Version of Record: https://www.sciencedirect.com/science/article/pii/S0025326X21008997
Manuscript_d2aafc97f6fcb9407f567741713f1407

Revised paper submitted to "Advances in Knowledge about the Sources, Fates and Consequences of Pollutants in Tropical Shelf Systems", a Special Issue in *Marine Pollution Bulletin* in Honour of Jon Brodie.
6 August 2021

Coral Reef Health in the Gulf of Honduras in Relation to Fluvial Runoff, Hurricanes, and Fishing Pressure

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Highlights

- Identification of four biogeographic reef zones in the Gulf of Honduras with significant differences in the local stressors analyzed.
- Fluvial runoff, hurricanes, and fishing pressure were evaluated and have different levels of impact in the four reef zones.
- Reef Health Index (RHI = 5.0 max) proved to be a valuable predictor of reef health in the four reef zones, ranging from poor (RHI = 2.1) to good (RHI = 4.3), in response to the local stressors, consistent with conventional ecological causal relationships.
- Recently discovered Cayman Crown Reef on the border between Belize and Guatemala experiences high fishing and fluvial stresses, but still has unexpectedly high coral cover (on average 49%) in the absence of hurricane damage.

Abstract

The Gulf of Honduras includes extensive coral reefs in Belize and Guatemala, classified into four biogeographic zones, which are differentially affected by runoff, hurricanes, and fishing. Runoff mostly impacts the coastal and adjacent channel reefs. The Belize Barrier Reef (BBR) experiences less runoff impact due to the prevailing cyclonic ocean circulation. Hurricane waves powerfully impact the BBR, only occasionally the lee-side of Glover's Reef, and rarely the coastal and channel reefs. Fishing pressure is most intense on the coastal and channel reefs, comparatively modest on the BBR, and low at Glover's Reef. The effects of the three local stressors were evaluated using observations from 24 sites in the Gulf of Honduras. Data were analyzed using the Reef Health Index (RHI), with the highest RHI (4.3) for two Glover's Reef sites, medium RHI (2.6) for 10 sites on the barrier reef, and lowest RHI (2.1) for 8 coastal reef sites.

Key words: Mesoamerican Reef; reef health index; fluvial runoff; hurricane impact; fishing pressure; Gulf of Honduras.

1. Introduction

The Mesoamerican Reef (MAR) is the most extensive barrier reef complex in the Americas, located in the western Caribbean Sea. The MAR extends for more than 900 km along the coasts of Mexico’s Yucatan peninsula, the entire coast and offshore atolls of Belize, and the Caribbean coasts of Guatemala and northern Honduras. In addition to the barrier reef, there are extensive fringing, patch, pinnacle reefs, inner-barrier reef rhomboid shoals, and four off-continental shelf atolls. The focus in this paper is the section of the MAR located in the Gulf of Honduras (Figure 1), south of Dangriga (Belize) and west of Glover’s Reef (Belize)/Puerto Cortez (Honduras) but not including the reefs of northern Honduras. The study area extends 125 km from the northern part of Columbus Reef (latitude N16.91°) to the coastal reefs of Guatemala in the south (Figure 1).

Our objective is to relate indicators of reef health in the Gulf of Honduras to the three main local stressors, (i) chronic and episodic fluvial sediment/nutrient runoff, and (ii) fishing pressure (both hypothesized to decrease towards the north), and (iii) intermittent impacts by hurricanes (hypothesized to increase towards the north). We explore ways to distinguish the influence of these three local stressors on the health of the reefs against the backdrop of global stressors, such as rising ocean temperatures and coral bleaching. Two reference sites on the western leeward side of Glover’s Reef atoll are least affected by fluvial runoff and fishing pressure, located within in a Marine Reserve with managed access, and protected from direct hurricane waves by the ocean-facing reefs of the atoll.

2. Physical Setting

The southernmost portion of the MAR complex in the Gulf of Honduras consists of the BBR, reefs fringing Glover’s Reef, a series of reefs along the coast of Guatemala, the Cayman Crown Reef in the channel south of the Sapodilla Cayes, and reefs scattered throughout the BBR lagoon. The southern BBR from Columbus Reef to the Sapodilla Cayes is semi-contiguous for approximately 100 km and separated from the Belize mainland by a 20 - 40 km wide coast-parallel lagoon (Heyman and Kjerfve, 2001). The 1,000 m isobath, from Glover’s Reef (an offshore atoll) via Gladden Spit to the Sapodilla Cayes, parallels the boundary between the North American and Caribbean lithospheric plates, with water depths exceeding 1,000 m within 6 km of the reef crest (Rosencrantz and Sclater, 1986).

A 28-km wide channel separates the Sapodilla Cayes at the southern end of the BBR from the coastal reefs of the Punta de Manabique peninsula (Guatemala). This channel connects the Gulf of Honduras and the BBR lagoon and is the major shipping lane to Puerto Barrios, Guatemala’s main Caribbean port. Located in the middle of this channel at the southern end of the Cayman trench (where the 1,000 m isobath forms an acute 50° angle; Figure 1), lies a recently discovered channel reef complex, the Cayman Crown Reef (Giró and Mojica, 2020). It covers some 90 km^2, consists of highly complex spur and groove structures with steep walls (Giró and Mojica, 2020), and includes a contiguous 10 km^2 area where water depths range from 0 to 10 m (Figure 1).

The Gulf of Honduras experiences persistent northeasterly trade winds, occasional ‘northers’ with mainly northeasterly winds November-January (Koltes and Opishinski, 2009), and south-flowing currents along the southern BBR as a result of cyclonic (anticlockwise rotating) meso-scale eddies in the Gulf of Honduras (Thattai, 2003; Ezer et al., 2005; Chérubin et al., 2006). These eddies form and separate from the westward flowing Caribbean current 3 - 5 times every year as it crosses the shallow ridge between Jamaica and Honduras/Nicaragua (Thattai, 2003; Ezer at al., 2005). The cyclonic eddies have diameters from 100 to 300 km, drift west towards the Belize Barrier Reef, and are easily mistaken for a single semi-stationary eddy in the Gulf of Honduras (Thattai, 2003; Ezer et al., 2005; Carrillo et al., 2015). The southern BBR thus experiences intermittent but dominant south-flowing currents seaward of the reef due to these cyclonic eddies and enhanced by the trade winds (Ezer et al., 2004, 2005).

Hurricanes frequently traverse the Gulf of Honduras, approaching the study area from the easterly sectors, mostly from the east southeast, with winds, waves, and rainfall impacting both natural and built environments, including the coral reefs of the Gulf of Honduras (National Ocean Service, 2020).

3. Methods

In this paper we assess the health of the reefs in the Gulf of Honduras along a south - north gradient in relation to differences in the three main local stressors (fluvial runoff, hurricane damage, and fishing pressure) with the aim of evaluating the main influences on the coral health in four biogeographic zones (Guatemalan coastal reefs, the Cayman Crown channel reefs, the BBR, and the reference reefs on the west-facing lee side of Glover’s Reef). This required the use of multiple disparate datasets, including Healthy Reefs Initiative’s Reef Health Data, modelled fluvial runoff, historical hurricane data along with some ancillary oceanographic time series measurements, and comparative estimates of fishing intensity based on number of fishers per fishing area.

3.1 Evaluating Reef Health

To assess the condition of the coral reefs in the Gulf of Honduras, we used the Healthy Reefs Initiative’s observations, which are available on www.healthyreefs.org/dataexplorer (2018 data) with measurements at four additional reef sites on Cayman Crown Reef in 2019, all following the AGRRA (Atlantic and Gulf Rapid Reef Assessment) protocol (www.agrra.org). The Healthy Reefs Initiative is a collaboration of more than 70 organizations, led by the Smithsonian Institution, incorporating science into conservation of the Mesoamerican Reef in Belize, Guatemala, Honduras and Mexico.

Reef Health is assessed with the following four key indicators:
• Coral cover - the percent of the reef surface covered by live stony corals contributing to three-dimensional framework of the reef structure, as measured in six 10 m transects per site.
• Fleshy macroalgae - the percent of the reef structure covered by fleshy algae, as measured in six 10 m transects per site.
• Herbivorous fish - an estimate of the biomass (g/100 m^2) of the parrotfish and surgeonfish families, as measured in ten 30m by 2m belt transects per site.
• Commercial fish - an estimate of the biomass (g/100 m^2) of the most heavily exploited commercial species, specifically fish species from the snapper and grouper families, as measured in ten 30 m by 2 m belt transects per site.

These indicators were selected from the conceptual descriptions of more than 50 potential indicators, whose relationships to different stressors and contributions to ecological 'health' are fully described in McField and Kramer (2007), and summarized in McField and Kramer (2006). The four key indicators used in the Reef Health Index (RHI) are ranked into 5 discrete categories, based on standardized grading criteria developed through an expert review process evaluating over 800 sites in the Wider Caribbean in the AGRRA database, with the fish biomass ranks adjusted to reflect updates to a and b values and adjustments for total vs fork length of each species of fish (McField et al., 2018). The four calculated ranks for each indicator are equally weighted into one mean value for the RHI, also presented in McField et al. (2020). The Healthy Reefs Initiative's reef evaluation and grading system was the first to develop specific target values for a variety of coral reef indicators in order to assist managers in interpreting their monitoring data and has now been adopted in other parts of the Caribbean (Flower et al., 2017).

3.2 Fluvial Discharge, Sediment Load, and Sediment Yield

Because the rivers in the study area are not systematically gauged, we relied on studies that modeled both discharge and sediment load based on climatological and basin data (Thattai et al., 2003). Although there exist numerous temperature and precipitation stations in the watersheds, the lack of long-term data within each of the watersheds makes it difficult to calculate the temporal variability of discharge reliably. Modeling of mean discharge for each basin was based on an empirical water balance model first proposed by Schreiber (1904), from which the annual discharge Q (m^3/s) for each river is calculated as

$$Q = \sum_{i=1}^{n} a_i \left(\frac{\Delta f}{r}\right)_i \frac{r_i}{2.592\ x\ 10^9}$$

where $\frac{\Delta f}{r}$ is the annual runoff ratio

$$\frac{\Delta f}{r} = \exp(\frac{e_0}{r})$$

where e_0 is potential evapotranspiration (mm yr^{-1}), r is precipitation (mm yr^{-1}), *a* (m^2) is the area of a sub-basin represented by a meteorological station, and n is the number of polygons within each basin. The annual potential evapotranspiration is an empirical function of mean temperature (indirectly accounting for latitude and elevation). The model has been successfully applied to a number of small tropical river systems (Kjerfve, 1990; Kjerfve et al., 1997; Heyman and Kjerfve, 1999; Thattai, 2003; Thattai et al., 2003) and verified with gauging data for Rio Grande, Belize. The average sediment load S (t yr^{-1}) was calculated by Thattai (2003) and Thattai et al. (2003) using the model by Morehead et al. (2003)

$$S = 2 \times 10^{-5} R^{3/2} A^{1/2} (0.2 \times 10^{0.0578T})$$

where R (m) is basin relief, A (km^2) is basin area, and T (°C) mean annual basin temperature. The sediment load divided by basin area (km^2) is the sediment yield Y (t yr^{-1} km^{-2})

3.3 Hurricane Impact Statistics

Summary statistics for all hurricanes and tropical storms that crossed an area south of N18.70° (Mahahual, Mexico) and west of W85.80° (north coast of Honduras) during the 60-year period, 1960 - 2019, were obtained from the National Ocean Service online database (National Ocean Service, 2020). We analyzed storm paths, storm category, central pressure and maximum sustained winds at both the peak of each storm and at the time of landfall in the Gulf of Honduras. Each of the four biogeographic zones in the study area was ranked for hurricane impact. In addition, we added information for Hurricane Mitch (1998), which skirted the Gulf of Honduras and made landfall in Honduras east of the study area, but generated large waves onto the barrier reef and had catastrophic impact across Central America, due to intense rainfall (Sheng et al., 2007).

3.4 Fishing Pressure

To estimate and rank the fishing pressure on the various Gulf of Honduras reef environments, we relied on reports from the Fisheries Departments in both countries, FAO reports, population data for coastal communities, and the total marine areas in each zone as detailed in the Healthy Reefs GIS database. The number of Belizean fishers per zone was examined based on published reports (Martinez et al., 2018). Numbers of fishers were then compared to the extent of the marine territorial sea for each country.

4. Results

4.1 State of the Coral Reefs

The findings for the 24 forereef sites are listed in Table 1. The measurement locations include 8 sites on the coastal reefs in Guatemala, 4 sites on the Cayman Crown Reef in the channel connecting the Gulf of Honduras with the BBR lagoon and Bahía de Amatique, 10 sites along the southern BBR, and 2 reference sites on the west-facing leeward forereef of Glover's Reef, which are protected from hurricane waves, have the lowest fishing intensity, and are rarely subject to fluvial sediment runoff. The mean depth of the 24 forereef monitoring sites is 10.2 ± 3.5 m. The descriptive statistics for the RHI data set is summarized in Table 2. These reef zones were delineated based on biogeographic physical characteristics (Kramer et al., 2015) with the separate consideration of the newly discovered Cayman Crown channel reefs (which were bisected by two sub-regions of the original HRI classification).

To explore and rank the relative impact that the local stressors have on reef health (as measured by the RHI), we used ANOVA to justify the treatment of the observations as representative of the biogeographic zones. We compared the mean values of coral cover, fleshy macroalgal cover, herbivorous fish biomass, commercial fish biomass, and the integrated Reef Health Index for the four reef biogeographic zones, i.e., coastal reef sites, channel reef sites, barrier reef sites, and the reference sites. We tested the null hypothesis that there is no difference in the means of each of the five measured reef parameters for the four biogeographic zones. We carried out five separate one-way analysis of variance assessments (ANOVA) with four environments/factors on the data in Table 1. We calculated the F-value as $MS_{Between}/MS_{Within}$ for each parameter separately and found the F-factors exceeding the critical F-factor at the $\alpha=0.05$ for four tests, coral cover ($p=0.001$), fleshy macroalgae cover ($p=0.003$), herbivorous fish biomass ($p=0.001$), and RHI ($p=0.001$), and at the $\alpha=0.10$ for commercial fish biomass ($p=0.082$). Thus, we rejected the null hypothesis in each of the five analyses, concluding that the means of four reef environment parameters are indeed highly significantly different, and the fifth parameter (commercial fish biomass) marginally different, from each other compared to the variation of the individual site observations within each zone, thereby justifying our treatment of all site-data as belonging to one of four unique biogeographic zones. The ANOVA tables are shown in Appendix 1.

The Guatemalan coastal reefs and the BBR display lower means of 20 ± 9% and 17 ± 5% live coral cover, respectively (Table 2). In contrast, the four sites on the Cayman Crown Reef in the southern channel, and the two reference sites on the lee side of Glover’s Reef, have much higher live coral cover, on average 49 ± 22% and 34 ± 0%, respectively. Measurements by Giró and Mojica (2020) recorded an amazing 77% live coral cover, mostly *Agaricia tenuifolia* (Figure 5), at the Cayman Crown Reef site 11 in 2019, certainly one of the highest current values anywhere in the Caribbean.

The Guatemalan coastal reefs have 19 ± 10% fleshy macroalgae cover, and the Cayman Crown Reef a similar 19 ± 9% fleshy macroalgae cover (Table 2), both areas fueled by nutrients from high nutrient input near the coast. The BBR sites display a very large fleshy macroalgae cover, on average 31 ± 8%, as can be expected on a reef frequently impacted by hurricanes, with a relatively constant supply of nutrients, and insufficient herbivory by grazing fish and invertebrates. In comparison, the two sites on Glover’s Reef display only 4 ± 1% fleshy macroalgae cover, suggesting that these sites experience very limited coral breakage by hurricane waves, lower nutrients, and higher herbivory as a result of the managed protection of the marine reserve.

Herbivorous fish, especially the abundant parrotfish and surgeonfish species, are significant grazers of macroalgae and algal turfs. The observed biomass of these herbivorous fish is very low on the Guatemalan coastal reefs, measuring an average 657 ± 902 g/100 m^2. On the Cayman Crown Reef and the BBR, the herbivorous fish biomass is much greater, 1,856 ± 1,547 g/100 m^2 and 2,417 ± 1,230 g/100 m^2, respectively. The reference zone on the forereef of Glover’s Reef has a still greater herbivorous fish biomass, measuring 5,751 ± 2,866 g/100m^2, indicating a healthy balance between coral cover, fleshy macroalgae cover, and herbivorous fish biomass.

The biomass of snappers and groupers is used as a proxy to gauge the level of fishing pressure, as these are the most heavily exploited fish families for human consumption. The observation trend is similar to that of the herbivorous fish biomass (Table 2). The lowest average commercial fish biomass, 344 ± 414 g/100 m^2, was measured on the Guatemalan coastal reefs, and the Cayman Crown Reef sites display similar low commercial fish biomass, 354 ± 344 g/100m^2, indicating sustained fishing pressure. The 10 sites along the BBR exhibited a somewhat greater commercial fish biomass, 857 ± 748 g/100 m^2. The two reference sites on the west-facing forereef of the Glover's Reef Marine Reserve, a national protected area since 1993, in contrast exhibited a high commercial fish biomass of 1,397 ± 159 g/100 m^2.

The Reef Health Index (RHI) is a summary measure achieved by equally weighting the four indicators described previously. The RHI ranges from 1 (lowest) to 5 (highest). The forereef sites on the sheltered western side of Glover's Reef are by far the healthiest reef sites, with an RHI measure of 4.3 (Table 2). The coastal reefs of Guatemala have the lowest RHI, 2.1 ± 0.6, with site 7 displaying the lowest RHI of all 24 sites, 1.5. The Cayman Crown Reef has RHI values of 2.8 ± 0.6, and the BBR have RHI values of 2.6 ± 0.6.

4.2 Fluvial Runoff

Based on several decades of meteorological measurements (Spangler and Jenne, 1990; Thattai et al., 2003), there exists a significant rainfall gradient from the inland region of MAR in Guatemala to Mexico in the north. Many locations in the river watersheds experience 4,000-5,000 rainfall annually. In Punta Gorda, the annual rainfall measures 3,700 mm, in Belize City 1,900 mm, and in northern Belize 1,200 mm. The rainfall is bimodally distributed with rainfall maxima in May - July and September - December (Thattai et al., 2003).

The simulated discharges for the Gulf of Honduras watersheds (Table 3) are shown in Figure 2a. In decreasing order of watershed area are Ulúa-Camélocon (Honduras), Motagua (Guatemala), Polochic–Dulce (Guatemala), and Sarstún (Guatemala/Belize border), which originate at 2,500–3,000 m elevations (Thattai et al., 2003). Ulúa with the largest drainage basin of 16,880 km^2 also has the highest average discharge of 370 m^{3}s^{-1}. However, watershed area does not translate directly into runoff. Besides differences in rainfall, Polochic–Dulce, which has only one-third of the watershed area of Ulúa, has mean runoff of 313 m^{3}s^{-1} due to its high annual rainfall (3,150 mm). Similarly, Sarstún has mean runoff of 146 m^{3}s^{-1} from its 2,117 km^2 watershed, which is almost comparable to that of Motagua (186 m^{3}s^{-1} from 13,168 km^2). River discharge varies by ±8% on average with a ±100 mm change in annual watershed rainfall (Thattai et al., 2003). The mean combined water discharge into the Gulf of Honduras measures 1,233 m^3 s^{-1}, which translates to 39 km^3 yr^{-1}.

The simulated annual sediment loads for the Gulf of Honduras drainage basins (Table 3) are shown in Figure 2b. In spite of having the highest regional sediment yield (869 t yr^{-1} km^{-2})

because of high elevations, steep relief, and high rainfall, the total annual sediment load of the Polochic-Dulce (5,070 t yr^{-1}) is less than the sediment loads of Ulúa-Camélocon (9,140 t yr^{-1}) and Motagua (8,930 t yr^{-1}) because the watersheds of these two rivers are much larger. The N-SPECT model implemented by Burke and Sugg (2006) reports comparable values. The sediment load from Sarstún on the Guatemala/Belize border was calculated to be 653 t yr^{-1}, and the eight smaller rivers in Belize a combined 1,234 t yr^{-1}. As the regional rivers lack deltas, an average 25,000 tons of sediments are annually discharged directly into Bahía de Amatique and the southern Gulf of Honduras with contaminants often bound to sediment.

The growing human population in the watersheds is coupled with inadequate or absent sewage treatment, environmental and land-use changes, and intense agriculture. The fluvial runoff, laden with sediments, nutrients such as phosphorus and nitrogen, and hydrocarbon contaminants (Herrera and Silva, 2014), reaches Bahía de Amatique and the Gulf of Honduras principally via the 12 medium-sized and small rivers. The total hydrocarbon values reported in the San Francisco River are high (65 mg l^{-1} and 60 mg l^{-1}), at the mouth of the Motagua river the values are lower (20 mg l^{-1}) but are still considered high. The poorly oxygenated waters of the coastal lagoons in the Manabique Wildlife Refuge carry traces of agrochemicals, such as nitrate (NO_3) and phosphorus (PO_4). These lagoons receive runoff from man-made channels, which drain livestock farms and intensive agricultural plantations (Herrera and Silva, 2014).

The river sediment load impacts the coastal reefs and the Cayman Crown channel reefs because of their proximity to the river mouths and their frequent location within a turbid near-shore zone, which is quite apparent from satellite images (Sheng et al., 2007; Chérubin et al., 2008). However, both buoyant matter (suspended and dissolved material) and colored detrital material (CDM) have been modeled (Chérubin et al., 2008) and measured by satellites (Burke and Sugg, 2006), respectively, across the Gulf of Honduras. Because of the persistent trade winds for much of the year and the predominant cyclonic circulation in the Gulf of Honduras, the river-derived sediments seldom reach north of the Sapodilla Cayes, and would thus have minimal impact on the sites along the BBR and the reference sites on the leeward side of Glover's Reef. However, during Hurricane Mitch, flooding-induced sediment/nutrient-laden waters did reach as far north as Glover's Reef (Sheng et al., 2007; Andréfouët et al., 2002).

4.3 Hurricane Impact

Hurricanes and tropical storms frequently approach, traverse, and/or make landfall in the greater Gulf of Honduras, a total of 15 hurricanes and 12 tropical storms during the 60 years (Table 4). They arrive in the Gulf of Honduras from the eastern sectors (from directions between 80°T and 110°T) with all hurricane tracks shown in Figures 3 a-c.

The first 20-year period, 1960 - 1979, had the greatest storm activity with 8 hurricanes and 4 tropical storms. In contrast, during the second 20-year period, 1980-1999, the region experienced only 3 tropical storms, in addition to the 'monster' category 5 Hurricane Mitch, which never actually traversed the Gulf of Honduras but produced intensive hurricane swells and strong winds for a total of seven days. Mitch approached the Gulf of Honduras for four days before veering south, stalling for 24 hours, and making landfall near Roatan, Honduras, then causing additional torrential rainfall, flooding, landslides, mudflows, and crop destruction as it tracked west across Honduras and Guatemala mainland into Mexico for another three days (Figure 3b) (Sheng et al., 2007). During the third 20-year period, 2000-2019, 6 hurricanes and 5 tropical storms impacted the Gulf of Honduras. Appendix 2 provides supplemental historical detail of the major hurricanes and their impacts.

Because hurricanes/tropical storms are cyclonic weather systems, as they travel towards the west, the greatest storm intensity, i.e*., impact focus*, occurs some ~20 km to the right of the storm track (in the northern hemisphere), including highest breaking waves, strongest sustained winds and wind gusts from across the ocean, and greatest storm setup (due to a combination of low atmospheric pressure and wave set-up). In contrast, ~20 km to the left of the storm track, winds are often reversed in direction, waves are confused and counter-acted by the winds, and wave setup is often non-existent (Stoddart, 1963).

Whereas winds and flooding cause most of the destruction to the built environment and the vegetation on the cayes during hurricanes (Stoddart, 1963), at the average depth of 10.2 m on the forereef where the RHI observations were made, breaking waves and associated intense wave-generated currents cause the main impacts on corals. Hurricane waves are the primary cause of coral breakage and toppling on the reefs (Woodley et al., 1981; Kjerfve et al., 1986). In situ hurricane wave measurements do not exist for the Gulf of Honduras but hindcasting by Kjerfve and Dinnel (1983) of Hurricane Greta (1978) at Carrie Bow Caye, BBR, indicated maximum wave heights of 10 m with wave periods up to 12 s.

Although 15 hurricanes and 12 tropical storms (Table 4; Figures 3a-c) travelled across the study area (as defined earlier), 1960-2019, including Hurricane Mitch, which affected the entire Gulf of Honduras from afar. However, only 7 of the remaining hurricanes and 3 tropical storms (bolded in Table 4) resulted in wave impact focus on the section of the barrier reef between Columbus Caye and Sapodilla Cayes, including two category 4 hurricanes, Hattie (1961) and Iris (2001); one category 3 hurricane, Greta (1978); two category 2 hurricanes, Francelia (1969) and Fifi (1974); and two category 1 hurricanes, Abby (1960) and Anna (1961). In comparison, during the same period, not a single hurricane similarly impacted the Guatemalan coastal reefs or the Cayman Crown channel reefs. Only one tropical storm, Kyle (1996), travelled across the Gulf of Honduras towards the southwest with landfall on the Punta de Manabique peninsula as a tropical depression, with focused wave impact on the coastal and channel reefs. The reef sites on the lee side of Glover’s Reef were in the path of several of the same hurricanes that impacted the barrier reef, but would not have experienced focused wave impact because of the shelter provided by Glover’s Reef.

In summary, the sites along the BBR were subjected to destructive hurricane wave *impact focus* by 7 hurricanes and 3 tropical storms, whereas the Guatemalan coastal reefs, the Cayman Crown channel reefs, and the reefs on the leeward side of Glover’s Reef would largely have escaped serious impact from destructive hurricane waves.

4.4 Hurricane Mitch Impact on the Barrier Reef

The most destructive hurricane during the 60-year period was category 5 Hurricane Mitch (1998) (http://www.hurricanescience.org/history/storms/1990s/mitch/), estimated to have caused more the $5 billion in damages. It was also the deadliest hurricane in the Western Hemisphere in more than 240 years, with at least 11,000 estimated deaths. The eye of Hurricane Mitch made landfall near Roatan, Honduras, and did not cross the Gulf of Honduras (Figure 3b; for further details see Appendix 2). The eye of Hurricane Mitch was at its closest 220 km east southeast of Gladden Spit and 250 km east of Sapodilla Cayes. As the diameter of the hurricane was 600 km (Figure 4a), intense winds and hurricane waves impacted most of the Gulf of Honduras. A S4 instrument, fortuitously moored on the forereef in 31 m water depth (the mean depth of the instrument was 27.8 m), recorded hourly oceanographic measurements (Figure 4b) during the approach and landfall of Hurricane Mitch. In spite of the distance from the hurricane center, the water level increased by 2 m due to the storm surge, completely over-washing the cayes along the reef crest. The near-bottom currents intensified with an average flow towards the south exceeding 0.5 m s^{-1} at the instrument depth, or 20 times greater than typical bottom currents during non-hurricane conditions. The water temperature dropped by 0.8°C and salinity increased by 1.4 indicating hurricane-induced mixing and upwelling of waters from at least 60 m or deeper (based on CTD casts). The time series represents hourly snapshots of the average hourly conditions but did not capture the wave heights and the intense wave-induced currents, which are the primary cause of coral breakage (Woodley et al., 1981; Kjerfve et al., 1986). The significant deep-water waves at Gladden Spit (stations 16 and 17) during the approach of Hurricane Mitch are estimated to have had a height of ~8 m and a maximum period of 12-13 s.

4.5 Fishing Pressure Impact

The Caribbean coast of Guatemala is relatively limited (1,560 km^2 of territorial sea) compared to that of the neighboring countries (Belize 18,659 km^2; Honduras 19,564 km^2). Guatemala's main fishing villages along the Caribbean coast are Livingston with 1,325 fishers, Puerto Barrios with 950 fishers, San Francisco del Mar with 139 fishers, and El Quetzalito with 46 fishers (FAO, 2001). Thus, these approximately 2,460 artisanal fishermen are distributed with an average density of 1.6 fishers/km^2, likely much higher in reef areas, knowing that not all the territorial waters are well suited for artisanal fishing.

Conversely, less than 2,600 fishers are licensed for all of Belize (Martinez et al., 2018) giving an overall fisher density of 0.1 fishers/km^2. In 2016, the managed access requirements resulted in approximately 140 fisherfolk licenses issued for Glover's Reef Marine Reserve and 130 fisherfolk licenses issued for Port Honduras Marine Reserve (Martinez et al., 2018). An estimated 300 fishers work along the southern barrier reef fishing from open 20-30' boats with outboard engines, in addition to an unknown number of additional transboundary/illegal fishers known to operate along the barrier reef, resulting in the level of fishing pressure being higher than on Glover's Reef.

According to historical data from the Guatemalan fisheries department (DIPESCA), shrimp fishing is considered overexploited, with a significant decrease in the shrimp catch since 2008. Other important fisheries in Guatemala, *Ariidae*, *Sciaenidae*, *Lutjanidae*, have been in significant decline since 2013 (MARN et al., 2020). Based on these numbers and the assessment by Perez (2020), we rank the highest fishing pressure as occurring on the coastal reefs of Guatemala, followed by high fishing pressure on the Cayman Crown channel reefs, which lie in close proximity but are made more challenging by the fact they occur along a disputed international border and within a major shipping lane. In comparison, the BBR experiences moderate fishing pressure; and the Glover's Reef sites relatively low fishing pressure.

5. Discussion

5.1 Effects of Local Stressors

The ecological data from the 24 reef sites support the concept that chronic stress from continual fluvial runoff onto the Guatemalan coastal reefs combined with the highest fishing pressure to be more damaging than intermittent stress by hurricane waves on the BBR, combined with moderate fishing pressure and low fluvial impact, which generally aligns with established ecological "intermediate disturbance' hypothesis often applied to coral reefs (Connell, 1978; Rogers, 1993). While this hypothesis has primarily been applied to measures of diversity, we suggest that the integrative nature of the reef health index would also apply to the intermediate disturbance theory, given the range of taxa included in the index.

Most of the sediment and nutrients entering the MAR do so via highly cultivated lands in Honduras and Guatemala (Burke and Sugg, 2006), including banana, citrus, palm-oil, and coffee plantations, and with discharge from shrimp aquaculture ponds (Gibson et al., 1998; López and Scoseria, 1996; Bolaños et al., 2018). As a result, they carry high sediment loads along with fertilizers, herbicides, and other pollutants entering the southern Gulf of Honduras, impacting coral reefs and reef biota (Gibson et al., 1998; Katz, 1989; Burke and Sugg, 2006; Chérubin et al., 2008). Excess nutrients lead to increased algal growth, which has numerous direct and indirect damaging ecological consequences for coral reefs (Fabricius, 2005), and with high sedimentation rates at time exasperating these effects in coastal waters (Rogers, 1990; McField et al., 1996).

Fluvial water and sediment deposition limit live coral cover on the coastal reefs, whereas hurricane waves destroy live coral cover on the forereef of the BBR, which in turn increases the availability of new surfaces for fleshy macroalgae to grow. Thus, both the coastal reefs and the BBR display lower live coral cover but for different reasons. The fleshy macroalgae cover is far greater on the BBR as compared to all other sites. An abundance of fleshy macroalgae on reefs indicates an ecological imbalance, but without distinguishing between multiple influences. Often, it involves a combination of water transparency, nutrient enrichment, reduced herbivory, and increased areas with dead coral surfaces available for colonization after massive coral mortality events, resulting from coral bleaching, disease, the impact of hurricane waves, or some combination of these factors.

Hurricane waves break corals, and temporarily rip up and remove fleshy macroalgae. If numerous corals are killed, bare rock surfaces will be exposed and colonized first by turf algae and subsequently by macroalgae, sponges and eventually new coral growth, although such ecological shifts typically take several years (Hughes, 1994; Hughes et al., 2007; Birkeland, 2019; Precht et al., 2020). The barrier reef is impacted by breaking hurricane waves reaching 10 m in height with instantaneous wave-induced flow greater than 2 m s^{-1} (Woodley et al., 1981; Kjerfve and Dinnel, 1983; Kjerfve et al., 1986). Coral reefs are then sandblasted, abrading the delicate coral tissues, removing small corals, and toppling even large coral heads, particularly those with significant bioerosion within their structures. This, in turn, establishes massive reef rubble areas that can prevent the recruitment of new corals for years to come. On the reef crest, there is often rubble accumulation from the hurricane surge (Rützler and Macintyre, 1982), sometimes boulder rampart build-up, and complete alteration of water flow regimes in the shallow back reef area behind the built-up reef crest. On the cayes, there is destruction of coconut palms, mangrove trees, shrubs, and man-made structures caused primarily by winds and the hurricane setup, not waves.

The Guatemalan coastal reefs and the Cayman Crown channel reefs are located far south of the hurricane tracks and rarely experience the great wave forces that impact the barrier reef, especially since the greatest wave *impact focus* occurs well north of the tracks. In fact, the barrier reef experienced 7 hurricanes compared to none for both the coastal reef sites (1 - 8) and the Cayman Crown reef sites (9 - 12), which on the other hand are more impacted by hurricane-induced fluvial runoff and sediment load but not the destructive hurricane wave forces.

The Cayman Crown channel reefs, which are located only 17 km from the Guatemalan coast (Figure 1), are situated near the regional river mouths, display greater live coral cover than both the coastal reefs and the barrier reef but almost identical fleshy macroalgae cover as compared to the coastal reefs. This is most likely a function of the local oceanography. The wide channel between the Sapodilla Cayes and the Punta de Manabique coast serves as the main water exchange between the Gulf of Honduras and the barrier reef lagoon/Bahía de Amatique. Our tentative observations indicate the existence of a low-salinity surface layer, with high sediment concentration and rich in nutrients, due to fluvial runoff, extending to a depth of 3-4 m in the channel, where strong non-tidal currents flow towards the east. Below the surface layer, waters with oceanic salinity and low turbidity on average apparently flow towards the west into the lagoon/Bahia de Amatique. This indicates the existence of a two-layered estuarine-like circulation in the channel. The net inflow in the lower layer 'washes' the Cayman Crown channel reefs with Caribbean waters, thus mitigating the impact of the fluvial sediment load, although this is a hypothesis at this time. As a result, the Cayman Crown channel reefs are affected less than expected by the sediment-laden runoff. Excess nutrients are available in both the fluvial runoff and in the oceanic inflow, which explains both the high live coral cover and the relatively high fleshy macroalgae cover. Thus, the Cayman Crown channel reefs remain in fair health although the fish population is rather low. In 2020, this was addressed with Guatemala establishing its first fully protected coral reef area in the Caribbean, and Belize extending the Sapodilla Cayes Marine Reserve to include its portion of the Cayman Crown Reef.

Clearly, the healthiest reefs in this study are the two sites (23 and 24) on the leeward side of Glover's Reef atoll, which are largely spared both destructive hurricane waves and continental runoff, and have been located within a managed MPA for 27 years, affording them low fishing pressure. Hurricane waves impact the sheltered west-facing Glover's Reef forereef only indirectly, thus leading to low coral breakage and high live coral cover. The lack of broken dead coral surfaces, infrequent fluvial nutrient pulses, and more abundant herbivores due to better enforcement of the regulation protecting these fish since 2009, all contribute to maintaining an extremely low coverage of deleterious fleshy macroalgae.

Fishing pressure is notoriously difficult to assess on a specific reef, but the four biogeographic zones addressed in this study are well distinguished into separate categories. However, the direct relationship between fishing pressure and resulting commercial fish biomass is never perfect, as many species of snappers and groupers are transient spawners. Snappers and groupers aggregate at forereef promontories such as Gladden Spit (Heyman et al., 2001, 2005). Promontories are characterized by variable energetic hydrodynamics, including upwelling, formation of local eddies, and internal waves, due to the sharp bend in the reef and the steep reef drop-off (Ezer et al., 2011). Gladden Spit is the location of spawning aggregations of Cubera snappers (*Lutjanus cyanopterus*) twice annually (Heyman et a., 2001; Heyman et al., 2005). Nevertheless, at the shallow (7.2 m) forereef site 16 at Gladden Spit, there was 0 g/100 m^2 commercial fish biomass, which likely reflects a combination of high local fishing pressure, the transient nature of spawning aggregations, and the fact that reef topographic complexity is relatively low on this high-energy shallow forereef (sites 16, 17), versus more well-developed reefs occurring in deeper waters, where most of the spawning aggregations occur (Heyman et al., 2005).

The impact of hurricane wave destruction on the forereef was evaluated along the BBR before and after Hurricane Mitch (1998). The greatest destruction along the southern barrier reef occurred in the Sapodilla Cayes, which had an 85% decline in live coral cover (McField, 2002). The destructive impact of hurricanes includes the wave-generated breakage of corals, especially branching corals, by high breaking waves, strong bottom currents, and sand and rubble acting as water-borne projectiles. On the other hand, the ecological effects of hurricane-induced massive flood events (e.g., as a result of Hurricane Mitch) can transport floodwaters and contaminants, albeit not sediments, 100 km or so, even as far north as to the reference sites (23 and 24) at Glover's Reef (Andréfouët et al., 2002; Sheng et al., 2007).

The BBR had significantly more coral cover in the early 1970's, maybe 60 - 70% live coral cover, with *Acropora palmata* defining the shallow forereef and reef crest, and *Acropora cervicornis* covering large areas of the deeper forereef and back reef areas (Miller and Macintyre, 1977; Rützler and Macintyre, 1982). This has been well documented at Carrie Bow Caye, where extensive sampling took place along a fixed 650 m long (projected length) transect, including lagoon, back reef, reef crest, inner forereef (depth 1 to 12 m), and outer forereef (deeper than 12 m) with repeated sampling and numerous experiments carried out as part of the

Smithsonian IMSWE (Investigations of Marine Shallow-Water Ecosystems) project (Rützler and Macintyre, 1982). The abundant branching corals found at Carrie Bow Caye and elsewhere along the MAR were devastated, primarily by coral disease, beginning in the 1980’s and persisting to the present, a stress occurring across all of our biogeographic zones and treatments.

5.2 Additional Effects of Global Stressors

Globally, coral reefs have been in decline since at least the 1970’s due to the interplay between global and local stressors. The main global stressors are rising ocean temperature, increasing ocean acidity, and increasing disease outbreaks. Global stressors are responsible for much of the decline of coral reefs in the Gulf of Honduras and elsewhere. The main effect of increasing ocean temperatures, i.e., heat stress, is coral bleaching, which is triggered when the water temperature exceeds the normal summer temperature and remains there for at least several weeks. Glenn et al. (2015) showed that the Caribbean-wide sea surface temperature (SST) warmed significantly during the 31-year period from 1982 to 2012, based on regional analysis of the Optimum Interpolation Sea Surface Temperature Analysis Product (OISST), which used Advanced Very High Resolution Radiometer (AVHRR) infrared satellite SST data from the Pathfinder satellite in addition to buoy and ship data. In the Caribbean, the SST trend increased at a rate of 0.0161 °C/yr using early rainfall season data and 0.0209 °C/yr using late rainfall season data with significant variability around the trendlines, i.e., anomalies. High SST anomalies and wide-spread Caribbean heat-stress events triggered mass coral bleaching events in 1995, 1998, 2005, 2010-2011, 2015, and 2017 in the MAR region (Muñiz-Castillo et al., 2019). The 1998 bleaching in the MAR was the most significant such event and resulted in widespread coral bleaching and mortality, further exasperated by the area-wide catastrophic destruction by Hurricane Mitch in October 1998 (McField, 2002; Kramer and Kramer, 2000; Peckol et al., 2003). The effects of bleaching can be long-lasting, as evidenced by coral cores and growth bands, showing that the 1998 bleaching event impacted corals from the Sapodilla Cayes for up to 8 years (Carilli et al., 2009).

6. Conclusions

Globally, coral reefs have experienced decline for more than 40 years in response to global warming, acidification, and disease. In addition, local stressors, i.e., fluvial runoff, hurricanes, and fishing pressure, have caused further impact and reef decline. The coral cover of 60 - 70% recorded in the early 1970’s along the BBR (Rützler and Macintyre, 1982) is now reduced to an average of 34% for the healthiest of the reefs on the protected forereefs of Glover’s Reef in the Gulf of Honduras. This zone has the highest Reef Health Index score (4.3 out of 5.), with only 5% macroalgae cover and very high herbivorous and commercial fish biomasses. However, with the addition of significant hurricane wave impact, medium-scale artisanal fishing, and only occasional runoff stressors, the average RHI falls to 2.6 (“poor”) along the BBR. In contrast, the coastal reefs, experience no hurricane impacts but register higher fishing pressure, and higher fluvial sediment runoff, producing a lower “poor” RHI of 2.1 (including 20% live coral cover, 19% flesh macroalgae cover, and 657 and 344 g/100 m^2 herbivorous and commercial fish biomasses, respectively).

Interestingly, the Cayman Crown channel reefs have a higher ‘fair’ RHI of 2.8, on average very high 49% live coral cover, 19% fleshy macroalgae cover, and relatively high herbivore biomass, but low commercial fish biomass. The surprisingly healthy Cayman Crown channel reefs are, with regulations passed in 2020, more protected from fishing. Improving our understanding of the physical oceanographic setting and dynamics, which seemingly mitigate some of the fluvial impacts on these reefs, can help explain why the Cayman Crown channel reefs, have better than expected reef health, and could help guide conservation efforts.

Overall, evaluating the four key indicators in the Reef Health Index in relation to the main local stressors in our analysis, offers a sound framework and approach for classifying reef threats within biogeographic zones to assist in marine spatial and networked protected areas planning to enhance marine conservation. The ecological data from the 24 reef sites support the concept that chronic stress from continual fluvial runoff onto the Guatemalan coastal reefs combined with the highest fishing pressure is more damaging than intermittent stress of hurricane waves on the BBR, combined with moderate fishing pressure and low fluvial impact. When even moderate fishing pressure and fluvial runoff are combined with higher frequency hurricane wave destruction, the average reef health condition drops to a ‘poor’. Our analysis finds that in the absence of additional local impacts like fluvial runoff, hurricane wave destruction, and high fishing pressure, healthy reefs are still attainable under current environmental and climatic conditions.

Acknowledgements

We would like to acknowledge the many data collectors within the Healthy Reefs Initiative who conducted the MAR reef surveys in 2018/2019 and for at least 12 years prior, and for contributing to the open source HRI database. Funding for HRI has been provided by numerous private foundations, including the Summit Foundation through the Smithsonian Institution. We would also like to acknowledge the National Ocean Service and the very rich NOS database on hurricanes and their characteristics. We thank Rafael Cuellar de Oliveira e Silva of Universidade Federal Fluminense for assisting with the production of the map of the Gulf of Honduras and the charts showing the hurricane tracks; Dr. Chuamin Hu of University of South Florida for providing the annotated SeaWIFS image of Hurricane Mitch; and Dr. Alessandro Filippo of Universidade do Estado do Rio de Janeiro for help with the Matlab m-files to plot the S4 oceanographic time series.

Declaration of Competing Interest

The authors declare that we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Revised paper submitted to "Advances in Knowledge about the Sources, Fates and Consequences of Pollutants in Tropical Shelf Systems", a Special Issue in *Marine Pollution Bulletin* in Honour of Jon Brodie.
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Table 1. Observations for 24 MAR outer forereef sites in the Gulf of Honduras in 2018/2019, extracted from Healthy Reefs Initiative 2018 data (www.healthyreefs.org).

	Site	Sampling Date	Depth (m)	Live Coral (%)	M-algae (%)	Herb. Fish (g/100 m^2)	Com. Fish (g/100 m^2)	RHI
1	Bahía de Amatique BZ1019/N 15.96 W88.80	18-Sep-2018	3.5	27	16	2,756	1,071	3.3
2	Punta de Manabique GT06/N15.97 W88.56	25-Jun-2018	8.5	8	12	148	31	1.8
3	Punta Manabique GT002/N15.97 W88.55	27-Jun-2018	10.9	15	14	922	99	1.8
4	Punta de Manabique GT04/N15.96 W88.55	25-Jun-2018	10.9	15	19	170	457	2.0
5	Punta de Manabique GT03/N15.96 W88.54	27-Jun-2018	11.0	23	18	152	53	2.0
6	Punta de Manabique GTM004/N15.94 W88.54	27-Jun-2018	11.3	34	6	371	106	2.3
7	Guatemala east coast GT007/N15.85 W88.31	26-Jun-2018	11.7	13	38	38	871	1.5
8	Guatemala east coast GT009/N15.85 W88.29	26-May-2018	13.4	23	26	702	60	1.8
9	Cayman Crown Reef GT10/N15.96 W88.28	19-Sep-2018	11.0	48	20	942	821	2.8
10	Cayman Crown Reef GT08/N15.95 W88.28	19-Sep-2018	10.8	24	24	4,171	392	3.3
11	Cayman Crown Reef 13CCNRC/N15.96 W88.28	28-May-2019	10.2	77	5	1,178	41	3.0
12	Cayman Crown Reef 011CCNRC/N15.97 W88.30	28-May-2019	11.4	47	25	1,131	162	2.0
13	Sapodillas, recurved spit BZ1019/N16.10 W88.33	18-Sep-2018	3.5	27	16	2,756	1,071	3.3
14	Northeast Caye BZ2027/N16.25 W88.18	18-Sep-2018	9.1	18	31	1,344	490	2.0
15	Queen Caye entrance 1032/N16.42 W88.04	15-Jul-2018	6.1	10	37	2,070	0	2.0
16	Gladden Spit 1038/N16.51 W87.97	16-Jul-2018	7.2	19	41	584	647	1.8
17	North of Gladden Spit 1044/N16.65 W88.07	30-Oct-2018	5.2	10	17	2,588	2,646	3.3
18	Belize Barrier Reef SWCGUZFR6/N16.75 W88.07	2-May-2018	11.9	14	29	4,893	488	2.8
19	Carrie Bow Caye SWCCZFR6/N16.81 W88.07	6-May-2018	15.2	20	31	2,522	449	2.5
20	Tobacco Reef SWCCZFR4/N16.83 W88.07	7-May-2018	15.5	16	37	1,274	536	2.0

21	Tobacco Reef SWCCZFR3/N16.85 W88.06	17-Jul-2018	15.5	21	35	3,593	1,530	3.5
22	Columbus Reef SWCGUZFR1/N16.91 W88.05	5-May-2018	15.5	15	33	2,541	713	2.3
23	Glover's Reef, lee side WFR4/N16.82 W87.85	9-Oct-2018	8.6	34	5	3,724	1,509	4.3
24	Glover's Reef, lee side WFR6/N16.84 W87.84	9-Oct-2018	7.9	34	3	7,777	1,284	4.3

Table 2. Descriptive statistics of the RHI data in Table 1.

Coastal	Coral	Macroalgae	Herb Fish	Com Fish	RHI
Mean	19.8	18.6	657.4	343.5	2.1
Stdev	8.5	9.7	901.9	413.9	0.6
n	8.0	8.0	8.0	8.0	8.0
Channel					
Mean	49.0	18.5	1,855.5	354.0	2.8
Stdev	21.7	9.3	1,547.0	343.7	0.6
n	4.0	4.0	4.0	4.0	4.0
Barrier					
Mean	17.0	30.7	2,416.5	857.0	2.6
Stdev	5.2	8.3	1,230.3	748.2	0.6
n	10.0	10.0	10.0	10.0	10.0
Glover's					
Mean	34.0	4.0	5,750.5	1,396.5	4.3
Stdev	0.0	1.4	2,865.9	159.1	0.0
n	2.0	2.0	2.0	2.0	2.0
Overall					
Mean	24.7	22.4	2,014.5	647.0	2.6
Stdev	15.4	15.4	15.4	15.4	15.4
n	24.0	24.0	24.0	24.0	24.0

Table 3. Simulated Gulf of Honduras watershed statistics, including watershed area (A), basin-averaged rainfall (r), average discharge (Q), sediment load (S), and basin sediment yield (Y), based on Thattai et al. (2003). The five smaller rivers in Belize are Middle, Golden Stream, Deep, Ycacos, and Indian Hill rivers.

Watershed	A	r	Q	S	Y
	(km^2)	(mm yr^{-1})	(m^3s^{-1})	(10^3 t yr^{-1})	(t yr^{-1} km^{-2})
Ulúa-Camélocon	16,880	1,900	370	9,140	541
Montagua-San Francisco	13,168	1,500	186	8,930	678
Polochic-Dulce	5,832	3,150	313	5,070	869
Sarstún	2,117	4,000	146	653	308
Moho	1,583	3,700	98	307	194
Grande	722	3,300	35	95	132
Monkey	1,292	2,800	49	617	478
Five smaller rivers in Belize	814	3,109	36	215	264
Totals	42,408		1,233	25,027	

Table 4. Summary statistics of hurricanes and tropical storms that crossed and made landfall in the Gulf of Honduras in the 60-year period, 1960 to 2019. The table shows storm characteristics, category, central pressure, and maximum sustained winds, both at the peak and when the storms made landfall. The data in the table have been extracted from the National Ocean Service online database (NOS, 2020). Legend: H = Hurricane (in bold), TS = Tropical Storm, TD = Tropical Depression, GoM = Gulf of Mexico, NA = not available. Hurricanes/tropical storms with impact focus on the barrier reef sites are bolded; also, the only TS/TD (Kyle, 1996) with impact focus on the Guatemalan coastal and Cayman Crown channel reefs.

Year	*Name*	*MAR cross*	*Category max/MAR*	*Pressure min/MAR (hPa)*	*Winds max/MAR (m/s)*	*Place of MAR cross/landfall*
1960	**H-Abby**	**15-Jul**	**1/1**	**995/NA**	**36/36**	**Gladden Spit (Sta. 16)/Independence**
1961	**H-Anna**	**24-Jul**	**2/1**	**976/NA**	**46/39**	**Sapodilla Cayes (Sta. 14)/Monkey River**
1961	**H-Hattie**	**31-Oct**	**5/4**	**914/924**	**75/67**	**Turneffe/Sta. 22)/Mullins River**
1964	TS-no name	09-Nov	TS/TD	997/1008	31/13	San Pedro (10 km north)
1969	**H-Francelia**	**04-Sep**	**3/2**	**973/NA**	**51/44**	**Sta. 14/Port Honduras/Punta Gorda**
1971	TS-Chloe	25-Aug	TS/TD	1004/NA	28/13	San Pedro
1971	H-Edith	11-Sep	5/TS	943/NA	72/31	Turneffe/30 km north of Belize City
1971	**TS-Laura**	**21-Nov**	**TS/TS**	**994/NA**	**31/31**	**Sta. 22/Placencia/Port Honduras**
1974	H-Carmen	02-Sep	4/4	928/928	67/67	Xcalak (Quintana Roo) (40 km north)
1974	**H-Fifi**	**19-Sep**	**2/2**	**971/NA**	**49/46**	**Sta. 14/Monkey River (5 km north)**
1977	TS-Frieda	19-Oct	TS/TD	1005/1010	26/10	North Turneffe/Belize City (8 km north)
1978	**H-Greta**	**19-Sep**	**4/3**	**947/964**	**59/51**	**Sta. 23/24/19/Dangriga**
1980	TS-Hermina	22-Sep	TS/TS	994/994	31/31	San Pedro
1993	TS-Gert	18-Sep	TS/TS	1000/1000	18/18	Belize City (later Cat 2 in GoM)
1996	**TS-Kyle**	**12-Oct**	**TS/TD**	**1001/1008**	**23/15**	**Rio Motagua mouth (4 km NW)**
1998	**H-Mitch**	**26/31 Oct**	**5/-**	**905/NA**	**80/-**	**Roatan, Honduras**
2000	H-Keith	03-Oct	4/TS	939/959	62/51	San Pedro/Turneffe/San Pedro
2001	TS-Chantal	21-Aug	TS/TS	997/999	31/31	Bacalar Chico National Park
2001	**H-Iris**	**09-Oct**	**4/4**	**948/948**	**64/64**	**Gladden Spit (Sta. 16)/Port Honduras**
2007	H-Dean	21-Aug	5/5	905/905	77/77	Mahahual (Quintana Roo)
2007	**TD-Felix**	**05-Sep**	**5/TD**	**929/1007**	**77/10**	**Sta. 13/Port Honduras**
2008	TS-Arthur	31-May	TS/TS	1004/1004	21/10	Hol Chan Marine Reserve
2010	TS-Alex	27-Jun	TS/TS	946/995	49/28	Turneffe/Belize City (later cat 2 in GoM)
2010	**TS-Matthew**	**25-Sep**	**TS/TS**	**998/1000**	**26/18**	**Sta. 15/Placencia**
2010	H-Richard	25-Oct	2/2	977/977	44/44	Turneffe (4 km south)/Southern Lagoon
2011	**TS-Harvey**	**20-Aug**	**TS/TS**	**994/995**	**28/28**	**Sta. 19 (Carrie Bow Caye)/Dangriga**
2016	H-Earl	04-Aug	1/1	979/979	39/39	Turneffe/Belize City (8 km south)

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Figure Captions

Fig. 1 Gulf of Honduras in the western Caribbean with the location of the 24 Healthy Reefs Initiative forereef sites. The Cayman Crown Reef is indicated by a polygon in the channel south of the Belize Barrier Reef, outlined by the 30 m isobath within which 4 sites are located. The lithospheric plate boundary is indicated by the 1,000 m isobath.

Fig. 2 (a) Modeled mean annual water discharge (m^3/s) and (b) modeled annual sediment discharge (10^3 t/yr) into the southern Belize Barrier Reef lagoon, Bahía de Amatique, and the Gulf of Honduras.

Fig. 3 Tracks of all hurricanes crossing and impacting the Gulf of Honduras (a) 1960 - 1979, (b) 1980 - 1999, and (c) 2000 - 2019.

Fig. 4 (a) NASA SeaWIFS (Sea-viewing Wide Field-of-view Sensor) satellite image of Category 5 Hurricane Mitch at 1756 GMT on 26 October 1998, while the hurricane was still heading west towards Gladden Spit and Belize, before veering south, fully 54 hours before making landfall in northern Honduras. At the time of the image, the central pressure was 905 hPa, and maximum sustained winds 80 m/s. The red dot indicates the location of the S4 instrument mooring just north of Gladden Spit (site 17). (b) Time series of ocean currents, water level, temperature, and salinity on the forereef (site 17), at a depth of 27.8 m, during the approach of Hurricane Mitch.

Fig. 5 Oblique view of site 11 (13CCNRC) on the Cayman Crown Reef in May 2019, with 77% live coral cover, mostly *Agaricia tenuifolia*. (Image by Ana Giró).

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APPENDICES

Appendix 1: ANOVA Tables

Live Coral Cover (%): One-way Analysis of Variance - 4 Environments

Source of Variation	SS	Df	MS	F	Prob	F-critical
Between Environments	2,810.37	3	936.79	8.67	0.0007	3.10
Within Environments	2,161.50	20	108.08			
Total	4,971.87	23				

Fleshy Macroalgal Cover (%): One-way Analysis of Variance - 4 Environments

Source of Variation	SS	Df	MS	F	Prob	F-critical
Between Environments	1,539.73	3	513.24	6.68	0.0026	3.10
Within Environments	1,536.98	20	76.85			
Total	3,076.71	23				

Herbivorous Fish Biomass (g/100 m^2): One-way Analysis of Variance - 4 Environments

Source of Variation	SS	Df	MS	F	Prob	F-critical
Between Environments	44,490,186	3	14,830,062	8.55	0.0007	3.10
Within Environments	34,709,804	20	1,735,490			
Total	79,199,990	23				

Commercial Fish Biomass (g/100 m^2): One-way Analysis of Variance - 4 Environments

Source of Variation	SS	Df	MS	F	Prob	F-critical
Between Environments	2,560,687	3	853,562	2.58	0.0822	2.38
Within Environments	6,617,565	20	330,878			
Total	9,178,251	23				

RHI: One-way Analysis of Variance - 4 Environments

Source of Variation	SS	Df	MS	F	Prob	F-critical
Between Environments	8.51	3	2.84	8.50	0.0008	3.10
Within Environments	6.67	20	0.33			
Total	15.18	23				

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Appendix 2: Sixty Years of Gulf of Honduras Hurricanes

During the 20 years from 1960 to 1979, 8 hurricanes and 4 tropical cyclones affected the study area in the Gulf of Honduras (Table 4). The most significant storm was Hurricane Hattie, a category 5 hurricane but category 4 when it made landfall at Mullins River, 18 km northwest of Dangriga, on 31 October 1961 (Figure 3a). The Saffir-Simpson Hurricane Wind Scale was not adopted until 1973, according to which 70 m s^{-1} sustained winds define a category 5 hurricane. Belize City and Dangriga were badly damaged by Hurricane Hattie, which caused some 250 deaths, including 45 on the reef cayes (Stoddart, 1963). The associated storm surge measured 2.7 m at Sandbore Caye (at the northern tip of Lighthouse Reef) just ahead of the arrival of the hurricane's eye but was hardly measurable at Half Moon Caye 29 km to the south. The storm surge exceeded 4.6 m at Caye Caulker 40 km to the right of the storm track, exceeded 3.7 m in Belize City 45 km to the right of the storm track, whereas the storm surge was 3.0 m in Dangriga to the left of the storm track (Stoddart, 1963). No wave measurements exist from Hurricane Hattie, but the wave heights would have been significantly higher on the right side of the track, where the cyclonic winds would have enhanced wave development rather than opposed the waves. The strongest winds would also have been more intense on the right side of the hurricane track and blowing towards the mainland with winds further to the south blowing at a somewhat lesser speed from land to sea as Hattie made landfall. However, it should be noted that as a hurricane approaches and passes a location, wind directions change both systematically and erratically, and wind gusts can be far stronger than the peak 72 m s^{-1} sustained winds measured at the international airport at Belize City in the early morning on 31 October 1961 (Stoddart, 1963). This pattern of a higher storm surge, greater waves, and more intense winds in the quarter to the right of the storm track holds true for all Caribbean and northern hemisphere hurricanes and tropical storms.

Hurricanes Abby (1960) and Anna (1961) were category 1 hurricanes when they crossed the Belize Barrier Reef at Gladden Spit and the Sapodilla Cayes, respectively, whereas Hurricanes Francelia (1969) and Fifi (1974) were category 2 hurricanes when they both crossed the barrier reef at site 14, Northeast Caye, on their way to inflict significance damage to Punta Gorda and Monkey River, respectively. Hurricane Fifi (1974) was particularly deadly and fierce with torrential rains, causing more than 8,000 deaths in Honduras and Guatemala, and destroying infrastructure and banana plantations in southern Belize. Hurricanes Edith (1971) and Carmen (1974) and all 4 tropical storms crossed the barrier reef north of Belize City, sufficiently far north to have little impact on the southern MAR in the Gulf of Honduras, although Tropical Storm Laura (1971) crossed the barrier reef near site 22 and then proceeded south-southwest to Port Honduras north of Punta Gorda, accompanied by heavy rainfall. Hurricane Greta crossed both sites 23 and 24 (Glover's Reef) and 19 (Carrie Bow Caye) and made landfall at Dangriga on 19 September 1978. Greta was a category 4 hurricane, category 3 at the time of landfall, with a minimum central pressure of 947 hPa, maximum sustained winds of 59 m s^{-1}, heavy rainfall, and caused significant property damage inland and tree damage on the cayes.

Kjerfve and Dinnel (1983) hindcast waves at Carrie Bow Caye for when Hurricane Greta (1978) approached the barrier reef and crossed the caye, which was located within the radius of maximum sustained winds (46 m s^{-1}). They calculated significant maximum breaking wave heights of 10 m on the forereef in spite of the partial protection provided by Glover’s Reef 23 km to the east. The shallow *Acropora palmata* zone near the reef crest suffered extensive breakage but the *Acropora cervicornis* zone on the inner forereef at a depth of 10 to 15 m was only moderately damaged (Kjerfve and Dinnel, 1983). However, the zone with abundant *A. cervicornis* in the backreef near Carrie Bow Caye was destroyed by Hurricane Greta (Rützler and Macintyre, 1982). Similarly, when Hurricane Allen passed just north of Jamaica in 1981, the breaking maximum waves on the eastern forereef measured 11.5 to 12.0 m and generated near-bottom wave-induced currents exceeding 2.4 m s^{-1} (Woodley et al., 1981; Kjerfve et al., 1986), breaking 85 to 96% of all branched corals, *A. palmata* and *A. cervicornis*, which prior to Hurricane Allen dominated the forereef terrace down to 6 m and 25 m, respectively (Woodley et al., 1981; Kjerfve et al., 1986). Some of the breakage was due to drag forces, some due to the impact of water-borne coral fragments transported shoreward forming a new boulder rampart on the reef flat.

During the next 20 years, 1980-1999, the study area experienced three tropical storms and one hurricane (Table 4, Figure 3b). Mitch is maybe the most deadly and destructive category 5 hurricane (Figure 4 a, b) in the Caribbean for more than a century (Sheng et al., 2007) – until 2020. Mitch made landfall in northern Honduras, east of Roatan, on 29 October 1998 as a category 5 hurricane after having traveled west for the previous 4-5 days before turning sharply south, acting as a generator for enormous waves that impacted with destructive force the Belize Barrier Reef to the north-west. The coral reefs of southern Belize were physically severely impacted by these waves (McField, 2002). The eye of Hurricane Mitch approached within 220 km of Gladden Spit before the hurricane made the sharp turn to the south into Honduras, traveled for three days at a slow rate towards the west into Guatemala, before turning north and continuing into Mexico and ultimately the Bahía de Campeche in the Gulf of Mexico (Figure 3b). During the overland passage, Mitch dumped an enormous amount of rain in Honduras, Nicaragua, and Guatemala, locally reported to be greater than 1,900 mm, caused severe flooding and catastrophic landslides, and resulted in more than 11,000 deaths and more than $5 billion in property damages. Most of the subsequent massive water and sediment runoff entered Bahía de Amatique and the Gulf of Honduras, dramatically changing ocean color measured in satellite-based analyses, showing that sediment-laden waters extended the impact zone north past Gladden Spit and Glover’s Reef (Andréfouët et al., 2002; Sheng et al., 2007). Mitch is the only hurricane in the 60-year period through 2019 to have made landfall along the 380 km long northern coast of Honduras (although half a dozen tropical storms/depressions have exited the northern Honduras coast moving west northwest into the Caribbean).

From 2000 through 2019, 6 hurricanes and 5 tropical storms impacted the southern MAR in the Gulf of Honduras (Table 4, Figure 3c). Hurricane Keith travelled directly west, then turned south to just north of Turneffe, then turned 180 degrees to the north, and made landfall at San Pedro on 1 October 2000, as a category 4 hurricane. Hurricane Iris, a small but very powerful category 4 hurricane with sustained 64 m s^{-1} winds, crossed Gladden Spit (sites 16 and 17), made landfall in Port Honduras north of Punta Gorda on 9 October 2001, and caused 24 deaths and significant destruction in southern Belize. Hurricane Dean made landfall at Mahahual, 64 km north of the

Mexico/Belize border on 21 August 2007, as a category 5 hurricane, but was too far north to impact the southern Gulf of Honduras significantly. Hurricane Felix, another deadly category 5 hurricane, made landfall in Nicaragua and Honduras with massive flooding and many deaths, but was reduced to a tropical depression before continuing west into the Gulf of Honduras and making landfall in southernmost Belize in 2007. Hurricane Richard, a category 2 hurricane, crossed Turneffe Reef and made landfall just south of Belize City on 25 October 2010, causing extensive flooding and damage to the forests while moving into the interior. This in turn lead to increased fires during the next dry season, followed by extremely high nutrient runoff and toxic algal blooms the subsequent rainy season (McField et al., 2012). From 2013 to 2019, two tropical cyclones affected Belize. Tropical Storm Harvey crossed the barrier reef at Carrie Bow Caye (Station 19) and made landfall in Dangriga on 20 August 2011; and Hurricane Earl, a category 1 hurricane, crossed Turneffe Reef and made landfall 10 km south of Belize City on 4 August 2016.

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The figures below are low-resolution versions of the final figures, which are submitted as high-resolution figures separately, some in both full color and greyscale.

Figure 1

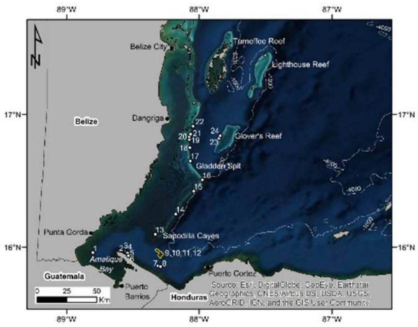
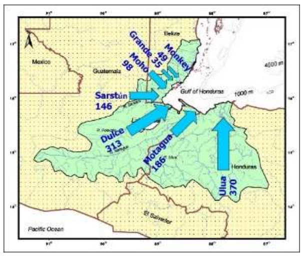


Figure 2a



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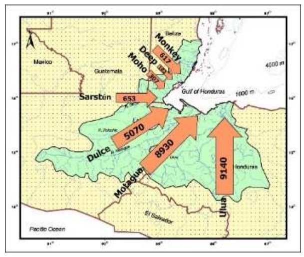

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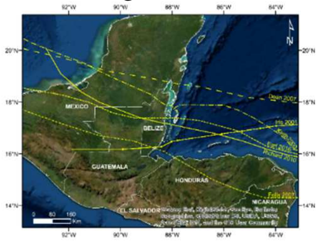

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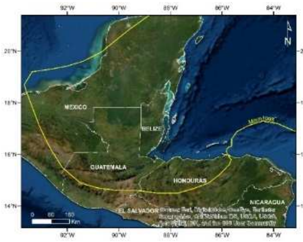

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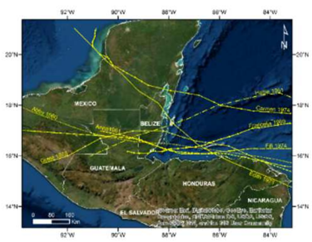

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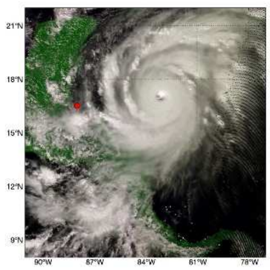

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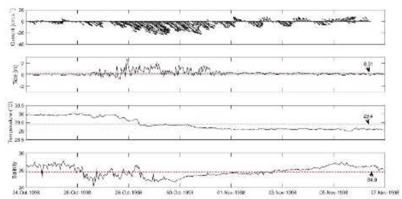

Figure 5