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Coral Reef Recovery in the Mexican Caribbean after 2005 Mass Coral Mortality—Potential Drivers

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Abstract: In 2005, an extreme heatwave hit the Wider Caribbean, followed by 13 hurricanes (including hurricanes Emily and Wilma) that caused significant loss in hard coral cover. However, the drivers of the potential recovery are yet to be fully understood. Based on recent findings in the literature of coral cover recovery in the Mexican Caribbean after the mass bleaching event and associated hurricanes in 2005, this study analyzed, through random-effects meta-analysis, the hard coral and macroalgae benthic development and potential drivers of change between 2005 and 2016 in the Mexican Caribbean. Therefore, we tested the relative effect of sea surface temperature (SST), chlorophyll-a water concentration, coastal human population development, reef distance to shore, and geographical location on both hard coral and macroalgae cover over time. Findings revealed increases of both hard coral (by 6%) and algae cover (by ca. 14%, i.e., almost three times the increase of corals) over 12 years. Although our findings confirm the partial coral recovery after the 2005 Caribbean mass coral mortality event, they also indicate rapid colonization of algae across the region. Surprisingly, only SST correlated negatively with changes in coral cover. Contrary to expectations, there was a significantly greater algae cover increase in the Central section of the Mexican Caribbean, which is characterized by a low population density. However, a constant discharge of nutrient-rich freshwater may have facilitated algae growth there. This study reports partial regional reef recovery, but it also indicates that local factors, particularly eutrophication, facilitate algae growth at a speed that is much faster than coral recovery.

Keywords: coral; meta-analysis; sea surface temperature

1. Introduction

Worldwide, coral reefs are jeopardized through a combination of natural and anthropogenic pulse disturbances. Unprecedented losses of coral cover are the result of coastal development, hurricane impacts, and heatwaves [1–3]. Some reefs around the world show coral recovery after such mass mortality events [4–9] For instance, corals in the Eastern Tropical Pacific recovered by 30% in 13 years after the El Niño phenomenon in 1982–1983 [7]. Likewise, in Seychelles, the coral cover increased by 23% in 13 years after the 1998 bleaching event [8]. The North-Western Australian reefs showed a 35% coral cover recovery within 12 years after the 1998 bleaching event [6]. The primary mechanism leading to coral recovery is the recruitment of sexually produced corals [10,11]. Additionally, high herbivore grazing capacity [6,10,12], high coral and fish diversity [13], and isolation from chronic anthropogenic pressures [13] can enhance coral recovery.

However, only very few studies have reported that reef condition improves after any mass mortality events in the Caribbean Sea. For example, Rodriguez-Martínez et al. [14] described a ca. 20% increase of *Acropora palmata* cover in the Northern part of the Mexican Caribbean after the impact of the hurricanes in 2005, while the hard coral cover was reported to double from 23% to 53% between 1995 and 2005 in Jamaica [15]. However, the only region-wide evidence of a recovery in coral cover was recently provided by a meta-analysis in the Mexican Caribbean, that showed a coral cover slight increase between 2005 and 2016, despite the macroalgae increase found during that same period [16]. On the contrary, many studies are reporting how reefs in the Caribbean Sea are failing to recover after such events [14,17–19], and other studies suggest that the coral and macroalgae cover has remained relatively constant since the mid-1980s [20]. Roff and Mumby [21] suggested that Caribbean coral reefs show lower resilience than Indo-Pacific reefs due to their fast macroalgae growth rate, lack of Acroporid corals, lower herbivore biomass, and missing groups of herbivores.

Pulse disturbances, such as the white band disease outbreak in the late 1970s [22], the mass mortality of the sea urchin Diadema in 1983–1984 [23], or the El Niño-induced bleaching event in 1998–1999, have affected Caribbean coral reefs. In 2005 (May to October), the Wider Caribbean was hit by a heatwave of +1.2 °C [24,25]. It was described by Eakin et al. [25] as one of the most extreme coral bleaching and mortality events affecting the Wider Caribbean [24,25]. On average, 50–95% of the coral colonies were bleached in the whole Caribbean and in the U.S. Virgin Islands, and ca. 51% of coral colonies died due to bleaching and subsequent coral disease [24].

During the warm period of 2005, the Mexican Caribbean (MC) was not impacted by the heatwave to the extent of other reefs in the Wider Caribbean [25]. However, the warm water anomaly contributed to the following record hurricane season in the same year [25,26]. The 2005 hurricane season ended with a record of 26 storms that included 13 hurricanes [24]. Storms of Category 5, including the hurricanes Emily (July) and Wilma (October), greatly impacted the Northern MC [26,27]. Unfortunately, just a few studies are assessing the effects of the 2005 mass mortality event. McField et al., [28] reported 9% overall coral mortality in Mexico, whereas surveys by Álvarez-Filip et al. [27] reported a 56% live coral cover decline after hurricanes Emily and Wilma at Cozumel Island. A recent meta-analysis showed that coral cover has since then slightly recovered (between 2005 and 2016) [16]. However, very little is known about the drivers that have promoted this coral cover increase.

The understanding of the environmental and anthropogenic conditions that favored the coral cover increase is particularly relevant because the Mexican Caribbean reefs have also been exposed to long-term chronic stress. The human population in Quintana Roo alone increased from 0.9 to 1.3 million (i.e., by 70%) between 2000 and 2010 [29]. Different studies point out that the degradation of reefs may be correlated with the tourism industry [30,31] and can facilitate phase shifts of coral reef communities towards algae dominance [31,32]. The tourism industry is one of the greatest challenges in the MC since it has developed tremendously since the mid-1970s [33]. Currently, over 10 million tourists arrive annually [34], and in 2016, the gross income of tourism for the Mexican state of Quintana Roo alone was $8810 Million US dollars [35]. The growing tourism can decrease water quality [19] as it is usually joined by increasing liquid and solid waste discharge into the ocean [36,37].

Here, we set out to analyze the development of hard coral and macroalgae cover, as an indirect measure of reef degradation [1,38,39], in high spatiotemporal resolution over the period 2005 to 2016, with particular interest in identifying the potential drivers affecting reef recovery. Sea surface temperature (SST), water chlorophyll-a concentration, coastal human population, and reef distance to the shore were selected as proxies of the most critical anthropogenic drivers of change impacting the MC reef tract reported in the literature [32,40,41]. Increasing SST, chlorophyll-a (as a proxy for eutrophication), and human population were expected to slow down coral recovery, while increasing distance to the shore was expected to enhance it.

2. Materials and Methods

2.1. Data Collation

Spanning approximately 400 km along the Mexican Caribbean, 254 quantitative benthic surveys (hard coral and macroalgae) were analyzed from 2005 to 2016 (Figure 1) after the bleaching event and the hurricanes Emily and Wilma. This data was a subset of the database used by Contreras-Silva et al. [16], however, only monitoring sites with at least three surveyed years were used for this study so that it was possible to conduct a general linear model (Figure 1, for PRISMA checklist see Supplementary Materials, Checklist S1). The data was gathered by the Biodiversity and Reef Conservation Laboratory, UNAM, and comes from fieldwork and the following sources: Arrecifes de Cozumel National Park (PNAC), Arrecife de Puerto Morelos National Park (PNAPM), Healthy Reefs for Healthy People (HRHP) initiative, Greenpeace, National Council of Science and Technology (CONACYT), Lanz-Landazuri et al. [42], Perera-Valderrama et al. [43], and Rodríguez-Martínez et al. [14]. The benthic surveys were conducted using AGRRA (Atlantic and Gulf Rapid Reef Assessment) versions 4 and 5 and SAM (for its Spanish acronym for Mesoamerican Reef System) protocols (Appendix A Table A1, Supplementary Materials, Table S2). The benthos protocol in AGRRA version 4 used intercept length measurement, whereas version 5 uses point intercept methodology (PIT) [44], the same as the SAM protocol. More detailed information is found in Contreras-Silva et al. [16]. It is also important to mention that the only permanent reef units in the database are those located in Puerto Morelos from 2012 to 2016. The rest of the sampling sites presented specific coordinates (from Global Positioning System—GPS) for a revisit period, namely the systematic sampling approach, which is most useful for primary trend analyses, where evenly spaced samples are collected for an extended time [45]. The number of replicates per site each year was considered high enough to neglect the spatial variability caused by the use of haphazard transects. One possible bias caused by the spatial variability would be the sampling of different coral reef types, and therefore, this factor was included in the analysis (Table 1). The hard coral and macroalgae (fleshy and calcifying) cover surveys corresponded to 48 reef sites along the Caribbean coast of Mexico (Figure 1). Each survey included the coordinates of each monitoring site. The water depths of the surveyed sites varied between 0.5 to 19.0 m and were between 21 and 5000 m away from the coast.

Table 1. Proxies effect on hard coral and macroalgae benthic cover in Mexican Caribbean coral reefs. Mean effect size using random-effects meta-analysis. Abbreviations: effect size (ES), standard error (SE), and Mexican Caribbean (MC).

Factor	Hard Coral Cover			Macroalgae Cover		
	ES	*p*-Value	SE	ES	*p*-Value	SE
Temperature	−39.331	**0.019**	16.81	-40.89	0.248	35.40
Chlorophyll-a water concentration	4.69	0.095	2.81	-48.98	0.716	135.08
Population rate	-0.06	0.173	0.04	-0.11	0.250	0.09
Distance to the shore	0.00	0.984	0.00	0.00	0.818	0.00
Initial cover	-0.01	0.48	0.02	-0.04	**0.021**	0.02
Reef type: fore reef	0.426	0.416	0.32	0.70	0.298	0.67
Reef type: posterior	−0.05	0.899	0.32	−0.97	0.238	0.83
Reef type: crest	0.24	0.416	0.30	0.89	0.138	0.60
Latitude	−0.03	0.844	3.65	−0.91	**0.001**	0.29
Sub-Region: Cozumel Island	0.45	0.720	0.63	−0.76	0.499	1.13
Sub-Region: North MC	0.16	0.806	0.66	−2.11	0.062	1.13
Sub-Region: Central MC	0.30	0.699	0.77	2.32	**0.031**	1.07
Sub-Region: South MC	0.32	0.654	0.71	0.10	0.937	1.25

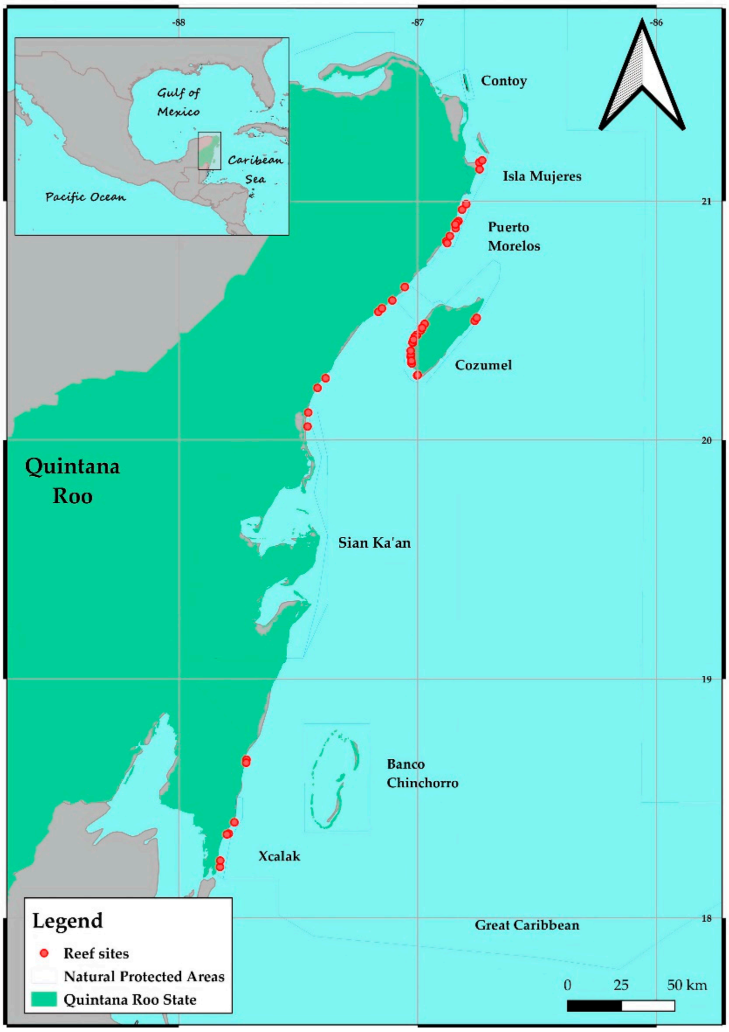


Figure 1. Study area (created with QGIS Development Team, 2019. QGIS Geographic Information System. Open Source Geospatial Foundation. http://qgis.org). Polygons in blue represent the Natural Protected Areas in the Region. The red dots are the reef monitoring sites used for the hard coral and macroalgae cover meta-analysis.

2.2. *Drivers of Change*

To study the effect of increasing sea surface temperature (threatening coral reefs worldwide) and coastal development (assessed as the primary driver of change affecting reefs in the MC according to Bozec et al. [40], Arias-González et al. [32], and Suchley and Alvarez-Filip [41]), four factors were selected as proxies: sea surface temperature (SST), chlorophyll-a water concentration, coastal human population, and coral reef distance to the shore.

2.2.1. Sea Surface Temperate (SST)

Remote sensing data for the SST (in °C, 0.25° spatial resolution) [46] was extracted from the Monthly Optimum Interpolation Sea Surface Temperature (OISST) database of the National Oceanic and Atmospheric Administration (NOAA) of the United States.

2.2.2. Coastal Development

Chlorophyll-a water concentration was used as a proxy for nutrient concentration and eutrophication, for example, as used by Duprey et al. [47], Reynolds and Maberly [48] and De'ath and Fabricius [49]. Chlorophyll-a concentration is directly correlated with nitrogen, phosphorous, and suspended solids [49]. For this, monthly satellite data from AQUA/MODIS (mg m^{-3}, 0.036° spatial resolution) was extracted from NASA (NASA GSFCOEL, 2018). The distance of the reef site to the coastline was measured using Google Earth Pro 7.3.0.3832 and the provided coordinates from each monitoring site (Supplementary Materials, Table S3. The human population data per locality of 2005 and 2010 were collected from the National Institute of Statistics and Geography (INEGI) of Mexico (Supplementary Materials, Tables S4 and S5). The data from the 2015 population was not included because the data for some locations included in the study had not yet been processed and were not available.

2.2.3. Spatial Variability

The latitude of each monitoring site was tested as a factor to account for spatial variability. Additionally, the coast of the Mexican Caribbean was divided into four sub-regions: North (North of the Sian Ka'an Biosphere Reserve), South (South of Sian Ka'an), Central (Sian Ka'an), and Cozumel Island (Figure 1), as proposed by Jordán-Dahlgren and Rodríguez-Martínez [50]. The reefs in each sub-region are exposed to different levels of anthropogenic pressure, e.g., the North MC is a hotspot for tourism and coastal development, while the Central MC comprises the entire Sian Ka'an Biosphere Reserve [36]. To test any spatial variability in hard coral and macroalgae benthic cover development, the sub-region to which each site belonged to and the latitude at which each monitored reef was located were also analyzed as factors for the meta-analysis. Most of the surveyed sites used in this study are in North MC and Cozumel, contrary to Central and South MC where only two and seven sites were surveyed, respectively. This vast difference in the number of sites per sub-region represents a bias in the results; however, no further reliable temporally replicated data was found for the MC, especially for the Central and South sub-regions of the Mexican Caribbean. Furthermore, the North MC was the most affected region by the hurricanes Emily (July) and Wilma (October) [26,27].

2.2.4. Further Factors

Additionally, the type of reef was also analyzed as a factor. The first hard coral and macroalgae cover reported for each monitoring site after 2005 were selected as initial cover and also analyzed as factors.

2.3. Data Processing

Annual averages of the sea surface temperature and chlorophyll-a water concentration data were calculated using the smallest spatial resolution as a radius for all 50 coordinates (Supplementary Materials, Tables S6 and S7). An annual rate of change was calculated for both SST and chlorophyll-a from 2005 to 2016 using a general linear model.

The threat of coastal development to reefs varies with distance to the source of pollution [51–54]. The closer the reefs are to cities and other human settlements, the biggest affectations they will encounter by terrestrial pollution. According to Burke et al. [52], this proxy is measured based on the location of human settlements as well as coastal population density. According to the authors, the highest coastal development impact on reefs occurs between 0 and 15 km distance to the shore with population densities varying between 50,000 and 1,000,000. Pollutants, such as sewage and industrial effluents, may travel approximately 5 km before starting to dissolve in the seawater [55,56]. An extra 5 km were added, assuming that rural and urban cities 5 km away from the coast still discharge human waste directly to the sea [57]. Therefore, all human populations found within a 10 km radius from the monitoring site were added to a total population per monitoring site. From this data, a population rate of change was calculated as follows:

$$\text{Population rate} = (\text{Population 2010})/(\text{Population 2005}) \tag{1}$$

To compare the human population rates of the four mentioned sub-regions of the MC, a Kruskal–Wallis rank-sum test was conducted.

2.4. Meta-Analysis

In this study, a random-effects meta-analysis of the hard coral and macroalgae cover was conducted in the statistics program R 1.0.136 using the metafor package [58]. A limitation of using monitoring data is the large random variability caused by the difference in survey methods, surveyors, and data source. This can highly limit the meta-analysis results [58,59]. The random-effect meta-analysis accounts for data variance and error by weighting the individual effect size by the inverse of its variance using the within- and between-study sampling errors to reduce the heterogeneity caused by the variability of methods and samples between studies [58,59]. According to Koricheva et al. [59], the control of type II error rates can be identified because the low power of individual studies to detect an effect is "corrected" by the accumulation of evidence across many studies; in our case, individual reef sites. By conducting a random-effects meta-analysis, it has been recognized in advance that there is a substantial between-study variation [59].

In this study, instead of using the relative annual rate of change as in Contreras et al. [16] or Alvarez-Filip et al. [60], we calculated the individual effect size (ES) as the slope over time of the hard coral and algae cover of general linear models (GLM) using the lm function. The GLM was used to detect a simple but statistical strong trajectory per reef site using its inverse variance as the weighting method. The mean effect size (MES) was then calculated using the "rma" command with each site's obtained individual effect size, and their corresponding standard error squared as the sampling error. The input of the meta-analysis was as follows: yi is the individual effect size and vi is the sampling error (SE) (Supplementary Materials, Tables S8 and S9).

$$\text{MES} = \text{rma (yi, vi)} \tag{2}$$

A random-effects meta-analysis of the SST and chlorophyll-a water concentration was also conducted. In this case, the slope of the yearly averages of each monitoring site and their standard error were used to calculate the mean effect size.

The individual effect of the selected factors on the hard coral and macroalgae cover development was determined using the same random-effects meta-analysis. The input for testing each fixed factor followed:

$$\text{ES} = \text{rma (yi, vi, mods = *factor*)} \tag{3}$$

To test for variability caused by the different number of monitoring years, monitoring methods, and number surveyors, these factors were also tested in the meta-analysis as fixed factors.

All analyses were performed in R1.0.136.

3. Results

The meta-analysis showed a significant increase in both hard coral and macroalgae cover between 2005 and 2016. The hard coral cover presented a mean effect size of 0.53 ± 0.11 (SE) ($p < 0.001$) (Figure 2, Supplementary Materials, Figures S10 and S11). This corresponds to a coral cover increase of 6.4% ± 1.3% (SE) over the study period. The mean effect size of the algae cover was 1.2 ± 0.25 (SE), i.e., a benthic cover increase of 14.4% ± 3.7% (SE) ($p < 0.0001$), i.e., almost three times the increase of the hard coral cover over the same period. However, as observed through the confidence interval in Figure 2, the difference between the hard coral and macroalgae cover was not significant.

The SST increased along the coast of Quintana Roo (Figure 3a). The mean effect size, resulting from the temperature meta-analysis was 0.026 ± 0.003 (SE), accounting for a sea surface temperature increase of 0.31 ± 0.03 (SE) °C ($p < 0.0001$) in 12 years (Figure 3a). The chlorophyll-a water concentration did not show any clear trend (effect size: 0, $p = 0.97$).

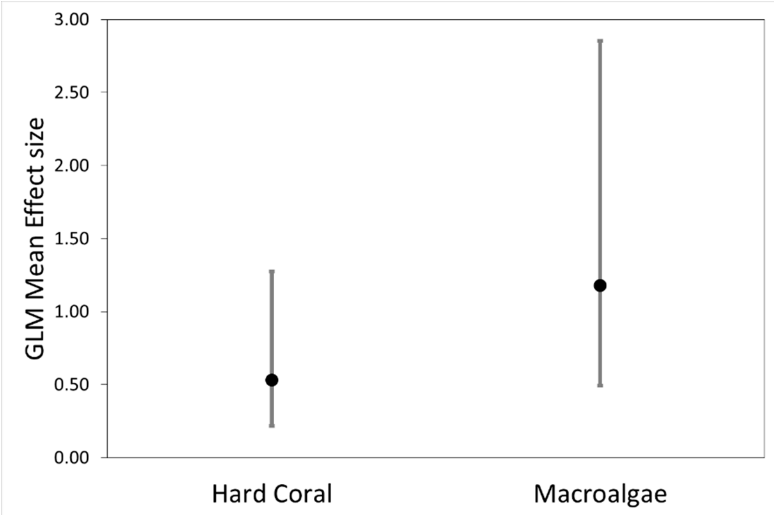


Figure 2. Mean effect size of the random effect meta-analysis on the hard coral and macroalgae cover along the coast of the Mexican Caribbean. Error bars are indicating 95% confidence intervals.

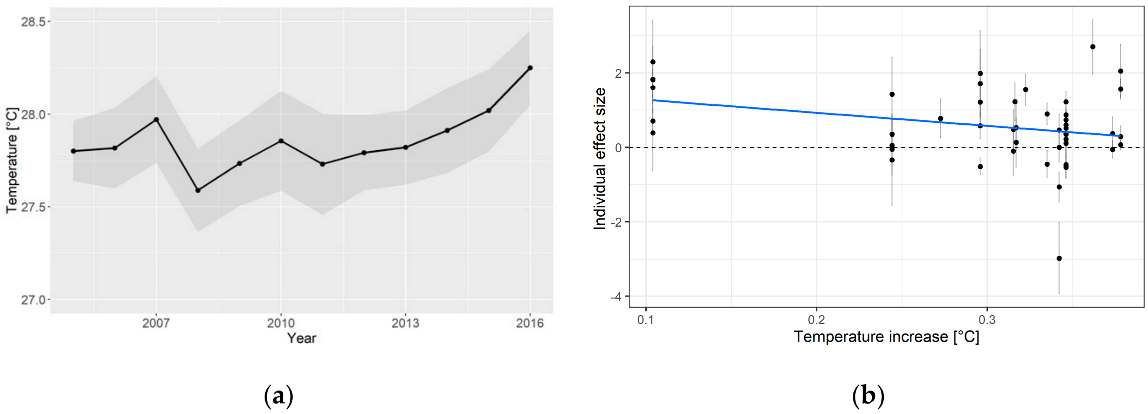
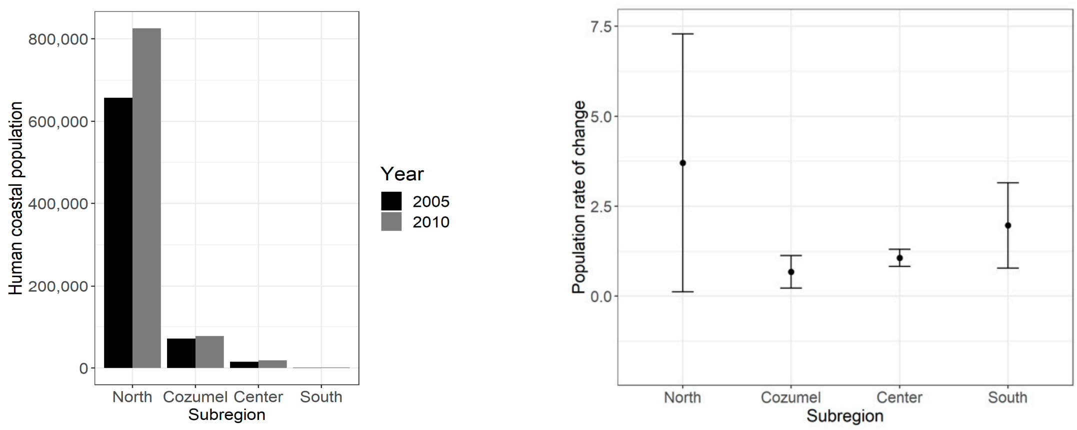


Figure 3. Sea surface temperature (SST) development and effect on the hard coral cover development from 2005 to 2016 using calculated yearly means (Supplementary Materials Table S6): (**a**) Yearly mean of monthly values from Optimum Interpolation Sea Surface Temperature (OISST) data from the National Oceanic and Atmospheric Administration (NOAA). Shade: 95% confidence interval (Meta-analysis p-value < 0.001). (**b**) Individual hard coral cover effect size against temperature increase per site. Error bars indicate standard error. Blue line indicates the negative correlation ($p = 0.019$).

The temperature was the only factor significantly affecting the hard-coral cover from 2005 to 2016 (Table 1). The hard coral cover increased less with higher temperature increase rate (Figure 3b). On the other hand, no significant effect of any individual factor (Table 1) was observed on the macroalgae cover during the study period. There was, however, significant macroalgae cover spatial variability, as the latitude ($p = 0.001$) significantly influenced macroalgae development. The meta-analysis showed a higher macroalgae increase at lower latitudes, particularly in the Central region (mean effect size: 2.3, i.e., 27.6%), while in the North and South sub-region, and Cozumel Island, it remained stable (Table 1). The sites with higher initial macroalgae cover showed faster macroalgae cover growth ($p = 0.021$).

The human coastal population was twice as high in 2010 than in 2005. However, the population change was variable between sub-regions (Figure 4). The highest rate of change was observed in North MC (3.7), while Cozumel Island showed the lowest one (0.7) (Figure 4b). The human coastal population growth rate (Figure 4b) was only significantly higher in North and South MC than in Cozumel Island (Wilcox pairwise comparison $p = 0.0002$).



(**a**) (**b**)

Figure 4. Coastal human population per locality in the Mexican Caribbean. Population data from the National Institute of Statistics and Geography (INEGI) (INEGI, for the Spanish original) from 2005 and 2010: (**a**) Coastal human population per MC sub-region in 2005 and 2010. (**b**) Mean population rate of change in the four sub-regions of the Mexican Caribbean from 2005 to 2010. Error bars indicate standard deviation. Kruskal–Wallis rank sum test p-value = 0.0002.

4. Discussion

This study aimed to identify potential drivers of coral and macroalgae increase along the Mexican Caribbean after the 2005 coral bleaching event and following hurricanes. The results showed a hard coral cover increase of approximately 6.4% in 12 years. These results reflect those of Contreras-Silva et al. [16], who also found a modest but significant coral recovery for the same period analyzed here but using a different meta-analysis approach. The macroalgae cover increased almost three times as fast, however, not significantly. The temperature was the only analyzed factor that showed an effect on coral cover development. Reefs exposed to higher temperatures showed a lower coral cover increase. The macroalgae cover increase did show spatial variation, the highest being in the Central Mexican Caribbean. However, these results cannot be extrapolated to the whole central area due to the small sample size and spatial variability (i.e., just two monitoring sites located in the north of the central area) and therefore need to be interpreted with caution.

Even though the coral cover increase suggests coral recovery after the events of 2005, the recovery rate was rather slow when compared to recovery rates (ca. 25–35% in 11–13 years) reported in other regions of the world [7–9]. For the Mesoamerica Reef, including the MC, subtle but significative increases have also been reported recently [34,39], supporting the trend described here. Still, this far, mainly local hard coral recovery cases have been reported elsewhere in the Caribbean [15,61]. In this region, Gardner et al. [18] found no evidence of coral recovery after impacts of hurricane between 1980 and 2001. The hurricanes in 2005 could have released suitable substrate for coral recruits to settle, as described by Rogers [62] and Graham et al. [10], or could have allowed coral recolonization through hurricane-generated asexual recruit, as observed by Lirman and Fong [63] in the Caribbean. Yet, it has to be considered that coral cover does not account for the recovery of the reef's diversity and functionality. A note of caution is due here since we do not analyze species composition. For instance, the coral recovery measured by coral cover could be reflecting an increase of fast-growing corals, as it has been reported by Guzmán and Cortés [64] in the eastern Pacific or by Estrada-Saldívar et al. [65] in the Caribbean, and Perera-Valderrama et al., [43] in North MC. This species composition change may cause a reduction of hard coral diversity and possibly decreasing ecosystem functioning [10,65,66]. Thus, as a next step, the species development after the 2005 events should be studied.

On the other hand, the simultaneous, and much faster, increase of macroalgae suggests that the free space left by lost hard corals due to the physical disturbance of the hurricanes in 2005 in the Mexican Caribbean [24] could have also been occupied by faster-growing macroalgae that may outcompete slow-growing hard corals [67,68]. These results, however, have to be interpreted carefully. Firstly, the macroalgae increase was not significantly higher than the hard coral cover. Secondly, the random factors describing the meta-analysis variability did affect the macroalgae mean effect size significantly (Appendix B Table A2).

The macroalgae cover development showed spatial variation. A higher increase in macroalgae cover was found in lower latitudes. The algae cover increased significantly by ca. 28% in the Central sub-region, where the lowest initial algae cover of ca. 9% was found. In the North sub-region (−25.3%) and Cozumel Island (−9.12%), with initial macroalgae cover of ca. 18% and 16% respectively, the algae cover decreased, however, not significantly due to the high between-sites macroalgae cover development variability (Figure 5). The Central Mexican Caribbean is composed of the Sian Ka'an Biosphere Reserve (Figure 1). The biosphere is characterized by a complex hydrological system composed of wetland and mangrove forests [69]. The coral reefs in Sian Ka'an may be exposed to the constant discharge of nutrient-rich freshwater that could benefit algae growth [69]. To our knowledge, this is the first time that such a fast macroalgae (~28% in 12 years) growth has been reported in reefs of the protected area. The Central MC was the least surveyed sub-region of the MC with only two monitoring sites, and this rapid change in the benthic composition needs to be more closely monitored.

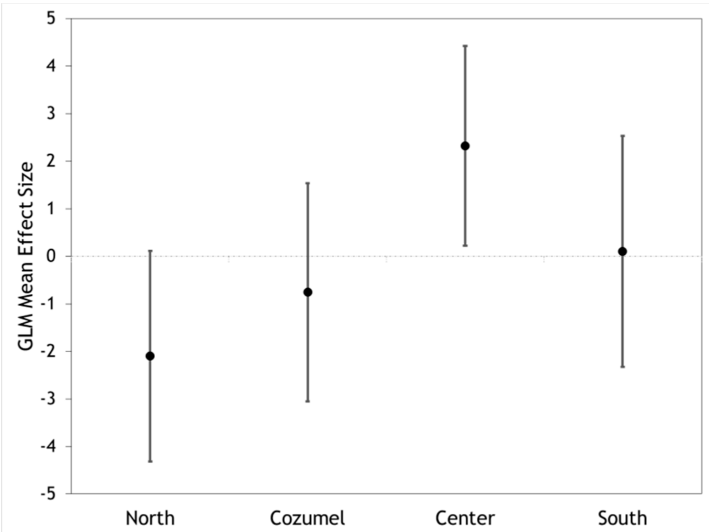


Figure 5. Macroalgae mean effect size of selected sub-regions of Quintana Roo (MC) calculated using a general linear model from 2005 to 2016. Error bars indicate 95% confidence intervals.

Four proxies of drivers of change were tested in this study: SST, chlorophyll-a, coastal human population, and the reef distance to the shore. According to literature, the selected proxies (increasing SST, increasing water chlorophyll-a concentration, increasing human coastal population, and short reef distance to the shore) usually impact coral reefs' benthic cover [52,70,71]. The SST did increase significantly, 0.31 °C from 2005 to 2012, at a similar rate to the ones reported in the literature [72,73]. Only the SST affected the hard coral cover. Results showed that with higher temperature increase, the coral recovery was slower (Figure 3b). A recent study by Muñiz-Castillo et al. [74] corroborates these findings. Hughes [1] and Nyström et al. [3] suggested that chronic disturbances, such as the slow increase in temperature, can slow down the recovery process. This may be the case in the MC showing a rather slow coral recovery after the mass mortality events in 2005. The rest of the tested factors did not show any effect on benthic macroalgae and coral cover, however, it does not mean that there is no effect, as Chollett et al. [73] discussed, the spatial resolution of the remote sensing data (water chlorophyll-a concentration) could be too broad to capture local small-scale variations [50], as it may average measurements over large distances (1 km in this case) [74]. Nevertheless, this is the only chlorophyll-a data available at such spatiotemporal scales, and this database has been used in other studies [75,76]. Another possibility may be the effect of a multitude of chronic (i.e., anthropogenic climate change) and emergent stressors (i.e., rapid coastal anthropization), in which the possibility of finding cause-effect indicators is minimized. The observed hard coral cover increase could have masked the effects of the analyzed factors. The human coastal population increased in all four sub-regions. North Quintana Roo had the highest coastal human population, as reported by the literature [77]. The Wilcox pairwise comparison showed no significant difference in the human population growth rate between North, Central, and South MC, suggesting that Central and South MC may be reaching the North MC coastal human population growth rates. It seems possible that these results indicate the coastal development expansion in the southward of the Mexican Caribbean, as pointed out by Bozec et al. [40]. Nonetheless, an essential factor to take into account in future research is tourism. Tourism in the MC contributes significantly to the Mexican economy and has been identified as negatively impacting MC coastal ecosystems [31,37,40].

The findings in this study also add up to the current discussion about the relative contribution of local versus global factors to reef degradation lead by Bruno and Valdivia [38] and Smith et al. [78]. Our findings suggest that global events do have catastrophic effects on the Mexican Caribbean reefs, yet the reefs showed recovery capacity. Firstly, this study indicated that the SST increase slowed down the hard coral recovery. Local factors, such as tourism and coastal development, were tested in this study, and no effect was found, however, the accuracy of the indicators chosen to test the effect of local factors might have influenced the results. These local factors are as important in previous studies in the region [32,40,41]. For that matter, these results instead show that the combined effect of global and local stressors may be leading to phase-shifts of coral reefs in the Caribbean in that local factors, in this case, primarily eutrophication, may prevent coral recovery due to stimulation of algae growth.

5. Conclusions

Our meta-analysis confirmed that the heat stress caused by increasing SST decreased the capacity of MC corals to recover after multiple impacts. Understanding how reefs are reshaping in light of multiple stressors is critical for developing coral reef conservation and monitoring strategies. This study yielded similar results as Contreras-Silva et al. [16], using a different methodology. This confirms the results that are generally limited by sample sizes and the within- and between-study variability. To better monitor the development of the coral reefs in the MC, a standardization of the survey methodology is recommended, using permanent sites and, if possible, transects. Still, to our knowledge, this is the first study investigating how anthropogenic factors affect coral reef recovery processes over long periods in the MC. This meta-analysis shows how simple surveys such as hard coral cover and macroalgae cover monitoring—two groups that are very easy to identify—can provide valuable information about spatiotemporal development of reef ecosystems, thereby supporting management efforts.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/12/9/338/s1, Checklist S1: PRISMA checklist, Table S2: Monitoring data including hard coral and macroalgae cover from 2005 to 2016 on all 48 sites, Table S3: Survey sites' distance to the shore measured using Google Earth Pro 7.3.0.3832, Table S4: Human population data per locality of 2005 collected from the National Institute of Statistics and Geography (INEGI) of Mexico, Table S5: The human population data per locality of 2010 collected from the National Institute of Statistics and Geography (INEGI) of Mexico, Table S11: Distance of transect monitored to closest shore measured using Google Earth Pro 7.3.0.3832, Table S6: Mean sea surface temperature extracted from NOAA's Monthly Optimum Interpolation Sea Surface Temperature (OISST) data from 2005 to 2016, Table S7: Chlorophyll-a data extracted from AQUA/MODIS satellite from NASA (NASA GSFCOEL, 2018), S8: Meta-analysis input with generalized linear models of hard coral cover over time, Table S9: Meta-analysis input with generalized linear models of macroalgae cover over time, Figure S10: Forest plot of the random-effects meta-analysis conducted on hard coral cover from 2005 to 2016, Figure S11: Forest plot of the random-effects meta-analysis conducted on hard coral cover from 2005 to 2016.

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Appendix A

Table A1. Monitoring methods, institutions, and years of each monitoring site from 2005 to 2016. Sub-regions: Northern (N), Cozumel (Co), Center (C), Southern (S).

Sub-Region	Site Name	Monitoring Methods	Monitoring Entity	Years Monitored
N	Bonanza	AGRRA V4, AGRRA V5, SAM, otro	PNAPM, CONABIO, thesis	2005, 2006, 2008, 2010, 2011, 2012, 2013, 2014, 2015, 2016
N	Cuevones	SAM, AGRRA V5	CONACYT, PNAPM	2011, 2014, 2016
N	Jardines	SAM, AGRRA (modified), AGRRA V5	PNAPM, thesis	2005, 2006, 2008, 2010, 2011, 2012, 2013, 2014, 2015, 2016
N	LaBocana	SAM, AGRRA (modified), AGRRA V5	PNAPM, thesis	2007, 2010, 2012, 2013, 2014, 2015, 2016
N	LaPared	SAM, AGRRA (modified), AGRRA V5	CONABIO, PNAPM, thesis	2007, 2010, 2012, 2013, 2014, 2015, 2016
N	Limones	AGRRA (modified), AGRRA V5, SAM, other	PNAPM, thesis,	2005, 2006, 2008, 2010, 2011, 2012, 2013, 2014, 2015, 2016
N	MX1017	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
N	MX1043	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
N	MX1050	AGRRA V4, AGRRA V5	HRI	2005, 2012, 2014, 2016
N	MX1055	AGRRA V4, AGRRA V5	HRI	2005, 2012, 2014, 2016
N	MX1057	AGRRA V4, AGRRA V5	HRI	2005, 2012, 2014, 2016
N	MX1116	AGRRA V4, AGRRA V5	HRI	2005, 2012, 2014, 2016
N	MX1117	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
N	MX1131	AGRRA V4, AGRRA V5	HRI	2005, 2014, 2016
N	MX1132	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
N	MX1133	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
N	RadioPirata	SAM, AGRRA V5	PNAPM	2008, 2013, 2014, 2015, 2016
N	Tanchacte.Norte	SAM, AGRRA V5, other	PNAPM, CONABIO	2005, 2006, 2007, 2008, 2009, 2010, 2012, 2013, 2014, 2015, 2016
N	TanchacteSur	SAM, AGRRA V5	PNAPM	2008, 2013, 2014, 2015, 2016
Co	CardonaMERASomero	SAM	PNAC	2009, 2011, 2014

Table A1. *Cont.*

Sub-Region	Site Name	Monitoring Methods	Monitoring Entity	Years Monitored
Co	Chankanaab	AGRRA V5, SAM	PNAC, CONACYT, Greenpeace	2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016
Co	ChankanaabBolonesMERAProfundo	SAM	PNAC	2009, 2011, 2014
Co	Colombia	SAM, AGRRA V5	PNAC, CONACYT	2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016
Co	ColombiaMERASomero	SAM	PNAC	2009, 2011, 2014
Co	Dalila	SAM, AGRRA V5	PNAC, CONACYT	2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016
Co	DzulHaMERASomero	SAM	PNAC	2009, 2011, 2014
Co	HananII	SAM, AGRRA V5	CONACYT, PNAC	2005, 2015, 2016
Co	Islote	SAM	PNAC	2005, 2007, 2008
Co	MX1048	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
Co	MX1053	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
Co	MX3009	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
Co	MX3054	AGRRA V4, AGRRA V5, SAM	HRI, CONACYT, PNAC	2005, 2015, 2016
Co	PalancarJardinesMERASomero	SAM	PNAC	2009, 2011, 2014
Co	Paraiso	SAM, AGRRA V5	CONACYT, PNAC,	2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016
Co	ParaisoMERASomero	SAM	PNAC	2009, 2011, 2014
Co	PasodelCedral	SAM, AGRRA V5	CONACYT, PNAC	2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016
Co	SanClemente	SAM, AGRRA V5	Greenpeace, PNAC	2009, 2011, 2016
Co	Tormentos	SAM, AGRRA V5	PNAC, Greenpeace	2009, 2011, 2014, 2016
Co	Yucab	SAM, AGRRA V5	CONACYT, PNAC	2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016
C	MX1008	AGRRA V4, AGRRA V5	HRI	2005, 2012, 2014, 2016
C	MX1042	AGRRA V4, AGRRA V5	HRI	2005, 2009, 2011, 2014, 2016
S	Mah01	AGRRA V5	HRI, CONACYT	2012, 2014, 2016
S	MX1020	AGRRA V4, AGRRA V5	HRI, CONACYT	2006, 2012, 2014, 2016
S	MX1065	AGRRA V4, AGRRA V5	HRI, CONACYT	2006, 2009, 2012, 2014, 2016
S	MX1136	AGRRA V4, AGRRA V5	HRI	2006, 2009, 2014, 2016
S	MX2067	AGRRA V4, AGRRA V5	HRI	2006, 2009, 2012, 2014, 2016
S	MXXCK01	AGRRA V4, AGRRA V5	HRI	2012, 2014, 2016
S	MXXCK02	AGRRA V5	HRI	2012, 2014, 2016

Appendix B

Table A2. Effect of the number of monitoring years, methods, and institutions on the hard coral and macroalgae mean effect size.

Factor	Hard Coral Cover			Macroalgae Cover		
	ES	p-Value	SE	ES	p-Value	SE
Number of years surveyed	0.04	0.223	0.03	-0.21	**0.004**	0.07
Number of methods	-0.07	0.698	0.18	-1.22	**0.001**	0.36
Number of surveyors	0.08	0.334	0.08	-0.56	**0.001**	0.16

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