs would have been higher, such as was documented for *Acropora cervicornis* in the back reef zone at Carrie Bow Cay, Belize (Still et al., 1982). Although a reef's susceptibility to damage was attributable in part on the individual characteristics of the hurricane and location of a reef, more detailed wind and wave-height data are needed to better hindcast the characteristics of Mitch and verify some of these trends.

The degree of hurricane Mitch damage at a given site was in large part dependent on a combination of the site's physical characteristics (e.g., depth, aspect), community composition, structural complexity, and previous disturbance history; which is similar to what has been found for other post-hurricane studies (e.g., Woodley et al., 1981; Rogers et al., 1982; Bythell et al., 1993). The bulk of physical destruction occurred on shallow reefs where storm energy and mechanical stress was highest. At the most impacted shallow sites in Belize and Honduras, 50-70% of the corals displayed physical damage leaving the reefs largely devoid of substantial structural complexity. Branching and foliaceous coral species (particularly *Acropora* spp., *A. tenuifolia* and *M. complanata*) were most susceptible to damage and were typically broken into smaller fragments. In many cases (especially in Belize), the storm resulted more in a loss of reef structure than live coral cover because bleaching-susceptible species like *A. tenuifolia* and *M. complanata* had already suffered partial or total tissue mortality during the weeks preceding Mitch. In addition, several massive mound species, like *Montastraea* and *Diploria*, were also affected in the shallow sites, usually being either knocked over or fractured. In many cases, we observed broken fragments and overturned heads of all species were abraded by the large amounts of rubble mobilized during and after the storm, or were buried into layers of rubble (up to 2m thick) often making it impossible to quantify the amount of lost colonies or tissue loss. Corals of all sizes (10cm-1+m in diameter) were affected, particularly smaller-sized corals, which may eventually affect population structures and reproduction fitness or success. After Gilbert and Keith hit Yucatan, Mexico, Jordán-Dahlgren et al. (1998) observed a shift in *Acropora palmata* sizes from large colonies pre-hurricane disturbance to smaller colonies post disturbance and a subsequent poor success of new recruits.

Overall, our data suggest reef type (depth, aspect) and community composition (e.g., species, colony morphology and size) accounted for much of the spatial variability between sites. For example, windward reefs in Belize and Mexico have been frequently subjected to large storm waves in the past, including hurricane Hattie in 1968 (Stoddart, 1969, 1974), Greta in 1979 (Kjerfve and Dinnel, 1983) and Gilbert in 1989 (Jordán-Dahlgren and Rodríguez-Martínez, 1998). As a result of these storms and the high wave energy characteristic of the region, many windward reefs were characterized by bare pavement interspersed with short blocky spurs, low coral cover, and lacked a well-developed *Acropora palmata* rampart. Although these reefs were subjected to large storm waves, in many cases the damage was not as severe as might be expected, simply because of the lack of substantial coral structure most prone to hurricane damage.

Mitch did not affect deep fore reef sites in the MBRS region as severely as the shallow sites, probably due to the lower wave energy at deeper depths and the lower abundance of delicate branching corals. Fore reef storm damage was most evident in Belize, in some cases down to depths of 20 m, and related mostly to a reef's location relative to the storm surge and community composition. The most dramatic impacts occurred where the top of fore reef spurs were composed of an unstable layer of interlocking old dead *A. cervicornis* on which massive corals were using as a foundation to grow on. Hurricane force waves breaking on these spurs dislodged many of the massive corals, particularly *D. strigosa* in the 20-40 cm size class range. These dislodged corals were then swept up into shallow water reefs leaving only a faintly distinguishable impression of where they had been growing. Piles of fresh coral heads and fragments up to two meters thick were observed on reef crest and back reefs of the more impacted sites (Photo ##). This type of damage was observed in southern Ambergris down to Chapel Cay, on selected fore reefs sites along the central and southern Belize barrier, the eastern side of Glovers atoll, and on the northeastern side of Guanaja.

Secondary effects

Apart from the immediate physical destruction imparted by wave energy, there were also numerous secondary effects from Mitch that are more difficult to quantify and may take years to fully become apparent. The most significant of these was the extensive runoff of low salinity, sediment-ladened water into the Gulf of Honduras in the weeks and months following Mitch. It is also likely that this mainland runoff contained high quantities of pesticides and fertilizers washed away during the storm (P. Dulin, personal communication). SEAWIFs imagery (Fig. 29) indicated that the post-Mitch plume of runoff appears to have influenced portions of the Bay islands for several weeks and even went as far north as Glovers Atoll in Belize (Andrefouet, unpublished data). Undoubtedly, sediment runoff would have added additional stress to corals already stressed from warm waters. Additional energy would have to be allocated towards removing thin layers of sediment which would increase energy demands and contribute to a continued state of stress and potentially to mortality (Hodgson, 1994). The only sedimentation we heard reported occurred at Cayos Cochinos, located 40 km from the mainland Honduras coast, where thin layers of sediment coated corals for months (4+) after Mitch (C. Garcia-Saez, personal communication; P.R. Kramer, personal observation).

Sedimentation and runoff may have contributed to some of the stress experienced by corals in November-December, 1998, but it is not thought to have had an immediate impact on any of the areas we examined. Supporting this contention is the fact that recent mortality rates were not significantly higher in Cayos Cochinos than the other Bay Islands or other parts of the MBRS not subjected to Mitch runoff. Furthermore, most of the recent mortality observed at Cayos Cochinos was attributed to bleaching and diseases rather than sedimentation. One possible explanation for the lack of significant sedimentation effects around Cayos Cochinos is that corals here are frequently exposed to sediment runoff because of their proximity to the mainland and may be better adapted. Yet it is possible that increased sedimentation did contribute to the high percentage (43%) of deep fore reef corals observed in a prolonged bleached state. Runoff and sedimentation were probably most damaging to inshore coral communities and hard grounds near the Honduran and Guatemalan mainland, but additional follow-up monitoring is necessary to determine long-term effects. The United States Geological Survey (USGS) is presently undertaking studies to determine the extent of Hurricane Mitch damage to these inshore areas.

Not all secondary effects of Hurricane Mitch were negative to reef sites in the region. There is considerable evidence that the passage of the hurricane may have benefited some areas by improving water quality, mainly by decreasing water temperatures thus alleviating some of the temperature stresses on corals. The passage of hurricanes is known to lower water temperatures by several degrees (3°C) as deeper water is upwelled to replace lost surface water (Shay et al., 1992). The large size and slow movement of Mitch probably also had the added effect of flushing out hot lagoon water in portions of the Gulf of Honduras and southern Belize lagoon where bleaching was already rampant. Several dive operators on Roatan and Guanaja described the inshore waters as "green and stagnant" in the weeks prior to the hurricane but noticed a dramatic improvement in water quality after Mitch passed. The cooler and cleaner waters possible carried in by Mitch may have relieved much of the temperature stress corals were experiencing prior to the hurricane, particularly in Honduras and southern Belize.

Large disturbances such as Mitch can also have a strong secondary influence on coral re-colonization process of some species by 1) producing fragments, and 2) affecting macroalgae that compete with corals for space. Numerous fragments of fragile species such as *A. palmata, A. tenuifolia* and *M. complanata* were often observed at storm damaged sites. However, most fragments had been washed into the shallow rubble zone where they suffered high mortality due to abrasion. In addition, many of these fragments were already dead (or dying) because of the bleaching event. In a few cases, fragments of *M. complanata* were observed reattached to the substrate. A more significant influence on coral recolonization is thought to occur from changing macroalgal abundances. Immediately following Mitch (weeks-scale), there was a dramatic decrease in macroalgal abundance across much of the MBRS (Local observations, and T. Williams, unpublished data). This initial decrease in macroalgae may have benefited surviving fragments and new recruits by decreasing competition for space. Fong and Lirman (1995, 1997) documented a large increase in asexual regeneration of *Acropora* populations following Hurricane Andrew that they correlated to a decrease in macroalgal abundance. Similarly, Rosesmyth (1984) found moderately high sexual recolonization of *A. palmata* in Jamaica immediately after hurricane Allen (1 recruit/m2), but that high mortality from predation and competition reduced recruitment success considerably in subsequent years. Jordán-Dahlgren and Rodriguez-Martinez (1998) found that macroalgae returned in record amounts in subsequent years after Hurricane Gilbert which in the long-term may have depressed coral recruitment. Additional follow-up monitoring is necessary to determine the extent of coral recolonization.

In summary, the physical forces generated by Hurricane Mitch had differential effects on the reefs in the MBRS region resulting in pronounced spatial variability of the extent and type of damage observed throughout the region. This variability emphasizes the importance of a reef's susceptibility to damage based primarily on the individual characteristics of a reef, as well as hurricane properties. Hurricane Mitch's most notable effects originated from its extended stationary position and its intensity. Hurricane Mitch caused significant localized increases in coral mortality, particularly to specific species, as well as a loss of reef structure and complexity. How reefs responded to these effects varied depending primarily on a reef's location, species present, and architectural complexity and ultimately will play a determining role in the potential for their recovery.

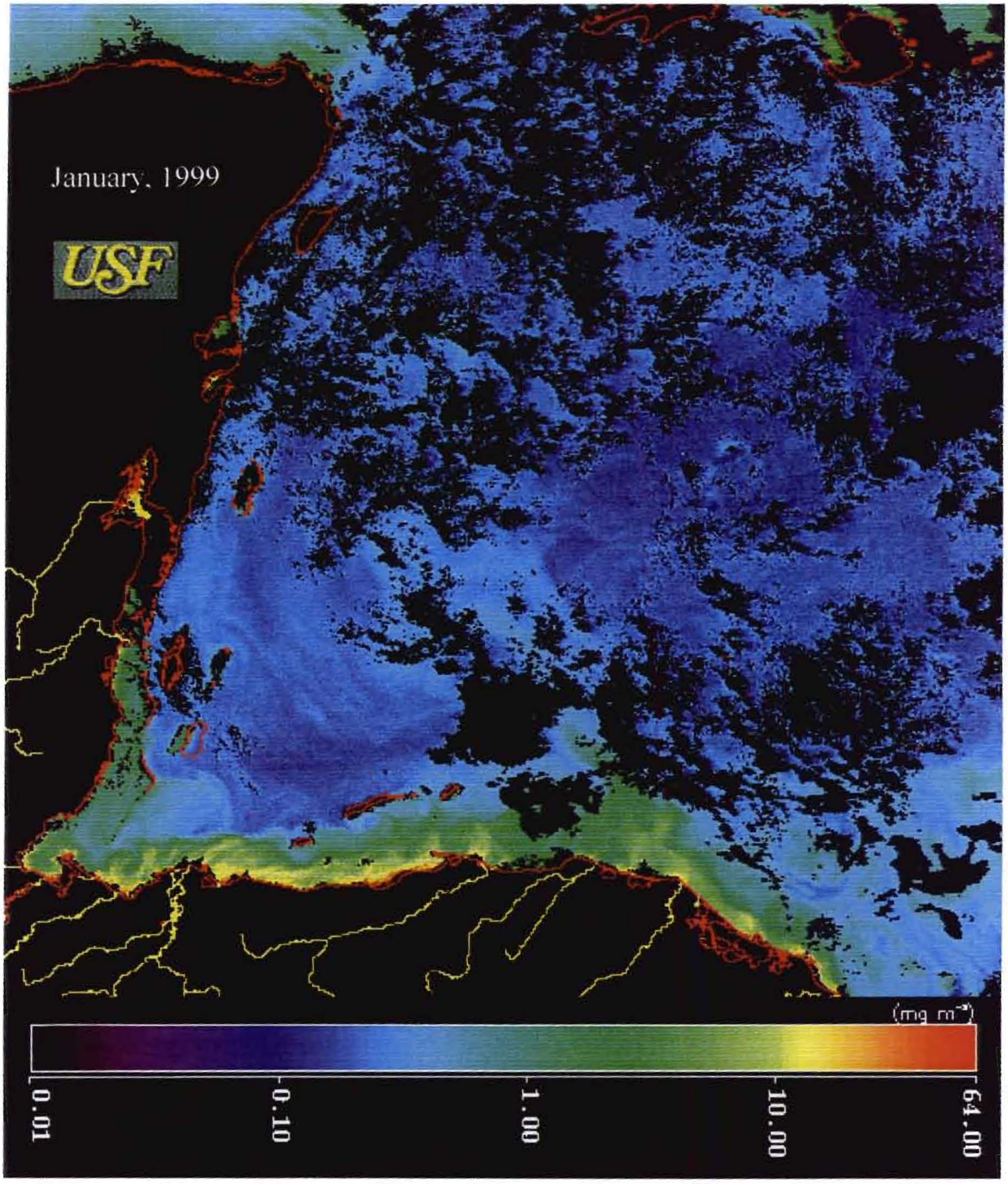


Figure 29: SEAWIF image of MBRS region taken in early January, 1999 showing widespread runoff along north coast of Honduras and into the Bay Islands -Cayos Cochinos and Utila. The scale bar indicates the approximate chlorophyll concentration in the water column (mg/m3). Image courtesy of S. Andrefouet.

Summary: Ecological Consequences and Future Perspectives

The longer-term ecological consequences of coral mortality and physical storm destruction experienced by much of the MBRS during 1998 will depend on complex interactions between recovery and degradation processes. Recovery processes include rates of growth and regeneration of the remaining surviving colonies (Rogers et al., 1982) and recruitment of new larvae (Bak and Engle, 1979) and will vary depending on a coral's life history and the manner in which it allocates resources. Over the next few years, reduced growth rates and diminished reproductive output might be expected for many coral species of the MBRS region. Szmant and Gassman (1990) showed that *Montastraea* spp. that do not recover their zooxanthellae within 7 months after bleaching have a low probability of producing reproductive outputs in the ensuing year. The high percentage of *Montastraea annularis* colonies showing remnant bleaching (~30%) up to 8 months after the peak bleaching event suggests that reproductive output during August-September 1999 and possibly longer, will be diminished for this species. Our data implies many small- to medium-sized corals on exposed fore reef sites suffered total mortality suggesting size-class distributions may have been disrupted. The loss of an age class or disruption of size-class frequencies may cause significant changes in population and community dynamics (Bak and Meesters, 1999; Done 1999). Although we did not measure coral sizes, we did observe that larger colonies were more likely to experience *partial* mortality which supports the hypothesis by Bak and Meesters (1999) that coral populations that undergo continued large-scale perturbations will progressively become skewed towards larger sizes.

Another likely consequence of the 1998 disturbance events for the MBRS region is the alteration of coral reef communities in terms of species richness and densities (e.g., Rogers, 1993; Bythell et al., 1993). In the east Pacific, local extinction of coral species following massive bleaching is well documented (e.g. Glynn, 1988, 1990). The degree of species extinction is largely dependent on scale. For the MBRS region, species extinction will be most evident at smaller spatial scales of sites (~100 m) to reefs (~10 km) but probably not at larger spatial scales of areas (~50km) and certainly not for the region (~500 km). One of the worst hit areas of the MBRS were the shallow reefs in the central and southern Belize lagoon. In many places, more than 70% of the coral is now dead resulting in local species extinction, particularly for the reef building species of *A. tenuifolia, M. complanata, A. palmata, M. annularis.* How changes in species composition of reefs will affect long-term integrity of coral reefs is currently unclear.

There is also the likelihood that severely disturbed reefs in the MBRS will shift from coral dominance to macroalgal dominance similar to what has been documented in other areas of the Caribbean (Ginsburg, 1994). In Jamaica, the synergistic stresses of hurricane Allen, overfishing, and the *Diadema* die-off resulted in a complete phase shift from a coral- to an algal-dominated state that has remained in many areas to this day (e.g. Hughes, 1992, 1994). Overtime, the moderate-to-severe damaged areas of the MBRS might be expected to lose much of their reef framework as bioerosion and physical breakage of standing dead corals takes place (Glynn, 1997) or from the possible reduction of calcifying organisms (Done, 1999). Depending on the rate of ensuing structural degradation of the remaining reef framework, ecological consequences might include the loss of habitat for many reef dwellers and possibly the complete disruption of food cycles. Species with strong habitat fidelity that inhabit shallow water reefs will be most affected. These might include corallivores, herbivores, and some meso-predators (grunts).

Our preliminary projections of how the MBRS reefs might respond to the 1998 disturbance events are briefly outlined based on criteria by Done (1999). In response to changing and increasing environmental perturbations, Done (1999) suggests reefs are likely to follow one or a combination of scenarios including: *Tolerance* (acclimation of corals, no major change), *Fast turnover* (community shift to smaller corals as life expectancy decreases), *Strategy shift* (hardier species replace more susceptible ones), and *Phase shift* (corals are replaced by another organism such as algae). In general, MBRS reefs that were categorized as "low" disturbance are likely to experience *tolerance*, whereas "moderate" and "severe" disturbance reefs are likely to undergo *fast turnover* or *strategy shifts*. The most severely disturbed sites have a high likelihood of experiencing *phase shifts*. Although these projections may be an over simplification of what may occur, they do provide guidance on potential scenarios. Which scenario or combination of scenarios the reefs of the MBRS region follow remains to be seen. However, it is likely that reestablishment of many of the sites to their pre-disturbance condition may take significant time and in some cases may never be achieved.

Future implications

The long term ecological consequences of bleaching and hurricane destruction in the MBRS will take years to fully emerge. The numerous complex interactions that occur on coral reefs make predicting any single outcome very near impossible. Important factors that must be considered include the frequency and intensity of future disturbances (Hughes, 1999), the ability of corals to adapt to the changing environmental conditions (Buddemeier and Fautin, 1993), and the degree to which human impacts are managed (Brown, 1996). Perhaps the largest threat to the future of the MBRS and other regions of the Caribbean comes from the likelihood of future bleaching events (Hoegh-Guldberg, 1999). There is increasing evidence that global warming is occurring and that sea surface temperatures are increasing. The decade of 1990 was the warmest on record and many databases show that there has been a gradual warming trend since 1970 most pronounced during global El Niño events. Sea surface temperature prediction models for the next 100 years suggest that the warming trend will continue and that bleaching events will become more frequent and more extreme in magnitude (Hoegh-Guldberg, 1999, Fig. 30). If these predictions are correct, than bleaching will be an annual occurrence over much of the Caribbean by the year 2015.

Socioeconomic effects

The socioeconomic effects of hurricane and bleaching coral mortality are more difficult to predict. Possible consequences may include a loss of revenue within the fisheries industry (reef finfish, crawfish), and possibly lower revenues in the tourism industry associated with diving and snorkeling activities. Overtime, the loss of reef structure may also increase coastal erosion on adjacent beaches. Further socioeconomic studies coupled with detailed monitoring need to be implemented to better determine the long-term consequences of the 1998 impacts to the MBRS region.

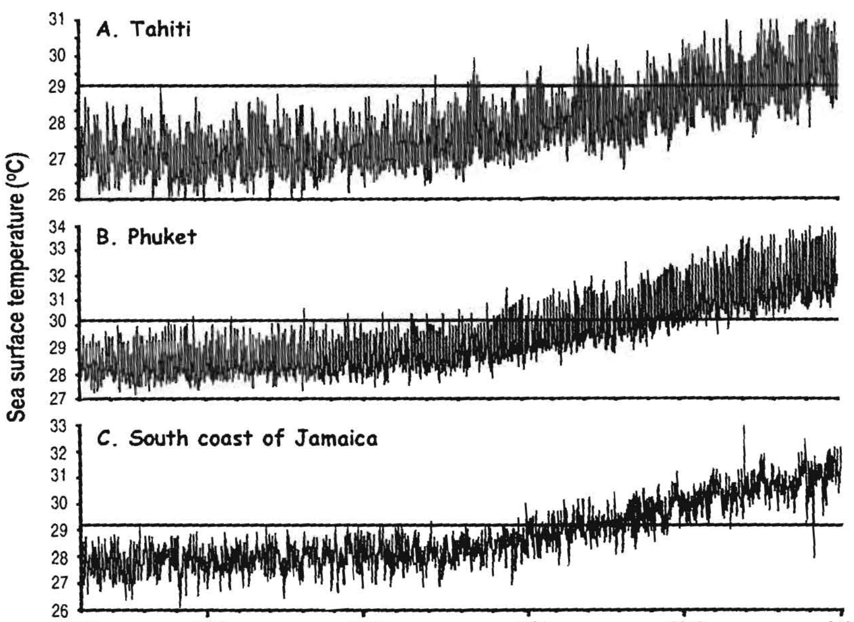


Figure 30. Sea surface temperature fluctuations in the past and predicted over the next 100 years. Graph from Hoegh-Guldberg, 1999.

Recommendations

The MBRS Initiative can contribute to the preservation, restoration, and sustainable use of coral reefs by contributing to the maintenance and restoration of the natural structure, composition, and ecological processes of this important community. The conservation of coral reefs will supply structural habitat (shelter and food) to numerous organisms, provide nursery and breeding habitat, maintain or increase biodiversity, and contribute to the protection and stabilization of imperiled and rare species. Management and restoration on such a regional landscape level as the MBRS should attempt to maintain or reestablish the natural structure, composition, and landscape processes that were historically lost as a result of human impacts. To improve our ability to restore some of these processes, it is essential to establish measurable management and restoration goals and long-term monitoring programs to evaluate the success of these goals. Below are recommendations for measurable goals and criteria to manage coral reefs in the MBRS region. We have separated this section into two sections: ecological loss and socioeconomic concerns. For each section we briefly list problems and concerns then present specific recommendations.

Ecological loss

Problems and concerns

1. Serious declines of several important reef builders (e.g., *A. tenuifolia*, *Montastraea annularis*, *Millepora complanata*).
2. Local extinction is likely for some coral species (*A. cervicornis*, *A. tenuifolia*, *M. complanata*).
3. High coral mortality will decrease likelihood of recovery or re-establishment of some corals.
4. Macroalgal abundances are likely to increase in disturbed areas and compete with corals.
5. High incidence of coral disease and high potential for continued mortality.
6. Loss of coral cover and reef structure can reduce reef habitat and structure for fishes/other invertebrates.
7. High potential for future bleaching events, particularly affecting areas that lack flushing.

Recommendations

1. Establish a region wide monitoring network to evaluate reef recovery and investigate the following:
   - Recovery of tissue of selected tagged coral colonies
   - Coral populations (e.g., species diversity, corals size)
   - Coral recruitment
   - Recent mortality
   - Coral disease
   - Macroalgal overgrowth
   - Reef architectural complexity and loss of reef structure
   - Fish populations (select species): diversity, density, size
   - Physical characteristics (e.g., temperature, current, turbidity)
   - Rate of change of habitat

   – Yes - Moveable - rotating protected areas

2. Establish immediate "temporary" or "restricted-use" marine protection areas to minimize further degradation or alteration of severely disturbed areas (see Tables 3-5). Monitor effectiveness of temporary protected areas in promoting reef recovery.

3. Identify important reef habitats with high biological production, high biodiversity, endangered and imperiled species, nursery and breeding areas, and sources and sinks of larvae and adults.

4. Develop a regional network of protected critical coral reef habitats to protect these important reef habitats.

Use the data on trajectory of bleaching + SST rise, + [illegible] to [illegible] where MPAs should be set up - even on a temporary basis. During coral spawning - all reefs should be protected

5. Conduct applied scientific research that investigates specific hypotheses or questions on reef recovery.

   - Investigate the extent of coral recovery after the removal of black band disease. Remove active black band and prevent algal growth/competition, particularly at popular tourist reefs.
   - Establish an experimental study that evaluates the effects of increased flushing in restricted flushing areas (e.g., Glover's) and determine if increased flushing helps decrease the amount of algal overgrowth, coral disease and improve overall reef condition.
   - Investigate the response of fish and other important species (e.g., lobsters) to the change in coral condition (i.e., change in quality or quantity of food or habitat).
   - Conduct restoration, transplanting, and augmentation techniques to improve degraded reef sites. Determine if coral recruitment enhancement techniques significantly increase coral recruitment or survival and are technologically and economically feasible.
   - Conduct intensive studies on specific imperiled coral species (e.g., *Acropora*, *Agaricia*, *Montastraea*) and determine status and likelihood of extinction.

6. Conduct applied scientific research that investigates specific hypotheses or questions on reef structure, composition and ecological processes.

   - Determine the quality and quantity of important habitats. Has the quality, structure and function of habitat been lost or altered due to natural and manmade impacts?
   - Investigate the extent of habitat use by species and life stages.
   - Investigate recruitment and linkage studies to determine source and sinks of coral larvae. How does the dynamic physical environment (e.g., transport) affect the movements of larvae, juveniles and adults?
   - Investigate the effects of natural and human stressors on habitats and populations and communities.

7. Develop a regional GIS-metadata database. The information from this report is in GIS-format and can be used as a basis for forming a regional database that will incorporate additional information that is available or collected.

8. Promote the implementation of marine protection policies by increasing funding at both regional and national levels.

Socioeconomic concerns

Problems and concerns

1. Impacts to reefs (i.e., loss of coral cover) from the hurricane or bleaching event may negatively impact tourism (divers, snorklers) by decreasing the aesthetic value and experience.

2. Impacts from the hurricane (e.g., wind damage, loss of docks) may have caused hardship on local businesses that rely on reefs for livelihood. Many fishermen lost time, traps or fishing gear during the hurricane and may suffer economic hardships.

3. Loss of coral cover and reef structure over time may lead to decrease in fish stocks and may impact socioeconomic livelihood of locals.

4. General lack of awareness has reduced stewardship for marine coastal areas.

5. Few established monitoring efforts, particularly on regional or transboundary scales and lack of resources and funding to monitor.

6. Lack of legal protection, marine protection policies or enforcement, especially on the regional level.

Recommendations

1. Collect existing socioeconomic data losses from hurricane because of impacts on reefs.

2. Conduct interviews with local tourism operators (e.g., dive shops, resorts) to evaluate if damage to reefs has resulted in loss of business, dissatisfaction of customers or reported loss of aesthetic value of reef habitat.

3. Conduct interviews with fisherman to determine if damage to reefs has resulted in a decrease in catch, if time/effort was affected, or economic loss occurred.

4. Determine what factors attract tourists to the MBRS and how important "healthy" reefs are.

5. Increase public awareness of coral reef habitat and instill stewardship.

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Appendix 1. Bleaching reports in the MBRS.

Country	Date	Reporter	Location	Water temp.	Bleaching Comments
Mexico	Aug.-Oct 1998	Eric Jordan	Quintana Roo	Aug ~30°C, Sept-29.5-30.5°C	Variable bleaching began. *Agaricia, Millepora* affected more than *Montastraea, Diploria*, although acroporid not affected. Bleaching less severe than 1995.
Mexico	Sept. 1997	Rodrigo Garza Perez CINVESTAV-IPN Unidad Mérida*	S. Yucatan Xcalak, Mahaual, Sian Ka'an		Massive bleaching beginning in Sept. 1997, mainly affecting *A. tenuifolia* Affected *Montastraea annularis* and *Diploria labyrynthyformis*
Mexico	Oct. 15 1998	Jose Hernandez CINVESTAV-IPN Unidad Mérida*	Mahahual, near Chetumal	88°F (31.1 °C)	Pale corals, has samples and color slides
Mexico	Aug.-Oct 1998	Eric Jordan	Quintana Roo	Aug ~30°C, Sept-29.5-30.5°C	Bleaching began, Variable bleaching, *Agaricia, Millepora* affected more than *Montastraea, Diploria*, acroporid not affected. Bleaching less severe than 1995.
Belize	Sept 2, 1998	Thomas Bright Glover's Reef Marine Station, Belize*	Crawl Caye (N. end of Victoria Channel)	High in upper 2 ft; sharp thermocline at 3 feet	Massive bleaching (85%) of *M. annularis* (knobby)Upper 6 inches of wa column was brown; little wind for 7 days prior to study
Belize	Sept. 15, 1998	Thomas Bright (see above)**	Entire Belizean Reef ecosystem	30-32 °C	Massive bleaching in *Millepora, Agaricia, Palythoa*, and *P.Porites*, High/patchy bleaching in *Montastraea, Siderastrea*, and *Diploria*, Low/patchy bleaching in *Dendrogyra* and *Acropora*
Belize	Sept 17-21, 1998	Melanie McField Univ. South Florida*	Gallows, Goffs Alligator, Calabash, Turneffe	-	Moderate/patchy bleaching (25-30% affected), Depths of 14-18 m
Belize	Sept. 23-Oct. 7, 1998	Melanie McField (see above)*	Glovers reef atoll	-	High bleaching (76% affected), Along western fore reef (near Baking Swash) at 12-15 m
Belize	Sept. 23-Oct. 7, 1998	Melanie McField (see above)*	Long Caye (eastern fore reef)	-	High bleaching (70-80% affected), Partial tissue mortality by early Oct., esp. in acroporids (compared to 1995); bleaching appears to be greater in northern and southern regions.
Belize	Late Oct.	Rich Aronson, Bill Precht Dauphin Island*	Central lagoon	28.5-29.8 °C 28.5-29.1 °C (at 9 m)	Massive bleaching, pale corals, recently mortality of *A. tenuifolia*
Belize	Late Oct.	Rich Aronson, Bill Precht*	Fore reef at Curlew Bank	29.6 °C 29.3 °C (at 9 m)	Patchy bleaching, massive bleaching, Only patchy bleaching of *A. tenuifolia*, while *A. cervicornis* and *A. palmata* showed no signs of bleaching (highly bleached in central lagoon).
Belize	Late Oct., 1998	Thomas Bright* (see above)	Lagoonal patch reefs adjacent to Middle Caye		Massive bleaching, Obvious mortality in A. *palmata*, P. *Porites*, and *Millepora* sp.
Belize	Late Oct., 1998	Thomas Bright* (see above)	Upper fore reef		Massive bleaching ,Corals were in initial steps of recovery when Hurric Mitch came through
Belize	1998	Jorge Cortés (Univ. de Costa Rica) and Marea Hatziolos (World Bank)**		32-38 °C in protected shallow waters	Large areas show extensive bleaching of almost all species, Rates overal status of Belize reefs as very good.
Belize	Jan. 5-12, 1999	Mark Bertness, John Bruno Brown Univ.*	Southern Belize		Massive bleaching for *A. tenuifolia* and *Millepora*, All colonies of *Porit* and *Montastraea* were healthy; Suspect that white band disease has eliminated *Acropora* colonies (Laughing Bird Key)
Belize	Jan. 7-8 1999	Rich Aronson, Bill Precht*	Central lagoon	25.5-26.5 °C	Massive bleaching of *A. tenuifolia*, Massive mortality of *A. tenuifolia* du bleaching and physical damage from Mitch; Bleaching and white band disease has virtually eliminated *A. cervicornis*
Belize	Jan. 7-8 1999	Rich Aronson, Bill Precht*	Curlew Bank		Bleaching of *A. tenuifolia*, other species are recovering from patchy bleaching, Most of foliose, branching, and massive corals appear to be recovering and regaining color.
Belize		Roy Caldwell, Kate Schafer, UC Berkeley	Spanish Bay Cay		Massive bleaching
Honduras	Mid-September	Marea Hatziolis, World Bank**	Roatan, Bay Islands		Up to 50% live coral cover bleached , Bleaching at depths 10-25 m, mo species affected especially *Agaricia, Montastraea, Diploria*

*Coral list server. Coral.aoml.noaa.gov Bleaching reports 1998-1999. ** Wilkinson. C.R. (ed.). 1998. Status of Coral Reefs of the World: 1998.Global Coral Reef Monitoring Network. Australian Institute of Marine Science. 184 pp.

Appendix 2. Coral diseases of the wider Caribbean. Information from:
http://ourworld.compuserve.com/homepages/mccartyandpeters/coraldis.htm

Disease	Description	Corals Affected	Geographic extent	Impact	References
Black-band disease	Black band approx. 1-2 in. wide leaving behind a bare white skeleton. Cause: cyanobacteria Infected colonies can infect healthy colonies that are it in contact with it but injured colonies are more susceptible. Conditions which increase the occurrence of BBD include sedimentation, high levels of nutrients, toxic chemicals and above-average water temperatures	*Montastraea cavernosa, M. annularis, M. franksi, M. faveolata, Diploria strigosa, D. labyrinthiformis Colpophyllia natans, Siderastrea sideria*	Caribbean Indo-Pacific and Red Sea	Can cause partial loss of tissue, remaining tissue can continue to grow after band disappears; bare skeleton can be colonized preventing coral settlement	Antonius; Rutzler & Santavy; Carlton & Richardson, 1995; Kuta & Richardson, 1996; Edmunds, 1991; Peters, 1993; Littler & Littler, 1996; & Bruckner et al., in press
Bleaching	Loss of algae and pigment forming white skeleton Cause: high temp/salinity levels, high turbidity/ sediment levels	*S. sideria, P. porites, M. faveolata*	World-wide	Can affect reproduction, growth, cause tissue degeneration, or cause death of affected area	Kushmaro et al., 1996; Ritchie & Smith, 1995; Upton & Peters, 1986; Edmunds, 1994; Rowen et al, 1997; Williams & Bunkley-Williams, 1990; Glynn, 1993; Birkeland, 1997
Dark spots disease	Discolored spots (dark purple/gray/ brown) usually circular. Cause: unknown	*S. sideria, S. radians*	Florida Keys Caribbean	Tissue and skeleton tend to build up after tissue dies in circular area	
Red band disease	Brick red or dark brown band which can easily be removed from coral surface. Cause: cyanobacteria and microorganisms	*Diploria strigosa, M. annularis, M. cavernosa, P. asteroides, S. sideria, C. natans*	Caribbean Brown band – GBR	Build up of sediment and algae in affected area preventing settlement of corals	Richardson, Santavy, Dinsdale
White Band Disease	Moves from the base of branches to tip peeling of coral tissue leaving bare white skeleton at a rate of 1/8 to 1/4 inch/day. Cause: unknown	*Acropora palmata* and *A. cervicornis*	Type I: Caribbean, Philippine GBR, Red Sea. Type II: Bahamas	Can spread very quickly killing a large percentage of coral in area	Gladfelter, 1982 Ritchie and Smith, 1995; Bythell and Sheppard, 1993 and Peters, 199
White plague	Tissue disappears at a rate of 1 or more cm/day leaving a bare white skeleton; sharp line between healthy tissue and bare skeleton. Cause: probably bacterium	About 18 species: *Diploria strigosa, A. agracites, Dichocoenia stokesii, Den. cylindrus*	Type I: world-wide Type II: Florida Keys	A rapid partial or complete loss of tissue	Dustan, 1997; Antonius, 198 Peters, 1984
White pox	Irregular patches of bare white skeleton usually on the surface or underside of branches. Cause: unknown	*Acropora*	Florida Keys	Killed large percentage of elkhorn, spreading throughout Keys & Bahamas	
Yellow blotch disease	Irregular blotch of light yellow tissue; inside area usually fills with algae and sediment Cause: unknown	*Montastraea faveolata, M. annularis*	Yellow blotch: FL Keys and Caribbean Yellow-band: Arabian	Affecting very old colonies and large amounts of tissue loss throughout Caribbean and Arabian Gulf	