THE MEXICAN CARIBBEAN REEFS: FROM BENTHIC CHANGES AND STRESSORS TOWARDS A SUSTAINABLE MANAGEMENT STRATEGY

DISSERTATION

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A DISSERTATION BY

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Dedication

I dedicate this thesis to my son Cosmo because, through your eyes, I can see that a different, better world is possible. I want you to dive and admire this other stunning underwater world full of magic and beautiful reefs.

This is also for you, *Mamita*, my most outstanding example of strength, unconditional love, and continued effort. I look at you and admire you so much. Despite my age, you continue giving me so much love and sweetness with infinite kisses. Thank you for your fortitude, your unequalled wisdom, and for always holding me with sure feet as if you were walking on the sea with the most outstanding security.

And this is for you, *Papi*, my oak tree, my slice of watermelon. You left this world too early to see me with my doctor's title. I honour your life every second, surprising myself with every bit of beautiful life detail like you always did. Your smile and laugh will perdure forever in my life, along with your honesty, willingness to help people, and thirst for knowledge. Love you to the moon and back, counting every star from where you see us each night.

“The truth is: the natural world is changing. And we are totally dependent on that world. It provides our food, water, and air. It is the most precious thing we have and we need to defend it.”

— David Attenborough

“The world is a dangerous place to live, not because of the people who are evil, but because of the people who don't do anything about it.”

— Albert Einstein

“Nothing in life is to be feared, it is only to be understood. Now is the time to understand more, so that we may fear less.”

— Marie Curie

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Abstract

The Mexican Caribbean is home to many coral reefs with a high ecological and economic value for people in the country and beyond. Nevertheless, these ecosystems are highly threatened due to a combination of global (anthropogenic climate change) and local stressors (mass tourism, land-based pollution, and overuse of resources). The decline of the wider Caribbean coral reefs has been alarming, with an average loss of 40 % of absolute coral cover since the late 1970s. However, the current literature lacks spatiotemporal information on the coral and macroalgae cover development and longitudinal studios regarding the stressors causing changes in Mexican Caribbean reefs. Therefore, this thesis aimed first to understand the benthic dynamics of change and the main stressors causing these changes to finally propose a conceptual framework to improve coral reef management.

A large-scale spatiotemporal analysis between 1978 and 2016 on coral and macroalgae cover in the Mexican Caribbean reefs was conducted through meta-analysis. Here, findings revealed that hard coral cover decreased from ~ 26 % in the 1970s to 16 % in 2016, whereas macroalgae cover increased from ~ 16 % in the 1980s to ~ 30 % in 2016. Both groups showed high spatiotemporal variability. Hard coral cover declined by 12 % from 1978 to 2004 but increased again by 5 % between 2005 and 2016, indicating some coral recovery after the 2005 mass bleaching event and hurricane impacts. Additionally, a cumulative impact assessment on hard coral and macroalgae benthic communities exposed to multiple stressors (thermal stress, nutrient inflow, sedimentation, hurricane impact, and anthropisation) was conducted using an extensive remote sensing data collection. These data were coupled with 91 coral reef monitoring sites from 2005 to 2016, and the estimates of the change in coral and macroalgae cover percentage were related to each factor considered a potential stressor impacting reefs. Results showed that sea surface temperature increased by 0.30 °C in 12 years, and bleaching susceptibility strongly influenced coral cover change, followed by the negative effect of anthropogenic activities, which incorporates the increasing pressures of urban hubs. The water quality predictors, primarily the particulate organic carbon (used as a proxy for sedimentation and nutrients),

only affected macroalgae cover. The only adverse effect on macroalgae was sea surface temperature and chlorophyll-*a* interaction. Analyses here revealed that global warming impacts on coral reefs occur parallel with local pressures, such as increases in nutrients and suspended sediments through coastal development. The future of Mexican Caribbean coral reefs is at high risk due to cumulative impacts from local and global stressors despite monitoring and restoration efforts over the past few decades, which begs the question of why and how protection and management may be improved. Consequently, a conceptual framework was generated focusing on an integrated management strategy to improve the understanding of the unique and vital services that coral reef ecosystems in the Mexican Caribbean provide. Within this spectrum, a Cybercartographic atlas was proposed because it offers an excellent method for creating a conceptual framework for such a management tool. The ultimate objective is to make arguments accessible that serve as a baseline for assisting and setting priorities for governance in political decisions.

Zusammenfassung

Die mexikanische Karibik beherbergt zahlreiche Korallenriffe, die für die Menschen im Land und darüber hinaus einen hohen ökologischen und wirtschaftlichen Wert haben. Dennoch sind diese Ökosysteme durch eine Kombination globaler (anthropogener Klimawandel) und lokaler Stressfaktoren (Massentourismus, landgestützte Verschmutzung und Übernutzung der Ressourcen) stark bedroht. Der Rückgang der Korallenriffe in der Karibik ist alarmierend: Seit den späten 1970er Jahren sind durchschnittlich 40 % des absoluten Korallenbestands verloren gegangen. In der aktuellen Literatur fehlen jedoch räumlich-zeitliche Informationen über die Entwicklung des Korallen- und Makroalgenbewuchses sowie Längsschnittstudien über die Stressfaktoren, die Veränderungen in den Riffen der mexikanischen Karibik verursachen. Daher zielte diese Arbeit zunächst darauf ab, die benthische Veränderungsdynamik und die Hauptstressoren, die diese Veränderungen verursachen, zu verstehen, um schließlich einen konzeptionellen Rahmen zur Verbesserung des Managements von Korallenriffen vorzuschlagen.

Eine groß angelegte raum-zeitliche Analyse der Korallen- und Makroalgenbedeckung in den Riffen der mexikanischen Karibik zwischen 1978 und 2016 wurde durch eine Meta-Analyse durchgeführt. Die Ergebnisse zeigten, dass die Steinkorallenbedeckung von ~ 26 % in den 1970er Jahren auf 16 % im Jahr 2016 zurückging, während die Makroalgenbedeckung von ~ 16 % in den 1980er Jahren auf ~ 30 % im Jahr 2016 anstieg. Beide Gruppen wiesen eine hohe raum-zeitliche Variabilität auf. Die Steinkorallenbedeckung ging von 1978 bis 2004 um 12 % zurück, stieg aber zwischen 2005 und 2016 wieder um 5 % an, was auf eine gewisse Erholung der Korallen nach der Massenbleiche von 2005 und den Auswirkungen der Hurrikane hindeutet. Darüber hinaus wurde eine kumulative Bewertung der Auswirkungen auf benthische Steinkorallen- und Makroalgengemeinschaften, die mehreren Stressfaktoren ausgesetzt sind (thermischer Stress, Nährstoffzufuhr, Sedimentation, Auswirkungen von Hurrikanen und Anthropisierung), anhand einer umfangreichen Fernerkundungsdatensammlung durchgeführt. Diese Daten wurden mit 91 Korallenriff-Überwachungsstandorten aus den Jahren 2005 bis 2016 verknüpft, und die Schätzungen der prozentualen Veränderung der Korallen- und Makroalgenbedeckung wurden zu jedem

Faktor in Beziehung gesetzt, der als potenzieller Stressor für die Riffe gilt. Die Ergebnisse zeigten, dass die Meeresoberflächentemperatur in 12 Jahren um 0,30 °C anstieg und die Anfälligkeit für Bleiche die Veränderung der Korallenbedeckung stark beeinflusste, gefolgt von den negativen Auswirkungen anthropogener Aktivitäten, die die zunehmende Belastung durch städtische Zentren einschließt. Die Prädiktoren für die Wasserqualität, in erster Linie der partikuläre organische Kohlenstoff (der als Stellvertreter für Sedimentation und Nährstoffe verwendet wird), wirkten sich nur auf den Makroalgenbewuchs aus. Die einzige negative Auswirkung auf Makroalgen war die Wechselwirkung zwischen Meeresoberflächentemperatur und Chlorophyll-*a*. Die Analysen zeigten, dass die Auswirkungen der globalen Erwärmung auf die Korallenriffe parallel zu lokalen Belastungen auftreten, wie z. B. der Zunahme von Nährstoffen und Schwebstoffen durch die Entwicklung der Küstengebiete. Die Zukunft der mexikanischen Korallenriffe in der Karibik ist aufgrund der kumulativen Auswirkungen lokaler und globaler Stressfaktoren trotz der Überwachungs- und Wiederherstellungsmaßnahmen der letzten Jahrzehnte stark gefährdet, was die Frage aufwirft, warum und wie Schutz und Management verbessert werden können. Folglich wurde ein konzeptioneller Rahmen entwickelt, der sich auf eine integrierte Managementstrategie konzentriert, um das Verständnis für die einzigartigen und lebenswichtigen Leistungen der Korallenriff-Ökosysteme in der mexikanischen Karibik zu verbessern. Innerhalb dieses Spektrums wurde ein cyberkartografischer Atlas vorgeschlagen, da er eine hervorragende Methode zur Erstellung eines konzeptionellen Rahmens für ein solches Managementinstrument darstellt. Letztlich geht es darum, Argumente zu finden, die als Grundlage für die Unterstützung und Prioritätensetzung bei politischen Entscheidungen dienen.

Resumen

El Caribe mexicano alberga numerosos arrecifes de coral de gran valor ecológico y económico para la población del país y fuera de él. Sin embargo, estos ecosistemas están altamente amenazados debido a una combinación de factores de estrés globales (cambio climático antropogénico) y locales (turismo masivo, contaminación terrestre y sobreexplotación de los recursos). El deterioro de los arrecifes de coral del Gran Caribe ha sido alarmante, con una pérdida absoluta del 40 % de la cobertura coralina desde finales de la década de 1970 hasta inicios del 2000. Sin embargo, la literatura actual carece de información espacio-temporal sobre la evolución de la cobertura de coral y macroalgas, así como de estudios longitudinales sobre los factores de estrés que causan los cambios en los arrecifes del Caribe mexicano. Por lo tanto, el objetivo de esta investigación fue entender la dinámica bentónica de cambio y los principales estresores causantes de cambios y finalmente proponer un marco conceptual para mejorar el manejo de los arrecifes coralinos en el Caribe Mexicano.

Mediante meta-análisis se estudió la dinámica espaciotemporal de la cobertura de coral y macroalgas en los arrecifes del Caribe mexicano entre 1978 y 2016. Aquí, los hallazgos revelaron que la cobertura de coral duro disminuyó de aproximadamente 26 % en la década de 1970 a 16 % en 2016, mientras que la cobertura de macroalgas aumentó de 16 % en la década de 1980 a aproximadamente 30 % en 2016. Ambos grupos mostraron una gran variabilidad espaciotemporal. La cobertura de coral duro disminuyó un 12 % entre 1978 y 2004, pero volvió a aumentar un 5 % entre 2005 y 2016, lo que indica cierta recuperación de los corales tras el blanqueamiento masivo de 2005 y los impactos de dos huracanes categoría 5. Adicionalmente, se realizó una evaluación del impacto acumulativo en la cobertura de coral duro y macroalgas expuestas a múltiples factores de estrés (estrés térmico, afluencia de nutrientes, sedimentación, impacto de huracanes y antropización) para ello se utilizó una amplia colección de datos de percepción remota. Estos datos se acoplaron a 91 sitios de monitoreo de arrecifes de coral de 2005 a 2016, con estimaciones del cambio en el porcentaje de cobertura de coral y macroalgas, esto a su vez se relacionó con cada factor, considerado como una posible causa de estrés que afecta a los arrecifes. Los

resultados revelaron un aumento de 0,30 °C en temperatura superficial del mar en los 12 años analizados, mostrando una alta susceptibilidad al estrés térmico, lo que impacta negativamente el cambio de la cubierta de coral. Las actividades antropogénicas, que incorporan las crecientes presiones de los núcleos urbanos, también presentaron un impacto negativo en la cobertura de coral. Sin embargo, los predictores de la calidad del agua, principalmente el carbono orgánico particulado (utilizado como variable indirecta de sedimentación y nutrientes), sólo presentaron un efecto positivo en la cobertura de macroalgas. El único efecto adverso sobre las macroalgas fue la interacción entre la temperatura superficial del mar y la clorofila-*a*. Los análisis de este estudio revelaron que los efectos del calentamiento global sobre los arrecifes de coral se producen paralelamente a las presiones locales, como el aumento de nutrientes y sedimentos en suspensión debido al desarrollo costero. A pesar de los esfuerzos de monitoreo y restauración de las últimas décadas, el futuro de los arrecifes coralinos del Caribe mexicano está en riesgo debido a los impactos acumulativos de los factores de estrés locales y globales; lo que nos lleva a plantear la pregunta de por qué y cómo se pueden mejorar la protección y la gestión de estos ecosistemas. En consecuencia, se generó un marco conceptual centrado en una estrategia de gestión integrada para mejorar la comprensión de los servicios únicos y vitales que proporcionan los ecosistemas de arrecifes de coral en el Caribe mexicano. Dentro de este espectro, se propuso un atlas cibercartográfico porque ofrece un método excelente para la creación de un marco conceptual para una herramienta de gestión de este tipo. El objetivo ulterior es acceder a argumentos que sirvan de base en la ayuda y establecimiento de prioridades de gobernanza en las decisiones políticas.

Chapter 1

GENERAL INTRODUCTION

Photo credits: CONABIO, *Acropora Palmata*

1 General Introduction

Coral reefs, often called the tropical rainforests of the oceans, are one of the planet's most beautiful and complex biological ecosystems that support many species through very high rates of biological productivity (Osborn & Briffa, 2004). Although they cover less than 1 % of the earth's surface, they significantly impact the atmosphere, ocean chemistry, diversity, and distribution of biogeographic life (Reaka-Kudla, 1997). Reef systems evolved through time of natural environmental fluctuations, evolving and adapting over hundreds of millions of years, and coping with disturbances, followed by recovery (Buddemeier et al., 2004). However, these are natural features of coral reef history (Buddemeier et al., 2004). The current long-term transformation, decline in abundance, diversity loss, and change in habitat structure (Pandolfi et al., 2003) sends a clear message that the speed and nature of present environmental changes are frequently surpassing the adaptive capability of coral reef organisms and communities to persist (Buddemeier et al., 2004). In addition, given the current effects of global anthropogenic climate change and the chronic local impacts jeopardising coral reefs, it is understandable why several researchers emphasise the current global reef crisis (Bellwood et al., 2004; Graham et al., 2014; Veron et al., 2009).

1.1 Caribbean Coral Reefs

Caribbean coral reefs are considered a biodiverse region where the corals cover ca 26,000 km^2 (Burke & Maidens, 2004) and are usually interconnected with seagrasses and mangroves (Jackson et al., 2014). The primary components of coral reefs are the scleractinian or hard corals, the so-called ecosystem engineers due to their reef-building capacity which generates a three-dimensional (3D) structure providing complex habitats for various associated biota (Jones et al., 1994). The 3D design of coral reefs has evolved over thousands of years by accumulating massive carbonate rock sequences, contributing to the complex reef development (Perry et al., 2013). Until around the 1970s, many Caribbean reefs were dominated mainly by branching corals *Acropora palmata* and *Acropora cervicornis* in the shallow crest and fore-reef areas (Reyes-Bonilla & Jordán-Dahlgren, 2017), and these species were primary providers of the 3D complexity with a cover of up to 50 % in the 1970s and beginning 1980s (Wilkinson et al., 2013). However, in the last four decades, these reefs have experienced significant losses in hard coral cover (Gardner et al., 2003) and 3D structure flattening (Alvarez-Filip, et al., 2009) due to natural and anthropogenic impacts.

1.2 The Mesoamerican reef system

Within the Caribbean region, the Mesoamerican Reef System is of ~ 1000 km length, spanning the coast of Mexico, Belize, Guatemala, and Honduras. It is an almost continuous reef system and a biodiversity hotspot recognised by the World Wildlife Fund (WWF) as one of 200 global priority ecoregions for essential biodiversity protection (Olson & Dinerstein, 2002). This area plays an essential role in the tourism-based economy of adjacent countries, where millions of people rely on them as a revenue source (McField & Kramer, 2006). The region hosts the most extensive and fully developed fringing reefs as well as a large area of mangroves and seagrass beds that are biologically and biogeochemically interconnected, i.e., species movement and energy flow interact and persist under natural, local and global anthropogenic impacts (Moberg & Folke, 1999). Despite a recent increase in marine research across the region, previous research has only been conducted in a few locations and has primarily focused on fish communities and hard corals (Gress et al., 2019).

1.3 The Mexican Caribbean

Mexico is the twelfth largest country in the world with regards of length of coastline and marine surface area (Fraga & Jesus, 2008). The Mexican coastline stretches along different seas along 11.500 km in three different provinces: the Gulf of California and the Pacific Coast, the Gulf of Mexico, and the Caribbean Sea.

The Mexican Caribbean extends ~ 450 km along the Yucatan Peninsula. The reef system borders the coast in a semi-continuous barrier with several geomorphological variations, back reefs, reef crests, and fore reefs, running parallel to the shore. Most of the region's continental and insular beaches are bordered by long fringing reefs and a shallow lagoon that is hundreds of meters wide, separating the reefs from the shore (Jordán-Dahlgren & Rodríguez-Martínez, 2003).

The Mexican Caribbean division for this study is based on coral geomorphological structure and differences in local oceanic circulation, marked by different terrestrial and socioeconomic influences (Rodolfo Rioja-Nieto & Álvarez-Filip, 2018) (Figure 1.1). Still, these reefs are biologically related via the primary current systems' up and downstream movement (Roberts, 1997). Here, we distinguish three geographical subregions along the Mexican Caribbean reef system: northern, centre, and southern, including Cozumel and Banco Chinchorro, as the two insular areas within these subregions (Figure 1.1).

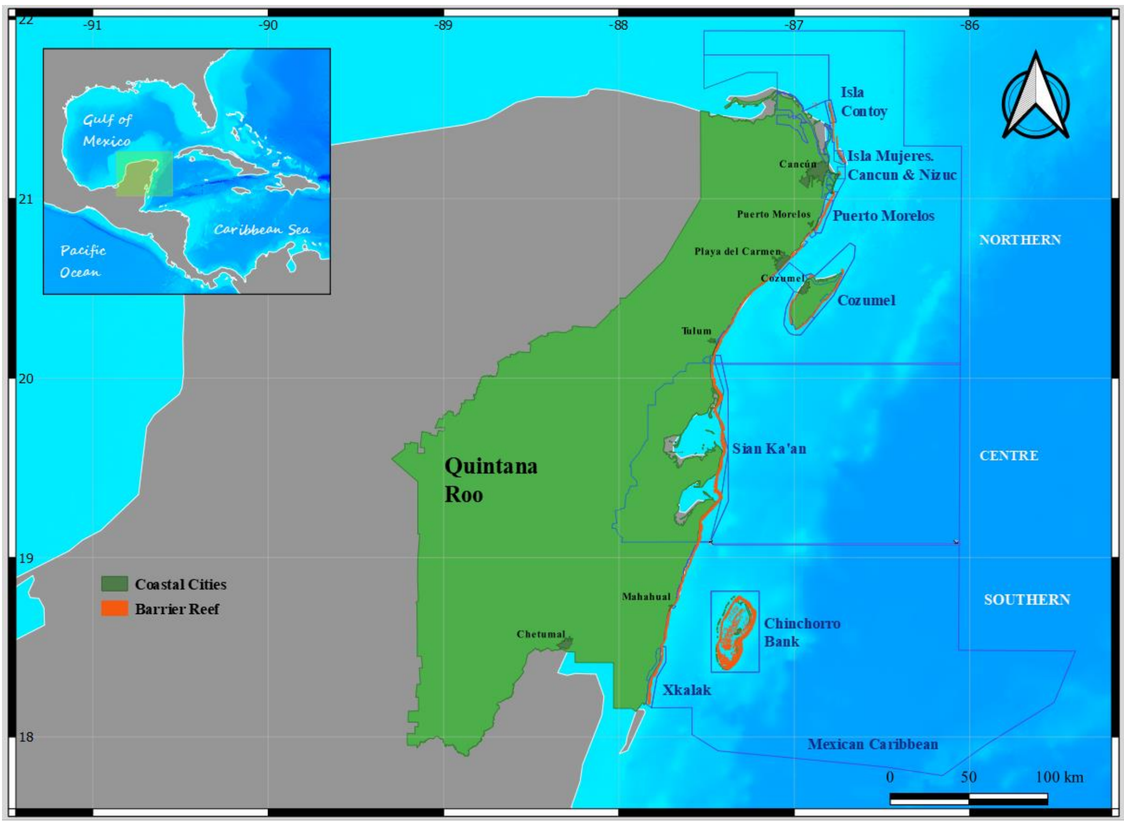

Figure 1.1 *Study area, main cities along the coast of Quintana Roo, the barrier reef, Natural Protected Areas and the three subregions, northern, centre and southern.*

1.3.1 The northern subregion

The northern reef area running from Isla Contoy until the Sian Ka'an Biosphere Reserve's limit is under the most pressure from coastal development because it hosts the biggest touristic hubs. It encompasses shallow fore reefs and reef crests that are overall small in area, once dominated by *A. palmata* (Rodriguez-Martinez et al., 2014). Deep fore reefs are often less developed and smaller. This region includes four NPAs in the category of National Parks: Isla Contoy, Costa Occidental de Isla Mujeres, Punta Cancun y Punta Nizuc, Puerto Morelos and Cozumel.

Cozumel Island

Cozumel is a crucial area due to its geological structure, the vast diversity of species, and their reefs' complexity. The reefs represent unique reef formations and one of the most significant nature reserves (Álvarez del Castillo-Cárdenas et al., 2008). In 1996 the region was designated as a natural protected area: the Cozumel Reefs National Park. The reefs here are among the most valuable and the best conserved within the Mexican Caribbean (Lara-Pulido et al., 2021), even though extensive and potentially unsustainable tourism activities have arisen since the late 1970s. Cozumel hosts several barrier reefs, including the world's most famous reef sites with high structural complexity and biodiversity (Solis-Weiss et al., 2007). In addition to their significance for biology and ecology, these reefs play an essential role in the region's economy and social structure (Alvarez-Filip et al., 2009). Cozumel is one of the primary areas of interest in the region due to three market categories: cruises, scuba diving, and high-performance sports (Palafox-Muñoz and Rubí-González, 2020). These activities pose growing concerns because of their unregulated development and lack of coastal ecosystems management streategies (Solis-Weiss et al., 2007).

1.3.2 The central subregion

The central region is defined by the Biosphere Reserve of Sian Ka'an, a UNESCO heritage place. This region has been protected on land and at sea since 1986 and therefore has experienced minimum local anthropogenic impacts for a long time (Walker et al., 2004). Well-developed reef formations characterise the region on the fringing reef, restricted to sites where the bottom topography has high relief (Jordan-Dahlgren et al., 1994). Unfortunately, despite protection, the reefs here are also heavily degraded, presumably due to higher groundwater discharge of freshwater (Null et al., 2014).

1.3.3 The southern subregion

This area runs from the southern limits of the Sian Ka'an reserve to the border with Belize. Reefs are well established over the southern Mexican Caribbean, where Spurs and grooves dominate the shallow and deep fore reefs (Garza-Perez & Arias-González, 1999). Nonetheless, recent research has identified the Southern region as an expanding hub of mass tourism development without adequate measures for sustainable management (Hirales-Cota et al., 2010). For example, between 2000 and 2006, a pier was constructed to accommodate large cruise ships, which fragmented the coral reef ecosystem with severe biodiversity consequences (Martínez-Rendis et al., 2015). In addition, coastal deforestation to sustain tourism facilities and households is rampant.

Banco Chinchorro

The reef system of Banco Chinchorro is located in the southern subregion. It is the nation's most extensive atoll-like reef complex system and presents an almost continuous reef crest represented by complex spur and groove systems (Loreto et al., 2003). The leeward edge comprises a network of shallow coral reef patches inside the lagoon and a series of small banks and islets. Besides coral reefs, the area is home to seagrass beds, sand beds, and mangroves. This area is not significantly affected by human activity. However, it has been exploited for scuba diving tourism and spiny lobster fishing (de Jesús-Navarrete et al., 2003).

1.3.4 Hydrogeology and Circulation

The Yucatan Peninsula is composed of permeable limestone that allows easy infiltration by water making the groundwater the only available permanent water resource in the region (Perry et al., 2003). Groundwater storage occurs in karst aquifers, which are connected to the surface by sinkholes locally called *Cenotes* (Bauer-Gottwein et al., 2011). Rings of *Cenotes* are a principal channel for groundwater movement in the northern Yucatan Peninsula (Perry et al., 2003). Despite the uniqueness of the region, the high infiltration and rapid flow make aquifers and coastal ecosystems more sensitive to anthropogenic pollutants such as agricultural fertilisers, urban run-off, and untreated sewage from leaking septic systems facilities that directly affect coastal ecosystems (Arandacirerol et al., 2011) (Figure 1.2).

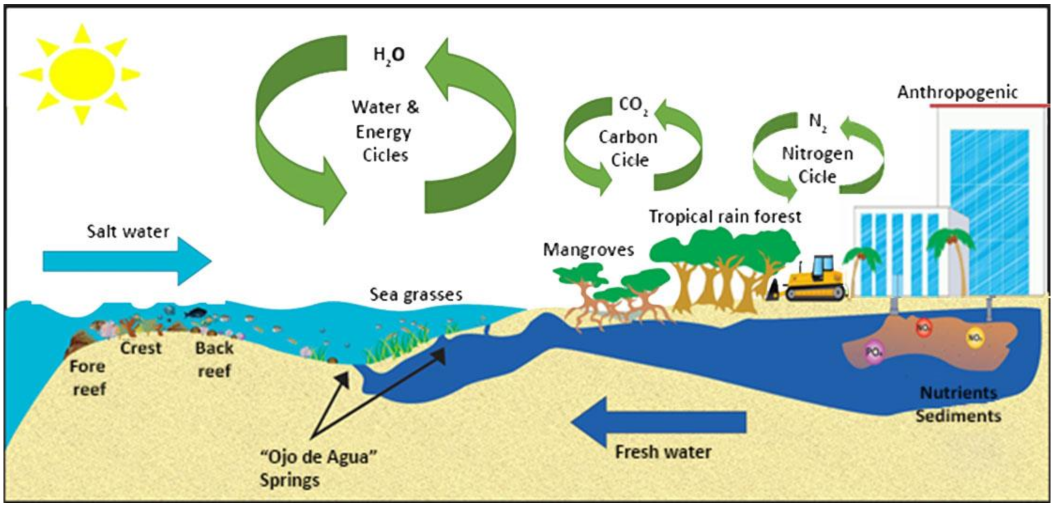

Figure 1.2 *A typical coastal system in the Mexican Caribbean. The main characteristic is karstic lithology, playing a determining role in the ecological dynamics of the system where water infiltrates rapidly into the aquifer generating a complex network of underground caverns, diminishing superficial runoff and surface water bodies. The infiltrated freshwater flows to the coast transporting nutrients and sediments from inland, released to the sea through the so-called "Ojos de Agua", and generating an exchange with seawater similarly. The terrestrial ecosystems are jungles and mangroves with an intrinsic relationship with marine ecosystems, seagrasses and coral reefs.*

Regional-scale fracture zones

The hydrodynamics of coral reefs involve water movement at various scales. The largest scales are characterised by eddies flow produced by island wakes and more minor depth-scale turbulent features influenced by reef topography, and at the smallest scales, those analogous to individual coral colonies (Monismith, 2007). According to the literature, geological factors and current flow directions vary locally along the Mexican Caribbean. For example, in the northern subregion, Cancun and Puerto Morelos are located in the Holbox fracture zone, whereas in the southern subregion, Xcalak is located in the Evaporite region, positioning Sian Ka'an in the centre as a transition zone between these two hydrogeological terrains with a potentially quite different groundwater system (Gondwe et al., 2010). According to observations, the currents in the area have a predominate northeasterly tendency along the shore. The direction of groundwater movement in the Holbox Fracture Zone is mainly to the northeast and the Evaporite to the southeast (Null et al., 2014). A comparison of the current patterns along the Mexican Caribbean coast reveals that the passage of eddies across the region may significantly impact the region's local dynamics (Cetina et al., 2006). These water movements will affect coral reef structure and nutrient cycling.

1.4 Reefs' economic goods and services value

Coral reefs are a cornerstone in sustaining marine biodiversity, providing goods and services crucial to society. Only in the Mesoamerican region, their annual economic revenue from tourism, commercial fishing, and coastal development reaches US$ 6.2 billion (U.N. Environment et al., 2018). The products and services coral reefs provide fall under broader categories since they support other crucial services. For example, provisioning encompasses food security and resources because of commercial and subsistence fishing (Crowder et al., 2008). Reduced coastal erosion (Bruckner, 2002) and climate control via carbon dioxide sequestration provided by the reefs' 3D structural complexity and reef development rate indicated in carbonate budgets are all included in the regulating services (Rioja-Nieto et al., 2019). Tourism and ocean leisure are sociocultural services made more appealing by charismatic species and vibrant reefs (Riera et al., 2016). Finally, supportive services include biogeochemical cycling, the production of white coral sand (Mata-Lara et al., 2018), and the preservation of habitats, including mangroves and seagrass beds.

1.5 Natural disturbances

Reefs may withstand some natural disturbances but are more susceptible to chronic stressors like pollution and poor water quality. Hurricanes are one of the most apparent natural disruptions to coral reefs, affecting reef ecosystems' structure and function. Hurricane intensity determines the extent and severity of damage; the most intense hurricanes immediately affect coral reefs' structural complexity. Evidence suggests that Caribbean reefs had adapted and survived these extreme conditions. They may even, contribute to biological diversity by limiting the dominance of competitors (Blackwood et al., 2011), freeing space for settlement by other species, i.e., branching fragments leading to re-growth (*Acroporids*). Other species with stronger morphologies, i.e., massive corals (*Montastrea*), have proven quite hurricane resistant. Hurricane damage may have longer-lasting effects because the equilibrium between disturbance and recovery appears to be compromised under the current anthropogenic influences (Roff et al., 2015). Recent research demonstrates that the emergence, prevalence, and risks of introduced species and diseases in the Caribbean are caused by anthropogenic factors, such as eutrophication and increases in sea surface temperature (Cramer et al., 2020; Van Woesik & Randall, 2017), thus reducing the resilience of the reefs and altering their community structure and function (Van Woesik & Randall, 2017).

1.6 Anthropogenic stressors

Anthropogenic Climate Change is now regarded as one of the main drivers of change in coral reefs systems (Bruno & Valdivia, 2016; Hughes et al., 2003; Obura, 2005; Yakob & Mumby, 2011) through increased sea surface temperature and extending further to changes in ocean circulation, precipitation, storm patterns, sea level rise, and ocean acidification (Figure 1.3), (Sampayo et al., 2008).

Rising temperatures have caused worldwide bleaching events as a stress response from corals and their symbiotic algae. The mutualistic symbiosis of the coral polyp and the zooxanthellae plays a vital role due to the exchange of nutrient resources, where the zooxanthellae photosynthesis provides the host up to 95 % of its energy requirements used for coral metabolism and calcification (Buchsbaum & Muscatine, 1971). In exchange, the host provides protection and inorganic nutrients (Stat et al., 2006). The disruption of this symbiosis has significant adverse effects on coral physiology and the entire ecosystem. Unusual, elevated sea surface temperatures cause coral stress, where the coral expels their photosynthetic algae, leaving the coral tissue bleached and more vulnerable to disease and death (Hughes et al., 2018). Mass bleaching events are reported worldwide, like in 1998, when 16 % of coral mortality was observed (Hughes & Others, 2017), or in 2005, in the Caribbean region, with coral mortalities up to 80 % (Schutte et al., 2010). Over the past 35 years, thermal stress events have become more frequent, intense, and prolonged. This trend is anticipated to continue when tropical seawater temperatures rise by another 1 to 3 °C

(IPCC, 2014; Hughes et al., 2018). The success of tropical coral reefs is related to the coral-zooxanthellae complex and successful association flourishing in oligotrophic and environmental equilibrated marine habitats. However, further changes in ocean chemistry due to anthropogenic climate change are expected to continue changing the environment in which coral reefs flourish (Graham et al., 2015).

Ocean currents and circulation play an important role in coral reef dynamics because, among other things, they can substantially impact the connectivity between reef systems, which can regulate larval dispersal and other processes (Sammarco et al., 1991). Although there is evidence of significant changes in some locations, it still needs to be determined how ocean currents will continue changing as the planet continues to warm. Likewise, the alteration in rainfall patterns and increased river flood can reduce salinity to levels unsuitable for coral reef environments (Lough, 2008). Storm tracks and atmospheric dynamics are changing, giving way to potentially more frequent tropical cyclones worldwide, affecting reef resilience to cope with such disturbances (Kerry, 2003). Rising sea levels may modify the hydrodynamic and sediment dynamics around coral reefs (Woodroffe & Webster, 2014). Due to the thermal expansion and melting of land-based ice, the sea level has already risen by around 20 cm globally during the previous Century, and the rate of rise appears to have accelerated in recent years by more than 3 mm each year diminishing coral light availability to growth (Meier et al., 2007).

Besides climate change, local human impacts are also becoming chronic stressors. They tend to increase in intensity as urban development escalates. The most apparent are land-based pollution, land-use change, agriculture, overfishing, and tourism. Overfishing leads to rapid deterioration of many species in marine habitats affecting food chains in the whole ecosystem (Hutchings & Reynolds, 2004). According to Méndez-Medina et al. (2015), 70 % of fisheries resources are fully exploited in the Caribbean, with overfishing as the critical factor driving collapse in some (Worm et al., 2009). As a result, many herbivores have been eliminated, reducing grazing and increasing algae growth with eventual subsequent phase shifts on many coral reefs (McManus & Polsenberg, 2004).

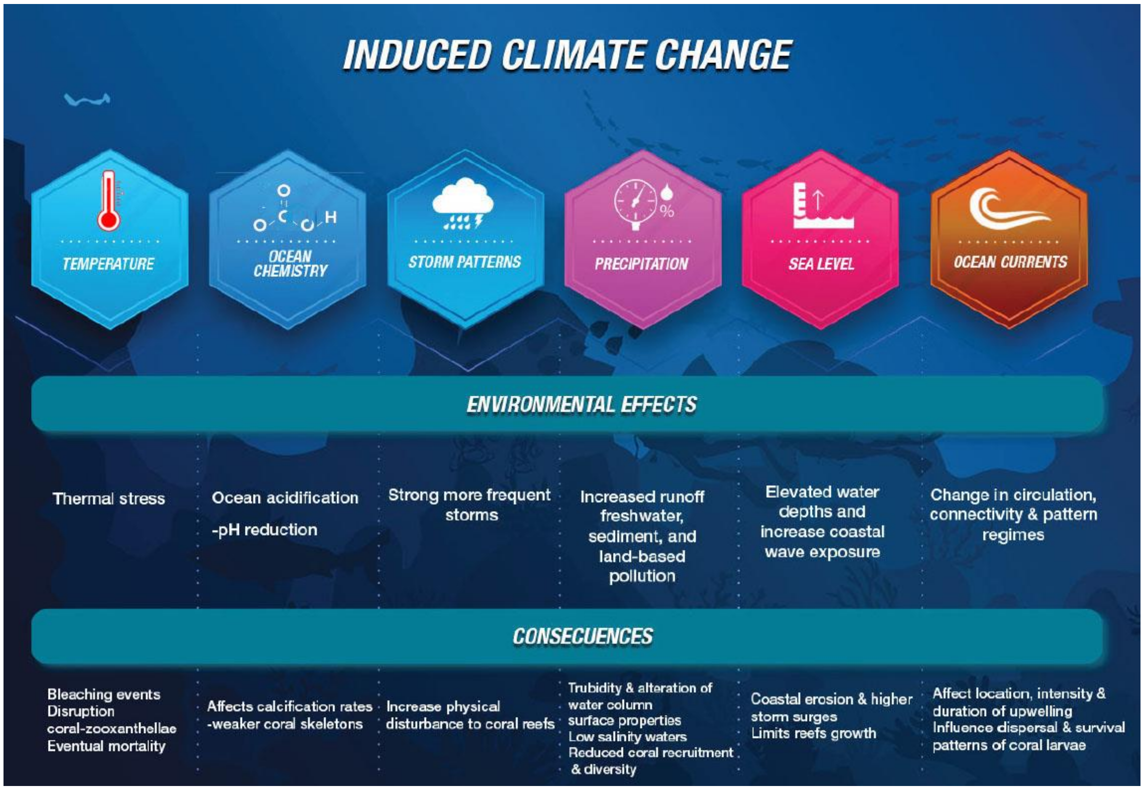

Figure 1.3 *Effects of anthropogenic-induced climate change on coral reefs.*

The additional effects of local anthropisation, linked mainly to the tourism industry, increased nutrients from agriculture, aquaculture practices, and overfishing, are considered the main force of change in coastal areas (Arias-González et al., 2011; Casey et al., 2010; De et al., 2023). The growing tourism has affected the water quality by several factors. Sedimentation, caused by the clearance of coastal landscape ecosystems, e.g. coastal wetlands, alters light availability in the generally oligotrophic environments where coral reefs best develop. As a result, phosphorous and nitrogen from fertilisers and sewage run-off enter the water column, leading to a eutrophication process, which accelerates overgrowth by algae and oxygen depletion (Pastorok & Bilyard, 1985). Moreover, sewage discharge and anchoring from vessels not only pollute the water with cargo and fuel spills, leaching of toxins (Ardisson et al., 2011) but also introduce exotic or non-indigenous species (i.e., red lionfish, *Pterois volitans*, which can modify the structure and composition of biotic communities, Mazzotti et al., 2005). Agricultural fields also induce run-off of sediment, nutrients and toxic substances (i.e., pesticide pollutants).

Nowadays, coral reefs are subject to multiple simultaneous global and local disturbances. When several stressors are present at once, their effects may be additive or can interact (Crain et al., 2008). Interactions can happen when two stressors interrelate directly or when the appearance of one stressor changes how an organism reacts to another (Bozec & Mumby, 2015). The likelihood of synergistic effects increases when stressors act via dependent and alternative pathways. Exposure to many stressors poses a serious concern since organisms can only withstand a certain level, possibly balancing their sensitivity and resilience to multiple stressors affecting the whole system (Fong et al., 2018). All the mentioned factors (threats) have already affected many coral reefs. Some reefs have been destroyed, while in others, significant changes in reef structure occur, impacting the variety of goods and services for society (Rogers & Miller, 2016).

1.7 Regional phase-shifts

Historically, before colonisation of the Caribbean region, there has been an anthropogenic influence on land and the sea. Fish populations were the first impacted (Newman et al., 2006). By the 1960s, some Caribbean regions had already shown signs of exhaustion, with a fish biomass reduction of up to 80 % (Hughes, 1994). Overfishing impacted the reef systems by diminishing the capacity to recover due to the decline of herbivores (Hughes & Connell, 1999), which reduces macroalgae growth control (Mumby, 2006). Furthermore, removal of dead coral (bioeroders) and grazing on turf algae are also affected (Green & Bellwood, 2009). Consequently, the reefs heavily depended on invertebrate herbivores to graze the macroalgae. Nevertheless, in the 1980s, the region suffered a massive population collapse (94-99 %) of one of the primary grazers, the long-spined sea urchin (*Diadema antillarium*), which added further to coral reef degradation (Lessios, 1988). This species continues to be suppressed (Lessios, 2015), and in the subsequent years, filamentous turf algae and macroalgae began to replace hard corals and crustose coralline algae as predominant groups in many reefs (Dubinsky & Stambler, 2011). At about the same time, an epizootic event, the white band disease, attacked the acroporids (*A. palmata* and *A. cervicornis*), leading to their partial disappearance, which had several consequences. First, erosion and bioerosion rates increased. Second, the replacement of complex coral species with the so-called weedy species occurred (Darling et al., 2012). Third, the reef area lost spatial heterogeneity; fourth, an imminent biodiversity loss occurred (Zubillaga et al., 2008). An additional increase in eutrophication, primarily through land-based pollution (Renfro & Chadwick, 2017), created conditions that enhanced the vulnerability of corals shifting to algal-dominated states in several Caribbean reef locations (Knowlton, 1992).

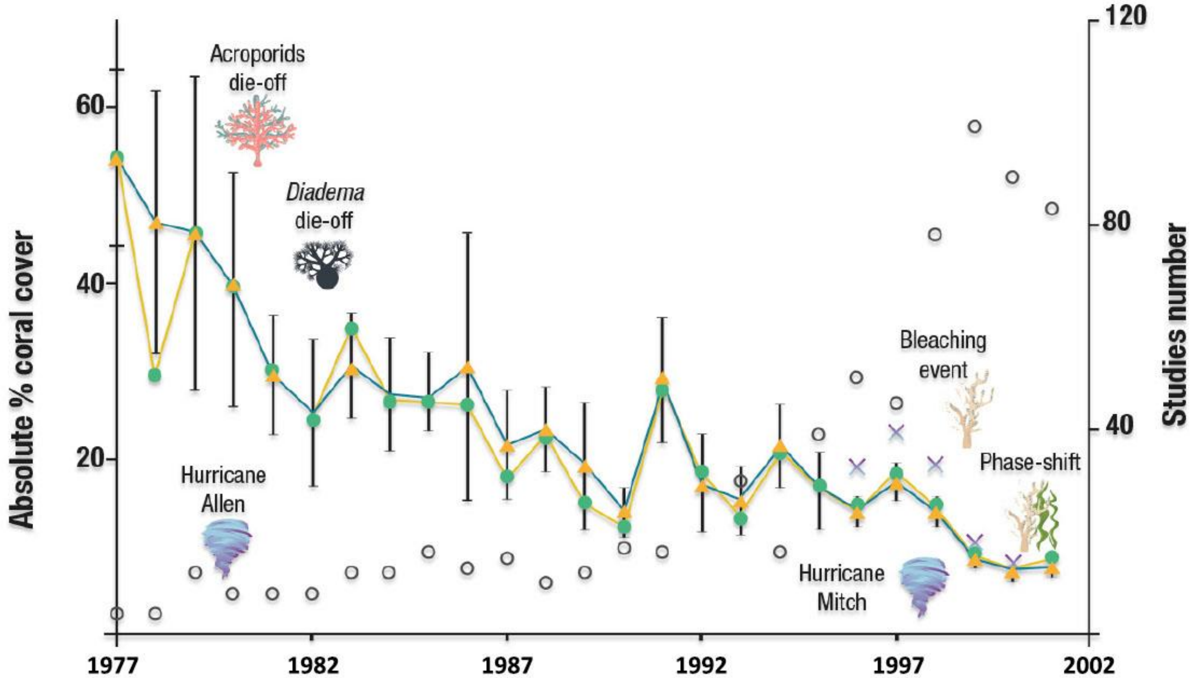

Figure 1.4 *Recent history of annual coral cover percentage in the Caribbean region. Green dots represent the absolute coral cover percentage from 1977 to 2000. Yellow triangles represent the annual coral cover estimates with 95 % bootstrap intervals. White dots represent the number of studies each year. Furthermore, the main historical ecological events in the Caribbean region are represented as the main hurricanes impacting the region, Acroporids and Diadema die-off, bleaching event, and regional phase-shift. Modified from Gardner et al. (2003).*

Figure 1.4 shows the hard coral cover decline for the wider Caribbean region ca ~ 80 % between 1975 and 2000 (Gardner et al., 2003); in the 2000s, a regional phase shift towards algae dominance is evident (Côté et al., 2005). Coral-to-algal dominance as of the most common transition in coral reefs (Alvarez-Filip et al., 2013); however, depending on the elements and mechanisms causing the change, soft coral and sponge domination could also occur, generating alternative stable states (Norström et al., 2009). For the Caribbean reefs, coral-to-algal phase shifts have already caused losses in reef accretion and structural complexity (Suchley et al., 2016), thus affecting its resilience (Mumby, 2017). Although there has been much discussion about whether algae may supplant coral, it is widely acknowledged that algae opportunistically occupy dead coral reef substrates, inhibiting coral recruitment and recovery in disturbed areas (Hughes et al., 2007). Significant declines in hard coral had affected ecosystem function, affecting their ability to return to a coral-dominated state.

There is a lack of longitudinal studies after 2000 in the Western Caribbean reefs. For the Mexican Caribbean reefs, phase shifts have been observed in some locations, either in the northern (Carriquiry et al., 2013) or the southern subregions (Martínez-Rendis et al., 2015). If these reefs presented alternative stable benthic states characterised by the different array of ecosystem processes, functions, and feedback mechanisms were not reported. Furthermore, information is still needed regarding any potential phase shift from coral to algae domination for the whole Mexican Caribbean region and the possible causes.

1.8 Problematic Trends in Mexican Caribbean Reefs

As in the rest of the world, the pressure on Mexican Caribbean reef ecosystems continues to rise and jeopardise the range of ecosystem services they provide to society. A pivotal issue in maintaining these vital services will be ensuring ecosystem resilience and health by attenuating current anthropogenic impacts. The biological effects of the many wastewater discharge components, including freshwater, nutrients (Wear & Vega Thurber, 2015), pathogens, and sunscreens (McCoshum et al., 2016), are harmful to corals and can cause bleaching, disease, and mortality (Vega Thurber et al., 2014). Further, the unique calcareous soil in the region allows an almost immediate wastewater effluent penetration in the aquifer system (Perry et al., 2009), reaching the sea despite inadequate or no treatment (Hernández-Terrones et al., 2015). The stony coral tissue loss disease is a novel contagious disease that has rapidly impacted the reefs in the whole region (Alvarez-Filip et al., 2019). In addition, since 2014, blooms of *Sargassum spp*. (*S. natans* and *S. fluitans*) further impair water quality and increase contamination (Salter et al., 2020). The degradation of these *Sargassum* mats not only releases nutrients and consumes oxygen but also decreases light availability on the seafloor, thereby affecting ecosystem functions such as benthic photosynthesis, degrading the ecosystem of the once-oligotrophic coral reefs (Wang et al., 2018).

Despite coral depletion in the Mexican Caribbean, tourism continues to be a flourishing economic development opportunity (Gil et al., 2015). It has developed tremendously since the mid-1970s (Spalding et al., 2001) and has been identified as an acute stressor in Quintana Roo (Molina et al., 2001). The gross income for the state in 2016 was $USD 2,992.781 (Sedetur, 2016), reflected in the hotel occupancy, which increased from 40 % in 2000 (Palafox-Muñoz, 2014) to 82 % in 2016 (Sedetur, 2016). As a result, the coastal vegetation is being replaced with hotels, residential areas and urban constructions (Figueroa-Zavala et al., 2015). For instance, mangrove coverage in Quintana Roo has declined by 25 % since 1985 (Hirales-Cota et al., 2010).

In a regional context, the Healthy Reefs for Healthy People initiative (HRI) is currently responsible for tracking the health of the Mesoamerican Reef System. This initiative enhances the current knowledge of the region's reef health by monitoring benthic coverage, fish herbivores, and sea urchin biomass with the AGRRA protocol every two years since 2003. In the Mexican Caribbean, coral reef monitoring efforts are generally conducted by scientists from universities, research centres, NGOs, and national institutions such as CONANP (the National Commission of Natural Protected Areas) and, more recently, CONABIO (National Commission for Knowledge and Use of Biodiversity). These inspections enhance the existing knowledge of the Mexican Caribbean reefs. Thus far, reef degradation is becoming more evident in the northern region along the Cancun-Tulum touristic corridor in areas such as Akumal and Puerto Morelos, as well as the offshore island of Cozumel (Spalding et al. 2001). In recent decades the Central (Sian Ka'an) and Mayan Zone (Mahahual-Xcalak) are also witnessing the consequences of reef degradation (Hirales-Cota et al. 2010).

Overall, the Mexican Caribbean reefs continue to degrade despite ecological monitoring, research efforts, and, for some areas, active management as natural protected areas since the early 1980s. Still, all this information permitted us to understand this region's history of reef change roughly. Active monitoring integrated into sustainable management strategies still needs to be enhanced. Furthermore, crucial regional information is needed:

1. A quantitative long-term spatiotemporal analysis of the Mexican Caribbean reefs' condition still needs to be improved. It is necessary to set a detailed knowledge baseline of its ecological history in a regional context, e.g., coral and macroalgae cover changes. Hard coral and macroalgae development trends are essential to understanding these reefs' current status and identifying changing patterns.
2. There is limited knowledge of global and local stressors impacting the Mexican Caribbean coral reef system, and most researchers have concentrated on how the reef reacts to individual causes rather than the interactions between them. Thus, in the face of increasing human impacts such as coastal anthropisation, reduced water quality, and effects from anthropogenic climate change, it is crucial to investigate the main drivers of coral reef impairment and their relative and synergistic impact on the Mexican Caribbean barrier reef.
3. Suitable scientific information is required to take action and slow down the reef's deterioration generating a science-based sustainable managing strategy to understand and manage anthropogenic impacts on coral reef systems.

Therefore, it is necessary to get an overview of the current status of the reefs and the dynamics that have occurred therein. Identifying the main stressors is critical to attempt to control, at least at the local level, the main drivers of change. Finally, it is mandatory to integrate ecological and social systems into a framework as a management tool at different multi-temporal scales with enough flexibility to address unpredictable feedback between systems components in the reef complex. The insights gained from the current investigation and other scientific efforts can be used to propose a new holistic approach to an integrated management strategy for the coral reefs, with the goal of ecological preservation for long-term socio-ecological sustainability. In the following subsection, this thesis' research questions are presented.

1.9 Research questions

1. How has the benthic composition changed in Mexican Caribbean (MC) reefs over the last four decades?
    a. How has hard-coral and macroalgae cover changed in the Mexican Caribbean?
    b. Are there spatial and temporal differences in change (1978-2016)?

2. What are the leading local and global drivers of change?
    a. Is the MC similarly affected by local and global factors?
    b. Are there spatial differences?

3. How to generate a conceptual framework for an integrated and sustainable management strategy?
    a. What elements need a well-coordinated future reef sustainable management tool?
    b. What could well-coordinated, future reef monitoring look like?

1.10 Chapters outline

This thesis combined remote sensing, statistical, and theoretical approaches to answer the main research questions. A broad introduction (chapter 1), three chapters presenting the PhD's research (chapters 2-4), and a general discussion (chapter 5) make up this thesis. Chapters 2-4 have already been published or are in the process of being published as standalone research pieces in international peer-reviewed journals. The second chapter of this work summarises the state of knowledge about the current status of coral reefs in the Mexican Caribbean, particularly on spatiotemporal changes. Then, the third chapter links spatiotemporal changes to critical environmental parameters to detect and evaluate causal relationships. In the fourth chapter, a proposal of a well-coordinated and sustainable management tool is proposed.

Chapter 2

Spatiotemporal benthic changes of coral and macroalgae cover

Chapter 2 explored benthic change patterns in Mexican Caribbean reefs through meta-analysis between 1978 and 2016, including 125 coral reef sites. Findings revealed that the total cover of hard coral declined by 12 % from 1978 to 2004. Then, a subtle increase of 5 % by 2016 was recorded after the 2005 mass bleaching event and hurricane impacts, indicating some coral recovery. Still, in 2016, more than 80 % of studied reefs were dominated by macroalgae, while hard corals dominated only 15 %; in contrast with 1978, when hard corals dominated all reef sites surveyed. This study is among the first within the Caribbean region to report local recovery in coral cover, while other Caribbean reefs have failed to recover. Most Mexican coral reefs are now no longer dominated by hard corals. To prevent further reef degradation, viable and reliable conservation alternatives are required.

This work was published in the journal "*Scientific Reports.*"

> **Contreras-Silva, A. I.**, Tilstra, A., Migani, V., Thiel, A., Pérez-Cervantes, E., Estrada-Saldívar, N., Elias-Ilosvay, X., Mott, C., Alvarez-Filip, L., & Wild, C. (2020). *A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean.* Scientific Reports.

Chapter 3

Main global and local stressors impacting benthic change

Chapter 3 explored the different global and local stressors generating change in Mexican Caribbean reefs. This chapter is divided into two individual publications. In the first publication, we analyse the potential drivers of reef change after the 2005 bleaching event and the impact of hurricanes Emily and Wilma. Following the methodology of Chapter 2, we further used random-effects meta-analysis to examine the possible change-causing factors on hard coral and macroalgae benthic development in the Mexican Caribbean between 2005 and 2016. Thus, we examined the temporal variations in hard coral and macroalgae cover as a function of sea surface temperature (SST), chlorophyll-*a* water concentration, coastal human population development, reef proximity to shore, and geographic location. Our findings support the partial coral rebound following the huge coral mortality event in the Caribbean in 2005 and show that algae are rapidly establishing themselves in the area. Only SST showed a negative correlation with changes in coral cover. Therefore, in a second publication, we conducted a cumulative impact assessment on hard-coral and macroalgae benthic communities exposed to multiple stressors (thermal stress, nutrient inflow, sedimentation, hurricane impact, and anthropisation), using an extensive collection of remote sensing data to examine the effects on the reef ecosystem further. Our findings also reveal that coral cover change is highly influenced by thermal stress expressed in bleaching susceptibility followed by anthropogenic activities, including the growing pressure from touristic hubs. The water quality predictors affected only the macroalgae cover, mainly the particulate organic carbon (used as a proxy for sedimentation and nutrients). The relationship between chlorophyll-*a* and sea surface temperature had the sole negative impact on macroalgae. Our studies demonstrate that local pressures like nutrient and suspended sediment increases transported by coastal development coexist with repercussions of global warming on coral reefs. Both studies document a partial recovery of coral reefs but also show that the algal development rate is significantly quicker than coral recovery. We conclude that the cumulative effects of local and global stressors seriously threaten the future of the coral reefs in the Mexican Caribbean.

Two publications were generated from this chapter. The first publication of this chapter is in the review process in the journal "*Ecological Applications.*"

> **Contreras-Silva, A. I.**, Navarro-Espinoza, E., Migani, V., Valderrama-Landeros, L., Velázquez-Salazar, S., Pardo-Urrutia, F., Tapia-Silva, O., Reuter, H. & Alvarez-Filip, L. (2023). *Effects of coastal anthropisation, hurricane impacts, and bleaching susceptibility in Western Caribbean coral reefs*.

The second was published in the journal "*Diversity.*"

> Elías Ilosvay, X., **Contreras-Silva, A. I.**, Alvarez-Filip, L., & Wild, C. (2020). *Coral Reef Recovery in the Mexican Caribbean after 2005 Mass Coral Mortality—Potential Drivers*. Diversity, 1–16.

Chapter 4

Conceptual framework for a reef management strategy

The Mexican Caribbean forms part of the Mesoamerican Reef system, a biodiversity hotspot and economically vital area for the region. In the Mexican Caribbean, 78 % of the population resides within 10 kilometres of the shore. The local economy, coastal livelihoods, and cultural customs are based on coral-based tourism. Since 1970, the tourist sector has proliferated, transforming the Yucatan region, where Cancun is located, from a small, isolated agricultural area to a prominent, international tourist destination in just forty years. With over two million visitors arriving in Cancun annually, whether by land or cruise ship, the landscape underwent significant change. The construction of airports, roads, resorts, and golf camps led to extensive deforestation of coastal vegetation and the filling of wetland areas. Despite federal ecosystems' protection as Natural Protected Areas and active monitoring efforts, the coral reefs continue degrading, which raises the question of why and how protection and management may be enhanced. Therefore, we aimed to develop a conceptual framework for an integrated management strategy. It addresses reversing unsustainable economic and social trends through effective science communication and enhances the understanding of the unique and essential services that coral reef ecosystems in the Mexican Caribbean provide. The ultimate goal is to gain access to justifications that act as a foundation for aiding and establishing priorities for governance in political decisions. So, we suggested geomatics as a transdisciplinary and integrative science that can generate solutions for complex systems like coral reefs. Cybercartographic atlases are artefacts that fall under this category and provide a valuable way to develop a conceptual framework for such a management tool. First, we define the ecological and social as independent subsystems for the Mexican Caribbean. Next, we constructed the conceptual framework's systemic components (ecological and social). Finally, we build on the combined strategy for coral reef management integrated into a cybercartographic atlas framework.

This work entitled: A cybercartographic atlas framework as an innovative and integrative tool for the sustainable management of Mexican Caribbean Coral Reefs is currently in preparation for "*Conservation Letters.*"

Contreras-Silva, **A. I.,** Rodriguez-Aldabe, Y., Alvarez-Filip, L. and Reuter H. (2023). *A conceptual framework for an integrated and sustainable management strategy in Mexican Caribbean Reefs.*

Chapter 5

Finally, Chapter 5 discusses the overall research findings of this research. The research is summarised by comparing it to the state-of-the-art background covered in the general introduction. Lastly, an overview is presented of the main findings and advancements for coral reef science and future developments that this thesis proposes.

1.11 Declaration of author contribution

Table 1.1 *PhD contributions to each research-based chapter's manuscripts*

	PhD student contribution (%)			
	Chapter 2	Chapter 3		Chapter 4
Activity	Paper 1	Paper 2	Paper 3	Paper 4
Concept & design	50	40	80	80
Acquisition of data	20	30	80	---
Data analysis and interpretation	80	50	80	---
Figures & Tables preparation	80	20	70	100
Drafting the manuscript	100	50	100	100

The PhD student entirely generated Chapter 1 and Chapter 5.

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Chapter 2

SPATIOTEMPORAL BENTHIC CHANGES OF CORAL AND MACROALGAE COVER

Photo credits right: CONABIO, *Orbicella Annularis*. Left: GoogleEarth.

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2 A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean

2.1 Abstract

Since the 1970s, the hard coral cover of coral reefs in the greater Caribbean has decreased by about 80 %. However, spatiotemporal assessments for sub-regions still need to be included. We used a meta-analysis of 125 coral reef sites between 1978 and 2016 to investigate the benthic change trends in the Mexican Caribbean reefs. Results showed that whereas macroalgae cover grew to 30 % in 2016, hard coral cover declined from 26 % in the 1970s to 16 % in 2016. High spatiotemporal variability was seen in both groups. The hard coral cover decreased by 12 % from 1978 to 2004 but increased by 5 % from 2005 to 2016, indicating some coral regeneration following the 2005 mass bleaching event and hurricane impacts. Only 15 % of the examined reefs were dominated by hard corals in 2016, compared to more than 80 % by macroalgae. This contrasts with 1978, when hard corals dominated all surveyed reef sites. Compared to other Caribbean reefs, which have not recovered, this study is among the first to document local coral cover recovery in the Caribbean. Hard corals no longer dominate the majority of Mexican Caribbean coral reefs. To prevent further degradation is mandatory to identify the leading global and local stressors impacting the reefs to propose alternatives to sustainable conservation alternatives.

2.2 Introduction

In a time when humans have a significant and lasting impact on nature, monitoring changes in coral reef ecosystems is crucial. Current anthropogenic climate change (Carilli et al., 2009) and local stressors (including overfishing, pollution, and sedimentation from coastal development) place coral reefs as the most endangered ecosystems on Earth (Bellwood et al., 2004). Rapid reversals in their health have been reported globally (Mercado-Molina et al., 2015), including reefs from the Caribbean region, where declines of the live hard coral cover of ~ 80 % between 1975 and 2000 have been documented (Côté et al., 2005; Gardner et al., 2003; Schutte et al., 2010). In the late 1970s, entire populations of reef-building coral species (i.e. *Acropora palmata* and *Acropora cervicornis*) collapsed due to the white-band disease (Aronson & Precht, 2001). Furthermore, the mass mortality of black sea urchins (*Diadema antillarum*), overfishing, and eutrophication (Hughes, 1994) have resulted in a proliferation of more opportunistic, fast-growing organisms such as (macro)algae that outcompete reef-building corals (Aronson & Precht, 2006; Dubinsky & Stambler, 2010; Hughes, 1994; Suchley et al., 2016). As a result, many Caribbean benthic coral reef communities changed drastically from low coral cover to persistent states of high cover (macro)algae in the process of so-called phase shifts (Aronson et al., 2004; Hughes & Tanner, 2000; McManus & Polsenberg, 2004; Roff & Mumby, 2012; Suchley et al., 2016). Efforts to mitigate or reverse phase shifts and reef degradation in the Caribbean include the development of new coral reef monitoring and managing strategies (Flower et al., 2017; Ladd & Collado-Vides, 2013; Melbourne-Thomas et al., 2011).

Monitoring efforts of Caribbean reefs began in the late 1970s at various reef locations for short durations (Jackson et al., 2012). It was until 1980 that the coral reef monitoring programs first began for some countries due to the evident reef degradation and increasing threats (Jackson et al., 2012). In the Mesoamerican Reef System (MAR), the monitoring officially began in 2005 with the Healthy Reefs for Healthy People Initiative (Rioja-Nieto & Álvarez-Filip, 2019). The World Wildlife Fund (WWF) recognises the MARs as one of 200 global priority ecoregions with essential biodiversity protection (Olson & Dinerstein, 2002). This ecoregion within the Caribbean spans 1600 km along Mexico, Guatemala, Belize, and Honduras coastlands and has experienced rapid changes within the last decades (Almada-Villela et al., 2002; Wilkinson, 2004). In the Mexican part, in particular, in Cozumel and the northern part of Quintana Roo, the 2005 bleaching event and subsequent hurricane impacts affected more than 50 % of coral colonies (Álvarez-Filip et al., 2009; Jackson et al., 2012). In 2007, hurricane Dean (category-5) hit the Southern Quintana Roo reefs affecting Mahahual and Chinchorro Bank (Jackson et al., 2012). In the following years, i.e., 2009-2011 and 2014-2017, Mexican Caribbean (MC) coral reefs were less affected by increasing sea surface temperatures (SST) (NOAA, 2018) and hurricane impacts (NOAA, 2019). Nonetheless, the rapid increases in macroalgae and the growing local threats diminish the capacity of the coral reefs to recover (Suchley et al., 2016).

Reefs in the MC have been threatened since the establishment of Cancun as an international tourist destination in the 1970s (Padilla, 2015). Tourism industry rapidly expanded through the region and has impacted reefs and other ecosystems through the construction of piers to receive massive tourist cruise ships (Martínez-Rendis et al., 2016), the clearing of vegetation to construct roads, houses, restaurants, and hotels (Figueroa-Zavala et al., 2015; Hirales-Cota et al., 2010), and recreational activities. Recreational activities provide the leading services for the tourism industry (Reyes-Bonilla & Jordán-Dahlgren, 2017). However, they also pose potential threats to reef communities, e.g. breakage of corals by divers and snorkelers, trampling, taking fish for aquaria, and oil contamination due to shipping, among others (Gil et al., 2015). Indeed, there are additional threats to the MC coral communities, such as invading species (e.g. lionfish, *Pterois volitans*) (Schofield, 2009) and the recent large floating mats of Atlantic *Sargassum spp*. reaching Western Caribbean coasts (Putman et al., 2018). The disintegration of these *Sargassum* mats releases nutrients and consumes oxygen, and decreases light availability at the seafloor, thereby affecting ecosystem functions such as benthic photosynthesis (Wang et al., 2018). All these threats impacted MC reefs, but their extent is still unknown.

The current degradation of MC reefs makes it necessary to set a detailed knowledge baseline of its ecological history in a regional context, e.g., changes in coral and macroalgal cover. Even though monitoring and research efforts have been regularly conducted in the MC since the early 1980s, this only permitted us to roughly understand the history of change for this region (Rioja-Nieto & Álvarez-Filip, 2019). Despite existing efforts, a quantitative long-term spatiotemporal analysis of the condition of MC reefs is still lacking. Hard coral and macroalgae development trends are essential to understand these reefs' current status and identifying patterns of occurred changes. In the last decade, meta-analysis has been a widely used tool applied in coral reef studies since it systematically combines a wide range of information, including monitoring and experimental field exploration, to provide an integrative view across time (Arnqvist & Wooster, 1995). Here, a meta-analysis of data from monitoring programs, peer-reviewed scientific publications, and grey literature was performed to describe the large-scale and long-term changes in MC coral reefs. This study aims to answer the following questions: 1) What extent does hard coral and macroalgae (calcareous and fleshy) benthic cover change in the MC over the last 38 years? 2) Are there temporal and spatial patterns of change?

2.3 Methods

2.3.1 Study area

Reefs in the MC occur along the coast of the state of Quintana Roo (Figure 2.1) and consist of various reef formations in terms of location, type, and degree of development (Jordan-Dahlgren & Rodriguez-Martinez, 2003; Rioja-Nieto & Álvarez-Filip, 2019). The MC can be divided into five core regions, i.e. Northern, Center, Southern, Cozumel, and Banco Chinchorro, each with particular characteristics and features (Rioja-Nieto & Álvarez-Filip, 2019).

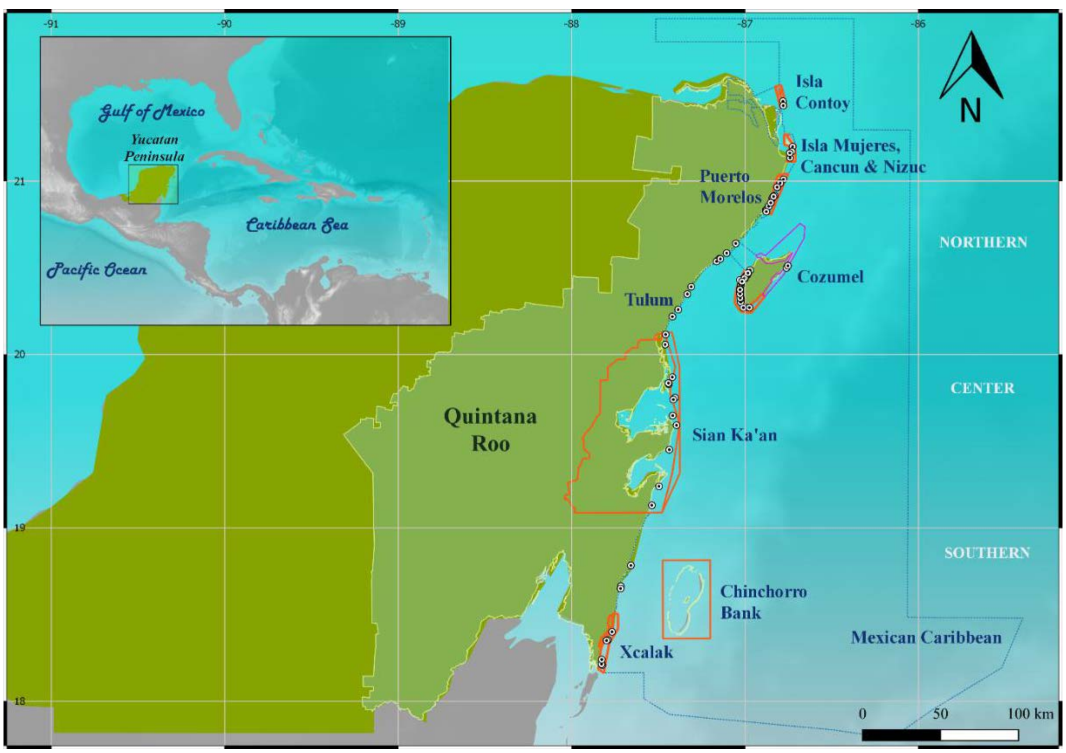

Figure 2.1 *Map of the study area. Polygons in orange and purple represent the MPAs in the region. The Mexican Caribbean Biosphere Reserve was decreed in 2016, after this project period of analysis, and therefore is represented with a blue dotted line. Dots represent the monitoring sites.*

The Northern region spans from Isla Contoy to Tulum. The forereef zones in this area are generally flat and gently sloped (Rodríguez-Zaragoza & Arias-González, 2015). It includes three MPAs: Isla Contoy, Puerto Morelos, Costa Occidental de Isla Mujeres, Punta Cancun & Punta Nizuc. Cozumel region is an island also located in the North in front of the coastline of the Yucatan Peninsula (Figure 2.1). The Center region is part of the Sian Ka'an Biosphere Reserve (Figure 2.1), one of Mexico's largest protected areas and a UNESCO world heritage site. The Southern region has ridges with a clear zonation of reef crest, front, slope, and terrace. This area also encompasses Arrecifes de Xcalak National Park (Figure 2.1). The last region is Banco Chinchorro atoll, located in the Southern part (Figure 2.1). However, due to a lack of monitoring information, it was omitted from the analysis. The MC region has an extensive network of MPAs. By 2016, nearly all the coral reefs have a protection status with the creation of the Mexican Caribbean Biosphere Reserve (Rioja-Nieto & Álvarez-Filip, 2019).

2.3.2 Data selection and extraction

The hard coral and macroalgae cover databases were collated from various sources, including published literature, research protocols, grey literature, and monitoring programs (Appendix B Table S2.3 and S2.4). For this study, the category of macroalgae included both fleshy and calcareous macroalgae; since many of the used sources did not report separate values for these categories and combined them into one single group. Literature searches were conducted using standard search engines (e.g. ISI Web of Science and Google Scholar) using specific terms (e.g., coral reef AND hard*coral* OR coral* AND algae* OR macroalgae* AND benthic* AND Mexico* AND Mesoamerican*reef* AND Mexican*Caribbean*). All the information was curated and systemised and is now included in the Caribbean Reef Information System (CRIS) from the Biodiversity and Reef Conservation, UNAM. The criteria for the potential inclusion of the study were as follows: (i) percentage cover of live hard coral and/or macroalgae; (ii) replicated measurements over time (not necessarily consecutive); (iii) if the authors use the exact location of survey (iv) the year of survey; (v) reports of the number and/or length of transects covered; and/or (vi) other variables e.g. water depth and reef zonation reported. If the studies reported monitoring and multi-temporal information, all sites defined in each study were used separately. Care was taken not to double-count coverage published in more than one study. If cover data were presented in graphical form, GetData (Wiebe et al., 2008) was used to extract the per cent cover. The raw monitoring information contributed a large number of sites to the dataset. The Northern subregion was sampled far more exhaustively than others (e.g. Center and Southern regions). Therefore, not all selected reef sites were surveyed in all years, although each was visited at least two times. The monitoring database included 2,458 coral cover surveys on 125 reef sites between 1978 and 2016. Macroalgae cover was measured in 2391 surveys on 94 reef sites between 1989 and 2016. From all the included studies, 32 % used the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol to measure the benthic cover, 36 % used the Synoptic Monitoring for the Mesoamerican Reef System (SAM) protocol, and 32 % did not mention the use of a monitoring protocol but the use of other sampling methodologies (mainly Linear Intercept Transect). Both protocols focus on specific monitoring sites; one of the main differences is the methodology to monitor benthic organisms. SAM protocol uses point intercept methodology with 30 m length transects, whereas AGRRA protocol uses line intercept methodology with 10 m length transect (Hill & Wilkinson, 2004; Obura, 2014). The majority of data analysed in this study were obtained during the same season (May to October) following recommendations of the monitoring protocols (e.g. AGRAA, SAM).

2.3.3 Data analysis

A regression analysis was performed to test the effect of time on overall yearly means of coral and macroalgae cover. Meta-analysis was used to analyse the temporal change in macroalgae and coral cover and how that change differed in the Northern, Center, and Southern regions of the MC.

Regression analysis

The mean cover for coral and macroalgae for each year was calculated, pulling all the sub-regions together. Since the cover of the coral and the macroalgae were not normally distributed, the data were tested using a Generalised Linear Model (GLM) with Gamma error distribution and log link function, which best fit these data.

Meta-analysis

Meta-analysis is one method of research synthesis supported by statistical procedures to merge the findings of individual primary studies (Viechtbauer, 2010). The fundamental statistical parameter is the ‘effect size’. It standardises the outcomes of different studies (Cooper et al., 2009a) such that different measures can be combined and compared initially. There are different effect size methods to choose from, depending on the data availability from primary studies (Cooper et al., 2009b; Koricheva et al., 2013). Meta-analysis was used to detect overall changes at different spatial and temporal scales and sub-grouped by the three regions. Percentages of hard coral and macroalgae coverage for MC reefs were extracted from all available data that met the inclusion criteria. The random-effects meta-analysis was conducted in R using the “metaphor” package (Viechtbauer, 2010). A random-effects model was used to represent the probability that any particular effect size is the best-approximating model to detect changes in coral reef ecosystems. The relative annual rate of change (ARC) was the effect size used to measure the change in percentage cover for both hard coral and macroalgae percentage over time. Because of the principle of compounding, the annual rate of change is calculated over a period. In this study, the ARC is implemented by comparing the percentage cover in the same reef site at two different times to obtain an average mean for the period of interest, and it is computed as follows:

$$\mathbf{ARC= (LogEnd\text{-}LogStart)/a} \qquad (1)$$

Where Start and End are the percentages of hard coral cover or macroalgae at the start and end of the time series, respectively, a is the time in years elapsed between both measures (Alvarez-Filip, Gill, Dulvy, et al., 2011; Paddack et al., 2009) — traditional meta-analysis weights within- and between-study sampling errors. However, the survey area has produced more biologically realistic weightings for coral reef benthic data (Côté et al., 2005).

For this reason, the weighting method for individual effect sizes was estimated using the spatial area covered in each survey (Alvarez-Filip, Gill, Dulvy, et al., 2011; Magdaong et al., 2014). The mean effect size (MES) input for the meta-analyses is yi, which corresponds to the individual effect size per reef site, and vi, which corresponds to the weighting method, defined as follows:

MES≈rma (yi, vi) (2)

Where rma is the function to fit the general linear models via mixed-effects in meta-analyses (Viechtbauer, 2010).

All data points were pooled per year and averaged regardless of the method used in the surveys. The temporal heterogeneity was examined in two periods before and after the 2005 mass bleaching event and hurricane impacts. The 2005 coral bleaching event was chosen as a cut-off point for data analyses because it was the warmest year in the Northern Hemisphere on average since reliable records in 1880 (McField et al., 2005) and also because insufficient data were available for previous bleaching events in the MC (small sample size between 1978 and 2004). Reef monitoring efforts in MC increased considerably after this bleaching event. Because the individual effect sizes were log-transformed, they were back-transformed to percentages of coral/algae cover for interpretation. Finally, a subset was made by grouping the surveyed sites by areas, i.e. (1) Northern, (2) Cozumel, (3) Center, and (4) Southern (Figure 2.1).

Previous research has established that independent effect sizes are a significant statistical premise of meta-analysis. Monitoring data are non-independent because various measures are conducted on the same experimental object over time. The meta-analysis addresses this non-independence by "treating each period as an individual study and the original studies as groups (Lajeunesse, 2010)." Thus, each effect size constitutes a separate unit of information (Koricheva et al., 2013; Mengersen et al., 2013). The data was ranked by the magnitude of effect size (independent of the direction) to assess the potential bias in this analysis. The largest effect size magnitude of each reef site was removed stepwise to define the number of studies that need to be removed to change the significance of the results (Côté et al., 2005). If excluding the largest effect size altered the significance of the results, that site was omitted from the analysis.

Sensitivity analysis

Several analyses were performed to determine the meta-analysis' sensitivity. The funnel plot is the most commonly used method to visually inspect the data (Fragkos et al., 2014). This method assumes that the results from smaller studies will mainly spread around the bottom because of more substantial random error, and the more robust studies will spread toward the top (Sterne et al., 2011). In ecological studies, results are inclined to be published if they show significant effects (Gates, 2002). In this regard, the database includes a large sample of monitoring data and grey literature, so the sample of studies is not only drawn from those already published studies.

All data analyses were implemented and analysed in the R Core Team (2018) software. The graphical representations for Windows were produced using R Statistics (R Development Core Team) and Sigmaplot 12.0 (Systat software).

2.4 Results

2.4.1 Coral and macroalgae cover between 1978 and 2016

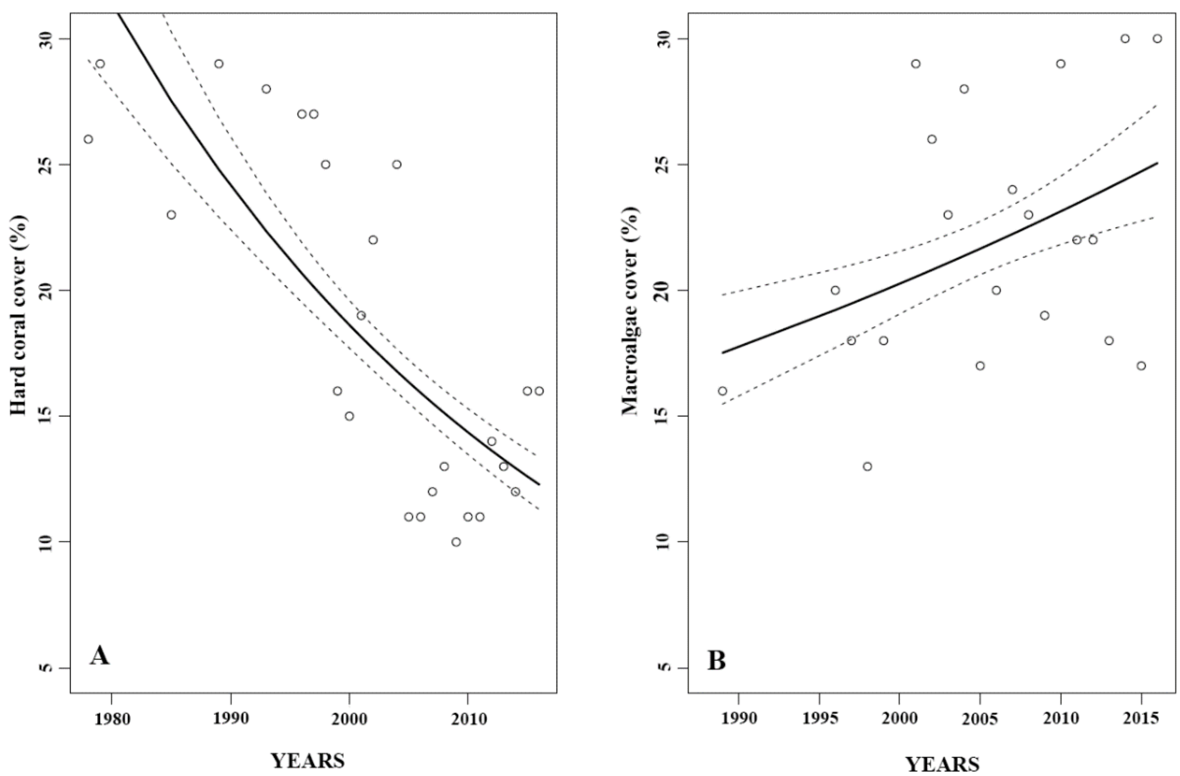

Figure 2.2 *Annual means of benthic cover. (A) Hard coral from 1978 to 2016 and (B) macroalgae cover from 1989 to 2016. The solid line represents the regression line calculated from the estimates of a GLM with Gamma distributed error and log-link function. In contrast, the dotted lines represent the upper and lower 95 % confidence interval.*

When considering the effect of time on the cover percentage, the region-wide hard coral cover declined by more than half during the last 38 years (from ~ 30 % in the 1970s to ~ 12 % in 2016; $p < 0.0001$; Figures 2.2A and 2.3). In contrast, macroalgae cover increased for the study region from ~ 17 % in the late 1980s to ~ 25 % in 2016 ($p < 0.05$; Figures 2.2B and 2.3).

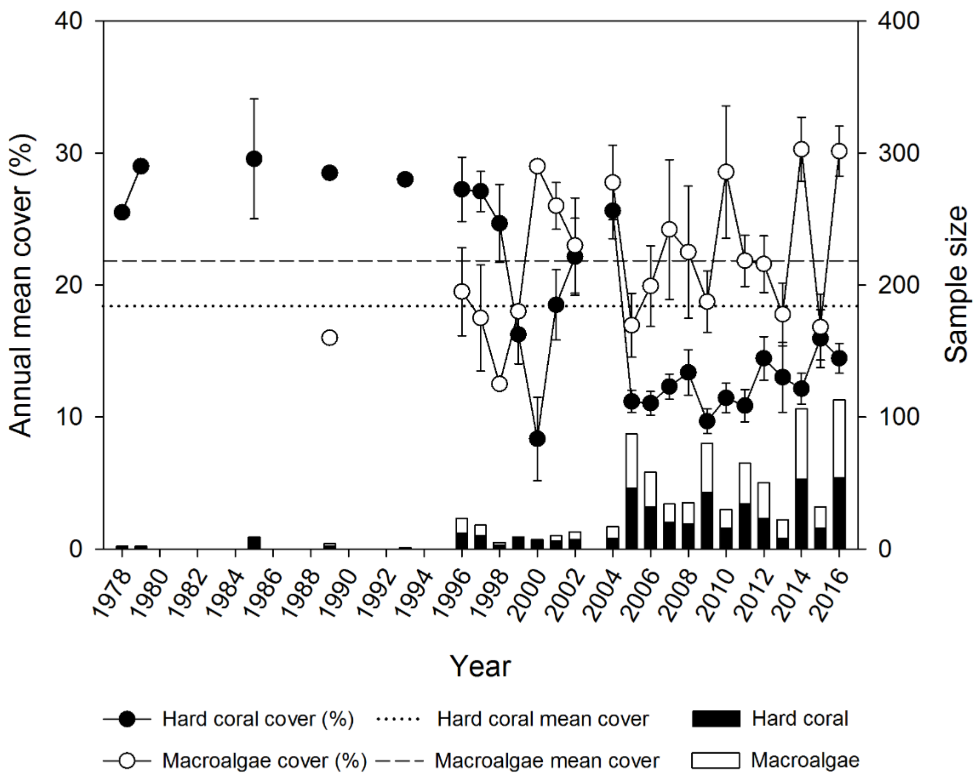

Figure 2.3 *Annual yearly means of hard coral and macroalgae cover (%) from 1978 to 2016. Circles represent hard coral cover (black), and macroalgae cover (white) as means ± S.E. (unless n < 3). Circles connected by the line represent subsequent years. The dotted and dashed lines represent the average hard coral cover and macroalgae. Bars represent the sample size (monitored years).*

In 2005, hard coral cover and macroalgae cover was lower than the previously available data point, except for hard coral cover in the Center region (Figure 2.4C). Whereas macroalgae increased and/or stabilised in subsequent years, hard coral cover only showed modest recovery, especially in the Cozumel and Center region, maintaining low coverage during the following years (Figure 2.4B and 2.4C).

The spatial patterns of hard coral and macroalgae cover present some differences between regions (Figure 2.4). Around the 2000s, macroalgae became the dominant biotic component in the North, Center, and South subregions, with a mean cover close to 30 % (Figure 2.4). In comparison, the coral cover was consistently low (< 15 %) for the North and South subregions. Data for the Center of the MC was sparse. It was not possible to depict clear temporal trends for any of the two variables. However, for this region, macroalgae cover has been consistently and significantly higher than coral cover since 2010.

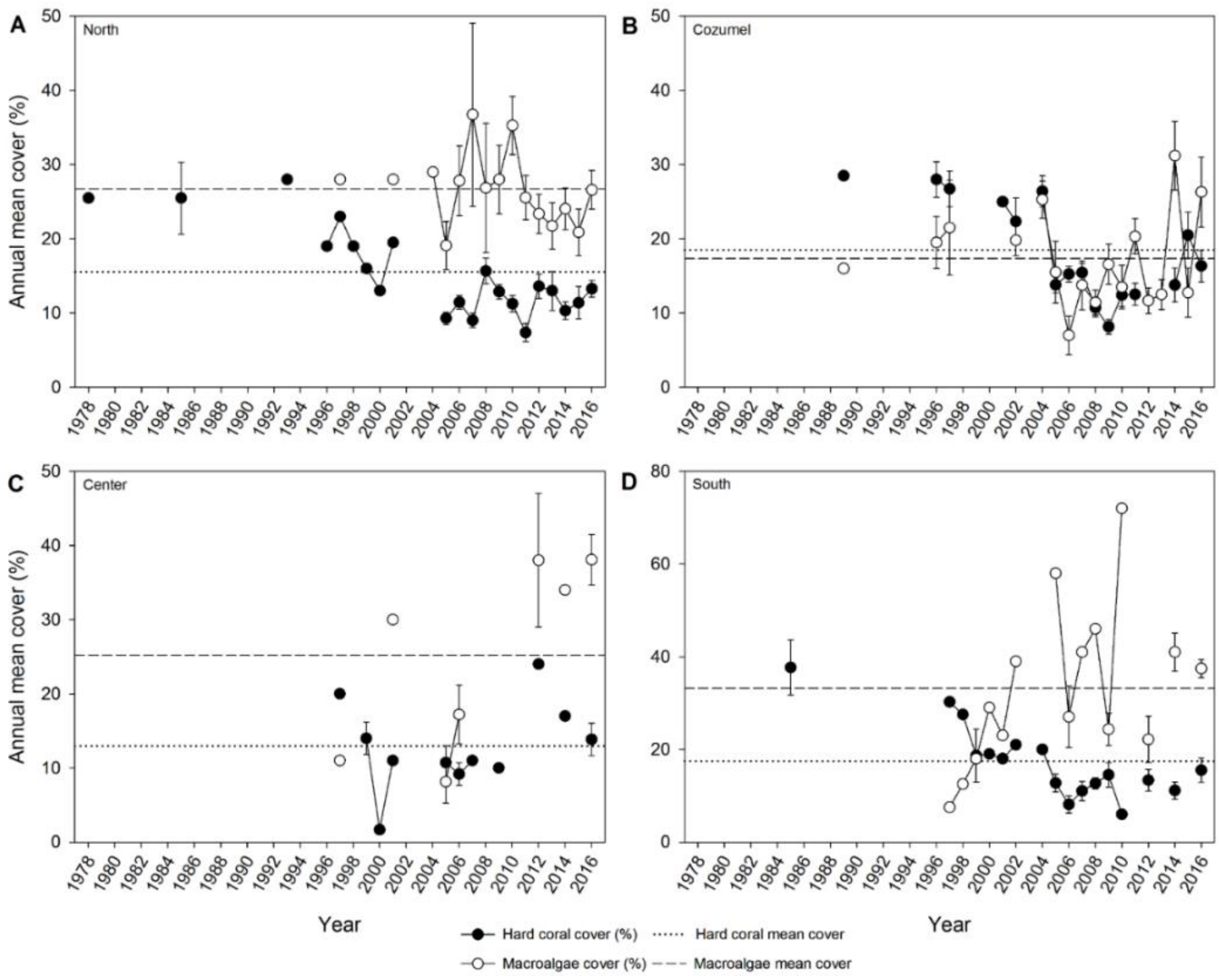

Figure 2.4 *Regional annual means of hard coral and macroalgae cover (%) from 1978 to 2016. (A) The Northern region, (B) Cozumel, (C) Center, and (D) Southern region. Circles represent hard coral cover (black), and macroalgae cover (white) as means ± S.E. (unless n < 3). Circles connected by the line represent subsequent years. The dotted and dashed lines represent the average hard coral cover and macroalgae in the studied time.*

For the Cozumel subregion, temporal trends show a decline for both macroalgae and coral cover in 2006 and a slight recovery for both variables. Cozumel is the only subregion in which the cover of macroalgae and coral has not yet diverged; nevertheless, it is notorious that macroalgae cover peaked in 2014 and 2016.

2.4.2 Meta-analysis: Temporal rates of change for the Overall MC

The relative annual rate of change (ARC) was the effect size used in the Meta-analysis to measure the change in percentage cover for hard coral and macroalgae percentage over time. Temporal patterns of coral change varied along the two analysed periods for the overall MC, presenting trajectories of decline and recovery (Figure 2.5).

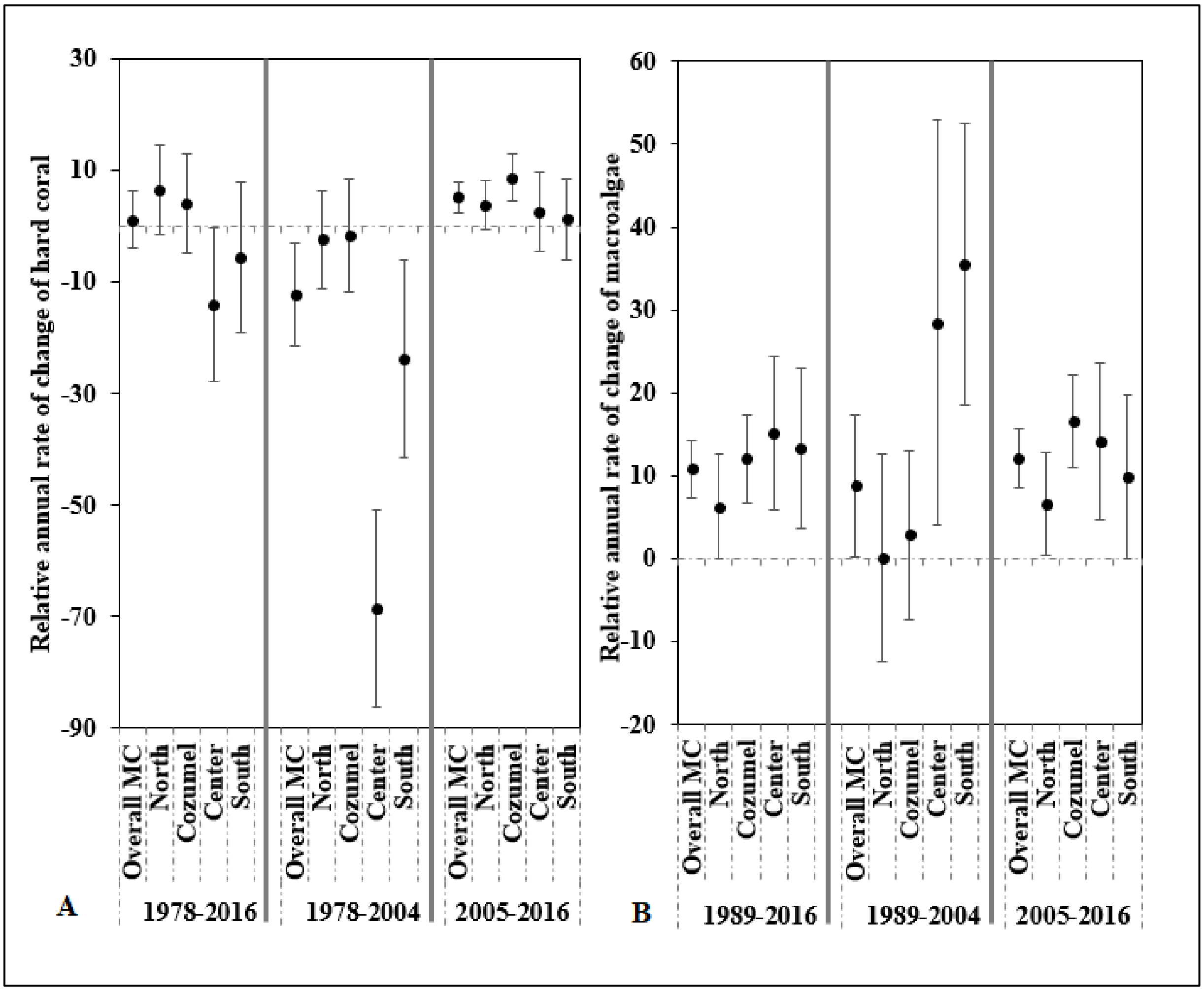

Figure 2.5 *Mean effect sizes of the relative annual rate of change (ARC) for (A) hard coral cover and (B) macroalgae cover from the weighted random meta-analysis by regions, sub-regions and periods: 1978-2016, 1978-2004, and 2005-2016. The ARC mean effect sizes are presented with a 95 % confidence interval for separate cover change analysis. The zero lines indicate no effect, and the significance of ARC effects is determined when the 95 % confidence interval does not overlap zero.*

The mean effect size for ARC in the hard coral cover decreased over the first period (1978 – 2004) and was significantly negative (ARC = ~ -12 %, $p = 0.0094$, $n = 35$; Figure 2.5A), meaning that on average there was a net loss of hard coral cover in the overall MC.

Conversely, the annual rate of change in the second period (2005 – 2016) was 5 % ($p < 0.001$, $n = 92$) for the overall MC (Figure 2.5A), meaning that there was a slight recovery in hard coral cover. However, when combined, the mean effect size for ARC remained stable throughout the entire study period (ARC = ~ 1 %, $p = 0.656$, $n = 125$; Figure 2.5A). The macroalgae mean effect size for ARC presented an increase in the whole period analysed (1989 – 2016) by ~ 11 % ($p < 0.0001$, $n = 94$; Figure 2.5B). See Appendix A Tables S2.1 and S2.2 for all spatiotemporal statistics.

2.5 Discussion

Our meta-analysis of ecological changes in the Mexican Caribbean showed that on a regional scale, coral cover experienced a steady rate of decline between 1978 and 2004, mainly driven by hard coral cover loss in the Center and South region and a slow relative increase in the second period (2005 – 2016), mainly driven by Cozumel (Figure 2.5A). On the contrary, macroalgae cover consistently increased across time and for most of the subregions in the MC (Figures 2.2 and 2.5). However, different trajectories of change for both coral and macroalgae were found with high spatiotemporal variability (Figure 2.5). It is also important to mention that regional trends in coral cover during the late 1970s and 1980s were of low resolution compared to the 2000s because of the earlier lack of monitoring efforts (Figure 2.3). Historically, the Northern and Cozumel regions were most exhaustively sampled over time, whereas fewer monitoring surveys were performed in the Center and Southern subregions. The Center and South subregions experienced the most outstanding rates of coral cover decline and highly significant increases in macroalgae cover between 1978 and 2004. For the second period (2005-2016), the same subregions were the only ones that did not show signs of coral recovery. As in the rest of the subregions, macroalgae cover increased (Figure 2.5). A different trend was observed for Cozumel and the North subregions. Between 1978 and 2004, only non-significant declines were observed for coral cover, and macroalgae cover remained relatively stable in these subregions. Nevertheless, it was not until the second period that the increase of macroalgae became more evident in the Cozumel and North subregions.

Since macroalgae compete with corals for space (Bozec & Mumby, 2015), macroalgae in the overall MC likely rapidly proliferated in response to declining coral cover. Phase shifts can occur due to various factors, including losing crucial herbivores and eutrophication that enhances benthic algal biomass (Lapointe, 1997). The results presented here reveal a phase shift from coral towards macroalgae domination in the overall MC (Figure 2.3) with high and significant variability among regions and periods of analysis (Figure 2.4). Certain conditions, such as nutrient enrichment, can increase macroalgae, especially in reefs near highly populated areas (Szmant, 2002a). Surprisingly, in the current study, the meta-analysis revealed a higher macroalgae increase in the more sparsely populated Center and Southern regions between 1989 and 2004 (Figure 2.5B). Between 2001 and 2013, the Southern region was subject to ~ 90 % of forest cover loss due to human settlement, agriculture, and livestock farming (Ellis et al., 2015), which may have caused increased sediment run-off. High sediment run-off can affect corals by increasing suspended sediment and nutrient levels, thus favouring macroalgae growth (Roberts et al., 2017).

Phase shifts from coral towards algae-dominated states have been widely reported in the Caribbean (Bruno et al., 2009). From 1978 to 2004, results reported here suggest that, on average, hard coral cover declined across the MC, and macroalgae increased (Figure 2.5). These results correspond with what was found in other local-scale and regional studies in the Caribbean (Côté et al., 2005; de Bakker et al., 2017; Gardner et al., 2003; Somerfield et al., 2008). Different successive biotic and abiotic impacts in the wider Caribbean may explain these outcomes. First, the diseases of hard coral species (i.e., *A. palmata* and *A. cervicornis*)(Aronson & Precht, 2001b) impacted the overall coral coverage compromising the architectural complexity of these reefs (Alvarez-Filip, Gill, & Dulvy, 2011). Secondly, the hurricane impacts, especially in shallow reefs, changed the physical structure of the benthos, as well as the local species distribution and habitat diversity (Rioja-Nieto et al., 2012). However, macroalgae colonisation in the MC is likely to be related to mortality events after the 1998 ENSO, resulting in mass bleaching and exacerbated by hurricane impacts, when opportunistic macroalgae began to colonise the free available space and continued increasing in MC reefs (Figure 2.2). Our findings suggest that the phase shift from coral towards macroalgae domination in MC started around the mid-2000s (Figure 2.3). First, there was an overall increase in macroalgae and a decrease in coral cover. Later, a marked phase shift from coral to macroalgae domination, where hard coral cover halved, and macroalgae cover increased (Figure 2.2). This regional-scale phase shift corresponds with the timing reported by previous studies that have assessed recent ecological changes at a local scale in the MC (Arias-González et al., 2017; Suchley & Alvarez-Filip, 2018).

Following the 2005 bleaching event and hurricane impacts, hard coral and macroalgae cover in the overall MC initially responded with similar declines in absolute cover, while their long-term responses displayed different trajectories defined by the fast (i.e., 11 years) recovery of macroalgae during the second period of study (2005 – 2016; Figure 2.3). Despite this increase in macroalgae cover, in the second period, hard coral cover in the overall MC exhibited a modest recovery (i.e. 5 %; Figure 2.5). However, the average mean effect size of ARC for the Northern, Center and Southern regions was positive, thus supporting the mean effect size for ARC for the overall MC towards a positive trend (Figure 2.5). Generally, it is more common to find recovery rates after mass mortality events in areas far away from anthropogenic impacts, such as the Seychelles Islands (Graham et al., 2015) and the archipelagos in the central Pacific Ocean (Smith et al., 2016). The coral settlement, calcification, and reproduction have been successfully compared to reefs near highly populated areas. However, current investigations in the Chagos Archipelago report that coral growth did not recover completely from warming events, thus keeping reefs in a low coral cover state (Sheppard et al., 2017). Likewise, in remote islands in the Central Equatorial Pacific, coral and reef fish species biomass was severely reduced after the 2015/16 bleaching event (Brainard et al., 2018). In the Great Barrier Reef (GBR), the coral community was recovering at a slow growth rate compared with previous bleaching events and pre-disturbance status (Sato et al., 2018).

MC reefs are directly exposed to chronic stressors. However, this study is one of the few within the Caribbean region that reports recovery. In the last decades, other Caribbean coral reefs have failed to recover after bleaching events (Huntington et al., 2011; Neal et al., 2017). This recovery does not necessarily suggest that the assemblage has recovered or maintained its previous diversity richness. Moreover, the recovery reported here, 5 % between 2005 and 2016, is still less than half of what was lost in 2005 and is slow compared with recovery rates found in reefs of the Pacific after widespread mortality (Gilmour et al., 2013; Graham et al., 2015; Johns et al., 2014). There are three potential explanations for the unexpected recovery in MC reefs: 1) The protection due to 13 Marine Protected Areas (MPAs) in the MC may have promoted the reported recovery (Mumby & Harborne, 2010), 2) these management actions may have helped to increase the resilience of MC reefs (Mellin et al., 2016), and 3) the dynamic of the water circulation and currents especially in the Northern region (Cetina et al., 2006a) may help to flush and diminish the adverse effects of land-based pollution sources (Storlazzi et al., 2018).

The Northern region of the MC had experienced more rapid rates of coastal modification since the 1970s when Cancun was conceived as an international tourist destination (Murray, 2007). Furthermore, this sub-region potentially has the highest coastal development pressure in the MC (Baker et al., 2013). Surprisingly, this region had the lowest macroalgae increase (i.e., ~ 6 %) for the entire study period (Figure 2.5). Three reasons may explain this result: first, this zone had an older history of reef degradation; the reefs were already impacted by the time the first surveys began (Jordan-Dahlgren, 1993). Second, the MPAs' actions helped conserve those systems during the last 20 years and, coupled with rehabilitation efforts, may have helped the reefs inside the reserves become more resistant (Suchley & Alvarez-Filip, 2018). One key example is Limones reefs in Puerto Morelos National Park which is the Cancun area of influence but has the highest coral cover (mainly *A. palmata*) within the Northern zone (2014). Third, the geology and local oceanographic conditions in the Northern region favour the formations of seasonal eddies (Suárez-Morales & Rivera Arriaga, 1998). Because of their velocities and turbulence, recirculating eddies may damage macroalgae production (Hurd, 2000). Also, eddies favour coral larval retention and recruitment patterns (Harriott & Fisk, 1988).

Coral reefs in Cozumel presented a ~ 9 % hard coral cover increase from 2005 to 2016. This area's high hard coral cover suggests a higher resilience, even though extensive unsustainable tourism activities have occurred since the late 1970s. The creation of Cozumel as a National Park in 1980 was a significant effort that may have helped to build reef resilience and cope with local anthropogenic impacts (Rioja-Nieto & Sheppard, 2008). The best-developed reefs in this area are located on the leeward of the Cozumel coast. According to Fenner (1988), the reef development in Cozumel in a sheltered area permitted better reef growth. Regardless of the good shape of Cozumel reefs, macroalgae cover remains high as in the rest of the MC reefs (Figure 2.4B) and exhibits an increasing trend (Figure 2.5) similar to other reefs around the globe (Mumby, 2017). This may be attributed to increasing nutrient uptake on the island due to the human population growth in the last decades (INEGI, 2015). However, water quality studies are still lacking.

The Center area in the MC encompasses one of the largest protected areas in the region: The Biosphere Reserve of Sian Ka'an, with protection on the sea and land since 1986, experiencing little local anthropogenic impacts (Walker et al., 2004). Surprisingly, coral reefs in this area experienced the most drastic decrease in hard coral cover and a substantial increase in macroalgae. Nevertheless, these results should be interpreted with caution due to the small sample size. Thus, for the first period analysed (1978 – 2004), the sample size is reduced to 3 time-series studies. Observational studies noted the importance of the size of protected areas and stated that protected areas themselves could improve coral reef health by protecting herbivorous fish, thus reducing macroalgae (Halpern, 2003; Mumby, 2006). However, due to management measures in MC reefs, the herbivorous fish biomass has increased in the last decade (Suchley et al., 2016). Therefore, the most reliable explanation for the reported reef degradation in this area may be caused by the natural water circulation carrying nutrients and pollutants stressing the corals in different ways (Cetina et al., 2006; Null et al., 2014). Gondwe et al. (2010) suggested through geochemical and phreatic analyses that Sian Ka'an has an entirely different groundwater system compared to, i.e., the Northern region. Indeed, systems surrounding Sian Ka'an experience a higher groundwater discharge of freshwater than the other coasts (Null et al., 2014). Moreover, this higher influx increases nutrient concentrations in the otherwise oligotrophic coastal wetlands of Sian Ka'an (Lagomasino et al., 2015). Consequently, nearby coral reefs may now be exposed to higher nutrient enrichment, sedimentation, and turbidity, resulting in a degraded state potentially favouring macroalgae overgrowth (Carpenter et al., 2008; Fabricius, 2005; Harborne et al., 2017; Pastorok & Bilyard, 1985; Szmant, 2002).

Recent studies have described the Southern part as a focal point for mass tourism development without proper selective management strategies, possibly causing a more rapid increase in the macroalgae coverage (Figueroa-Zavala et al., 2015; Martínez-Rendis et al., 2016). As mentioned, herbivores are essential biotic factors regulating macroalgae (Holbrook et al., 2016). However, this is not the case in these reefs. Evidence suggests that in the Southern region, macroalgae increase is not related to a reduction in herbivores (Arias-González et al., 2017). This may indicate that it did not increase sufficiently to control and restrict macroalgae growth or that macroalgae are unpalatable. It has been suggested that different fish species have specific preferences for certain types of algae (Adam et al., 2015), thus impacting the benthic community differently. Besides, critical grazers such as the sea urchin, *D. antillarum*, continue to be rare on most reefs since its region-wide die-off in the 1980s (Lessios, 2016; Steneck & Lang, 2003), and although the populations of herbivorous fishes have increased, its biomass is likely far below historical baselines due to the impacts of decades of overfishing and habitat degradation (Paddack et al., 2009). Further anthropogenic local impacts, i.e. the pier construction (2000 – 2006) to receive massive cruise ships, fragmented the ecosystem facilitating coral degradation and overgrowth of macroalgae. The lack of adequate management in the reefs in the Southern region poses higher local pressure on the coral reefs.

The current coral reef crisis is represented by a shift in species composition and ecosystem functions and services (Woodhead et al., 2019). Meta-analyses benefit coral reef research due to the synthesis of a large amount of data under the specific objectives of the analysis. Primary information deriving from monitoring campaigns is valuable. However, if this information is not integrated and analysed into the bigger picture, researchers will likely be unable to detect and predict the consequences of the changes (Hillebrand et al., 2018). Moreover, identifying the significant factors impacting coral reef health along the MC would help determine which areas require the most protection from anthropogenic activities. Even with the high number of MPAs and the creation of the MC MPA in 2016, monitoring active management and resources are still limited (Carriquiry et al., 2013). Meta-analyses enable long-term coral and algae cover assessment to set the baseline for a monitoring strategy based on science-based management that ensures coral reef biodiversity in the MC and the wider Caribbean.

Coral disturbance regimes continue to intensify, while recovery capacities depend on human impacts (Birkeland, 2015). The potential use of this study is to set the basis to understand how the reefs have changed through time and what measures should be taken to respond to and counter those changes for management. Individual studies integrated into long-term longitudinal research can be used as basic information for management strategies. However, standardised future monitoring methods are highly recommended for the MC to follow up on the further development of these ecosystems.

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Chapter 3

MAIN GLOBAL AND LOCAL STRESSORS IMPACTING BENTHIC CHANGE

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Two publications were generated from this chapter.

The first publication is in the review process in *Ecological Applications*:

Contreras-Silva, A. I., Navarro-Espinoza, E., Migani, V., Valderrama-Landeros, L., Velázquez-Salazar, S., Pardo-Urrutia, F., Tapia-Silva, O., Reuter, H. & Alvarez-Filip, L. (2023). *Effects of coastal anthropisation, hurricane impacts, and bleaching susceptibility in Mexican Caribbean coral reefs*.

The second was published in *Diversity*:

Elías Ilosvay, X., **Contreras-Silva, A. I.,** Alvarez-Filip, L., & Wild, C. (2020). *Coral Reef Recovery in the Mexican Caribbean after 2005 Mass Coral Mortality—Potential Drivers*. Diversity, 1–16.

3.1 Effects of coastal anthropisation, hurricane impacts, and bleaching susceptibility in Mexican Caribbean coral reefs

3.1.1 Abstract

Coral reefs worldwide face unprecedented cumulative impacts originating at various scales, driven by global anthropogenic climate change and local human pressures. In the Mexican Caribbean, coastal development intensified in the 1970s without overall management or planning to safeguard the affected ecosystems. Using an extensive collection of remote sensing data, we conducted a cumulative impact assessment on hard-coral and macroalgae benthic communities exposed to multiple stressors (thermal stress, nutrient inflow, sedimentation, hurricane impact, and anthropisation) to analyse the effects on the reef ecosystem. These data were coupled with 91 coral reef monitoring sites from 2005 to 2016, and the estimates of the change in coral and macroalgae cover percentage were related to each factor considered a potential stressor impacting reefs.

Our results show that bleaching susceptibility strongly influences coral cover change, followed by the negative effect of anthropogenic activities, which incorporates the increasing pressures of urban hubs. The water quality predictors, primarily the particulate organic carbon (used as a proxy for sedimentation and nutrients), only negatively affected macroalgae cover. The only adverse effect on macroalgae was sea surface temperature and chlorophyll-*a* interaction. Our analyses show that global warming impacts on coral reefs occur parallel with local pressures, such as increases in nutrients and suspended sediments through coastal development. We conclude that the future of Mexican Caribbean coral reefs is at high risk due to cumulative impacts from local and global stressors. Our findings highlight the importance of managing coastal development projects such as roads, ports, and resort constructions to sustain tourism in the face of climate change.

3.1.2 Introduction

The impacts of multiple anthropogenic stressors on coral reefs at global and local scales are increasing (Halpern et al., 2015; Hughes et al., 2017). Anthropogenic climate change is recognised as the primary driver of coral depletion worldwide, but it is not the only threat coral reefs face. Evidence suggests that local chronic stressors also impose multiple impacts (from genes to community) on reef systems (Halpern et al., 2007; Welle et al., 2017). In some regions, local or regional scale threats are considerably more critical than climate change because they rapidly restructure coral reefs (McLean et al., 2016). Generalist coral species (encrusting and massive growth forms) tend to tolerate low-light water dynamics dominating urban habitats, whereas specialists (i.e., *Acropora sp.*) may collapse under polluted waters (Carlson et al., 2019). Some authors suggest that managing local stressors increases coral reefs' resilience (Graham et al., 2014; Roberts et al., 2017; Suchley & Alvarez-Filip, 2018). For example, after mass bleaching events in the Mesoamerican Reef, marked differences in recovery rates were found between coral colonies exposed to different chronic pressure levels (Carilli et al., 2009). Furthermore, a consensus points out that global and local stressors acting in synchrony increase the risks of coral reef depletion (Osborne et al., 2017).

Even though the impact of coastal anthropisation on coral ecosystems is well recognised, knowledge is still limited for many regions. Mora (2008) found a positive correlation between the increase in human population and coral mortality and macroalgae abundance; macroalgae also increased in areas near cropland. Similarly, Ramos-Scharrón and others (2015) reported in Puerto Rico that coral cover decreased as land cover changed to urban settlements. In Bonaire, Caribbean islands, Roberts and collaborators (2017) identified increased coral cover in watersheds dominated by forest coverage. In contrast, Bruno and Valdivia (2016) found no correlation between human population density (within 50 km) and reef conditions. However, other studies demonstrated that reefs with minimum human activity or close to unpopulated areas were still dominated by reef-building corals, in contrast to those influenced by heavily populated areas (Renfro and Chadwick, 2017; Smith et al., 2016). Overall, these cases support the view that coral degradation is frequently exacerbated by local anthropogenic pressures, i.e., coastal development.

Several recognised mechanisms link coastal development and coral reef degradation, usually causing a chain reaction with immediate to long-term implications (Holon et al., 2018). Land-based pollution is one of the main problems identified along with densely populated coastlines (Wear and Vega Thurber, 2015), resulting in poor water quality due to the runoff of nitrogen and phosphorus from human and agricultural watersheds. Prior studies also identified areas of hypoxia (Cosme et al., 2017) due to increased sedimentation (Syvitski et al., 2005) and the contamination of column water by heavy metals (Reichelt-Brushett and Harrison, 1999) and toxic substances (Negri et al., 2011). Anthropogenic nutrient enrichment is one of the most relevant factors of coastal development affecting coral reefs in three main ways. First, eutrophication can enhance algal growth (Jessen et al., 2012), which actively competes with corals for space and light (Fung et al., 2011). Second, it can increase the severity and prevalence of coral disease (Bruno et al., 2003). Third, it can increase corals' susceptibility to bleaching by lowering the thermal threshold at which corals bleach (Bruno et al., 2003; Vega Thurber et al., 2014).

The Mexican Caribbean extends ~ 450 km along the Yucatan Peninsula in Mexico. It is a biodiversity hotspot because it encompasses mangroves, seagrasses, and coral reefs, closely interconnected regarding species movement and energy flux (Rioja-Nieto et al., 2019). Nonetheless, widespread eutrophication occurs along the coastline due to increasing tourism and urban growth. Tourism, which depends on natural resources, is the area's central axis of economic development (Palafox-Muñoz et al., 2011). Unfortunately, coastal development is carried out with limited management or planning to safeguard the adjacent ecosystems, i.e., coastal wetlands (Sevilla et al., 2018). The wetlands along the Mexican Caribbean shoreline are an essential transition zone between terrestrial and aquatic ecosystems (Adame et al., 2013), providing a large number of ecosystems services, e.g. mangroves in the coastline function as natural water filters (Carugati et al., 2018), offer protection from disastrous events, such as hurricanes and tidal bores, and can diminish shoreline erosion (Carugati et al., 2018). They also provide food, breeding grounds, and nursery sites for various terrestrial and marine organisms, including many marketable species and juvenile reef fish. However, the Mexican Caribbean shoreline lost 38.6 % of its mangrove forest from 1981 until 2005 (Valderrama et al., 2014). The northern area experienced an annual decrease of 19 % between 1970 and 1990 with the planned megaprojects of Cancun, San Buenaventura and Puerto Cancun (Pérez and Carrascal, 2000). In the central region of Sian Ka'an, natural forest fires are the leading cause of environmental hazards (Ellis et al., 2020). Recent evidence suggests that clearing and degradation of coastal forests can increase sedimentation rates on coral reefs and reduce fish population biomass due to the elimination of nursery habitats provided by these ecosystems (Adam et al., 2015).

Longitudinal analyses of global and local stressors impacting the Mexican Caribbean coral reef system still need to be included. However, small-scale studies have reported that multiple stressors interaction (overfishing, coastal anthropisation, thermal stress) resulted in coral reef depletion (Arias-González et al., 2017; Randazzo-Eisemann et al., 2021, 2022). Therefore, in the face of increasing human impacts such as coastal anthropisation, reduced water quality, and effects from anthropogenic climate change, it is crucial to investigate the main drivers of coral reef impairment and the relative impact on the Mexican Barrier Reef. In this study, we used an extensive collection of remote sensing data to generate mangrove and anthropogenic change indexes, coupled with data from 91 reef monitoring sites for corals and 85 sites for macroalgae from 2005 to 2016. Additionally, we included nutrients (chlorophyll-*a*, particulate organic carbon) and turbidity (diffuse attenuation coefficient Kd490). To account for thermal stress, we used the Sea Surface Temperature from MODIS (Moderate Resolution Imaging Spectroradiometer) and degree heating weeks (bleaching alert), and hurricane intensity from NOAA (National Oceanic and Atmospheric Administration) Historical Hurricane Tracks. These variables accounted for various anthropogenic and natural stressors in the Mexican Caribbean reef system.

This paper investigates how various stressors in the Mexican Caribbean impact the coral and macroalgae cover change and if there are spatial differences of affectations. We started by defining a buffer of influence at which the coastal anthropogenic development affects the reef environment. Then, we used the relative impact of the coastal stressors, represented in change indices, applying this buffer. Next, we extracted the satellite image data at specific reef sites through a weighting average of the pixels surrounding the site. We then ask whether the stressors impact differently the coral and macroalgae cover changes along the Mexican Caribbean to finally analyse the relative influence of each stressor using regression-based methodologies. We suggest priority areas for adequate coral reef management in the Mexican Caribbean coastline (~ 450 km).

3.1.3 Methodology

Study area

The Mexican Caribbean stretches for around 450 km. With back reefs, reef crests, and fore reefs running parallel to the beach, the reef system forms a semi-continuous barrier that borders the shoreline. This region is economically divided into three main subregions — Northern, including the Island of Cozumel; Centre, defined by Sian Ka'an natural reserve; and Southern, including Banco Chinchorro atoll, not incorporated in this study (Figure 3.1).

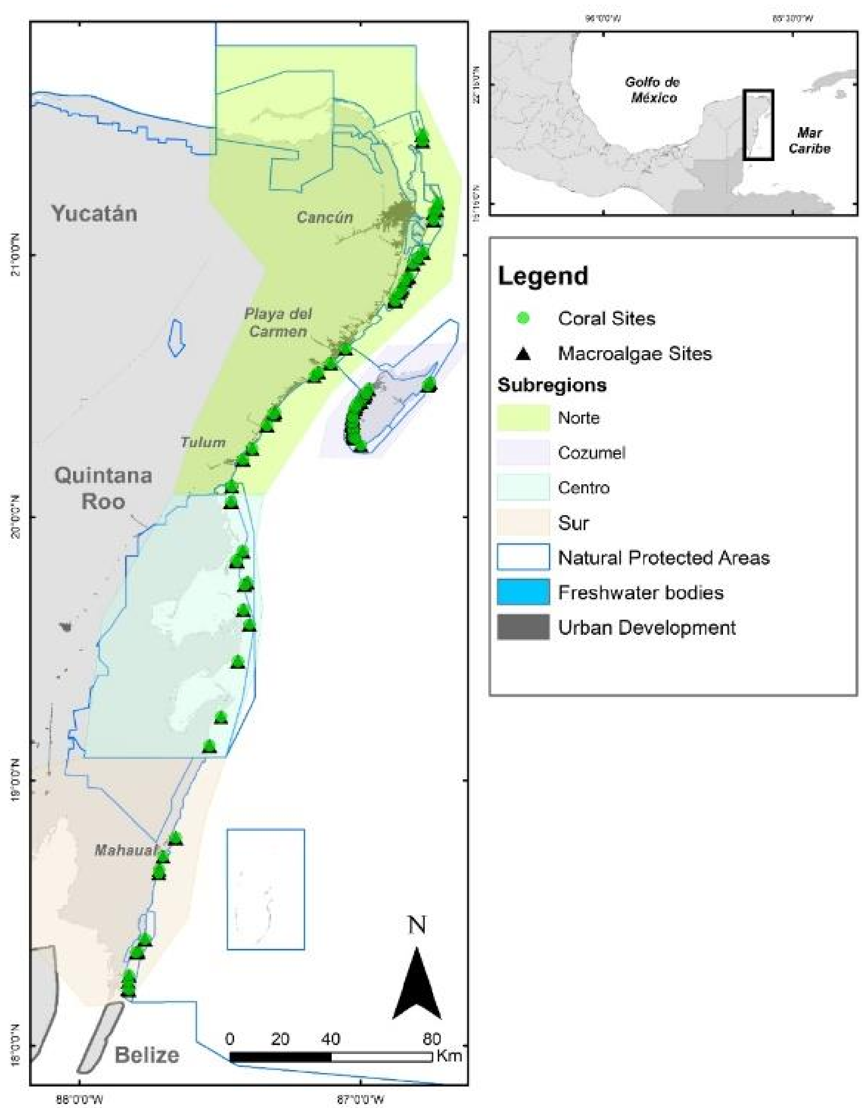

Figure 3.1 *Regional distribution of reef sites of hard-coral (green circles) and macroalgae (black triangles) which had at least two samplings between 2005 and 2016.*

Lithology of the study area

The Mexican Caribbean lithology is a permeable limestone that infiltrates almost immediately all the water run-off making the groundwater the only available water resource in the region (Perry et al., 2003). Despite this unique characteristic, the high infiltration and rapid flow make aquifers and coastal ecosystems more sensitive to anthropogenic pollutants such as polution from urban development, including untreated sewage from leaking septic systems facilities that directly affect coastal ecosystems (Arandacirerol et al., 2011).

Data

Biological data

We analysed the change in cover percentage of hard-coral (91 sites) and macroalgae (85 sites, including all fleshy and calcareous species) along the Mexican Caribbean divided into four regions North, Center, South, and the Island of Cozumel (Figure 3.1). We used a subset of the database on reef sites described by Contreras-Silva et al. (2020), sampled between 2005 and 2016 because of their spatial and temporal resolution.

Remote sensing data products

This study used remotely sensed data for Sea Surface Temperature (SST), bleaching stress as an index of SST, and water quality (attenuation coefficient K-490, chlorophyll-*a*, and particulate organic carbon), mainly from the National Aeronautics and Space Administration (NASA) Moderate Resolution Imaging Spectroradiometer (MODIS) from Aqua satellite at 500 m spatial resolution (NASA Goddard Space Flight Center, 2020). We used Google Earth Engine (GEE) platform to download the imagery. The water attenuation coefficient was downloaded from NASA Ocean Color Web at 1000 m spatial resolution (https://oceancolor.gsfc.nasa.gov/). The bleaching alert derived from Degree Heating Weeks was downloaded from NOAA Coral Reef Watch (https://coralreefwatch.noaa.gov/product/5km/index.php). All imagery was processed with GRASS GIS 7.8 (see Appendix B Figure S3.1 for imaging downloading, processing, and data extraction details).

The explanatory variables chosen to represent land characteristics were: the index of coastal anthropisation and mangrove change index and to represent the potential seascape stressors in reef systems: hurricane impact index, SST, bleaching alert, and water quality (Table 3.1). We analysed SST and bleaching alert as global stressors, whereas the other variables refer to local stressors (i.e., coastal anthropisation and water quality).

Table 3.1 *Description of environmental stressors used for the cumulative impact assessment (2005–2015)*

Proxies to stressors	Justification	Source of information	Scaling of data
Thermal stress (SST)	Sea surface temperature increase is the leading cause of bleaching events and ecological shifts in coral reef ecosystems (Kayanne, 2017; Obura, 2009).	Monthly mean SST (℃) images were calculated using MODIS products from Aqua Climatology	500 m spatial resolution
(Bleaching alert)	Based on a 7-day maximum composite of degree heating weeks to account for daily variations in the level of thermal stress monitored in highly fluctuating coral reef locations.	Coral Reef Watch from NOAA	5000 m
Turbidity (Attenuation coefficient Kd490)	Turbidity intensification is one of the main stressors to coral reefs. Because it affects light availability for photosynthesis, it is a vital water parameter in tropical corals. The diffuse attenuation coefficient at 490 m is directly related to scattering particles in the water column, either organic or inorganic, and thus is an indicator of water clarity.	Monthly Kd490 (1/m) images were calculated using MODIS products from Aqua Climatology (NASA).	1000 m

Nutrient concentration and eutrophication (Chlorophyll-*a*)	Low water quality is a significant issue of coral reef degradation. Chlorophyll concentration is an excellent indicator for measuring phytoplankton biomass and primary production; therefore, it is also helpful to monitor water quality. Waters with high levels of nutrients from fertilisers, septic systems, sewage treatment plants and urban runoff may have high chlorophyll-*a* concentrations.	Monthly chlorophyll-*a* concentration (mg/m^3) images were calculated using MODIS products from Aqua Climatology (NASA).	500 m
Eutrophication & pollution (Particulate organic carbon)	Eutrophication is one of the main stressors for coral reefs. It reduces light penetration in the otherwise oligotrophic reef waters and may bring a proliferation of macroalgae. In the water, particulate organic carbon (POC) comprises living material (phytoplankton, zooplankton, bacteria etc.) and detritus. It can be a good indicator of productivity, and detritus components of POC could be used as an indicator of pollution.	Particulate organic carbon concentration (mg/m^3) images were calculated using MODIS products from Aqua Climatology (NASA).	500 m

A coastal buffer of influence for reef sites

Considering that the coastal zone is highly dynamic and varies in space and time (Kay and Alder, 2005), it can have different meanings depending on the main focus of interest and how the 'coastal pressure' is analysed. In our approach to linking the coastal zone to reef ecosystems, we first defined a buffer of influence where the coast exerts the highest pressure on coral reefs. Therefore, it can have different meanings depending on the main focus of interest and how the ‘coastal pressure’ is analysed. In this work, we take the concept used in the Queensland Coastal Protection and Management Act (1995): "The coastal zone is coastal waters; and all areas to the landward side of the coastal waters. There are physical features, ecological or natural processes or human activities that affect or potentially affect, the coast or coastal ecosystems". This definition also coincides with the Mexican National Politic for Coasts and Seas, which refers to the coastal zone as the geographic space of mutual interaction between the marine environment, terrestrial environment, and the atmosphere.

Human population density and environmental deterioration are inextricably linked (Riegl & Glynn, 2020). Dramatic population growth in the tropics accelerates the rate of urbanisation leading to reef degradation by coastal destruction (Baker et al., 2013). Consequently, our goal was to establish an adequate land-sea buffer of influence based on the human settlements that are highly concentrated in the coastal area (Wolanski, 2005) thus exerting the greatest pressure on the reef system. To generate this buffer of influence, we had to consider the high soil permeability and the lack of superficial run-off of the study area taking into account that the contaminants can be dispersed in the aquifer to an unknown extent. This characteristic makes it difficult for a watershed approach to link the coastal zone with reef ecosystems due to the increased complexity of the groundwater processes.

Therefore, we performed the land-sea buffer of influence in three steps:

1) Create different buffers incrementing from 2.5, 5, 10, and 15 km to a 50 km radius.
2) Buffers in step 1 were intercepted with the population density that defines an area; in Mexico, this is called AGEB (geostatistical core area, urban or rural), defined by the National Institute of Statistics and Geography (INEGI by its Spanish acronym).
3) Calculate the population density in each distance buffer for our analysis. We took the buffer size where the inflexion point in the distance to the coast and population percentage was presented.

With this approach, we capture the region with the highest population density nearest to the coast, ensuring that this is the spatial scale where coast development mainly affects reef systems.

Indices

Hurricane index

Hurricanes affect coral reefs by disrupting the benthic community, local species distribution and habitat diversity (Gardner et al., 2005). The Historical Hurricane Tracks from NOAA (https://www.ncei.noaa.gov/data/) were used to calculate the aggregate activity of hurricanes and other tropical storms that could affect coral, and macroalgae cover at the Mexican Caribbean regional scale. The components of this index included:

1) The number of cyclones occurring at a fixed location (reef site) over a specific period
2) The cyclonic strength
3) The distance of the site from the eye of the hurricane
4) The monitoring period of the reef sites

In this way, we estimated the potential effect of hurricanes on the reefs based on hurricane category and the distance from the site to the hurricane eye. The hurricane category was established at the closest point to each site, evaluating the maximum energy with which the hurricane affected the reef. We considered that corals downwards to 20 m depth may still be fragmented and detached (Scoffin, 1993). Therefore, we generated three hurricane-risk regions (Appendix B, Figure S3.2). These risk regions were defined from the model produced by Mrowiec et al. (2016), in which they simulate the evolution of a hurricane and its internal dynamics. Because the hurricane strength is derived from wind speed measurements: central pressure, direction, range, forward velocity, and duration (Scoffin, 1993), the simulated storm reaches a maximum speed of 80 m/s, equivalent to 5 in the Saffir-Simpson category, and has a radius greater than 300 km (Appendix B, Figure S3.3). Therefore, Risk 1 sites at a maximum distance of 30 km from the path of the hurricane receive the total or greatest hurricane intensity (100 % to ~ 80 % of the top wind speed). Risk 2 sites between 30 km and 50 km of the path of the hurricane receive 80 % to ~ 60 % of the maximum wind speed. Risk 3 areas, between 50 km and 100 km, where the wind speed range is ~ 60 % to 40 % of the maximum wind speed (see Appendix B for further details).

Mangrove change index

The data used in this study consisted of an extensive remote sensing collection generated by the . Specifically, we used the mangrove distribution maps for the Quintana Roo state (for methodological details, see: Valderrama et al., 2014). This data was generated using Spot imagery and RapidEye for specific zones with high cloud coverage at a 10 m spatial pixel resolution. The land cover and land use were mapped using eight classification categories (Table 3.2) (a description of these categories are discussed in Valderrama and Collaborators (2014)). The accuracy of users and producers of the resulting maps was 93 % and 90 %, respectively. Using this classification, we generated a two-time change detection analysis (2005–2015). We focused our analysis on mangrove changes given its ecological functions, goods and services, and ecological connectivity with reef systems (Mumby and Hastings, 2007).

Table 3.2 *The class definition for the 2005 and 2015 maps of the mangrove and adjacent land cover in Mexico according to Valderrama et al. (2014)*

Classes	
1. Anthropogenic (human) development	5. Mangrove
2. Crop and animal husbandry	6. Damaged mangrove
3. Vegetation without mangroves and wetlands	7. Wetlands without mangroves
4. Bare soil	8. Water bodies

Based on the mangrove change map, we created a mangrove change index. This index resulted from reclassifying this change map according to the adaptive cycle and cross-scale effects concept from Walker et al. (2004).

According to the adaptive cycle concept, the ecosystem can be subject to a change series; however, the changes do not infer static systematic cycling (Walker et al., 2004). Appendix B, Figure S3.4, presents a complete adaptive mangrove cycle; it shows intermediate changes (which can or cannot occur) until complete anthropisation. The processes are constructed on observed system changes where the system can move backwards or forward (see Appendix B for further details).

Index of changes in anthropisation

Effects of direct and indirect anthropogenic activities continue to increase progressively in coastal areas. The term anthropisation derives from the hemeroby concept: "the measure of the human influence on ecosystems" (Kowarik, 2014). Martínez-Dueñas (2010) takes this approximation to generate the relative integrated anthropogenic index (INRA) within a spatial and land cover analysis framework used to measure: "the degree of modification of an ecosystem due to anthropogenic effects." The relative integrated anthropogenic index used in this work encompasses different processes defined in Velazquez-Salazar et al. (2019). As a base cartography, we use the index derived from the mangrove distribution map from CONABIO. The 'anthropogenic development' category was then subclassified to evaluate coastal anthropogenic impacts in the Mexican Caribbean (Appendix B, Table S3.1). The subclassification was an adaptation of the CORINE Land Cover Programme from the European Environmental Agency (2004), complemented with data from the Mexican National Institute of Statistics and Geography (INEGI by its Spanish acronym). Finally, we used the relative integrated anthropogenic index from Velazquez-Salazar et al. (2019) to calculate a change map for 2005–2015 (see Appendix B for further details), which we used to model the land influence on the reef system.

Model of land-sea influence

We used a land-sea influence model (Navarro-Espinoza et al., in prep.) to quantify coastal anthropisation effects on Mexican Caribbean coral reefs. This model is a spatial methodology designed to relate the inland impacts on marine ecosystems and was modified for this study. The main inputs of this model are 1) the raster layer of the phenomena to analyse (in this case, the mangrove index and the anthropisation index) and 2) the vector layer containing the coordinates in the marine ecosystem to be related (91 reef sites for coral and 85 for macroalgae). Figure 3.2 shows the different steps that encompass the model:

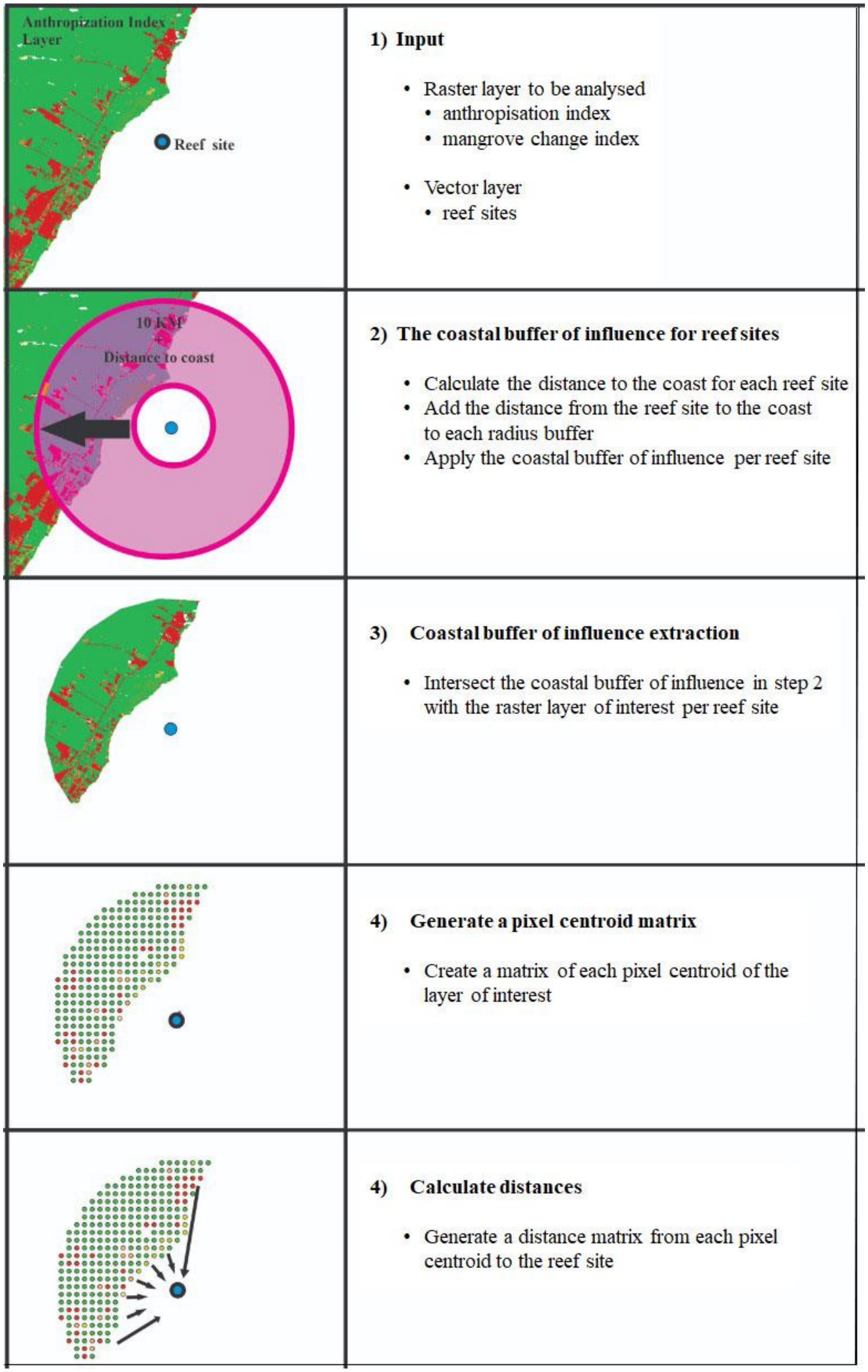

Figure 3.2 *Graphical model of the land-sea influence.*

We used the following equation 1 to calculate the anthropogenic index I:

$$I = \frac{\sum \frac{H}{\sqrt{D}}}{A_T} \qquad 1$$

Where:

D= distance within each coastal buffer of influence to the reef site

H= layer of interest (anthropogenic index, mangrove change index)

AT= total area of the buffer of influence

To facilitate the application of the model to each reef site, we used the graphical modeller of GRASS GIS 7.8.3 generated by a chain of operations wrapped into a single algorithm (see Appendix B, Figure S3.6 for further details).

Effects of stressors on benthic cover change

The effects of the stressors impacting coral and macroalgae cover change were assessed using linear mixed-effects models (LME); individual models were constructed for coral and macroalgae. We used 'lmer' in the 'lme4' package (Bates et al. 2015) in the R environment. Because the reef sites are nested in four subregions, we used the regions as a random effect to account for possible spatial autocorrelation. Depth was used as a fixed effect because it controls not only the reefs' construction pattern but also critical environmental conditions i., e., light dynamics. The 'lmer' function can easily handle nested and crossed cases without model modification (Bates 2005, Quiné and Berg 2008). The response variables were the change of coral or macroalgae cover measured in reef sites and were examined independently with LMER models using maximum likelihood. Each predictor (independent variable) was measured cumulatively, so there is only one value of the respective variable for each reef site. We also standardised all the predictors to facilitate the interpretation of the results. We included all explanatory variables in the model as fixed components when we first began the analysis. The significance was assessed using the 'lmer' Test's analysis of variance (ANOVA) tables produced from type II sums of squares with Satterthwaite degrees of freedom. Multiple stressors (predictors) effects were tested, fitting the model with an interaction term. Model selection was performed through sequential testing of the predictors. One of the purposes of model selection is a trade-off between model complexity and accuracy. Choosing the best model is challenging as the number of models grows exponentially with the number of factors. Therefore, the analysis started with the most complex model (all predictors and interaction terms) and sequentially removed or added the terms until no other variables could be deleted or added without a loss of fit. Finally, this algorithm determines the most informative predictors explaining the benthic change (coral and macroalgae) along the Mexican Caribbean. The reported results are based on tested predictors screening criteria of $p < 0.05$.

For the model validation, we assessed: 1) the distribution of the model residuals to guarantee they met the model assumptions. 2) The relationship between the model residuals and predictions to confirm the absence of spatial and temporal residual correlations, and 3) posterior predictive fit. Finally, R-squared was used to determine how closely the data resembled the fitted regression line. All statistical analyses were performed in R version 4.0.2 (R Development Core Team, 2020).

Random Forest

We fitted a Random Forests model in R version 4.0.2 (R Development Core Team, 2020) as a complementary approach to assess the predictive power of the variables tested in the LME regression when modelling the response variable (Cutler et al., 2007). It is a statistical learning technique that creates several decision trees using bootstrap samples of a data set (Hengl et al., 2018). Because this model is intended to be predictive, it allows us to assess if our covariates contain information concerning the state of the response variable while not requiring strict statistical assumptions about the distribution and stationarity of the target variable (Hengl et al., 2018). We used the default hyperparameters in R to predict the response variable (coral and macroalgae cover change) using all the independent variables (water quality, SST, bleaching alert, anthropogenic index of change, and mangrove change).

To assess its accuracy, we used the Out of Bag (OOB) error and OOB confusion matrix (Breiman, 2001).

3.1.4 Results

The coastal buffer of influence

Based on the buffer analysis (Figure 3.3a), we found that 78.45 % of the population is concentrated 10 km from the coastline and that the increase in population drops off after that (3.3b). Therefore, we used this 10 km buffer area to model the inland influence on our reef sites. First, a single model was calculated per reef site generating an individual inland influence (coastal anthropisation index and mangrove change index). We then used these results in the LMER models.

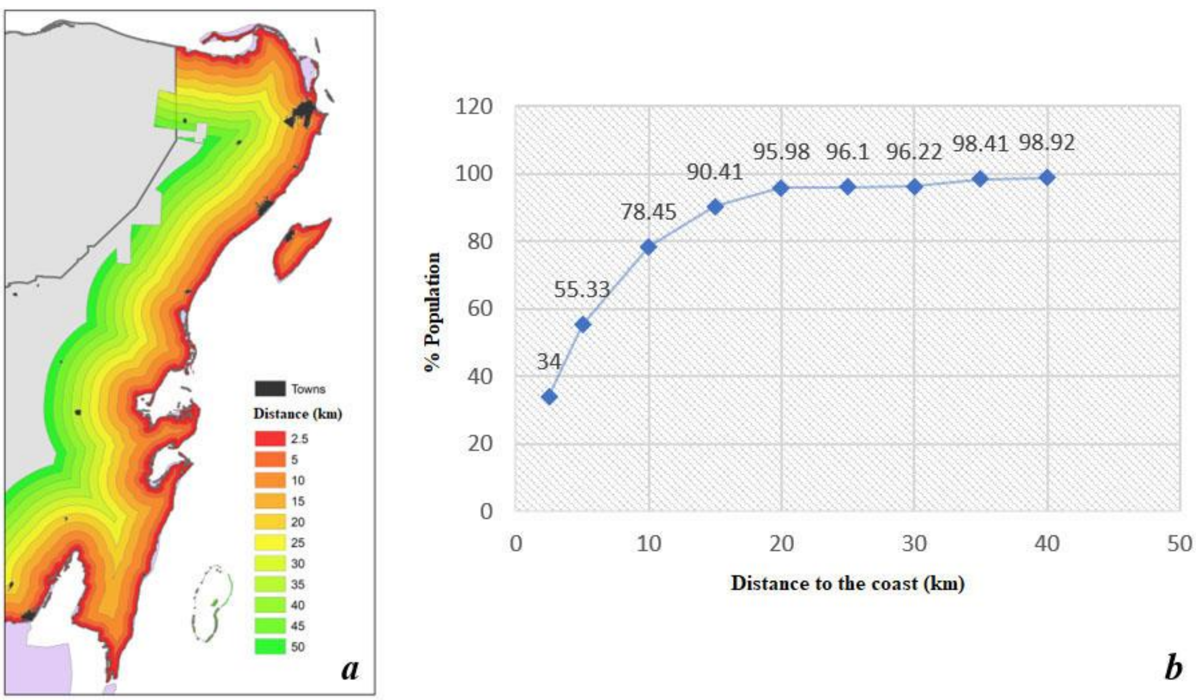

Figure 3.3 *a) Multiple distance buffers of influence the local population gathers. b) Concentration of the population with the distance to the coast. At 10 km, 78 % of the population concentrates. It is the buffer where the majority of the population is gathered.*

Indices

Hurricane index

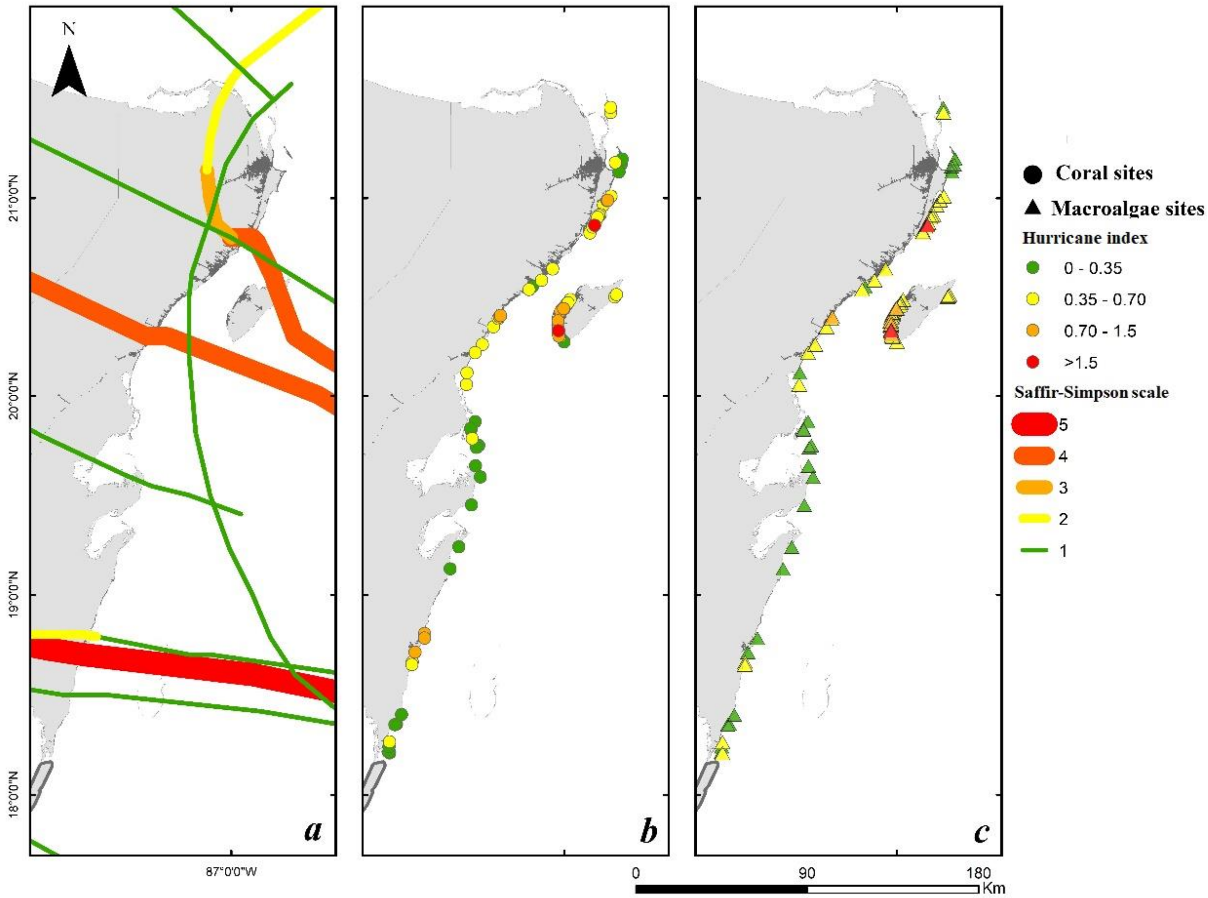

Figure 3.4 *Hurricane index for the Mexican Caribbean reef sites. a) Significant storms that passed in the Mexican Caribbean between 2005 and 2016, b) Hurricane index for coral sites and c) Hurricane index for macroalgae sites.*

Figure 3.4a shows the significant storms and categories that passed the Mexican Caribbean during the study period. Figures 3.4b and 3.4c show the assigned score for each reef damage category at each site for coral and macroalgae, respectively. Only three hurricanes between 2005 and 2016, categories 4 and 5, passed within 100 km of the Mexican Caribbean coastline, directly affecting 85 % of reef sites. In 2005 two hurricanes (Emily and Wilma) in category-4 significantly affected the reefs in the northern region. The southern region was hit in 2007 by Hurricane Dean (category-5).

Mangrove index of change

The mangrove index in Figure 3.5 resulted from the mangrove change map between 2005 and 2015. It was reclassified to generate a holistic index of change we could easily apply in our inland influence model analysis. The spatiotemporal (2005 – 2015) land cover change analysis for the Mexican Caribbean indicates that the major changes occur to the class 'other vegetation' (mainly represented by lowland rainforest), from this class approximately 10,600 ha changed to crop and animal husbandry and roughly 7,600 ha to anthropogenic development during the study period. In addition, the class of mangroves changed in total 1,441 ha to disturbed mangroves and 915 ha to other wetlands. It is essential to mention that the major changes were found in the northern Island of Cozumel and a lesser extent, in the Southern region.

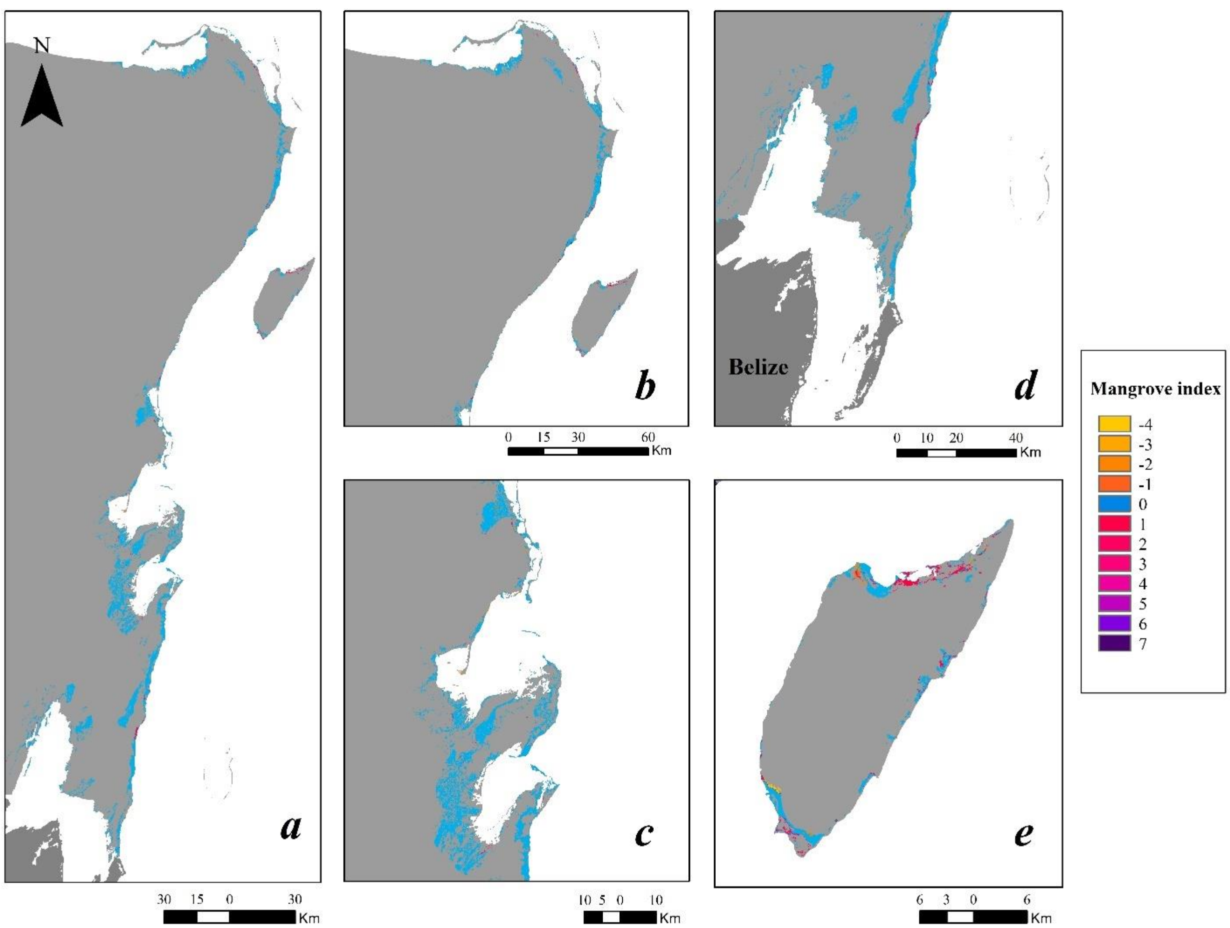

Figure 3.5 *a) Mangrove index of change, b) Northern, c) Centre, d) Southern, and e) Island of Cozumel.*

Anthropogenic index

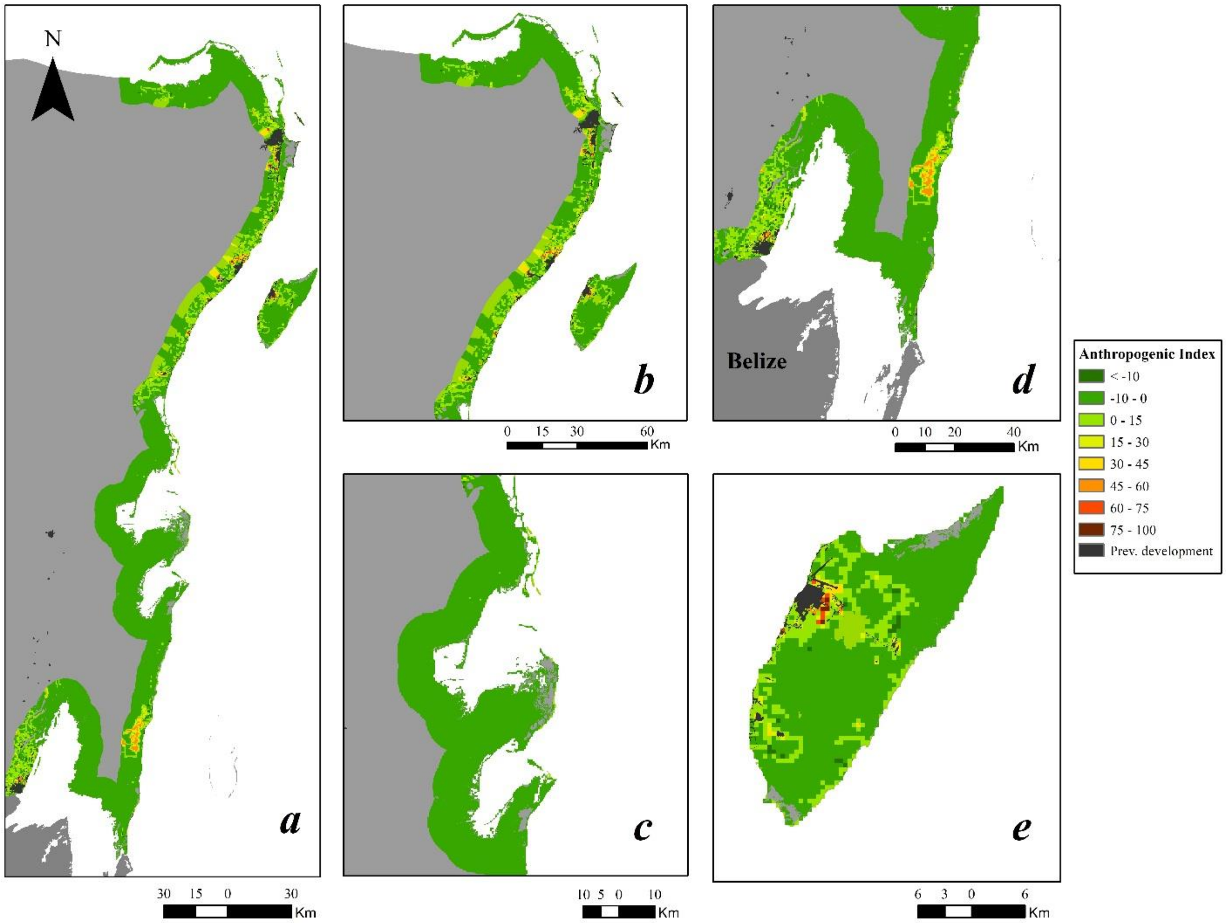

Figure 3.6 *Map of the anthropogenic changes 2005–2015 in the whole Mexican Caribbean (a) and by subregions, b) Northern, c) Centre, d) Southern and e) Island of Cozumel. The significant changes are expressed in dark red, the green areas are no change, and the negative numbers are vegetation gain.*

The level and dynamics of anthropisation vary significantly along the Mexican Caribbean. Findings reveal that the most critical activities in the Mexican Caribbean exerting anthropogenic pressures on the coastal area are: touristic areas, human settlements, transport routes, industrial areas, airports and landing strips (Figure 3.6). Thus, the primary anthropogenic pressure was 'touristic areas', increasing from 4,894 ha in 2005 to 7,819 ha in 2015, presenting a net change of 2,925 ha. 'Human settlements' followed with a net change of 2,853 ha; 10,777 ha were constructed in 2005, increasing to 13,630 ha in the regions built-in during the period till 2015. Transport routes presented an increase of 2,675 ha from 2005 to 2015. 'Industrial zones' increased by 536 ha, and airports and landing strips more than doubled their occupied area for the study period, 681 ha in 2005 compared to 1,645 ha in 2015. Figure 3.6 shows the anthropogenic index change between 2005 and 2015 for the Mexican Caribbean (a) and subregions (b - e). The major anthropisation expansion occurred on the Island of Cozumel (3.6 e), followed by the Southern region around Mahahual town (3.6 d). Even though the urban growth in the Northern area (3.6 b) around Cancun was ubiquitous since the 1980s, the development continued southwards along the coast until the Central region of Sian Ka'an in a persistent pattern.

Effects of stressors on benthic cover change

Based on 91 coral reef sites, our LME model showed that global and local stressors impact Mexican coral reefs (Table 3.3). Bleaching stress had a consistent negative effect on coral cover change (p-value = 0.002), followed by coastal anthropisation (p-value = 0.026). The hurricane influence positively affected the change in coral cover (p-value = 0.009). The interaction between the coral cover change stressors showed no significant effect. However, for the 85 macroalgae reef sites, the interaction effect of sea surface temperature and chlorophyll-*a* had a negative effect (p-value = - 0.0062).

Table 3.3 *LME model results. Abbreviations: Estimate (ES), standard error (SE)*

Factor	Coral cover change			Factor	Macroalgae cover change		
	ES	SE	p-value		ES	SE	p-value
Coral cover change	0.795	0.169	**0.008**	Intercept	2.121	0.347	0.103
Anthropogenic index	-0.265	0.13	**0.041**	SST	-0.461	0.314	0.124
Mangrove index	-0.211	0.118	0.073.	Chlorophyll-*a*	-2.082	0.720	0.228
Hurricane ifluence	0.321	0.138	**0.020**	POC	1.844	0.578	**0.001**
Beaching susceptibility	-0.708	0.237	**0.002**	SST*Chlorophyll-*a*	-1.004	0.347	**0.003**

The water quality predictors did not significantly differ in the coral cover change. Nonetheless, for macroalgae cover change, particulate organic carbon, the proxy for sedimentation and nutrients, also had a positive effect (p-value = 0.0014).

The R-squared explained the variance of 25 % for coral and 20 % for macroalgae. However, the Random Forest algorithm reported an internal out-of-bag estimate of 39.56 % for corals and 37.65 % for macroalgae.

3.1.5 Discussion

The present study is an integral approach including ecological data and remotely sensed information analysed with statistical methods to estimate the leading stressors in Mexican Caribbean reefs. Findings revealed that most Mexican Caribbean reefs are vulnerable to various threats, i.e., coastal development and water pollution, and are susceptible to temperature stress. These stresses may significantly influence the resilience and resistance of these reefs to cope with the imminent effects of anthropogenic climate change. According to previous research (Contreras-Silva et al., 2020), the benthic cover, specifically hard coral and macroalgae, rapidly declined in 2005 after the effects of the mass bleaching event and two category-5 hurricanes' impact. However, for the period analysed (2005-2016), both groups showed different paths marked by a rapid macroalgae increase (30 % in absolute cover), in contrast to the subtle recovery of hard coral cover (5 % in absolute cover). The results here indicate that coral cover change was impacted by thermal stress accumulation, because local temperature dynamics can change the physiologic endurance of coral populations to heat stress, which can also influence coral susceptibility to bleach (Schoepf et al., 2019). We did not find any indication that the tested stressors impacted the Mexican Caribbean subregions differently. Specifically, models on quality predictors, i.e., turbidity and sedimentation, positively affected the macroalgae cover change (showing an increase of 30 % for the period analysed, Contreras-Silva et al., 2020). It is well known that increasing sewage input, agricultural runoff, and sedimentation are potential changes associated with growing human densities that reduce water quality, promoting macroalgae increase (Burkepile et al., 2013). The hurricane index we tested positively affected coral cover change, probably because the damage extent is immediate after disturbance; here, we analysed 11 years with only two hurricanes in 2005 significantly affecting the northern and one impacting the southern Mexican Caribbean reefs.

Recent data suggest that the temperature threshold for coral bleaching has increased with global warming (DeCarlo et al., 2019). For the period of analysis (2005 - 2016), the sea surface temperature increased by 0.30 ℃ (Elías Ilosvay et al., 2020) and the heat stress of the Mexican Caribbean region oscillated between 2 ℃ (low-level thermal stress) and 3 ℃

(accumulating thermal stress) hotspots. Our results indicate that coral cover change was impacted by thermal stress accumulation, more likely hindering coral recovery (Donner, 2009), because local temperature dynamics can change the physiologic endurance of coral populations to heat stress, which can also influence coral susceptibility to bleach (Schoepf et al., 2019).

While numerous studies have examined the impacts of thermal stress on coral reefs (Bruno et al., 2007; Donner, 2009; Lough et al., 2018), there are few studies analysing local anthropogenic impacts along the Mexican Caribbean reefs (i.e. Randazzo-Eisemann et al., 2021, Banaszak, 2021; Rioja-Nieto and Álvarez-Filip, 2018; Suchley & Alvarez-Filip, 2018). Moreover, in the study area, the potential recovery of reef-building corals in the Mexican Caribbean is compromised by diseases (Alvarez-Filip et al., 2019; Randazzo-Eisemann et al., 2022) and the negative feedback loops associated with increased macroalgae cover and coral community change to the so-called coral "weedy" species (Doubleday and Connell, 2018; Perera-Valderrama et al., 2017). In the last four decades, coral reefs in this region have undergone severe cover changes (Contreras-Silva et al., 2020) with further implications for physical reef functionality (González-Barrios and Álvarez-Filip, 2018; Melo-Merino et al., 2022).

The water quality stressors did not significantly affect the coral cover change, probably due to the large-scale remote sensing data used (Hedley et al., 2018) and/or the temperature stress masking effects. Nonetheless, the local conditions in the Mexican Caribbean are continuously changing, primarily because of urban growth, pollution, and the arrival of the pelagic *Sargassum* since 2014. The risk of groundwater pollution is higher in karstic regions, including the Yucatan Peninsula, because rainfall permeates straight down towards the aquifer, potentially jeopardising the adjacent coastal environment (Personné et al., 1998).

Generating the 10 km buffer of influence allowed us to model the land-reef impacts by testing different stressors. However, our results are rather conservative because the inland-reef impacts depend not only on anthropogenic use. Regional geophysical and geomorphological factors also play an essential role (Hubbard, 2015; Medina-Valmaseda et al., 2020). Even though our model included reef depth, we missed data on lithology and slope characteristics.

The coastal anthropogenic development, resulting from the anthropogenic index, served as an indicator of how human activities affect coral reefs (such as nitrification and land-based runoff) (Cinner et al., 2017). The latter is the main contributor to coastal pollution, with most wastewater entering tropical waters without prior treatment (Hernández-Terrones et al., 2011, 2008, 2015). This index accounts for all anthropogenic features independent of the distance to population hubs. Therefore, it allows for the inclusion of many human activities like roads, bridges, farms, and landfills that could negatively affect reefs despite low nearby populations. The coastal anthropogenic stress in this area is expected to be exacerbated shortly due to the sustained construction of touristic facilities and increased water discharges that comprise agrochemical compounds, presumably from golf courts. Investigations showed that decreasing water quality causes an increase in the frequency and intensity of disease outbreaks (Randall and Van Woesik, 2017). In addition, since 2014, the Caribbean region has experienced the new stony coral tissue loss disease that endangers the reef community and the ecosystem services reefs provide to society (Alvarez-Filip et al., 2019).

According to this research, the rapid macroalgae increase from 2005 to 2016 of 30 %, reported by Contreras-Silva et al. (2010), was led by augmented nutrient inputs (POC). Marine macroalgae utilise various dissolved and particulate (in)organic carbon to photosynthesise and play an essential role in contributing to primary production (Diaz-Pulido et al., 2007) and marine organic carbon storage (Raven, 2018). Tropical macroalgae also play an essential role in building and cementation the reef framework, enabling coral settlement (crustose calcareous macroalgae) and creating habitats for other reef species (Ramírez-Viaña et al., 2021). However, when macroalgae replace reef-building coral species in the ecological phase shifts (Martínez-Rendis et al., 2015), they can also decisively transform whole reef systems. Warming temperatures benefit some taxa's primary productivity, especially weedy species like turf algae (Mertens et al., 2015). However, further studies in macroalgae composition are needed. We also found a negative interaction between temperature and chlorophyll-*a*, meaning that whereas macroalgae benefit from a high nutrient and sedimentation load, increasing temperatures harm tropical macroalgae by decreasing their growth rate (Koch et al., 2013). Likewise, temperature rise could reduce biomass production and generate phenological shifts in their canopy foundation, disturbing their capacity to sustain tropical marine ecosystems (Fulton et al., 2019). It is also important to mention that rising temperatures may benefit some tropical species over temperate zones in the long term by escalating their habitats to formerly colder, deeper regions, thus leading to geographical shifts of algal communities (Hernandez et al., 2018).

The hurricane index developed here represents a simple measure of hurricane impact on reefs; it provides a comprehensive overview of categorising storm intensity and spatial and temporal variability of events. Unsurprisingly, the hurricane impacts presented a rather positive effect on the coral cover. As is well known, in short periods, hurricanes can cool down high temperatures (Manzello et al., 2007) and their immediate damage is the physical impact on reef structure, changing the coral cover. Based on this index, the most significant reef damage levels generally occurred at sites closest to the hurricane eye, and sites far away from the main track of the storm may have received minor damage. In 2005, the northern region of the Mexican Caribbean and the Island of Cozumel experienced such impacts (Alvarez-Filip et al., 2009). On the bright side, the strength of waves associated with hurricanes can detach macroalgae from reefs, removing their biomass and reducing the coverage on reefs. It is a natural process that cleans space by removing macroalgae allowing new coral recruits (Rogers, 1993). In branching corals, fragmentation attachment facilitates fast growth and effective asexual reproduction recolonising new spaces (Edmunds, 2019). In the study period, the most severe hurricanes were Wilma and Emily for the northern region in 2005; and in 2007, hurricane Dean mostly impacted the southern region near Mahahual town. Only typical tropical storms were recorded in the subsequent years, indicating that the reefs had enough time to recover after the hurricane impacts.

Finally, the Random Forest supported our model and confirmed that the predictors tested here contain valuable information concerning the response variable. Nonetheless, incrementing the amount of factors might increase the explanatory power. Moreover, statistically significant p-values continue to show correlations even when the R-squared is low, and the interpretation of the coefficients is the same (Neter et al., 1989). Because the explained variance increases with the number of predictor factors included, for future work, we suggest including high spatial resolution satellite imagery such as Sentinel, available since 2016. Sentinel data are uncomplicated and inexpensive, able to map large areas at coarse spatial resolution and analyse and monitor changes in reefs and coastal ecosystems. Generating information from remote sensing and spatial analysis complements in situ measurements (Harvey et al., 2015). Given the enormous complexity of the marine and continental processes that lead to changes in coral and macroalgae cover, it is mandatory to take advantage of current technology.

3.1.6 Conclusion

This study comprehends a thorough approach to identifying global and local stressors impacting the Mexican Caribbean reef system. Our results reinforce the need for a nuanced, locally tailored approach to coral reef conservation that considers multiple cumulative stressors beyond the effect of the imminent anthropogenic climate change. New conservation efforts are required to maintain the biological significance of the region and to produce strategic conservation priorities. We suggest national-scale prioritising policies to protect reef biodiversity in the Mexican Caribbean.

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4.1 Coral reef recovery in the Mexican Caribbean after 2005 mass coral mortality - potential drivers

4.1.1 Abstract

In 2005, an extreme heatwave hit the Wider Caribbean, followed by 13 hurricanes (including 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 analysed 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 hard coral and macroalgae cover over time. Findings revealed increases in 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 algae colonisation 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 Mexican Caribbean's Central section, 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.

4.1.2 Introduction

Worldwide, coral reefs are subjected to natural and anthropogenic disturbances. Unprecedented loss of coral cover results from coastal development, hurricane impacts, and heat waves (Hughes, 1994; Goreau et al., 2000; Nyström et al., 2000). Some reefs around the world show coral recovery after such mass mortality events (e.g. Halford et al., 2004; Myhre and Acevedo Gutiérrez, 2007; Gilmour et al., 2013; Glynn et al., 2014; Graham et al., 2015; Pisapia et al., 2016). For instance, the Eastern Tropical Pacific corals recovered 30 % in 13 years after the El Niño phenomenon in 1982-1983 (Glynn et al., 2014). Likewise, the coral cover in Seychelles increased by 23 % in 13 years after the 1998 bleaching event (Graham et al., 2015). The North-Western Australian reefs showed a 35 % coral cover recovery within 12 years after the 1998 bleaching event (Gilmour et al., 2013). The primary mechanism leading to coral recovery is the recruitment of sexually-produced corals (Graham et al., 2011; Holbrook et al., 2018). Additionally, high herbivore grazing capacity (Mumby and Harborne, 2010; Gilmour et al., 2013; Graham et al., 2011), high coral and fish diversity (Hooper et al., 2005), and isolation from chronic anthropogenic pressures (Gilmour et al., 2013) can enhance coral recovery.

However, few studies have reported that reef condition improves after mass mortality events in the Caribbean Sea. For example, Rodriguez-Martínez et al. (2014) described a ca. 20 % increase in *Acropora palmata* cover in the Northern part of the Mexican Caribbean after the impact of the hurricanes in 2005. Hard-coral cover was reported to double from 23 % to 53 % between 1995 and 2005 in Jamaica (Idjadi et al., 2006). However, the only region-wide evidence of a recovery in coral cover was recently provided by a meta-analysis in the Mexican Caribbean, which showed a slight increase of coral cover between 2005 and 2016, despite the macroalgae increase found during that same period (Contreras-Silva et al. 2020). On the contrary, many studies are reporting how reefs in the Caribbean Sea are failing to recover after such events (Connell, 1997; Gardner et al., 2005; Baker et al., 2008; Rodríguez-Martínez et al., 2014), other studies suggest that the coral and macroalgae cover has remained relatively constant since the mid-1980s (Schutte et al., 2010). Roff and Mumby (2012) 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 (Aronson and Precht, 2001), the mass mortality of the sea urchin *Diadema* in 1983-1984 (Jackson et al., 2014) or the El Niño induced bleaching event in 1998-1999 have affected Caribbean coral reefs. In 2005 (May to October), the Wider Caribbean was subjected to a heatwave of + 1.2 °C above summer maximum values (Wilkinson and Souter, 2008; Eaking et al., 2010). It was described by Eakin et al. (2010) as one of the most extreme coral bleaching and mortality events affecting the wider Caribbean (Wilkinson and Souter, 2008; Eaking et al., 2010). On average, 50 – 95 % of the coral colonies bleached, and in the U.S. Virgin Islands, ca. 51 % died due to bleaching and subsequent coral disease (Wilkinson and Souter, 2008).

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 (Eakin et al., 2010). However, the warm water anomaly contributed to the following record hurricane season in the same year (Trenberth and Shea, 2006; Eakin et al., 2010). The 2005 hurricane season ended with a record of 26 storms, including 13 hurricanes (Wilkinson and Souter, 2008). Storms of Category 5, including hurricanes Emily (July) and Wilma (October), greatly impacted the Northern MC (Trenberth and Shea, 2006; Álvarez-Filip et al., 2009). Unfortunately, just a few studies are assessing the effects of the 2005 mass mortality event. McField et al. (2005) reported 9 % overall coral mortality in Mexico, whereas surveys by Álvarez-Filip et al. (2009) reported a 56 % live coral cover decline after hurricanes Emily and Wilma at Cozumel Island. A recent meta-analysis showed that coral cover has slightly recovered (between 2005 and 2016; Contreras-Silva et al. 2020). However, very little understanding is known about the drivers that have promoted this coral cover increase.

Understanding the environmental and anthropogenic conditions favouring the increased coral cover 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 (INEGI, 2010). Different studies point out that the degradation of reefs may be correlated with the tourism industry (Gil et al., 2015, Martínez-Rendis et al., 2015) and can facilitate phase shifts of coral reef communities towards algae dominance (Martínez-Rendis et al., 2015; Arias-González et al., 2017). The tourism industry is one of the greatest challenges in the MC since it has developed tremendously since the mid-1970s (Spalding et al., 2001). Currently, over 10 million tourists arrive annually (Rioja-Nieto and Álvarez-Filip, 2019), and in 2016 the gross income of tourism for the Mexican state Quintana Roo alone was $ 8810 Million US dollars (Sedetur, 2017). The growing tourism can decrease water quality (Baker et al., 2013) as it is usually joined by increasing liquid and solid waste discharge into the ocean (Molina et al., 2001; Padilla, 2015).

Here we set out to analyse the development of hard coral and macroalgae cover, as an indirect measure of reef degradation (Hughes, 1994; Bruno and Valdivia, 2016; Suchley et al., 2016), 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 (Bozec et al., 2008; Arias-González et al., 2017; Suchely and Alvarez-Filip, 2018). 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.

4.1.3 Methodology

Data Collation

Spanning approximately 450 km along the Mexican Caribbean, 254 quantitative benthic surveys (hard coral and macroalgae) were analysed from 2005 to 2016 (Figure 3.7) after the bleaching event and the hurricanes Emily and Wilma. This data was a subset of the database used by Contreras-Silva et al. (2020); 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. The UNAM Biodiversity and Reef Conservation Laboratory gathered the data and came 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), Landazuri et al. (2002), Perera-Valderrama et al. (2016), and Rodríguez-Martínez et al. (2012). The benthic surveys were conducted using AGRRA (Atlantic and Gulf Rapid Reef Assessment) versions 4 and 5 and SAM (Mesoamerican Reef System) protocols (Appendix B, Table S3.2). The Benthos protocol in AGRRA version 4 used intercept length measurement, whereas version 5 used point intercept methodology (PIT; Loya 1972) as the SAM protocol

(Appendix B, Table S3.2). More detailed information is found in Contreras-Silva et al. (2020). It is also important to mention that the only permanent reef units in the database were those in Puerto Morelos from 2012 to 2016. The remaining sampling sites presented specific coordinates (from GPS systems) for a revisit period. The systematic sampling approach is most useful for primary trend analyses, where evenly spaced samples are collected for an extended time (Burton and Pitt 2002). The number of replicates per site and each year was considered high enough to neglect the spatial variability caused by haphazard transects. One possible bias caused by the spatial variability would be the sampling of different coral reef types; therefore, this factor was included in the analysis. The hard coral and macroalgae (fleshy and calcifying) cover surveys corresponded to 48 reef sites along Mexico's Caribbean coast (Figure 3.7). 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 5,000 m away from the coast.

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. (2008), Arias-González et al. (2017), and Suchley and Alvarez-Filip (2018)) four factors were selected as proxies: sea surface temperature (SST), chlorophyll-*a* water concentration, coastal human population and coral reef distance to the shore.

Sea surface temperate (SST)

Remote sensing data for the SST (in °C, 0.25° spatial resolution) (Banzon et al., 2016) was extracted from the Monthly Optimum Interpolation Sea Surface Temperature (OISST) database of the National Oceanic and Atmospheric Administration (NOAA) of the United States.

Coastal development

Chlorophyll-*a* water concentration was used as a proxy for nutrient concentration and eutrophication as used, e.g., by Duprey et al. (2016), Reynolds and Maberly (2002) and

De'ath and Fabricius (2010). Chlorophyll-*a* concentration directly correlates with nitrogen, phosphorus and suspended solids (De'ath and Fabricius, 2010). For this, monthly data satellite 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. The human population data per locality of 2005 and 2010 were collected from the National Institute of Statistics and Geography (INEGI) of Mexico. 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.

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 3.7) as proposed by Jordán-Dahlgren and Rodríguez-Martínez (2003). The reefs in each subregion are exposed to different levels of anthropogenic pressure, e.g., the North MC is a hotspot for tourism and coastal development. In contrast, the Central MC comprises the entire Sian Ka'an Biosphere Reserve (Molina et al. 2001). To test any spatial variability in hard coral and macroalgae benthic cover development, the sub-region to which each site belonged and the latitude at which each monitored reef was located were also analysed as a factor 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-region of the Mexican Caribbean. Furthermore, the North MC was the most affected region by the hurricanes Emily (July) and Wilma (October) (Trenberth and Shea, 2006; Álvarez-Filip et al., 2009).

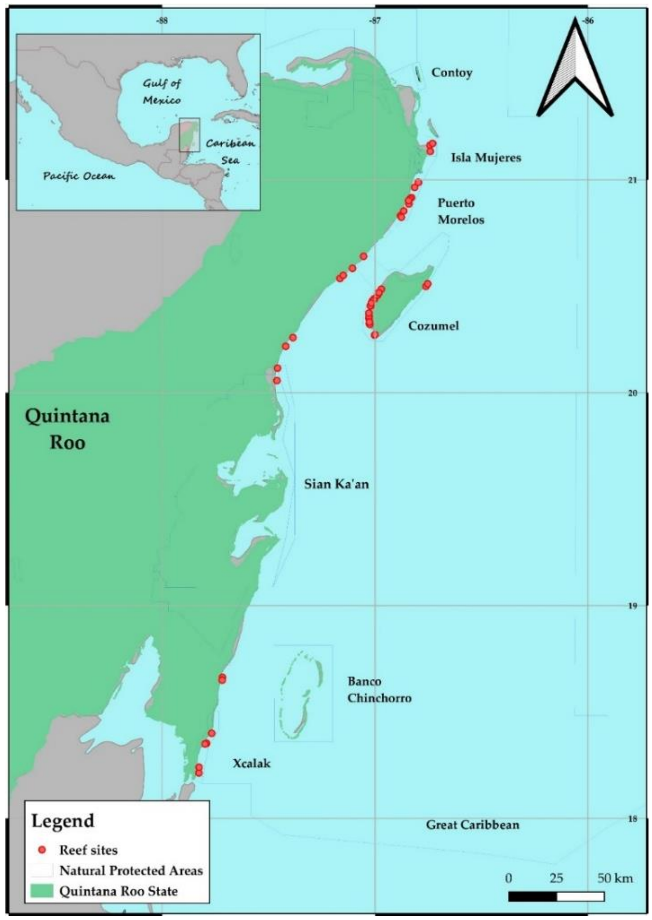


Figure 3.7 *Study area (created with QGIS Development Team, 2019. QGIS Geographic Information System. Open-Source Geospatial Foundation. http://qgis.org). Polygons in blue represent the Natural Protected Areas in the Region. The red dots are the reef monitoring sites for the hard coral, and macroalgae cover meta-analysis.*

Further factors

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

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. 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 the distance to the source of pollution (Bourke et al., 2005; Bourke et al., 2011; Ramos-Sharon et al., 2015; Roberts et al., 2017). The closer the reefs are to cities and other human settlements, the bigger affectations they will encounter from terrestrial pollution. According to Bourke et al. (2011), this proxy is measured based on the location of human settlements and 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 dissolving in the seawater (Chow et al., 2004; Osadchiev and Korshenko, 2017). An extra 5 km was added, assuming that rural and urban cities 5 km from the coast still discharge human waste directly to the sea (Hernández-Terrones et al., 2015). Therefore, all human populations within a 10 km radius of the monitoring site were added to the total population per monitoring site. From this data, a ratio was used to compare the change in population size as follows:

Population ratio= (Population 2010)/(Population 2005)

A Kruskal-Wallis rank-sum test was conducted to compare the human population differences of the four mentioned sub-regions of the MC.

Meta-analysis

This study conducted a random-effects meta-analysis of the hard coral and macroalgae cover in the statistics program R 1.0.136 using the metafor package (Viechtbauer, 2010). A limitation of monitoring data is the large random variability caused by the difference in survey methods, surveyors and data sources. This can limit the meta-analysis results (Koricheva et al., 2013; Viechtbauer, 2010). 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 (Koricheva et al., 2013; Viechtbauer, 2010). According to Koricheva and Gurevitch (2013), the control of type II error rates can be identified because the low power of individual studies to detect an effect is “corrected” by accumulating 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 (Koricheva et al., 2013).

In this study, instead of using the relative annual rate of change as in Contreras-Silva et al. (2020) or Alvarez-Filip et al. (2011), we calculated the individual effect size as the slope over time of the hard coral and algae cover of generalised linear models (GLM) using the glm function. The GLM was used to detect a simple but statistically 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 sampling error. The input of the meta-analysis was as follows: yi, the individual effect size and vi, the sampling error.

MES = rma (yi, vi)

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 follows:

ES = rma (yi, vi, mods = *factor*)

To test for variability caused by the different number of monitoring years, monitoring methods and the number of surveyors, these factors were also tested in the meta-analysis as fixed factors. All analyses were performed in R1.0.136.

4.1.4 Results

The meta-analysis showed a significant increase in 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 3.8). This corresponds to a 6.4 ± 1.3 (SE) % coral cover increase 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 3.8 the difference between the hard coral and macroalgae cover was not significant. Figure 3.9 presents macroalgae cover spatial differences, with the central region as the only significant increase.

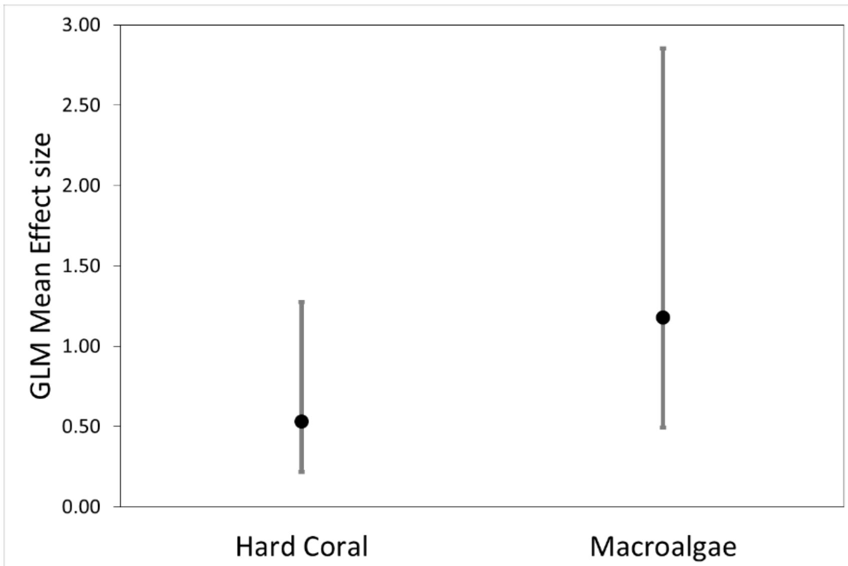


Figure 3.8 *Mean effect size of the random effect meta-analysis on the hard coral and macroalgae cover along the coast of the Mexican Caribbean. Error bars indicate 95 % confidence intervals*.

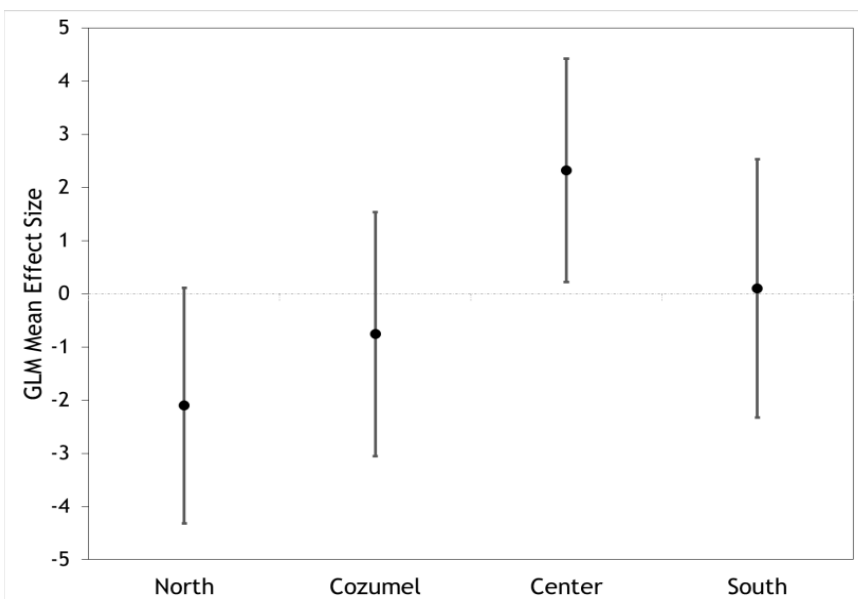
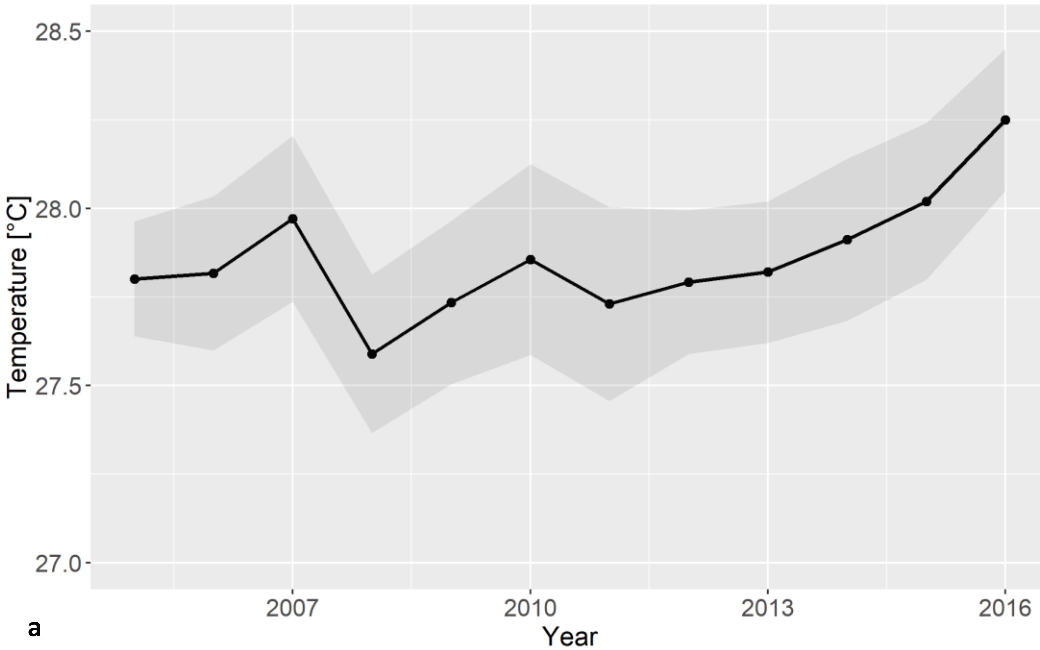


Figure 3.9 *Macroalgae mean effect size of selected subregions of Quintana Roo (MC) calculated using a general linear model from 2005 to 2016. Error bars indicate 95 % confidence intervals.*



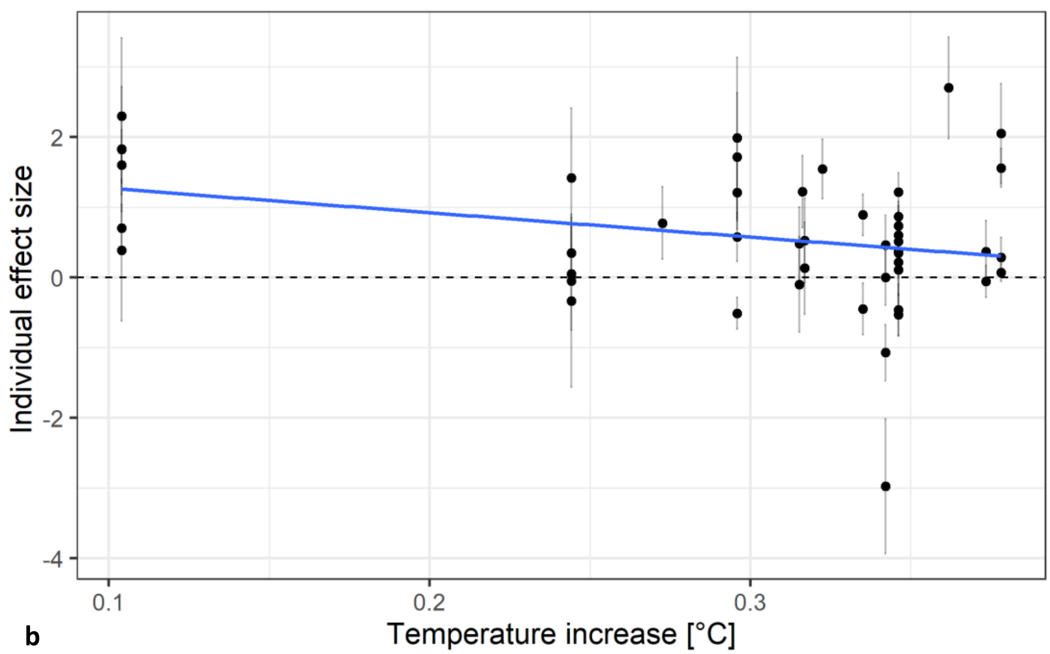


Figure 3.10 *Sea Surface Temperature development and effect on the hard coral cover development from 2005 to 2016 using calculated yearly means (supplementary material dataset S5):* ***a)*** *Yearly mean of monthly values from Optimum Interpolation Sea Surface Temperature (OISST) data from the National Oceanic and Atmospheric Administration (NOAA). Shade: 95 % confidence interval (Meta-analysis p-value <0.001);* ***b****) Individual hard coral cover effect size against temperature increases per site. Error bars indicate standard error. Blueline indicates a negative correlation (P = 0.019).*

The SST increased along the coast of Quintana Roo (Figure 3.10a); 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 3.10a). The chlorophyll-*a* water concentration showed no clear trend (effect size: 0, $P = 0.97$). This was the only factor significantly affecting the hard-coral cover from 2005 to 2016 (Table 3.4). The hard-coral cover increased less with a higher temperature increase rate (Figure 3.10b). Conversely, no significant effect of any individual factor (Table 3.4) 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 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 subregion and Cozumel Island, it remained stable (Table 3.4). The sites with higher initial macroalgae cover showed faster macroalgae cover growth ($P = 0.021$).

Table 3.4 *Proxies effect on hard coral and macroalgae benthic cover in Mexican Caribbean coral reefs mean effect size using random-effects meta-analysis*

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: forereef	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	0.3	0.89	0.138	0.6
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

The human coastal population was twice as high in 2010 as in 2005 (Figure 3.11a). However, the population change was variable between subregions (Figure 3.11b). The highest rate of change was observed in North MC (3.7). At the same time, Cozumel Island showed the lowest one (0.7). The human coastal population growth rate (Figure 3.11b) was only significantly higher in North and South MC than in Cozumel Island (Wilcox pairwise comparison $P = 0.0002$).

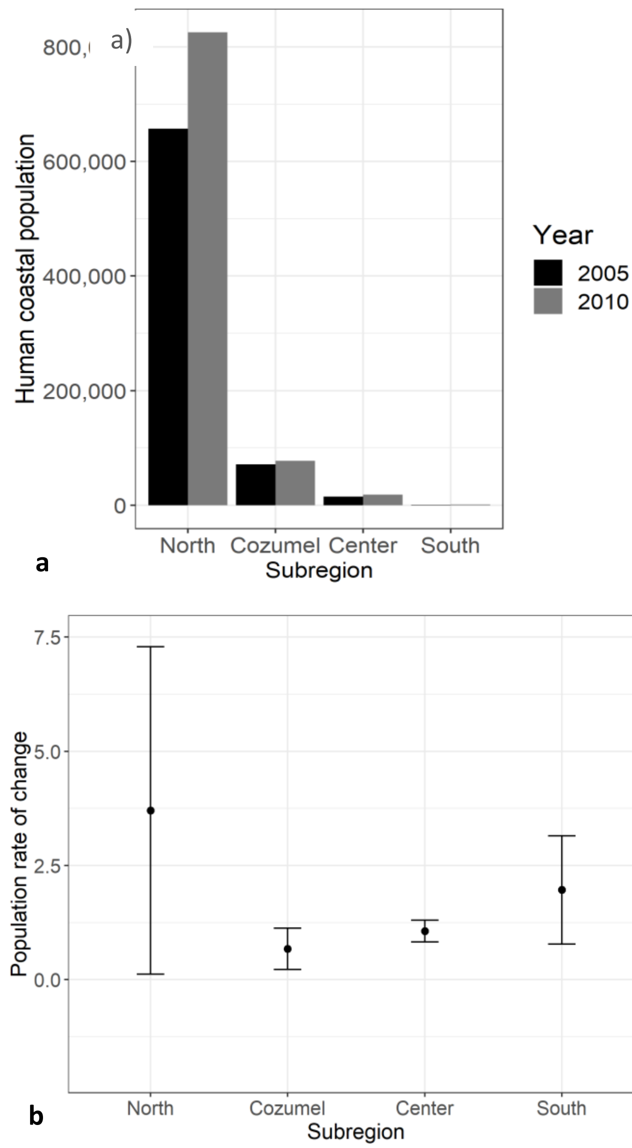


Figure 3.11 *Coastal human population per locality in the Mexican Caribbean. Population data from the National Institute of Statistics and Geography (INEGI) (INEGI, for the Spanish original) from 2005 and 2010: (a) Coastal human population per MC subregion in 2005 and 2010; (b) Mean population rate of change in the four subregions of the Mexican Caribbean from 2005 to 2010. Error bars indicate standard deviation—Kruskal-Wallis rank sum test p-value = 0.0002.*

4.1.5 Discussion

This study aimed to identify potential drivers of coral and macroalgae increase along the Mexican Caribbean after the 2005 bleaching event and following hurricanes. The results showed a hard-coral cover increase of approx. 6.4 % in 12 years. These results reflect those of Contreras-Silva et al. (2020), who also found a modest but significant coral recovery for the same period analysed 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 analysed factor that affected 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 north of the central area) and therefore need to be interpreted cautiously.

Even though the coral cover increase suggests coral recovery after the events of 2005, the recovery rate was relatively slow when compared to recovery rates (ca. 25 – 35 % in 11- 13 years) reported in other regions of the world (e.g. Glynn et al., 2014; Graham et al., 2015; Pisapia et al., 2016). For the Mesoamerican Reef, including the MC, subtle but significative increases have been reported recently (e.g. Suchley et al., 2016; Rioja-Nieto and Alvarez-Filip, 2019), supporting the trend described here. Still, thus far, mainly local hard coral recovery cases have been reported elsewhere in the Caribbean (Edmunds and Carpenter, 2001; Idjadi et al., 2006; Martínez et al., 2014). Gardner et al. (2005) found no evidence of coral recovery after hurricane impacts between 1980 and 2001 in this region. The hurricanes in 2005 could have released suitable substrate for coral recruits to settle, as described by Rogers (1993) and Graham et al. (2011) or could have allowed coral recolonization through hurricane-generated asexual recruit, as observed by Lirman and Fong (1997) in the Caribbean. Nevertheless, 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 analyse species composition. For instance, the coral recovery measured by coral cover could be reflecting an increase in fast-growing corals, as has been reported by Guzmán and Cortés (2007) in the eastern Pacific or by Estrada-Saldívar et al. (2019) in the Caribbean, and Perera-Valderrama et al., (2016) in North MC. This species composition change may cause a reduction of hard coral diversity and possibly decrease ecosystem functioning (Alvarez-Filip et al., 2013; Graham et al., 2011; Estrada-Saldivar, 2019). Thus, the species development after the 2005 events should be studied as a next step.

Alternatively, the simultaneous and much faster increase of macroalgae may suggest that the free space left by lost hard corals due to the physical disturbance of the hurricanes in 2005 in the Mexican Caribbean (Wilkinson and Souter, 2008) could have also been occupied by faster-growing macroalgae that may outcompete slow-growing hard corals (McCook et al., 2001; Barott et al., 2012). 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 significantly affected the macroalgae mean effect size (Appendix B, Table S3.3).

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 subregion (-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 variability of macroalgae cover development (Figure 3.9). The Central Mexican Caribbean comprises the Sian Ka'an Biosphere Reserve (Figure 3.7). It is characterized by a complex hydrological system composed of wetland and mangrove forests (Mazzotti et al., 2005). The coral reefs in Sian Ka'an may be exposed to the constant discharge of nutrient-rich freshwater that could benefit algae growth (Mazzotti et al., 2005). To our knowledge, this is the first time that such a fast macroalgae growth (~ 28 % in 12 years) has been reported in the protected area's reefs. The Central MC was the least surveyed subregion, with only two monitoring sites, and this rapid change in the benthic composition needs to be more closely monitored.

This study tested four proxies of change drivers: 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 (Edinger et al., 2000; Hughes et al., 2003; Burke and Maidens, 2004). The SST did increase significantly to 0.31 °C from 2005 to 2016 at a similar rate to the ones reported in the literature (Strong et al., 2008; Chollett et al., 2012). Only SST affected hard-coral cover.

Results showed that with higher temperature increases, coral recovery was slower (Figure 3.10b). A recent study by Muñiz-Castillo et al. (2019) corroborates these findings. Hughes (1994) and Nyström et al. (2000) suggested that chronic disturbances, such as slow temperature increase, can disadvantage recovery. This may be the case in the MC, showing a relatively slow coral recovery after the 2005 mass mortality events. The other 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. (2012) discussed, the spatial resolution of the remote sensing data (water chlorophyll-*a* concentration) could be too broad to capture local small-scale variations (Jordán-Dahlgren and Rodríguez-Martínez, 2003), as it may average measurements over large distances (1 km in this case) (Chollett et al., 2012). Nevertheless, this is the only chlorophyll-*a* data available at such spatiotemporal scales, and this database has been used in other studies (Acker et al., 2008; Gohin, 2011)). 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 relationships is minimized. The observed hard coral cover increase could have masked the effects of the analysed factors. The human coastal population increased in all four sub-regions. North Quintana Roo had the highest coastal human population, as reported by literature (INAFED, 2010). The Wilcox pairwise comparison showed no significant difference in the human population growth rate between North, Central and South MC. This suggests Central and South MC may reach 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. (2008). Nonetheless, tourism is an essential factor to consider in future research. Tourism in the MC contributes significantly to the Mexican economy and has been identified as negatively impacting MC coastal ecosystems (e.g. Bozec et al., 2008; Martínez-Rendis et al., 2015; Padilla, 2015).

The findings in this study also inform the current discussion about the relative contribution of local versus global factors to reef degradation (Bruno and Valdivia 2016; Smith et al. 2016). Our findings suggest that global events have catastrophic effects on the Mexican Caribbean reefs, yet the reefs showed recovery capacity. Firstly, this study indicated that the SST increase slowed 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 regional studies (Bozec et al., 2008; Arias-Gonzalez et al., 2017; Suchley & Alvarez-Filip, 2018). 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 the stimulation of algae growth.

4.1.6 Conclusion

Our meta-analysis confirms 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. (2020) using a different methodology. This confirms the results that are generally limited caused 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 transects. Still, to our knowledge, this is the first study investigating how anthropogenic factors affect coral reef recovery processes over extended 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 the spatiotemporal development of reef ecosystems, thereby supporting management efforts.

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Chapter 4

CONCEPTUAL FRAMEWORK FOR A REEF MANAGEMENT STRATEGY

Photo credits: CONABIO, *Orbicella Annularis*

This work is in preparation for *Conservation Letters*:

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4 Reef Cybercartographic Atlas framework as an innovative and integrative tool for the sustainable management of Mexican Caribbean Coral Reefs

4.1 Abstract

Coral reefs are among the most endangered ecosystems in this era due to anthropogenic climate change and chronic local impacts. Mexico is an emerging country and home to the state of Quintana Roo, where Cancun, a top tourist destination, is located. Here tourism forms the foundation of the local economy, coastal livelihoods, and cultural practices. Coral reefs are the basis of tourism, contributing to 9 % of the country's GDP. Despite monitoring and restoration efforts, coral reefs here have deteriorated over the past few decades, which begs the question of why and how protection and management may be improved. To enhance coral reefs' sustainability and governance, managers, scientists, divers, fishers, and the local community should be involved in creating a national policy. Thus, we aim to generate a conceptual framework for an integrated management strategy to improve the understanding of the unique and vital services that coral reef ecosystems in the Mexican Caribbean provide and successfully invert the unsustainable economic and social trends through adequate scientific communication. The ultimate objective is to access arguments that serve as a baseline in assisting and setting priorities for governance in political decisions. We propose Geomatics as a transdisciplinary and integrative science able to generate solutions for complex systems such as coral reefs. Within this spectrum, Cybercartographic atlases offer an excellent method for creating a conceptual framework for such a management tool.

4.2 Introduction

Since historical records, humanity has continued to alter Earth's biophysical dynamics (Steffen et al., 2015). Consequently, ecosystems are confronted by increasing risks as human activities intensify and spread. Therefore, interest in protecting nature has emerged in contemporary society as it has become aware of our severe environmental crisis. Coral reef ecosystems are one of the most impacted ecosystems worldwide, mainly by the effects of local anthropogenic activities and climate change, an issue that requires immediate policy response (Woodhead et al., 2019). Coral reef loss implicates biodiversity decline and losses for the nearly 400 million people who rely on them for food, coastal protection, and work (Cinner et al., 2017).

In the Western Caribbean, the Mesoamerican Reef system is considered a biodiversity hotspot and an economically vital area because it sustains more than two million people from four countries: Guatemala, Honduras, Belize, and Mexico (McField & Kramer, 2006; Padilla, 2015). Mexico is an emerging country and home to the state of Quintana Roo, where about eighty per cent of the population lives within 10 km of the Caribbean coast. Here tourism forms the foundation of the local economy, coastal livelihoods, and cultural practices. Coral reefs are the keystone of the local economy (Padilla, 2015), reef-based tourism contributes 9 % of the country's GDP, and the state is home to Cancun, a top tourist destination in the world (Fraga & Robledo, 2022). The tourism industry has developed rapidly since 1970. In just forty years, the Yucatan region where Cancun is situated went from remote agricultural to a significant, popular tourist destination. The landscape changed dramatically to sustain over two million guests arriving in Cancun each year, whether they travel on land or cruise ships, resulting in an uncontrollably expanding business growth such as airports, roads, resorts, and golf camps, accompanied by massive deforestation, loss of mangroves, and filling of wetland regions (Padilla, 2015).

Coral reef protection in the Mexican Caribbean has become the focus of governmental agencies in the last decades; however, it has not been given enough attention to drive a fundamental change in public policy. The country's primary legal document at the federal level relating to nature protection is the General Law for the Ecological Equilibrium and Protection of the Environment. However, its application to natural resource usage, conservation, preservation, and restoration tactics is limited (Rioja-Nieto et al., 2019). Only since 2016 has the whole reef area been covered by governmental biodiversity protection and was nominated as Natural Protected Area (NPA). Before 2016, 16 local NPAs with different protection statuses were established along the coast (Ardisson et al., 2011). Locally, several monitoring programs have been devised and implemented, mainly in the last 20 years, with support from government agencies, civil society, and academia. In the

Mesoamerican region, the Healthy Reefs for Healthy People Initiative, HRI, since 2003, has been responsible for tracking the reef system's state (McField & Kramer, 2006). Besides HRI, numerous monitoring programs have been set in motion, analyzing the different status and health indicators, e.g., AGRRA (Lang et al., 2010); CARICOMP (Carrillo-García & Kolb, 2022; Hodgson, 2001; Kjerfve et al., 1998; Martínez-Fernández et al., 2020; Martínez-Fernández et al., 2021; Selig et al., 2013); Reef Check (Hodgson, 2001). Carrillo-Garcia and Kolb (2022) reviewed ten existing monitoring protocols and proposed a monitoring indicators framework for the Western Caribbean. A framework or model addressing biophysical and ecological factors is undoubtedly relevant and a big step forward. Nevertheless, it could be more robust to the magnitude of the reef landscape and associated ecosystems if it included the human dimension. Several authors point out that integrated social, economic, institutional, and environmental measures and their interconnections should be used to analyze complex systems such as coral reefs to set solid conceptual foundations for effective political action (Martínez-Fernández et al., 2020; Martínez-Fernández et al., 2021; Selig et al., 2013). Therefore, besides social and academic pressure, it is crucial to combine data from many sources and analyse and process them so that managers and decision-makers can quickly understand the problems.

Despite monitoring and restoration efforts, coral reefs in the Mexican Caribbean have deteriorated over the past few decades (Contreras-Silva et al., 2020; Molina-Hernández et al., 2022), which begs the question of why and how protection and management may be improved. Several authors highlight the importance of integrating local users and communities to enhance coral reef sustainability and governance (Morrison et al., 2020; Turner et al., 2014; Turner et al., 2017). According to Anthony et al. (2020), evaluating governance efficacy with regards to managers, scientists, divers, fishers, and the local community is the first step to determining what has to be changed and how. Thus, we aim to generate a conceptual framework for an integrated management strategy to improve the understanding of the unique and vital services that coral reef ecosystems in the Mexican Caribbean provide and successfully invert the unsustainable economic and social trends through adequate scientific communication. The ultimate objective is to access arguments that serve as a baseline in assisting and setting priorities for governance in political decisions.

Integrating ecological and social systems into a framework as a management tool at different multi-temporal scales is challenging. Moreover, it has to be flexible enough to address foreseen and unpredictable feedback between systems components in the reef complex. Hence, we proposed Geomatics as a transdisciplinary and integrative science able to generate solutions for complex systems such as coral reefs. Within this spectrum, Cybercartographic atlases are artefacts that offer a suitable method for creating a conceptual framework for such a management tool (Reyes, 2005). In this paper, we first briefly provide an overview of the reef system in the Mexican Caribbean. Then, we develop the conceptual framework's systemic components and elaborate on the joined approach for a coral reef management cybercartographic atlas framework.

4.3 The Cybercartographic Atlas Framework

Creating societies that facilitate the sustainability of coral reefs depends on understanding and managing human-environment interactions at the local, national, and regional levels with implications in the international and global context (Bache & Flinders, 2004). Therefore, analysing the natural and social systemic components through different but integrated conceptual approaches is essential. Geomatics is an emergent discipline defined as the set of sciences involving the acquisition, conversion, processing, generation, analysis, management, representation and dissemination of geographic information. Complex solutions in Geomatics offer the possibility of investigating the different pressures of the reef system in a holistic and transdisciplinary way. With the premise of understanding the complexity and driving factors of change in coral reef ecosystems, a suitable approach to construct a conceptual framework for a management strategy is provided by cybercartographic atlases.

Cybercartography is "the application of geographic information processing to the analysis of topics of interest to society and the display of the results in ways that people can readily understand" (Taylor, 2013). It is conceived as a construction process framed in interdisciplinary knowledge incorporating a holistic method to analyse the emerging significant global changes in this contemporary era (Reyes et al., 2013).

The rapid degradation of coral reefs worldwide and the environmental services vital to society makes it mandatory to address current socio-ecological challenges for sustainable management. Thus, a better way of understanding reef complexity within the range of environmental stressors caused by human activity must involve a variety of tools informing that the services provided to society are also under threat, including linguistic, mathematical, statistical, visual and cartographic languages. Cybercartographic atlases are open communication paradigms created from three perspectives: as a meta-model: several models contained in a large model; as a knowledge representation, where problems can be observed with an integral or holistic approach; and as a communication artefact, including the use of virtual maps, geo-text, films, photos, space maps, satellite images, computer simulations, graphs, sound, and diagrams as part of its development (Martinez & Reyes, 2005). Through this kind of atlases, there is a perspective of problem-solving, support for public policy processes and consultation among local stakeholders (Taylor, 2019), providing a meeting point for dialogue and subsequent action (decision making).

A cybercartographic atlas construction requires a systematic approach with comprehensive spatial representation. An atlas's complete development and implementation include three main stages: 1) conceptual framework formulation, 2) product design, 3) product dissemination and application, and 4) stage of feedback, monitoring and evaluation of the atlas itself. However, for a complete artefact creation, all stakeholders, including civil society, academy, government, and other authorities in charge of natural resources planning and management, should be involved to understand the entire product creation, development and its consequences (Martinez & Reyes, 2005). Therefore, this study concerns itself only with the first stage.

4.3.1 Meta-model definition

To generate an integrated framework for the sustainable management of Mexican reefs, it is essential first to define the conceptual approach to understand the ecological dynamics (ecology-seascape-landscape) and social variables (social drivers). Figure 4.1 portrays a graphic representation of the subsystems' theoretical concepts as the metamodel of the cybercartographic atlas:

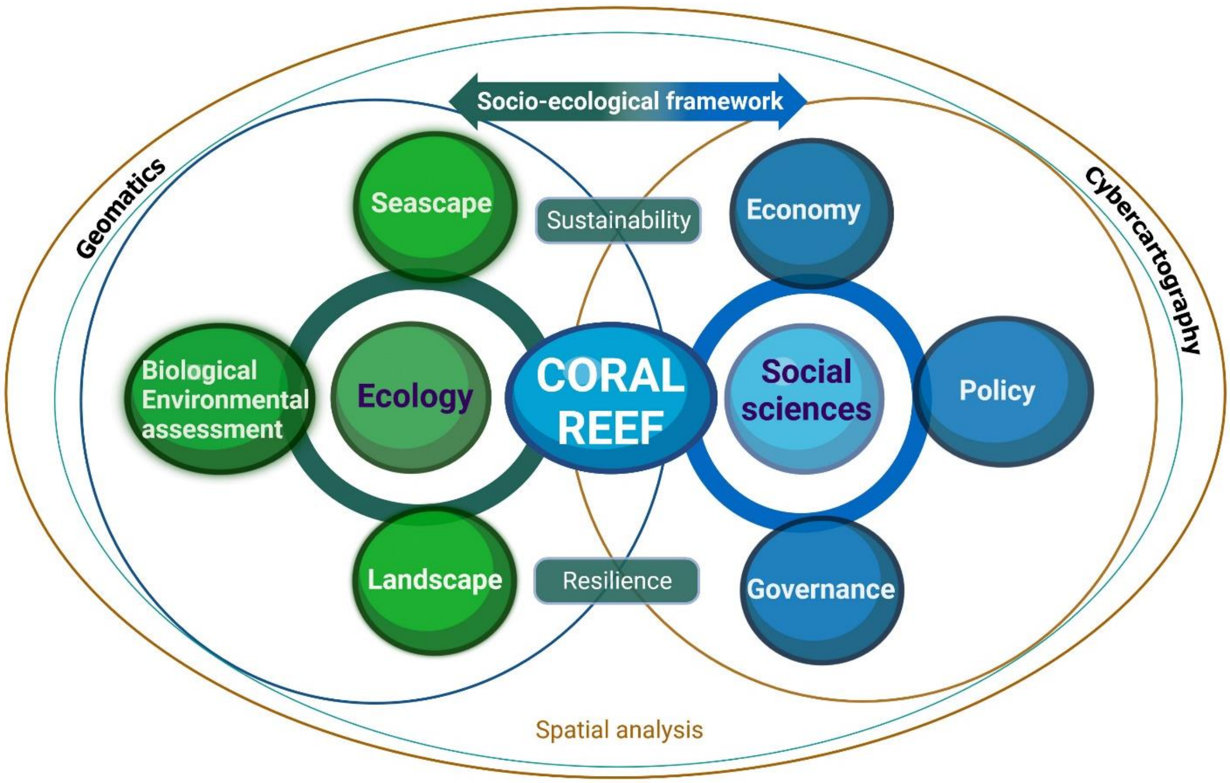

Figure 4.1 *Metamodel: defined by the theoretical frameworks for each subsystem*

In the centre: the reef, conceived as the integrative attractor axis because here, all processes, natural and social, rotate around and within the reef. Ecology provides the knowledge base of three main elements in the natural subsystem: the seascape, where individual species, communities, and habitats interact in an intricate and complex network of interconnections. The biological and environmental assessment devoted to providing the base information of the reef's bio-ecological foundation as well as geophysical and biophysical variables, and landscape ecology is a crucial ecology subdiscipline because a complex network of physical, economic, social, and political forces act at various spatial scales, exerting several forces on the landscape. Due to governance, the local community plays an essential role as the primary user of reef resources in the social subsystem. Additionally, general economic and sectoral policies, often developed by higher levels of government and decision-making organizations, directly impact natural resource management. Thus, management is regulated by policies, which develop through time as a direct result of different mechanisms of social choices and individual cases as mediated by various stakeholder groups.

The double-ended arrow in Figure 4.1 containing the Socio-ecological framework encompasses both natural and social systems. In this way, we define a new way in integrating ecological, biological, and physical processes at different spatiotemporal scales, including social, cultural, and economic processes. Thus, interconnections between actors and stakeholders via information sharing and action are required. Because, in the Anthropocene, the coral reef ecosystems are no longer solely under the influence of natural processes, the idea is to understand the underlying mechanisms causing changes and their impacts thoroughly.

The term ‘sustainability’ in Figure 4.1 portrays the importance of maintaining coupled human-coral reef systems in a desired state for many generations. Sustainability prioritises outcomes and generational equity being the centre of science and policy (Brown, 2016). The ultimate purpose is to produce knowledge and solutions for management and planning, expressed in policies to safeguard the reef system with undoubtedly societal benefits (Jianguo, 2012). In this context, resilience plays two essential roles. The first is resilience within the reef ecosystem, defined as the system's capacity to rebound after disturbance (Holling 2002). However, in a period of anthropogenic climate change, we considered it critical to align the resilience definition as in Glaser et al. (2018), prioritising resilience studies aiding in understanding and overcoming chronic, unwelcome, and hence lousy resilience (prioritising immediate stability above long-term sustainability) in addition to safeguarding the mechanisms and feedbacks we want to preserve. As a result, resilience should increase the system's ability to deal with unknown changes, disequilibrium, and uncertainty (Brown, 2016). The second aspect deals with resilience management on different spatiotemporal scales, focusing on changing and adapting decision-making according to the reef ecosystem development (Walker et al., 2002). We aligned with Weise et al. (2020), considering three different management/decision situations focused on safeguarding ecosystem services on a specific temporal scale. 1) Reactive when there is an imminent risk to ecosystem services resilience, and there is a high pressure to act; 2) adjustive when the threat is generally recognised yet there is still time for adaptation management; and 3) provident, when timescales are very long, and the nature of the threats is uncertain, resulting in a low capacity for action. Considering these decision contexts, what is required is to preserve and strengthen the reef ecosystem while transforming the social subsystem and enhancing resilience as a whole. With this, we can ensure that acute threats to ecosystem services are prioritised above longer-term management interventions.

Spatial analysis in Figure 4.1 encloses both subsystems because of the system dynamic and also because the study and management of reef systems are intrinsically dependent on contextual spatial patterns at different spatial scales within the land-seascape (Cumming, 2011). The system's computational, geographical, visual, and cartographic models are inserted here.

This framework intends to set the basis and explore how management plans can be improved for reef national policy protection for the Mexican Caribbean reefs across the different subregions. In the following section, we synthesise the arguments and elaborations for the concepts' inclusion in the cybercartographic atlas framework. We first define the two extensive subsystems: Ecological and Social, separately. Then, we identify the main elements of each subsystem and integrate the specific subdisciplines. Finally, both subsystems will be integrated into a holistic approach.

4.3.2 The Ecological system

Coral reefs are open, dynamic complex systems with intrinsic robustness and resilience that have contributed to their longevity and stability over millions of years before the Anthropocene era (Hatcher, 1997; Pandolfi, 2011). They sustain high levels of photosynthesis and calcification rate (Gattuso et al., 1999). They are among the most crucial foundation species, creating coral colonies and reef structures and serving as habitats for many reef organisms (Angelini et al., 2011). These characteristics account for the high level of coral reef biodiversity. We propose Ecology as the primary discipline in reefs studies since it provides a robust and flexible framework to understand the relationships between different organisms and their environment. Ecological studies are crucial to developing effective management strategies promoting the protection and conservation of reef ecosystems. At the same time, it is the umbrella for other relevant disciplines, such as landscape ecology.

Landscape ecology is an interdisciplinary field that investigates landscape structure, function, and change (Liu & Taylor, 2004). In this study, we also take the approach of seascapes that best define the reef area *per se*. The fundamental tenet of landscape ecology is that ecological systems are affected by the composition and spatial structure of the landscape mosaic and that the resulting systems could be very different if the composition or organisation of the mosaic were different (Boström et al., 2011). As a result, a landscape is conceived as one or more ecological systems where humans, even if not permanently, are included as a system component (Jameson et al., 2001).

We present an overview of the natural subsystem conceptual representation in Figure 4.2. One of the leading scientific disciplines for this study is landscape ecology because it integrates biodiversity at many scales, from individual habitat patches to the level of entire biomes or associated ecosystems, such as mangroves and seagrasses, including natural and external anthropogenic impacts (Wu, 2008) (Figure 4.2). To integrate the different organisational levels in reef systems, the approach of Reuter et al. (2005) was taken, thus linking the organisms, species, or processes being studied to the spatiotemporal scales appropriate to the specific analysis of interest when conducting biological assessments (Figure 4.2). Evaluating the changes in composition and the causes of these changes in the reef system is mandatory to overcome existing shortcomings in ecological surveys. The key attributes and processes studied necessary to monitor reefs refer to structure, function, and composition/change in landscape ecology. The reef system is considered an open complex system because tides, currents, and other water motions make it easier to interchange nutrients, sediments, and organisms with other elements of the marine environment, including chemical contaminants and diseases (Monismith, 2007; Nagelkerken, 2009). Thus, the reef's intrinsic openness is expressed with dotted lines in Figure 4.2. Further, environmental and biophysical variables, i.e., sea-surface temperature, primary ocean productivity, chlorophyll-*a*, sediments, currents, waves, and depth, play an essential role in reef ecosystems. The same variables directly or indirectly influence the landscape, exemplified as the first level or major scale of analysis in Figure 4.2.

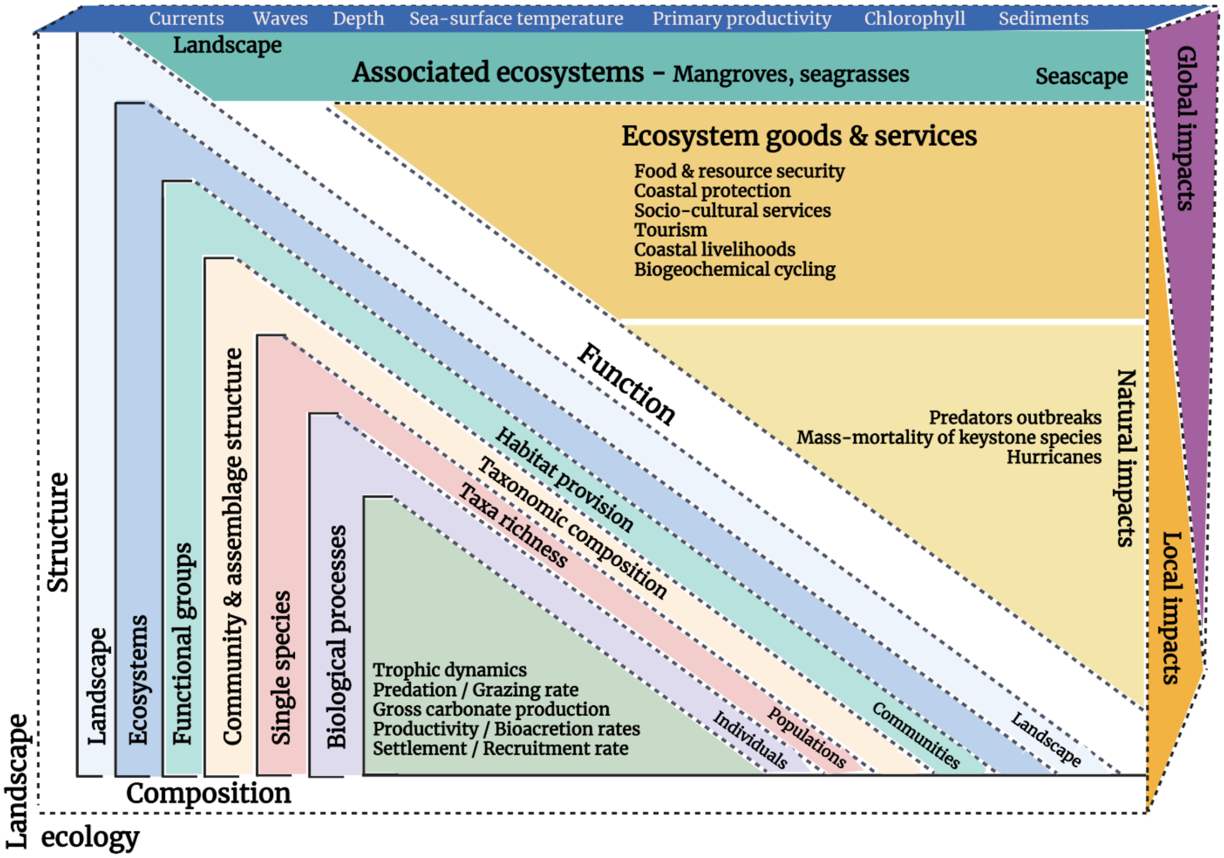

Figure 4.2 *Conceptual definition of the atlas' natural subsystem. The left triangles represent attributes and processes studied in landscape ecology: structure, function, and composition. The sub-triangles represent the different biotic organisational levels at each scale of analysis. The triangles on the right side show the most critical associated ecosystems and the provision of goods and services. Global and local impacts influence the whole subsystem.*

The ecosystem concept encompasses the analyses of organic networks based on the positive and competitive aspects of interaction, i.e., competition and predation. In the reef system, the different communities are represented in functional groups, e.g., bacteria, plankton, algae, octocorals, hydro-corals, sponges, and scleractinian corals, as the principal architects of the complex three-dimensional (3-D) structures. This contributes to the evolution of biological diversity and genetic library for future generations (Rodolfo Rioja-Nieto & Álvarez-Filip, 2018). Three factors are crucial in establishing and maintaining the biodiversity of coral reefs: the reef habitat area, living coral cover, and topographic complexity (Bellwood et al., 2006). In the Mexican Caribbean, the 3-D structure complex depends mainly on critical reef-building species such as *Acropora* and *Orbicella*, providing higher habitat heterogeneity and rugosity of these systems (Alvarez-Filip et al., 2013).

Ecological communities are the outcome of various assembling processes. The community assemblage structure comprises the taxonomic composition of the reef, relative abundance and dominance of species i.g., commercial fish, size frequency and distribution of communities, i.g., benthic assemblage structure, coral morphology, and coral population colony. Individuals include taxa richness and composition, crucial to analyse key taxa of regional ecological importance (Hodgson, 1999) and rare or endangered key taxa, e.g., commercially valuable fish/invertebrate species. Here an analysis of diseases, anomalies, contaminant levels, metabolic growth rate, and reproductive condition fecundity is also crucial. The finest scale of analysis encompasses all biological processes providing unique local characteristics (Jameson et al., 2001) (Figure 4.2).

Coral reefs are associated with two main ecosystems in the landscape, seagrass and mangroves, that intrinsically interact and benefit (Guannel et al., 2016; Lamb et al., 2017). Seagrass and mangrove provide nursery habitats for some fish and invertebrate reef species. Furthermore, both ecosystems retain and stabilise sediments, also working as areas of nutrient cycling. The wide range of ecological services these three ecosystems together provide benefit more as a group than a single of these habitats or any two combined (Guannel et al., 2016). Consequently, the response of these interconnected habitats at landscape-scape scales must be evaluated.

The natural impacts on reef systems are substantial because they shape them through disturbance and recovery processes. Hurricanes, for example, are the most evident natural disturbances affecting the structure and function of reefs (Gardner et al., 2005). Evidence suggests that reefs in the Caribbean region had acclimatised and persisted to these adverse conditions. For instance, the once-dominant species *A. palmata* may have been able to withstand hurricane disruption due to the fragment cementation of their populations. In contrast, other species, such as *Montastrea annularis,* generally were hurricane-resistant (Bythell et al., 1993). However, the current anthropogenic influence appears to shift the equilibrium between disturbance and recovery toward coral decline. The mass mortality of the grazing urchins *Diadema antillarum* in 1983–1984 resulted in reef ecosystem health decreases with further implications on ecological services, and populations are still repressed today. Similarly, the potential impact of invasive species, i.e., the red lionfish

(*Pterois volitans*) in the region, has emerged as a new menace in recent years. Overall, it is crucial to monitor these biological invasions because they affect the reefs' fauna and diminish the reef's resilience.

Finally, coral reefs' goods and services are essential to society bringing many benefits. These are divided into broader categories because they underpin other vital services. For example, provisioning encloses food and resource security due to commercial and subsistence fishing (Crowder et al., 2008). Within the regulating services are shoreline protection given by the reefs' 3-D structural complexity and reef growth rate expressed in carbonate budgets (Perry & Alvarez-Filip, 2019), reduction of coastal erosion (Bruckner, 2002), and regulation of climate through carbon dioxide sequestration (Rioja-Nieto et al., 2019). The socio-cultural services include tourism and ocean recreation, exacerbated by charismatic species and colourful reefs (Riera et al., 2016). Lastly, supporting services include biogeochemical cycling and white coral sand generation (Mata-Lara et al., 2018), undoubtedly a source of economic benefit (Miloslavich et al., 2010). Assessment of the economic value of coral reefs is essential to safeguard them for future generations.

4.3.3 The Social system

As an interdisciplinary area, the research of this paper focuses on understanding the functioning of the social system aspects in the Mexican Caribbean reef system and on developing normative societal goals for future implementation, such as those inherently connected to sustainability. Figure 4.3 presents the complex social system, which acknowledges the close ties between people and the natural world (Ahlborg et al., 2019). It is important to note that the main driver of change is the economic model that leads to further accumulation and concentration of capital. Capitalism drives land-use change, natural resource overexploitation, pollution, and anthropogenic climate change. The four dimensions (Figure 4.3) in their local expression and their connections (Panarchy type, a set of hierarchically interacting structured scales, (Allen et al., 2014), as well as their coupling (of the positive) or advocacy of the non-local (in the negative), thereby ensuring local sustainability in the current adverse environmental context. In this conceptualisation, the interdependence, linkages, and relationships across structures, dimensions, and scales are paramount because of the significant transformation in social structures. As the new millennium gets underway, a new form of creating sustainable societies should develop. The role of governments, institutions, society, organised groups, and nation-states is fast changing in this age of quick, unexpected, and unforeseen environmental changes with far-reaching effects on natural resources. Management strategies are changing due to pressure, choice, and the need to adapt to survive toward sustainable development (Schrerer et al., 2013).

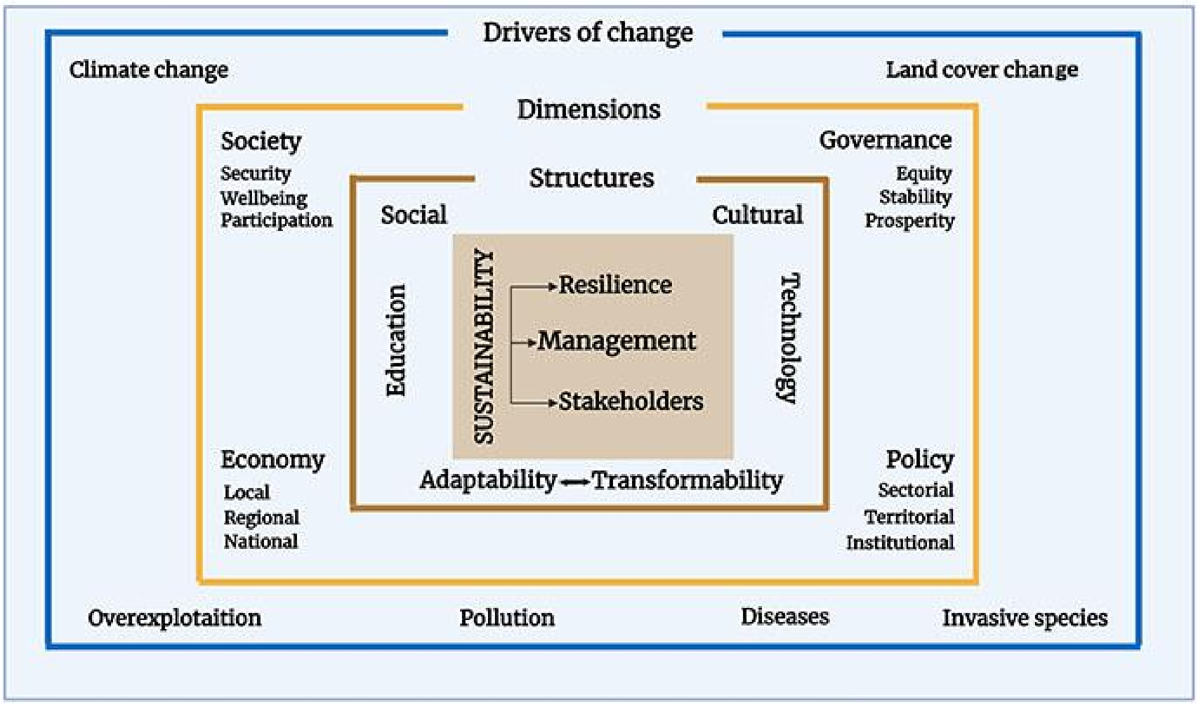

Figure 4.3 *Conceptual definition of the atlas social subsystem. Drivers of change, dimensions and structures.*

Therefore, sustainability is the leading framework for managing complex systems to ensure the reef system's long-term viability and well-being and advance equity, justice, and cultural diversity. As we discussed in the metamodel, resilience management is proposed to be the primary tool for stakeholders because it pursues to increase the reef systems' ability to absorb and adapt to shocks while preserving their functions and services, acknowledging the constant and inherent uncertainty, variability, and unpredictability of these systems. Thus, reef management must remain adaptive, integrating flexible strategies to changing conditions able to transform through local organisation solutions, ensuring their stability over time (Holling et al., 2002) (Figure 4.3). We emphasise that social and cultural structures should ensure the long-term viability of cultural diversity and heritage and incorporate local traditional knowledge and practices into management strategies.

Further, society, governance, economy, and policy are considered different but interlinked dimensions that influence each other. To ensure the good use and management of reef systems, it is vital to understand how decisions made in one context (or part of the system, related to one goal) can impact other goals (parts) (Figure 4.3).

In this work, we define *society* as the people who live, work and use the natural resources in the Mexican Caribbean according to their values, beliefs, and cultural community practices. The search for the necessary conditions to flourish and contribute to the public benefit in the Mexican Caribbean is based on: participation, security and well-being (Darvill & Lindo, 2015). Consequently, we consider that the society is civil, based on the rule of law, situated between the state and the market, where disputes between the two will impact it, and there is a sphere of open public debate (Setianto & Widianarko, 2023).

Governance is essential because it exchanges legislation responsibilities in the mediation process among nested government entities at various local, regional, national, and international levels. Then governmental actors, market parties, and civil society organisations regulate, in this case, coastal and maritime activities and their effects. The participation of many stakeholders at several levels and the coordination and integration of various sectoral marine operations will impact the legitimacy of integrated marine governance. Moreover, when marine governance is applied to managing natural resources, it should be considered dynamic, contextual, and constantly adjusting to changing situations (Tatenhove, 2011).

Additionally, economic development in reef systems relies on maintaining sustainable and direct access to ecosystem services while safeguarding marine biodiversity. The burden on the environment and coastal resources in the Mexican Caribbean are rising due to the quickly expanding tourism industry. Several factors influence the demand for tourism, including increased free time and economic expansion. Unless its rapid growth is controlled to be compatible with sustainable development, it may even be detrimental to local societies and traditional customs, reducing total economic gains (Hickel, 2019).

Concerning policy, we consider the importance of rules, regulations, and laws that govern natural resource management. Thus, we aim to assist in creating a national policy for the protection of reefs to be developed and implemented consistently with societal values, effective governance, local knowledge, ecological economics, and, most importantly, sustainability.

Finally, the drivers of change in Figure 4.3 are the main stressors negatively impacting the reef system. As coral reef ecosystems deteriorate, so does their capacity to deliver the vast goods and services providing an opportunity for recreation, resource extraction, inspiration, education, and economic subvention. Overfishing, destructive fishing, poor coastal and urban development, deforestation, unsustainable tourism, and land-based pollution are the most significant drivers for local anthropogenic disturbances, in addition to the global stresses of anthropogenic climate change: sea surface temperature rise, sea level rise, and ocean acidification.

4.4 The integrated framework

The interest in creating an integrated conceptual framework as a sustainable management tool for the Mexican Caribbean coral reefs lies in protecting these beautiful, complex, but highly impacted ecosystems. Therefore, it is mandatory to understand their spatial, ecological, and geographical variability and the interactions and impacts of human systems at different scales. With this information, we aim to facilitate/enhance an integrated conservation policy for Caribbean coral reefs.

Figure 4.4 represents a holistic approach to the cybercartographic atlas framework as the conceptual basis for this work since it acknowledges the close ties between society and the natural world, which could exist as separate entities within a landscape (Ahlborg et al., 2019). At the bottom of the figure lies the socio-ecological framework, including humans as active ecosystem members already integrating the two external arrows, ecological and social subsystems. Thus, social-ecological systems are conceptualised as complex adaptive systems with different stakeholders as crucial system components whenever the objectives include long-term sustainability (Walker et al., 2002). They also are nested, multilevel systems with several feedback loops involving numerous elements, making it potential for adaptation on various time scales.

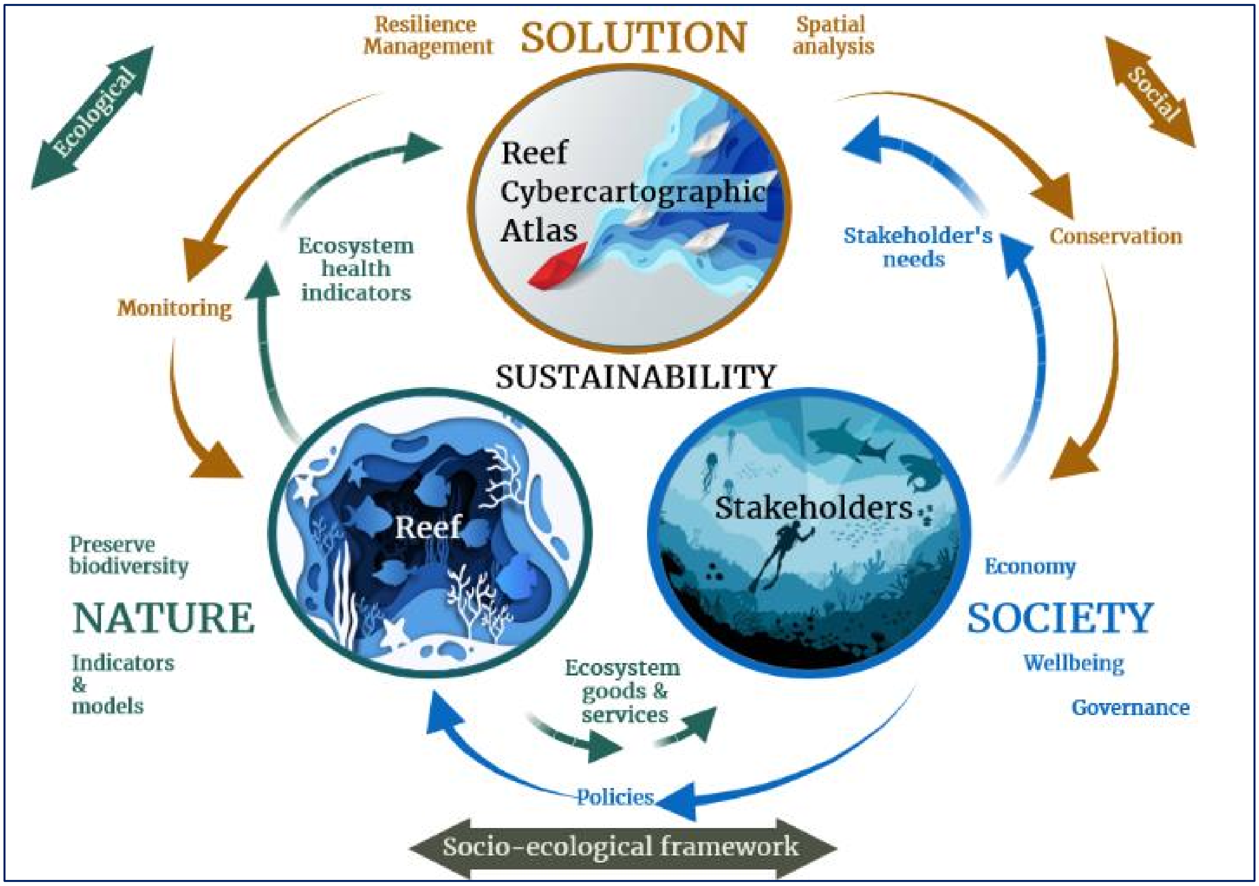

Figure 4.4 *The integrated conceptual framework of the cybercartographic atlas.*

The ecological component of the integrated framework is based on the valuation of the reef system and is expressed as “Nature” (Figure 4.4). It focuses mainly on the one hand, the preservation and enhancement of reef biodiversity through different indicators and models based on the assessment of the ecosystem structure (e.g., biodiversity, community structure, habitat extent, and abiotic conditions), ecosystem assemblage (population dynamics, reef accretion/bioerosion, food webs), and connectivity (terrestrial-marine, genetic, ecological, biogeographic, energy fluxes). On the other hand, the spatial relationships between reefs and other ecosystems, the energy flowing within them, and the ecological dynamics of the landscape mosaic over time (Boström et al., 2011). A link here with ecological monitoring programs already set into motion is fundamental for three main reasons. First, even though the different monitoring program methods are not standardised, they bring important information regarding the status and health of the reef system. Second, this information can be used to assess the structure, function, and change of reef systems because when the reef's structure is modified, its function is modified, generating a change that affects the environmental services it provides to society. Third, it might not be possible to directly integrate the existing and current information from the different programs. However, it could generate historical analyses and define what metrics should be improved and the importance of improving monitoring efficiency. This kind of analysis can serve as a basis for linking the internal and external impacts in the system, assessing the past, analysing the present, and planning the future, leading to the resilience management and reliable conservation efforts of these areas.

The oceanic environmental variables are essential to consider and can be mostly retrieved from international monitoring programs based on remote sensing; however, the spatial resolution might be too coarse, and not all parameters will be available. Some critical variables in coral reef health are nutrients, primary productivity, salinity, sea surface temperature, water turbidity, current patterns, and winds. These are important because species respond differently depending on environmental conditions to larval production, behaviour, and competition (Carr et al., 2011). Moreover, an increased awareness of how physical, biological, and chemical processes shape coastal marine ecosystems and how human activities affect these processes is necessary to establish vital management objectives.

Another vital component in the integrated conceptual framework is the human groups or "Society" represented by stakeholders (Figure 4.4) because the citizens' well-being is essential for economic success; therefore, governance is needed to moderate guiding the economy while boosting welfare factors and the efficiency of its government. Society benefits from adequate coral reef management, which can spur sustainable local development, eventually improving people's standard of living, promoting social cohesion, and reducing inequality, poverty, and crime. Moreover, economic growth based on the sustainable use and management of reef resources generates progress because it can foster entrepreneurship, innovation, and profitability. Therefore, the stakeholders' importance as the transforming agents of the physical-ecological dynamics generates a direct or indirect influence on the reef system. According to Orr (2014), collaboration among stakeholders is essential to building a society in an economic and environmental region, and they can be divided into specific groups:

- Formal social organizations: all organizations recognized by the governmental institutions linked with coral reefs in the Mexican Caribbean.
- Public and governmental institutions: within the three levels of government in Mexico: municipal, state, and federal.
- Private for-profit organizations: private companies.
- Private non-profit, non-governmental, and academic organizations: e.g. scientific institutes, research centres, and foundations; conservation organisations
- Local communities

In addition, one of the critical requirements in the Agenda for Sustainable Development since 1992 is broad public engagement in decision-making. This includes the requirement that people, groups, and organizations participate in environmental impact assessment processes and be informed of and involved in choices, particularly those that may impact the communities where they work and reside. Information about products and activities that have or are anticipated to substantially impact the environment and information on environmental protection measures kept by national authorities should be accessible to individuals, groups, and organizations (United Nations, 2023). Therefore, one fundamental condition is to have a clear influence map of different regional stakeholders, grouping them by relevance according to their different use and management of Mexican Caribbean reefs and linking them in the cybercartographic Reef Atlas through a social network scheme (Burton, 2019). The Atlas aims to meet the requirements of critical stakeholders to be consulted and articulate them in the form of needs and problems. Thus, linking them in the Atlas is a tool to mitigate, avoid and prevent current and future social conflicts.

The cybercartographic atlas is the proposal for a solution in coral reef management for Mexican Caribbean reefs (Figure 4.4). In the current Anthropocene geological era, coral reef managers should rapidly expand their support of ecosystem resilience from a narrow focus on stress reduction to include broader support of ecosystem processes that minimise sensitivity, improve recovery, and enhance adaptation, landing in resilience management, always taking into account natural and social systems as a whole (Box 4.1).

Box 4.1 *Basics of ecological and social assessments*

Reef status data (conventional monitoring)	Relevant Social components
Key functional groups as indicators of ecosystem health: corals, fish, algae, and other benthos organisms. **Definition of the spatial extent** of analysis: consideration of neighbouring reefs/regions. **Analysis of temporal trends:** reef development and projections (modelling).	**Land change** key indicators: regional approach, land classes, population density, sewage treatment, run-off. **Analysis of drivers** of reef transformation. **Processes of reef reconfiguration**: socio-ecological implications.

In this regard, the generation of improved information based on spatial analysis and linking the social and ecological needs with current problems based on ecological and social assessments will set the basis to propose a theoretical and practical solution tool coherent between the needs and the generation of knowledge through this atlas. Because non-fixed norms influence the reef system's socio-ecological dynamics, the idea is to keep the system's dynamism in mind by maximising the existing information and proposing improvements to monitor reef systems in biodiversity conservation interests adequately. Through this cybercartographic artefact, we aim to observe reef changes over time in response to alterations in the social and biophysical world and understand how they evolve. Only with this premise can the artefact have vital decisional flexibility to self-organise along desirable trajectories to achieve adequate system management, also creating awareness in society.

Managers' and stakeholders' toolbox

Improved management in the Mexican Caribbean reefs will allow the negotiation of mental maps between decision-makers and their users (linking their requirements with current/pressing problems and present needs). In such a way, a basis for public policy and consensual social action is built, allowing the emergence of new knowledge and driving actions parallelly related to natural and social processes in this geographical space. Thus, robust and legitimised management is achieved, understood as organising and managing resources to achieve a purpose: managing the reef system in a given time and space within an agenda based on ecological and social access to information (Box 4.2) for decision-making actions.

Box 4.2 *Basic information stored in the cybercartographic*

Access to information:
- Up-to-date information on:
    - Water quality
        - Chlorophyll-*a*, Turbidity, Nutrients
    - Biophysical variables
        - Sea surface temperature, solar radiation, salinity, bathymetry, wind
    - Habitat and reef structure
        - Extent, reef type, geomorphic zonation, benthic and substrate community composition, three-dimensionality structure
    - Resource maps
        - Location and status of critical associated habitats, mangroves, seagrasses
    - Ecosystem processes and services
- GIS – geographical info and attributes
    - Linked with local regional and global monitoring programs – platforms
- Information repository
    - Organised information
    - Historical information
- Linkage to management processes

Figure 4.5 represents an interface example of the proposed cybercatographic atlas. In the centre, an "indicators dashboard" is shown. The idea is to analyse through different indicators the change of state of the socio-ecosystem to see if it is moving towards or away from the desired state. The infinity symbol relates the inputs, processes, and outputs of the different components to finally monitor the coral's condition and the local society's welfare. In this way, we can continuously compare reality with the desired state and take actions to improve the inputs and the system base. However, it is currently only a theoretical approximation addressing specific problems identified in the development of this research. To produce the final content framework of the atlas to be used in public policy processes of Mexican Caribbean reefs, the key stakeholders should be part of the tool development and design to guarantee its necessities, guidance, and application.

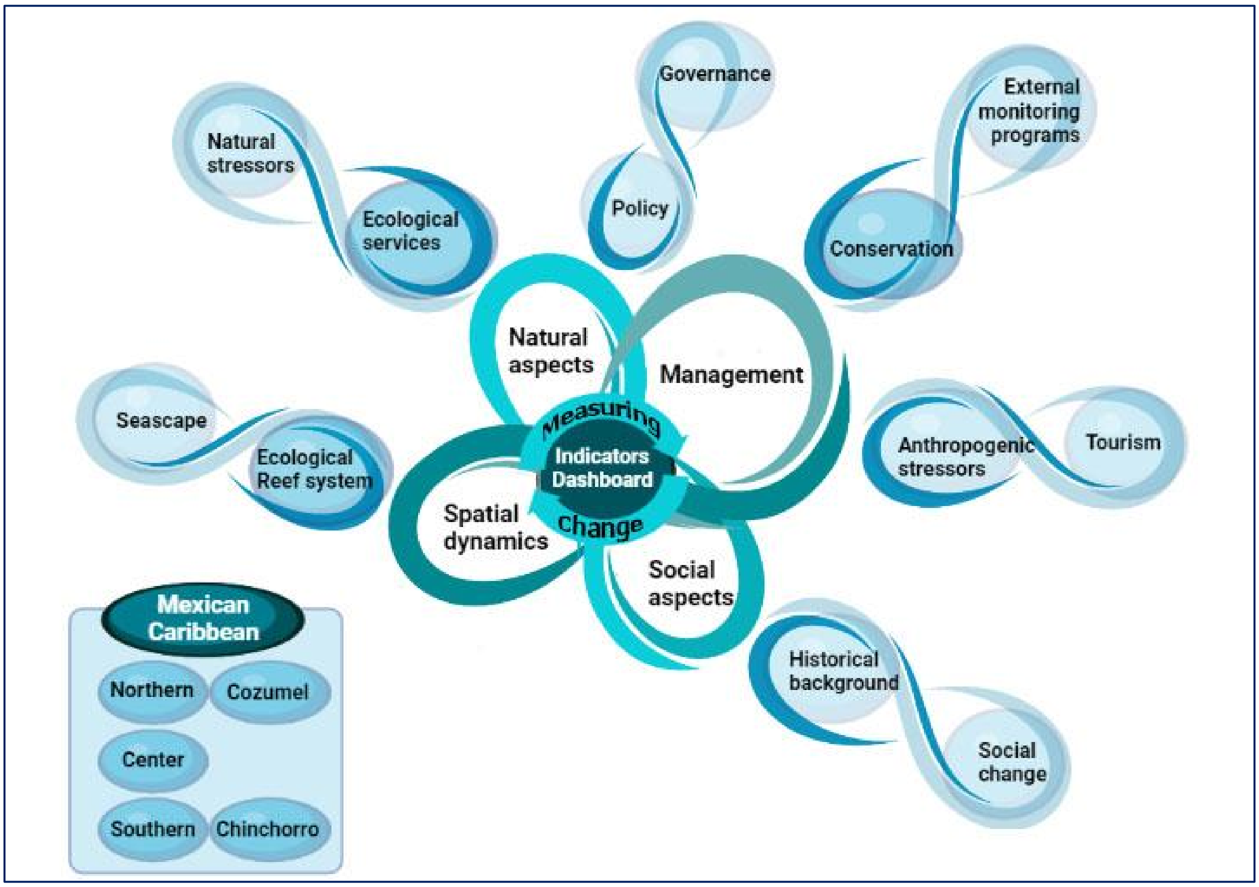

Figure 4.5 *Content framework for the Mexican Caribbean Cybercartographic Atlas.*

1 Generate a stakeholder analysis

The Reef Atlas is intended to support with reliable information the enhancement of national and regional environmental policies in reef ecosystems. Therefore, stakeholder analysis, as an actor mapping, is crucial if decision-makers want to understand who will be impacted by their decisions and actions and who has the potential to influence their result (Brugha & Varvasovszky, 2000). There is a wide range of methodologies to generate stakeholder analysis; we propose the identification of the main stakeholders in the Mexican Caribbean coral reefs with a permanent and evolving participation at every phase of Atlas development and implementation. This will allow the dynamic nature of stakeholder needs, priorities, and interests to be captured throughout the performance and beyond.

2 Conceptual framework discussion with stakeholders

This conceptual framework was based entirely on the literature. Thus, it is essential to discuss with the main previously identified stakeholders the actual scopes, gaps and other requirements of the Reef Atlas and modify it if necessary for current and near-future necessities.

3 Reef Atlas design and development

The Reef Atlas will be designed based on the necessities of the main stakeholders on a platform with a user-friendly interface available for computers and mobile phones with and without an internet connection.

The information content will provide a wide range of geospatial data, social and ecological indicators. The data collection will be divided by theme for the Mexican Caribbean region or at the module (subregions) level. Here, the organisation and combination of qualitative and quantitative information will be expressed in different forms, such as text, statistical graphics, photographs, maps, and scientific articles. It will be open enough to incorporate new information efficiently.

4 Reef Atlas dissemination and implementation

One of the Reef Atlas objectives is that the actors and stakeholders can articulate new visions and new forms of action based on a wide range of scientific information. Rather than data collection, it seeks to provide ways of organising quantitative and qualitative information and generate knowledge facilitating the perception of their natural resources and the role they play in it.

The Reef Atlas is assumed to be a living, dynamic tool with constant information updates. Therefore, development and implementation are vital and require permanent resources and an organisation guaranteeing permanence. The National Commission of Protected Areas in Mexico (CONANP) could be the host. Nonetheless, there must be enduring participation and presence of local communities and academies between other crucial regional institutions and organisations; the main stakeholders interested in the adequate use and management of the reef systems.

4.5 Conclusion

Conservation is typically an economic issue in many nations, and circumstances connect activities that transcend national boundaries. It is a pressing issue; management of the reef environment has evolved into a competition between exploitation and conservation. Environmental exploitation and deterioration (such as the coral reef crisis, land clearing, and carbon dioxide emissions) now affect all habitats. To establish the essential agreements, infrastructures, practices, and policies, we must acquire integrated knowledge of coral reefs' socio-ecological systems. Through a coral reef cybercartographic artefact, we can comprehend in a synaptic way the global environmental context to manage reef ecosystems and species locally inserted in the significant human dimension within public policies. Specifically, the cybercartographic atlas framework proposed here can strengthen the diagnosis of ecological and social conditions and according to problems by engaging with temporal dynamics, integrating insights from multiple stakeholders/actors, and exploring interactions between multiple stressors.

In this way, the atlas is a crucial tool inserted in consensus and geospatial management processes. Geoinformation relates to "real world" issues. Technically speaking, it asserts that only one world can be quantified using various techniques at various scales and perspectives. However, ultimately, everything must be logically and physically locatable in that one world. We intend that the cybercartographic atlas will be able to drive new synergies between users since it will include the key actors to determine their current needs and problems in reef systems at different scales. Thus, linking them in the cybercartographic solution will serve as a tool with a mediator function and mitigate, avoid, and prevent current and future conflicts.

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Chapter 5

GENERAL DISCUSSION

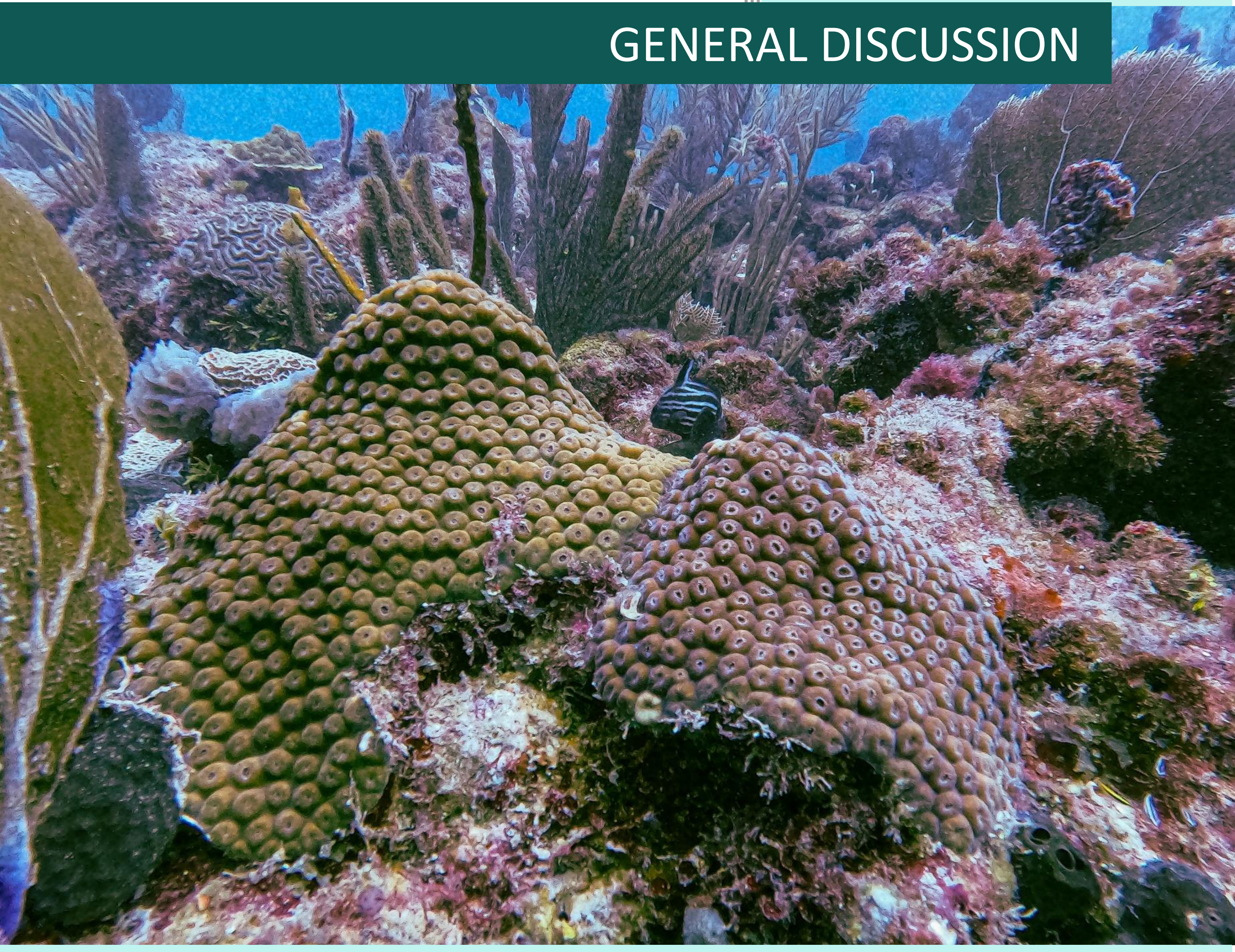

Photo credits: Mauricio Martinez-Clorio, *Orbicella Annularis*

5 General Discussion

5.1 Outline

Environmental changes have strongly affected the earth's biota throughout the history of natural life (Pandolfi, 1999). Reef systems exhibit such changes, evolving and adapting over hundreds of millions of years, coping with repeated disturbances, followed by recovery or regrowth (Buddemeier et al., 2004). However, these are natural features of coral reef history. The current Era has already witnessed coral reef depletion, and the losses in reef habitats and biodiversity are now to be counted. Along with more traditional management techniques and assertive action to stop global warming, new and potentially more complex interventions must be applied for coral reefs to stay resilient and provide their functions continuously (Buddemeier et al., 2004). Coral reefs in the Mexican Caribbean region offer numerous benefits for coastal inhabitants and visitors, including subsistence, recreational and commercial fishing, snorkelling, diving, and maritime activities, providing structural and reef-based tourism as a substantial contributor to the local economy through ecosystem services. These important reefs have degraded due to local impacts and anthropogenic climate change. However, the extent of further impacts has yet to be quantified, while further effective assessment tools and management strategies are yet to be proposed. Therefore, this study focused on contributing to these research problematics and knowledge gaps concerning the Mexican Caribbean region.

5.2 Key Findings and Advancements for Coral Reef Science

This thesis aimed to fill gaps in knowledge relevant to the historical status of the health of Mexican Caribbean coral reefs by analysing spatiotemporal changes in the coral and macroalgae communities and then identifying key drivers of change or stressors. Analysing such changes and identifying the main stressors causing them is essential to establish the basis of an integrated sustainable management tool, which the region still lacks. Figure 5.1 summarizes the main findings of this research.

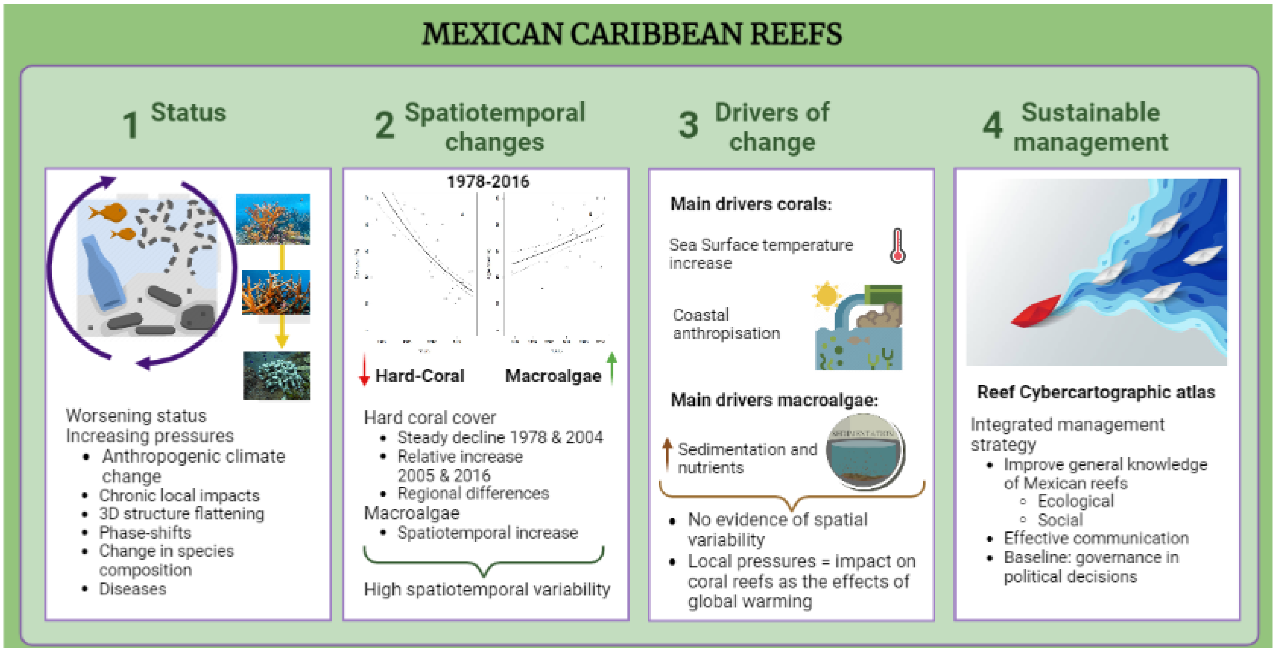

Figure 5.1 *Graphical abstract of the key findings of this research. Status refers to the environmental changes impacting Mexican Caribbean reefs. In spatiotemporal changes, the reefs moved from a coral dominated to a coral-dominated state. Sea surface temperature is the most conspicuous driver of change in reef systems, followed by the impacts of coastal anthropisation. These three elements set the basis for a sustainable reef management strategy to ensure the reefs continue providing vital ecosystem services to society.*

Key findings

Chapter 2

Spatiotemporal benthic changes of coral and macroalgae cover

1. This study was the first longitudinal analysis on Mexican Caribbean reefs exploring benthic change patterns through meta-analysis between 1978 and 2016, summarizing information at a finer subregional scale across the Caribbean.
2. Coral cover decreased from ~26 % in the 1970s to 16 % in 2016. In contrast, for the same period, the macroalgae cover increased from ~ 15 % in the late 1980s to 30 % in 2016, with both groups showing high spatiotemporal variability between the four subregions studied.
3. From 1978 to 2004, the coral cover declined by 12 %. Then, a relatively slow coral reef recovery of 5 % was recorded between 2005 and 2016 after bleaching events

and hurricane impacts. However, this increase in coral cover was mainly observable on Cozumel reefs.

4. Between 1978 and 2004, a steady rate of coral decline was observed primarily in the centre and southern subregions.
5. A local phase shift around the 2000s was recorded from coral to algae-dominated reefs as in the rest of the Caribbean regions. For most Mexican Caribbean sub-regions, macroalgae cover has steadily increased for the period analysed (1987 to 2016).
6. Most Mexican Caribbean reefs are now dominated by macroalgae in contrast to the 1970s when hard corals dominated the surveyed reefs despite mild bleaching events, hurricane impacts and diseases.

Chapter 3

Main global and local stressors impacting benthic change

7. A severe heatwave and 13 storms, including hurricanes Emily and Wilma, struck the wider Caribbean in 2005, significantly reducing the hard coral cover.
8. From 2005 to 2016, the main stressors causing changes in the Mexican Caribbean coral cover were the sea surface temperature anomalies directly correlated with bleaching susceptibility, followed by the effects of anthropogenic activities, which include the growing pressures from urban hubs. The great majority of the population in the Mexican Caribbean lives within 10 km of the coastline (78 %).
9. Only the macroalgae cover was influenced by the water quality predictors, mainly the particulate organic carbon (used as a stand-in for sedimentation and nutrients). Furthermore, the relationship between chlorophyll-*a* and sea surface temperature had the sole negative impact on macroalgae.
10. We did not find evidence during the analysis period that the tested factors affected the coral and macroalgae cover differently along the Mexican Caribbean (2005-2016).

Chapter 4

Conceptual framework for a reef management strategy

11. Even though the coral reef monitoring activities in the Mexican Caribbean started in 1980 through various conservation and management initiatives implemented by NGOs, local/federal government institutions, and international organisations (Legislation, strategic action plans, NPAs, monitoring, education, and awareness campaigns, among others), the Mexican Caribbean reefs continue to degrade, losing their biodiversity and the ecosystem services that are important to society.
12. Although each natural protected area in Mexico has a management programme, a large-scale integrative management plan is still required as the set of instruments that determines the conservation and usage strategies of such Natural Protected Areas.
13. We proposed a sustainable, long-term, and novel conceptual model: a Reef cybercartographic atlas aimed at safeguarding the reef ecosystems of the Mexican Caribbean.
14. By considering economic growth and maintaining biodiversity and natural spaces, the Reef Atlas will be a comprehensive and integrative tool to help understand the socio-environmental problems and serve as the basis for reorienting reef usage and management policies.
15. Generating new forms of environmental governance with informed personnel is needed to conserve and enhance the coral reefs' ecological services in the Mexican Caribbean.
16. Access to available and up-to-date regional scientific information, i.e., coral reef ecosystem services, ecological monitoring (e.g., AGRRA), coastal spatial planning, and satellite monitoring programs (e.g., NOAA bleaching alert), among others, will be facilitated and stored in the Reef atlas.

The following section will discuss the results of this thesis concerning the three research questions proposed for this work.

5.3 Chapter 2

How has the benthic composition changed in Mexican Caribbean reefs over the last four decades?

Chapter 2 of this thesis focused on understanding, through meta-analysis, the dynamics of change in coral and macroalgae cover on Mexican Caribbean reefs from 1978 to 2016. An ecosystem's condition or "health" must be measured using a benchmark or comparative historical standard (McCormick & Cairns, 1994). Unfortunately, there is a shortage of historical data on ecological conditions for most reefs in the Caribbean region. Integrating existing data sets to robustly assess spatiotemporal patterns of large-scale environmental change helped us understand the extent of ecosystem deterioration. As a reference, scientists adopted the use of coral and macroalgae cover as the two significant indicators of coral reef health (Gardner & Gill, 2006). Our findings revealed that hard corals no longer dominate most reefs in the analysed period. There were apparent temporal and subregional differences in benthic change. First, the speed of change was accelerated for both groups across regions. A phase shift from around the 2000s was reported from coral to algae domination as in the rest of the Caribbean. Coral coverage rapidly decreased while macroalgae quickly increased from 1978 to 2004, and in 2005 both groups decreased after two category-5 hurricane impacts. From 2005 to 2016, the speed of negative change slowed down for corals showing a subtle recovery. However, the macroalgae quickly increased again despite hervibore biomasss increasing across the region (Arias-González et al., 2017; Suchley et al., 2016). In 2016, the general ecological condition of the reefs was already showing signs of deterioration, with a coral cover of less than 25 %, whereas macroalgae often exceeded 40 % coverage. Many reefs across the Caribbean also showed this trend during the period of analysis (de Bakker et al., 2017; Gardner et al., 2003; Somerfield et al., 2008).

5.4 Chapter 3

What are the leading local and global drivers of change?

Chapter 3 examined the impacts of single and multiple stressors on corals. We highlighted human influences on the relationship between changing coastal development and ecological change in the Mexican Caribbean from 2005 to 2016. In the "Anthropocene" epoch, humans have developed from a species with little impact on Earth to a significant source of disturbance, threatening coral reefs worldwide (Birkeland, 2015). The impact of regular natural disturbance regimes on coral reefs has been the subject of numerous studies. Nevertheless, more research in the Mexican Caribbean needs to be conducted on the intricacy of disturbances and the change in responses of corals and macroalgae to such pressures, mainly anthropogenic stressors.

The adverse effects that increasing temperatures cause on corals are broadly recognised (Eakin et al., 2010; Schoepf et al., 2019). Moreover, research demonstrates that other stressors with little or no impact on corals when ocurring alone can have a significant effect when occurring in conjunction (simultaneously or sequentially) with other stressors (Ateweberhan et al., 2013). Therefore, we incorporated analyses of stressors reported in the literature to demonstrate if they synergistically affected Mexican reefs. Phase shifts are an example of environmental changes caused by interacting disturbance regimes. Coral-to-algal dominated state is a typical manifestation of these phase shifts in the Mexican coral reefs (Chapter 2), with temperature stress and land-based pollution through coastal anthropisation appearing to be some of the significant change-driving mechanisms. Still, today's Mexican Caribbean reefs are impacted by novel diseases (Alvarez-Filip et al., 2019) and other stressors (e.g., overfishing, introduced species) that should be included in future research, presenting critical structural and ecological challenges in these reefs.

According to literature (Baumann et al., 2016; Osborne et al., 2017), reefs exposed to warmer conditions exhibit a slower increase in coral cover. This study's most significant heat-stress events (1998, 2005, 2010–2011 and 2014–2016) corresponded to the most severe bleaching episodes reported globally. To a certain extent, those events also affected the Caribbean region, including Mexican reefs. However, this region has a long history of heat stress exposure (Chollett et al., 2012). Mexican Caribbean reefs were indeed affected by those global bleaching events. Still, the most aggravating impacts were the subsequent impacts of hurricanes Emily and Wilma (category-5) in 2005 (Trenberth & Shea, 2006). Sequential heat stress events (2014-2016) appeared not to heavily impact Caribbean reefs as observed for other reef regions, such as, i.e. the Arabian Sea (De et al., 2023). However, more acclimation studies are needed to corroborate the existence of heat-tolerant species in the region (Muñiz-Castillo et al., 2019).

Unfortunately, as with the rest of the reefs in the world, local and global stressors seriously threaten the future of the coral reefs in the Mexican Caribbean. The stressors tested here affected all subregions equally. We did not find spatial patterns impacting the reefs. Further, we demonstrated that the main drivers of change at the local level are primarily due to coastal anthropisation and subsequent land-based pollution, coexisting with the effects of global warming. Evidence elsewhere suggests reef areas are more susceptible to land-based pollution from coastal anthropisation and weather-related environmental change (Muslim & Jones, 2003). Even though the cumulative effects of the tested stressors here did not appear significant, we cannot conclude that their interactions do not affect coral and macroalgae development. Further local scale analyses are needed to measure the correlations of in-situ sampling, i.e., water quality parameters, to improve large-scale data, i.e., remote sensing. Doing so can generate accurate information at larger scales and effectively monitor the reef's condition.

5.5 Chapter 4

How to generate a conceptual framework for an integrated and sustainable management strategy?

Considering the status of Mexican Caribbean reefs and the role of the multiple stressors impacts, it is crucial to anticipate the future conditions of these reefs, understand how to manage them, and urgently prepare for changes in the provision of ecosystem services. The existing tools in the region to assess the status of reef systems are based on several monitoring and mapping efforts from international (Healthy Reefs Initiative, MARFUND) and national initiatives (CONANP through Natural Protected Areas, CONABIO) with assistance from civil society and academic institutions. However, an integrated sustainable management strategy is still pending. Therefore, we proposed creating a theoretical framework to support this need.

Our proposal is an enduring, sustainable and efficient conceptual model: a Reef cybercartographic atlas aimed at safeguarding the reef ecosystems of the Mexican Caribbean while considering economic growth and ensuring the maintenance of biodiversity and natural spaces. These conceptual models will serve as the basis to propose alternatives that allow the use and management of reef system resources as an opportunity to promote sustainable development; because coastal and marine areas of the Mexican Caribbean are subject to strong, diverse, and intense environmental impacts originating from economic activities. The Reef Atlas will help understand, through comprehensive and integrative visions, the socio-environmental problems as the basis for reorienting reef use and management policies. These need to be transversal, based on the multidimensionality of complex socio-ecological processes, including society and strengthening of governance.

The conceptual framework first focused on understanding contemporary society's environmental problems. In this way, the atlas can help reinforce comprehensive public policies and transcend to new schemes of effective coordination between institutions to generate new forms of environmental governance with informed personnel to conserve and enhance the coral reefs' ecological services. Promoting the proper use of information is mandatory. Thus, access to available and up-to-date scientific data will be facilitated and stored in the Reef atlas.

5.6 Potential future developments

Promoting adequate management and actions based on scientific information that supports coral reef resilience is of utmost importance for sustainability. Management must consider ecological disasters and the main stressors impacting the reefs to promote resilience in reef systems. The ulterior objective is maintaining coral diversity while improving their ability to provide ecological services (Chapter 4). Other management techniques should include in-situ water quality measurements, e.g., from oceanographic buoys to calibrate satellite measurements at regional scales correctly. Integrating different monitoring strategies, e.g., emerging aerial, surface and underwater autonomous vehicles technologies to generate real-time information, may enhance management (Chapter 3). Therefore, further longitudinal analysis should include data on factors such as herbivore biomass to test their effectiveness on macroalgae control (Chapter 2) and their relationship with decreasing water quality. This is important because most Mexican Caribbean reefs underwent phase-shifts from coral to algae domination despite maintaining herbivorous fish biomass in the last decades (Arias-González et al., 2017; Suchley et al., 2016). And in the face of novel coral diseases, further studies on alternative stable states and changes in hard-coral species should be proposed for the whole region, including Banco Chinchorro Atoll. Conversely, it would be interesting to study key reef-building coral taxa (e.g., *Acroporids sp*. resistance and resilience) and grazing species such as urchins and parrotfishes to gain further insights into the complex processes taking place in the region (Chapter 2).

Overall, the Mexican Caribbean reef's health status shows a tendency to decrease, as observed in other global regions, i.e., Western Atlantic and the Central Pacific and, to a lesser extent, the Indo-West Pacific and Indian Ocean, accompanied by a global increase of macroalgae cover due to land-based pollution (Tebbett et al., 2023). Further, the seascape has grown increasingly fragmented from the standpoint of corals because of pollution from coastal anthropisation, habitat degradation (Chapter 3), and coral reproductive failure (Shlesinger & Loya, 2019). The reduced connection between reefs can potentially impair spatial resilience, which may affect the ability of perturbed reefs to reorganise on a regional scale (Nyström & Folke, 2001). To prevent further coral reef depletion, managers must encourage spatial resilience as a determining factor in reef endurance over more significant extended periods if coral reefs are open, interconnected complex systems (Cumming, 2011; Dubinsky & Stambler, 2011b).

Environmental stressors and disturbances working on broader geographical scales, such as global warming, must also be addressed to manage coral reefs effectively, especially concerning spatial resilience (Hughes et al., 2003). It is a significant yet neglected research area to understand how combined disturbances impact coral reefs. Further research into adaptability and acclimation is also necessary since they might be crucial to coral survival during the next century of climatic change (Barnard et al., 2021). Furthermore, we must understand how much the system's redundancy can support ecosystem performance (Norberg, 2004) and how much coastal fragmentation affects the reef tract. Finally, to create a management tool to safeguard the reefs in the Mexican Caribbean, the Reef Atlas conceptual framework should be discussed with stakeholders, managers and civil society to enhance it and put it into motion (Chapter 4).

5.7 Concluding Remarks

Current analyses state that the variety, frequency, and intensity of disturbances affecting coral reefs will continue to increase (Jones et al., 2022; Vercelloni et al., 2020). Since the 1990s, Hoegh-Guldberg (1999) already anticipated that in 20 to 30 years, significant coral bleaching episodes would happen more frequently and almost annually. Today we witness that some corals cannot adapt to environmental changes as quickly as required over the next century, leading to the the currently observed global coral reef deterioration (Jones et al., 2022; McWilliam et al., 2020). According to recent studies, 40 % of the reefs may disappear by 2050 (Douglas, 2020). Although coral reefs have historically recovered from significant catastrophes, recovery can no longer be taken for granted. Mexican Caribbean reefs have historically recovered from major catastrophes, but this may no longer be true given the accelerated climatic change, modified disturbance regimes, and compounding disturbances. This perspective is shown by the rising number of coral reefs that switch to alternative states instead of reorganising after disturbance events that may have been absorbed in the past. As a result, it is urgent to re-evaluate coral reef resilience against the already-known effects of anthropogenic climate change. We already witness coral reef changes in species composition and a lower capacity to recover. Therefore, managers must be flexible enough to adjust their goals to account for sustainability and resilience. We can protect coral reefs locally and nationally through improved laws and regulations, so we may enhance their ability to cope and adapt to anthropogenic environmental change.

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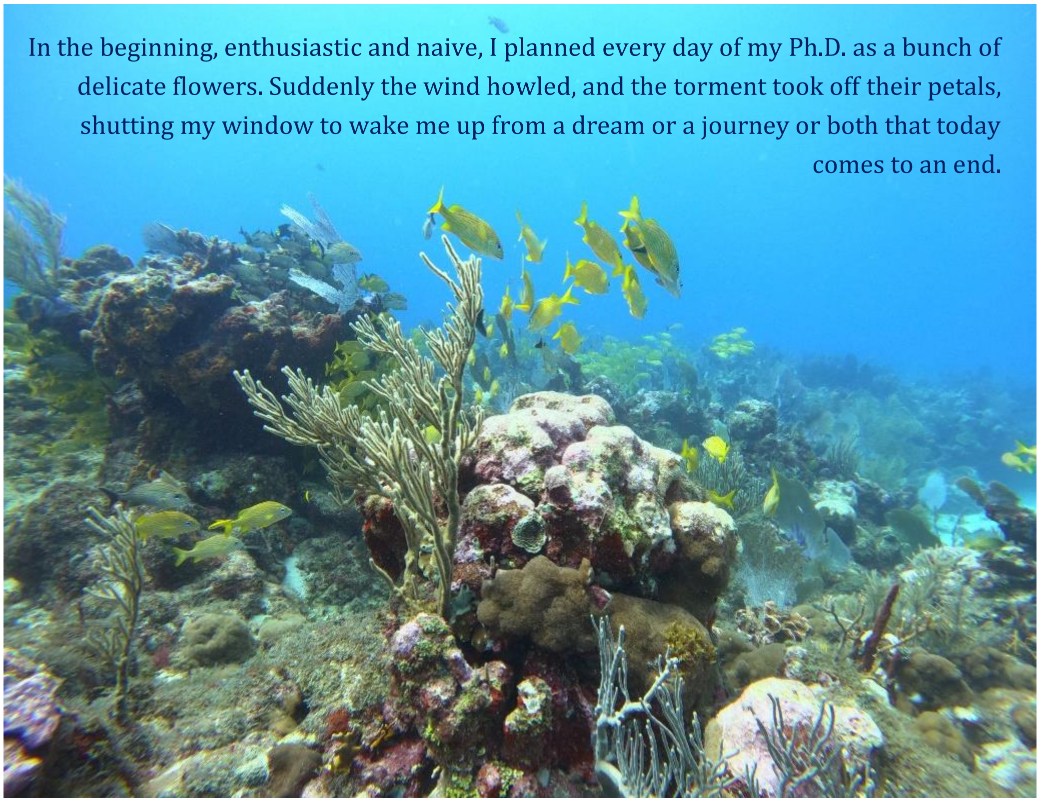

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Appendix A Supplementary Material Chapter 2

Supplementary Table S2.1 *Estimates resulting from the hard coral meta-analyses divided by periods of time, general result,s and by sub-regions. ES denotes the mean effect size (ARC), n denotes the sample size, SE denotes standard err,or and p the significance of the statistical analysis*

	1978-2016				1978-2004				2005-2016			
	ES	SE	n	*p*	ES	SE	n	*p*	ES	SE	n	*p*
Overall MC	1.18	2.64	125	0.656	-12.16	4.68	35	0.0094	5.19	1.36	92	0.0001
North	6.47	4.12	50	0.1161	-2.40	4.51	16	0.5952	3.78	2.31	32	0.1022
Cozumel	4.05	4.55	41	0.3736	-1.67	5.45	11	0.76	8.75	2.18	35	<0.0001
Center	-14.15	7.06	17	0.0451	-68.55	9.04	4	<0.0001	2.59	3.56	13	0.4681
South	-5.58	6.86	18	0.4159	-23.82	9.01	4	0.0082	1.30	3.71	12	0.7272

Supplementary Table S2.2 *Estimates resulting from the macroalgae meta-analyses divided by periods of time, general results and by sub-regions. ES denotes the mean effect size (ARC), n denotes the sample size, SE denotes standard error and p the significance of the statistical analysis*

	1989-2016				1989-2004				2005-2016			
	ES	SE	n	*p*	ES	SE	n	*p*	ES	SE	n	*p*
Overall MC	10.87	1.77	94	<0.0001	8.77	4.35	15	0.0437	12.06	1.84	85	<0.0001
North	6.28	3.19	29	0.0489	0	12.31	2	1	6.60	3.16	28	0.0365
Cozumel	12.05	2.72	40	<0.0001	2.87	3.73	11	0.44	16.55	2.87	34	<0.0001
Center	15.20	4.76	13	0.0014	28.51	12.44	2	0.02	14.10	4.82	12	0.0034
South	13.36	4.96	12	0.007	35.60	8.69	2	<0.0001	9.85	5.04	11	0.0506

Supplementary Table S2.3 *Reef sites used for hard coral cover analyses. MPA refers to Marine Protected Area, and Pub refers to the origin of the information (0 refers to monitoring or grey literature data; 1 refers to published data). NA = not available*

Num	***Site_code***	***Latitude***	***Longitude***	***Region***	***Municipality***	***Depth***	***MPA***	***Pub***
1	Akumal.Garcia	20.398	-87.3052	Northern	Tulum	10	0	0
2	Akumal.Garza	20.406	-87.30056	Northern	Tulum	10	0	0
3	Akumal.Harvell	20.398	-87.3061	Northern	Tulum	NA	0	0
4	Akumal.Rodriguez	20.383	-87.3151	Northern	Tulum	7	0	1
5	Boca.Paila.Garza	19.975	-87.4284	Center	F.Carrillo.Puerto	10	1	0
6	Bonanza	20.965	-86.81408	Northern	Puerto.Morelos	2	1	0
7	Cancun.Barranco	21.181	-86.75833	Northern	Isla.Mujeres	NA	1	1
8	Cardona.Mera.Somero	20.408	-87.01955	Cozumel	Cozumel	5	1	0
9	Cardona.ReefKeeper	20.414	-87.02031	Cozumel	Cozumel	NA	1	0
10	Chankanaab	20.44	-87.00295	Cozumel	Cozumel	12	1	0
11	Chankanaab.Bolones	20.44	-87.00295	Cozumel	Cozumel	NA	1	0
12	Chankanaab.Bolones.Mera.Profundo	20.44	-87.00512	Cozumel	Cozumel	18	1	0
13	Chankanaab.Mera.Somero	20.439	-86.99961	Cozumel	Cozumel	12	1	0
14	Chitales.Jordan	21.141	-86.7437	Northern	Cancun	NA	1	1
15	Colombia	20.324	-87.02719	Cozumel	Cozumel	12	1	0
16	Colombia.Mera.Profundo	20.31	-87.02565	Cozumel	Cozumel	18.5	1	0
17	Colombia.Mera.Somero	20.32	-87.02437	Cozumel	Cozumel	6.5	1	0
18	Colombia.ReefKeeper	20.326	-87.01681	Cozumel	Cozumel	NA	1	0
19	Cozumel.Barranco	20.426	-87.0159	Cozumel	Cozumel	NA	1	1
20	Cozumel.Garcia	20.329	-87.0269	Cozumel	Cozumel	10	1	0
21	Cuevones	21.162	-86.74199	Northern	Isla.Mujeres	7	1	0
22	Dalila	20.349	-87.02906	Cozumel	Cozumel	12	1	0
23	DzulHa.Mera.Somero	20.459	-86.98709	Cozumel	Cozumel	3	1	0
24	Hanan	20.505	-86.757	Cozumel	Cozumel	5	1	0
25	Hanan.II	20.499	-86.761	Cozumel	Cozumel	8	1	0
26	Islote	20.441	-87.00233	Cozumel	Cozumel	15	1	0

27	Ixlache	21.435	-86.78	Northern	Isla.Mujeres	2	1	0
28	Jardines	20.833	-86.87844	Northern	Puerto.Morelos	2	1	0
29	La.Bocana	20.875	-86.85172	Northern	Puerto.Morelos	4	1	0
30	La.Pared	20.824	-86.87753	Northern	Puerto.Morelos	4	1	0
31	Las.Redes_13	20.389	-87.31028	Northern	Tulum	13	0	1
32	Limones	20.988	-86.79719	Northern	Puerto.Morelos	3	1	0
33	Mah01	18.663	-87.71636	Southern	Othon.P.Blanco	11	0	0
34	Mahahual.Arias	18.712	-87.70329	Southern	Othon.P.Blanco	15	0	1
35	Mahahual.Garza	18.712	-87.70333	Southern	Othon.P.Blanco	10	0	0
36	Mahahual.Harvell	18.723	-87.6971	Southern	Othon.P.Blanco	NA	0	0
37	Mahahual.Rodríguez	18.805	-87.6583	Southern	Othon.P.Blanco	10	0	1
38	Media.Luna_13	20.402	-87.30272	Northern	Tulum	13	0	1
39	MX1005	19.75	-87.40317	Center	F.Carrillo.Puerto	17	1	0
40	MX1006	19.829	-87.4399	Center	F.Carrillo.Puerto	18	1	0
41	MX1008	20.057	-87.46059	Center	F.Carrillo.Puerto	17	1	0
42	MX1010	20.348	-87.33246	Northern	Tulum	16	0	0
43	MX1017	21.171	-86.72976	Northern	Isla.Mujeres	6	1	0
44	MX1020	18.65	-87.71769	Southern	Othon.P.Blanco	11	0	0
45	MX1026	19.13	-87.53735	Center	F.Carrillo.Puerto	8	1	0
46	MX1028	19.239	-87.49639	Center	F.Carrillo.Puerto	14	1	0
47	MX1034	19.591	-87.39506	Center	F.Carrillo.Puerto	10	1	0
48	MX1035	19.74	-87.4135	Center	F.Carrillo.Puerto	6	1	0
49	MX1037	19.869	-87.4194	Center	F.Carrillo.Puerto	12	1	0
50	MX1042	20.115	-87.45794	Center	Tulum	9	1	0
51	MX1043	20.259	-87.38535	Northern	Tulum	8	0	0
52	MX1047	20.39	-87.31046	Northern	Tulum	10	0	0
53	MX1048	20.358	-87.02822	Cozumel	Cozumel	12	1	0
54	MX1050	20.536	-87.16451	Northern	Solidaridad	11	0	0
55	MX1053	20.486	-86.97072	Cozumel	Cozumel	5	1	0
56	MX1055	20.584	-87.10606	Northern	Solidaridad	7	0	0
57	MX1057	20.641	-87.05353	Northern	Solidaridad	2	0	0
58	MX1059	18.209	-87.82293	Southern	Othon.P.Blanco	7	1	0

59	MX1062	21.01	-86.77834	Northern	Isla.Mujeres	12	1	0
60	MX1065	18.353	-87.7907	Southern	Othon.P.Blanco	12	1	0
61	MX1066	21.46	-86.78122	Northern	Isla.Mujeres	7	1	0
62	MX1109	19.647	-87.41732	Center	F.Carrillo.Puerto	2	1	0
63	MX1116	20.551	-87.14924	Northern	Solidaridad	2	0	0
64	MX1117	20.218	-87.41906	Northern	Tulum	3	0	0
65	MX1131	20.916	-86.8288	Northern	Puerto.Morelos	4	1	0
66	MX1132a	20.987	-86.79642	Northern	Puerto.Morelos	2	1	0
67	MX1132b	20.987	-86.79642	Northern	Puerto.Morelos	2	1	0
68	MX1133	21.133	-86.74054	Northern	Isla.Mujeres	4	1	0
69	MX1134	21.199	-86.72548	Northern	Isla.Mujeres	6	1	0
70	MX1136	18.35	-87.79838	Southern	Othon.P.Blanco	1	1	0
71	MX2007	19.835	-87.44176	Center	F.Carrillo.Puerto	13	1	0
72	MX2033	19.45	-87.43655	Center	F.Carrillo.Puerto	11	1	0
73	MX2067	18.4	-87.76702	Southern	Othon.P.Blanco	10	1	0
74	MX3009	20.272	-86.99994	Cozumel	Cozumel	7	1	0
75	MX3021	18.783	-87.65809	Southern	Othon.P.Blanco	12	0	0
76	MX3054	20.511	-86.7524	Cozumel	Cozumel	12	1	0
77	MXXCK01	18.214	-87.82744	Southern	Othon.P.Blanco	9	1	0
78	MXXCK02	18.24	-87.82623	Southern	Othon.P.Blanco	7	1	0
79	Palancar.Herradura	20.331	-87.02742	Northern	Cozumel	NA	1	0
80	Palancar.Jardines.Mera.Profundo	20.334	-87.02722	Cozumel	Cozumel	22	1	0
81	Palancar.Jardines.Mera.Somero	20.332	-87.0262	Cozumel	Cozumel	6	1	0
82	Palmas.Mera.Profundo	20.455	-86.99373	Cozumel	Cozumel	25	1	0
83	Paraiso	20.469	-86.98303	Cozumel	Cozumel	10	1	0
84	Paraiso.Mera.Somero	20.469	-86.98147	Cozumel	Cozumel	4	1	0
85	Paraiso.Norte.ReefKeeper	20.475	-86.97957	Cozumel	Cozumel	NA	1	0
86	Paraiso.Sur.ReefKeeper	20.472	-86.98232	Cozumel	Cozumel	NA	1	0
87	Paso.del.Cedral	20.374	-87.02894	Cozumel	Cozumel	13	1	0
88	Puerto.Morelos	20.862	-86.8559	Northern	Puerto.Morelos	2	1	0
89	Puerto.Morelos.Harvell	20.847	-86.867	Northern	Puerto.Morelos	NA	1	0
90	Puerto.Morelos.Posterior.Jordan	NA	NA	Northern	Puerto.Morelos	NA	1	0

95	PuertoMorelos.Rodriguez	20.989	-86.7941	Northern	Puerto.Morelos	5	1	1
96	Punta.Allen.Rodríguez	19.784	87.4338	Center	Tulum	10	1	1
97	Punta.Francesa.Mera.Profundo	20.357	-87.02963	Cozumel	Cozumel	17	1	0
98	Punta.Francesa.Mera.Somero	20.362	-87.0272	Cozumel	Cozumel	7	1	0
99	Punta.Maroma_10.Jordan	NA	NA	Northern	Solidaridad	10	0	0
101	Punta.Maroma_Posterior.Jordan	NA	NA	Northern	Solidaridad	5	0	0
104	Punta.Nizuc_Posterior.Jordan	NA	NA	Northern	Benito.Juarez	5	1	0
105	Punta.Sur.Mera.Profundo	20.301	-87.02476	Cozumel	Cozumel	20	1	0
106	Punta.Sur.Mera.Somero	20.298	-87.0194	Cozumel	Cozumel	4	1	0
107	Radio.Pirata	20.854	-86.86501	Northern	Puerto.Morelos	1	1	0
108	San.Clemente	20.408	-87.02197	Cozumel	Cozumel	8	1	0
109	San.Francisco.Mera.Intermedio	20.397	-87.02603	Cozumel	Cozumel	12	1	0
110	Santa.Rosa.Bolones	20.377	-87.02933	Cozumel	Cozumel	17	1	0
111	Santa.Rosa.Mera.Intermedio	20.378	-87.02849	Cozumel	Cozumel	11	1	0
112	Sta.Rosa.bajo	20.376	-87.02953	Cozumel	Cozumel	12	1	0
113	Tampalam.Centro	19.146	-87.53611	Center	F.Carrillo.Puerto	20	1	0
114	Tampalam.Norte	19.154	-87.53333	Center	F.Carrillo.Puerto	20	1	0
115	Tanchacte.Norte	20.912	-86.83608	Northern	Puerto.Morelos	20	1	0
116	Tanchacte.Sur	20.902	-86.84227	Northern	Puerto.Morelos	20	1	0
117	Tormentos	20.432	-87.01257	Cozumel	Cozumel	8	1	0
118	Tunich.Mera.Profundo	20.415	-87.0205	Cozumel	Cozumel	24	1	0
119	Uvero.Harvell	18.952	-87.61	Southern	Othon.P.Blanco	NA	1	0
120	Xcalak.Harvell	18.26	-87.8237	Southern	Othon.P.Blanco	NA	1	0
121	Xcalak.Fore.Steneck	18.32	-87.813	Southern	Othon.P.Blanco	13	1	1
122	Xcalak.Garcia	18.264	-87.8233	Southern	Othon.P.Blanco	10	1	0
123	Xcalak.Patch.Steneck	18.265	-87.828	Southern	Othon.P.Blanco	2	1	1
124	Yalku.Rodríguez	20.406	-87.2998	Northern	Tulum	10	0	1
125	Yucab	20.421	-87.01747	Cozumel	Cozumel	13	1	0

Supplementary Table S2.4 *Reef sites used for macroalgae (calcareous and fleshy) analyses. MPA refers to Marine Protected Area, Pub refers to the origin of the information, 0 refers to monitoring or grey literature data, whereas 1 refers to published data. NA = not available*

Num	*Site_code*	*Latitude*	*Longitude*	*Region*	*Municipality*	*Depth*	*MPA*	*Pub*
1	Akumal.Garcia	20.4	-87	Northern	Tulum	10	0	0
2	Akumal.Garza	20.4	-87	Northern	Tulum	10	0	0
3	Boca.Paila.Garza	20	-87	Center	F.Carrillo.Puerto	10	1	0
4	Bonanza	21	-87	Northern	Puerto.Morelos	2	1	0
5	Cardona.Mera.Somero	20.4	-87	Cozumel	Cozumel	5	1	0
6	Cardona.ReefKeeper	20.4	-87	Cozumel	Cozumel	NA	1	0
7	Chankanaab	20.4	-87	Cozumel	Cozumel	12	1	0
8	Chankanaab.bolones	20.4	-87	Cozumel	Cozumel	NA	1	0
9	Chankanaab.Bolones.Mera.Profundo	20.4	-87	Cozumel	Cozumel	18	1	0
10	Chankanaab.Mera.Somero	20.4	-87	Cozumel	Cozumel	12	1	0
11	Colombia	20.3	-87	Cozumel	Cozumel	12	1	0
12	Colombia.Mera.Profundo	20.3	-87	Cozumel	Cozumel	19	1	0
13	Colombia.Mera.Somero	20.3	-87	Cozumel	Cozumel	6.5	1	0
14	Colombia.ReefKeeper	20.3	-87	Cozumel	Cozumel	NA	1	0
15	Cozumel.Garcia	20.3	-87	Cozumel	Cozumel	10	1	0
16	Cuevones	21.2	-87	Northern	Isla.Mujeres	7	1	0
17	Dalila	20.3	-87	Cozumel	Cozumel	12	1	0
18	DzulHa.Mera.Somero	20.5	-87	Cozumel	Cozumel	3	1	0
19	Hanan	20.5	-87	Cozumel	Cozumel	5	1	0
20	Hanan.II	20.5	-87	Cozumel	Cozumel	8	1	0
21	Islote	20.4	-87	Cozumel	Cozumel	15	1	0
22	Ixlache	21.4	-87	Northern	Isla.Mujeres	2	1	0
23	Jardines	20.8	-87	Northern	Puerto.Morelos	2	1	0
24	La.Bocana	20.9	-87	Northern	Puerto.Morelos	4	1	0
25	La.Pared	20.8	-87	Northern	Puerto.Morelos	4	1	0
26	Limones	21	-87	Northern	Puerto.Morelos	3	1	0
27	Mah01	18.7	-88	Southern	Othon.P.Blanco	11	0	0

28	Mahahual.Arias	18.7	-88	Southern	Othon.P.Blanco	15	0	1
29	Mahahual.Garza	18.7	-88	Southern	Othon.P.Blanco	10	0	0
30	MX1005	19.8	-87	Center	F.Carrillo.Puerto	17	1	0
31	MX1006	19.8	-87	Center	F.Carrillo.Puerto	18	1	0
32	MX1008	20.1	-87	Center	F.Carrillo.Puerto	17	1	0
33	MX1010	20.3	-87	Northern	Tulum	16	0	0
34	MX1017	21.2	-87	Northern	Isla.Mujeres	6	1	0
35	MX1020	18.6	-88	Southern	Othon.P.Blanco	11	0	0
36	MX1026	19.1	-88	Center	F.Carrillo.Puerto	8	1	0
37	MX1028	19.2	-87	Center	F.Carrillo.Puerto	14	1	0
38	MX1034	19.6	-87	Center	F.Carrillo.Puerto	10	1	0
39	MX1035	19.7	-87	Center	F.Carrillo.Puerto	6	1	0
40	MX1037	19.9	-87	Center	F.Carrillo.Puerto	12	1	0
41	MX1042	20.1	-87	Center	Tulum	9	1	0
42	MX1043	20.3	-87	Northern	Tulum	8	0	0
43	MX1047	20.4	-87	Northern	Tulum	10	0	0
44	MX1048	20.4	-87	Cozumel	Cozumel	12	1	0
45	MX1050	20.5	-87	Northern	Solidaridad	11	0	0
46	MX1053	20.5	-87	Cozumel	Cozumel	5	1	0
47	MX1055	20.6	-87	Northern	Solidaridad	7	0	0
48	MX1057	20.6	-87	Northern	Solidaridad	2	0	0
49	MX1059	18.2	-88	Southern	Othon.P.Blanco	7	1	0
50	MX1062	21	-87	Northern	Isla.Mujeres	12	1	0
51	MX1065	18.4	-88	Southern	Othon.P.Blanco	12	1	0
52	MX1066	21.5	-87	Northern	Isla.Mujeres	7	1	0
53	MX1109	19.6	-87	Center	F.Carrillo.Puerto	2	1	0
54	MX1116	20.6	-87	Northern	Solidaridad	2	0	0
55	MX1117	20.2	-87	Northern	Tulum	3	0	0
56	MX1131	20.9	-87	Northern	Puerto.Morelos	4	1	0
57	MX1132a	21	-87	Northern	Puerto.Morelos	2	1	0
58	MX1132b	21	-87	Northern	Puerto.Morelos	2	1	0

59	MX1133	21.1	-87	Northern	Isla.Mujeres	4	1	0
60	MX1134	21.2	-87	Northern	Isla.Mujeres	6	1	0
61	MX1136	18.3	-88	Southern	Othon.P.Blanco	1	1	0
62	MX2007	19.8	-87	Center	F.Carrillo.Puerto	13	1	0
63	MX2033	19.5	-87	Center	F.Carrillo.Puerto	11	1	0
64	MX2067	18.4	-88	Southern	Othon.P.Blanco	10	1	0
65	MX3009	20.3	-87	Cozumel	Cozumel	7	1	0
66	MX3021	18.8	-88	Southern	Othon.P.Blanco	12	0	0
67	MX3054	20.5	-87	Cozumel	Cozumel	12	1	0
68	MXXCK01	18.2	-88	Southern	Othon.P.Blanco	9	1	0
69	MXXCK02	18.2	-88	Southern	Othon.P.Blanco	7	1	0
70	Palancar.Jardines.Mera.Profundo	20.3	-87	Cozumel	Cozumel	22	1	0
71	Palancar.Jardines.Mera.Somero	20.3	-87	Cozumel	Cozumel	6	1	0
72	Palmas.Mera.Profundo	20.5	-87	Cozumel	Cozumel	25	1	0
73	Paraiso	20.5	-87	Cozumel	Cozumel	10	1	0
74	Paraiso.Mera.Somero	20.5	-87	Cozumel	Cozumel	4	1	0
75	Paraiso.Norte.ReefKeeper	20.5	-87	Cozumel	Cozumel	NA	1	0
76	Paraiso.Sur.ReefKeeper	20.5	-87	Cozumel	Cozumel	NA	1	0
77	Paso.del.Cedral	20.4	-87	Cozumel	Cozumel	13	1	0
78	Puerto.Morelos	20.9	-87	Northern	Puerto.Morelos	2	1	0
79	Punta.Francesa.Mera.Profundo	20.4	-87	Cozumel	Cozumel	17	1	0
80	Punta.Francesa.Mera.Somero	20.4	-87	Cozumel	Cozumel	7	1	0
81	Punta.Sur.Mera.Profundo	20.3	-87	Cozumel	Cozumel	20	1	0
82	Punta.Sur.Mera.Somero	20.3	-87	Cozumel	Cozumel	4	1	0
83	Radio.Pirata	20.9	-87	Northern	Puerto.Morelos	1	1	0
84	San.Clemente	20.4	-87	Cozumel	Cozumel	8	1	0
85	San.Francisco.Mera.Intermedio	20.4	-87	Cozumel	Cozumel	12	1	0
86	Santa.Rosa.Bolones	20.4	-87	Cozumel	Cozumel	17	1	0
87	Santa.Rosa.Mera.Intermedio	20.4	-87	Cozumel	Cozumel	11	1	0
88	Sta.Rosa.bajo	20.4	-87	Cozumel	Cozumel	12	1	0
89	Tanchacte.Norte	20.9	-87	Northern	Puerto.Morelos	20	1	0

90	Tanchacte.Sur	20.9	-87	Northern	Puerto.Morelos	20	1	0
91	Tormentos	20.4	-87	Cozumel	Cozumel	8	1	0
92	Tunich.Mera.Profundo	20.4	-87	Cozumel	Cozumel	24	1	0
93	Xcalak.Garcia	18.3	-88	Southern	Othon.P.Blanco	10	1	0
94	Yucab	20.4	-87	Cozumel	Cozumel	13	1	0

Supplementary Table S2.5 *PRISMA 2009 Checklist*

Section/topic	#	Checklist item	Reported on page #
TITLE			
Title	1	Identify the report as a systematic review, meta-analysis, or both.	1
ABSTRACT			
Structured summary	2	Provide a structured summary including, as applicable: background; objectives; data sources; study eligibility criteria, participants, and interventions; study appraisal and synthesis methods; results; limitations; conclusions and implications of key findings; systematic review registration number.	1
INTRODUCTION			
Rationale	3	Describe the rationale for the review in the context of what is already known.	2
Objectives	4	Provide an explicit statement of questions being addressed with reference to participants, interventions, comparisons, outcomes, and study design (PICOS).	2
METHODS			
Protocol and registration	5	Indicate if a review protocol exists, if and where it can be accessed (e.g., Web address), and, if available, provide registration information including registration number.	-
Eligibility criteria	6	Specify study characteristics (e.g., PICOS, length of follow-up) and report characteristics (e.g., years considered, language, publication status) used as criteria for eligibility, giving rationale.	7
Information sources	7	Describe all information sources (e.g., databases with dates of coverage, contact with study authors to identify additional studies) in the search and date last searched.	8
Search	8	Present full electronic search strategy for at least one database, including any limits used, such that it could be repeated.	7
Study selection	9	State the process for selecting studies (i.e., screening, eligibility, included in systematic review, and, if applicable, included in the meta-analysis).	7
Data collection process	10	Describe method of data extraction from reports (e.g., piloted forms, independently, in duplicate) and any processes for obtaining and confirming data from investigators.	-
Data items	11	List and define all variables for which data were sought (e.g., PICOS, funding sources) and any assumptions and simplifications made.	7
Risk of bias in individual studies	12	Describe methods used for assessing risk of bias of individual studies (including specification of whether this was done at the study or outcome level), and how this information is to be used in any data synthesis.	-

Summary measures	13	State the principal summary measures (e.g., risk ratio, difference in means).	7
Synthesis of results	14	Describe the methods of handling data and combining results of studies, if done, including measures of consistency (e.g., I^2) for each meta-analysis.	8
Risk of bias across studies	15	Specify any assessment of risk of bias that may affect the cumulative evidence (e.g., publication bias, selective reporting within studies).	9
Additional analyses	16	Describe methods of additional analyses (e.g., sensitivity or subgroup analyses, meta-regression), if done, indicating which were pre-specified.	9
RESULTS			
Study selection	17	Give numbers of studies screened, assessed for eligibility, and included in the review, with reasons for exclusions at each stage, ideally with a flow diagram.	3
Study characteristics	18	For each study, present characteristics for which data were extracted (e.g., study size, PICOS, follow-up period) and provide the citations.	-
Risk of bias within studies	19	Present data on risk of bias of each study and, if available, any outcome level assessment (see item 12).	-
Results of individual studies	20	For all outcomes considered (benefits or harms), present, for each study: (a) simple summary data for each intervention group (b) effect estimates and confidence intervals, ideally with a forest plot.	-
Synthesis of results	21	Present results of each meta-analysis done, including confidence intervals and measures of consistency.	3
Risk of bias across studies	22	Present results of any assessment of risk of bias across studies (see Item 15).	-
Additional analysis	23	Give results of additional analyses, if done (e.g., sensitivity or subgroup analyses, meta-regression [see Item 16]).	-
DISCUSSION			
Summary of evidence	24	Summarize the main findings including the strength of evidence for each main outcome; consider their relevance to key groups (e.g., healthcare providers, users, and policy makers).	4-7
Limitations	25	Discuss limitations at study and outcome level (e.g., risk of bias), and at review-level (e.g., incomplete retrieval of identified research, reporting bias).	6-7
Conclusions	26	Provide a general interpretation of the results in the context of other evidence, and implications for future research.	6-7
FUNDING			
Funding	27	Describe sources of funding for the systematic review and other support (e.g., supply of data); role of funders for the systematic review.	-

Appendix B Supplementary Material Chapter 3

3.1 Effects of coastal anthropisation, hurricane impacts, and bleaching susceptibility in Mexican Caribbean coral reefs

Downloading and data extraction from remote sensing imagery

Downloading data from Google Earth Engine (GEE)

This study focused on satellite datasets in GEE that correspond to the Mexican Caribbean seascape, including AQUA from MODIS imagery, sea surface temperature (SST), chlorophyll-*a* and particulate organic carbon. The images were retrieved online from (https://developers.google.com/earth-engine/datasets/catalog/NASA_OCEANDATA_MODIS-Aqua_L3SMI#bands) (See Appendix 1 script example to export data from GEE platform).

Sea surface temperature (SST)

Several institutions, including NASA, routinely conduct global surface temperature change analyses. Increases in SST are significant in coral reefs, causing coral stress. Temperatures above 1ºC for prolonged periods (four or more weeks), coral tissue bleaching results by disrupting the symbiotic zooxanthellae-coral. Here we use SST as the leading global stressor impacting coral reefs in the Mexican Caribbean.

Chlorophyll–*a*

Chlorophyll-*a* water concentration was used as a proxy for nutrient concentration and eutrophication, for example, as used by Duprey et al. (2016), Reynolds and Maberly (2002) and De'ath and Fabricius (2010). In addition, chlorophyll-*a* concentration is directly correlated with nitrogen, phosphorous, and suspended solids (De'ath and Fabricius, 2010).

The algorithm used to generate this product returns the near-surface concentration of chlorophyll-*a* in mg m-3, calculated using an empirical relationship resultant from in situ measurements of chlorophyll-*a* and remote sensing reflectances in the blue-to-green region of the visible spectrum1.

Particulate organic carbon (POC)

POC is one of the leading organic carbon pools found in the ocean. It comprises living material (Phytoplankton, zooplankton, bacteria, between others) and detritus. POC is important in terms of the global carbon cycle. It is the main pathway by which organic carbon formed via photosynthesis in the ocean's surface layers is transferred to deeper ocean layers where it may be sequestered. It is measured for various reasons and, for example, can be a good indicator of productivity in the euphotic zone. Regarding seaports, the biotic and detritus components of POC could be used as pollution indicators.

In this study, we used a MODIS Aqua product from NASA. The platform retrieves an image whose algorithm returns the concentration of particulate organic carbon (POC) in mg m-3. POC is calculated using an empirical relationship derived from in situ measurements of POC and blue-to-green band ratios of remote sensing reflectances between 547 and 565 nm in the green region.

Coefficient attenuation coefficient Kd490

The diffuse attenuation coefficient Kd490 in water indicates how strongly light intensity attenuates at a specified wavelength within the water column. The value of Kd490 represents the rate at which light at 490 nm is attenuated with depth. This parameter has broad applicability in ocean optics, as it is directly related to the presence of scattering particles in the water column, either organic or inorganic. Thus, it indicates water turbidity represented in the visible blue to the green region of the spectrum penetrating the water column. For example, a Kd490 of 0.1/meter means that light intensity will be reduced to one natural log within 10 meters of water. Thus, for a Kd490 of 0.1, one attenuation length is 10 meters. A higher Kd490 value means a smaller attenuation depth and lower clarity of ocean water.

The algorithm used to generate this product returns the diffuse attenuation coefficient for downwelling irradiance at 490 nm (Kd_490) in m-1, calculated using an empirical relationship derived from in situ measurements of Kd_490 and blue-to-green band ratios of remote sensing reflectances in the blue-green spectral region 490 - 565 nm. The water attenuation coefficient was downloaded from 2005 until 2016 from NASA Ocean Color Web (https://oceancolor.gsfc.nasa.gov/) at 1000 m spatial resolution. A minimum of two images per month for each year were downloaded. The majority of the images had a percentage of cloud coverage. Therefore, an interpolation was performed with the r.fillnulls function in GRASS GIS 7.8.3. Monthly, followed by annual averages, were created.

References

Duprey, N. N., Yasuhara, M., & Baker, D. M. (2016). Reefs of tomorrow: eutrophication reduces coral biodiversity in an urbanized seascape. Global Change Biology, 22(11), 3550–3565. https://doi.org/10.1111/gcb.13432

De'ath, G., & Fabricius, K. (2010). Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecological Applications, 20(3), 840–850.

Reynolds, C. S., & Maberly, S. C. (2002). A simple method for approximating the supportive capacities and metabolic constraints in lakes and reservoirs. Freshwater Biology, 47(6), 1183–1188. https://doi.org/10.1046/j.1365-2427.2002.00839.x

[1]Chlorophyll–*a* [https://oceancolor.gsfc.nasa.gov/atbd/chlor_a/]

[2]POC [https://oceancolor.gsfc.nasa.gov/atbd/poc/]

[3]K490 [https://oceancolor.gsfc.nasa.gov/atbd/kd_490/]

Model to extract data

We used the graphical modeler of GRASS GIS 7.8.3 to easily extract the data from the satellite images at specific reef site. The model in Figure S1 shows a chain of operations wrapped into a single process, independently of how many steps and different algorithms it involves, the model was executed as a single algorithm, thus saving time and effort.

The group of instructions in Figure S1 are as follows: 1) Projection of the input image which contains the parameter of interest. 2) Vector importation of the file containing the reef sites. 3) This step generates a weighted average (3 x 3 window) of the pixels surrounding the reef site. 4) A new column is added to the attribute table of the vector containing the reef sites. 5) Extract the average value of the image of interest and write the value in the new column created in step 4. 6) As a result, a new vector with the new extracted data is generated.

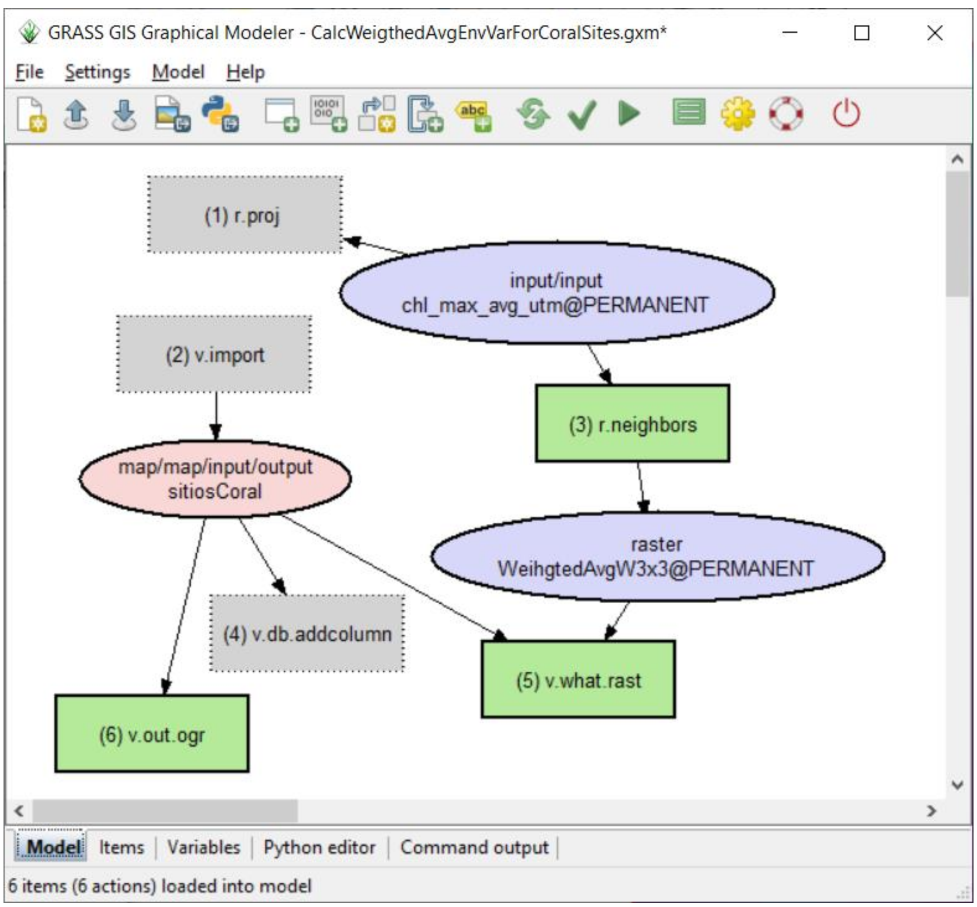

***Figure S3.1** Graphical visualization of the model to extract satellite data concordant with each reef site.*

Appendix S3.1.2. Scripts GEE. Example to export sea surface temperature data

```
var dataset = ee.ImageCollection('NASA/OCEANDATA/MODIS-Aqua/L3SMI')
            .filterDate('2005-01-01', '2005-12-31');
var dataset = ee.ImageCollection('NASA/OCEANDATA/MODIS-Aqua/L3SMI').filterDate('2005-01-01', '2005-12-31').select(['sst']);
print('Dataset: ', dataset);
var count = dataset.size();
print('Count: ', count);
var Visibility = {'palette': ['blue', 'red'],'min': 20, 'max': 40};
Map.setCenter(-86.8, 21.0, 4);
Map.addLayer(dataset.mean(), Visibility,'sst_2005');
var mean = dataset.reduce(ee.Reducer.mean());
Map.addLayer(mean, Visibility,'sst_2005_mean')


var geometry = ee.Geometry.Rectangle([-85, 22, -89, 15.0]);
Export.image.toDrive({
 image: mean,
  description: "sst_mean_2005",
  scale: 500,
  region: geometry,
  fileFormat: "GeoTIFF",
 });
```

Hurricane Index

To calculate the potential effect of hurricanes on coral and macroalgae cover, we designed an index based on four factors:

1. The number of cyclone events experienced by each sampling site
2. The intensity of each cyclone event
3. The distance of the site from the eye of the hurricane
4. The monitoring years of the reef sites

We downloaded the historical storm paths from NOAA (https://www.ncei.noaa.gov/data/). First, we selected the number of cyclone events per reef site from 2005 to 2016. Then, we chose only those trajectories events at a distance no greater than 100 km within the Mexican Caribbean area.

We considered two variables to estimate hurricanes' potential effect on the reefs: the hurricane's category and the distance from the site to the hurricane's eye. This was done by weighting the wind speed variation as a reference for the wave that causes damage to the reefs. The hurricane category was established at the closest point to each site, evaluating the maximum energy the hurricane most affected the reef.

Similarly, we took the site's distance from the path (hurricane's eye) as a tangential wind variation parameter. For this purpose, three hurricane-risk regions were generated (Figure S2.1). Risk 1, sites at a maximum distance of 30 km from the hurricane's path receive the hurricane's total or greatest intensity (100 to ~80% of the top wind speed). Risk 2, sites between 30 km and 50 of the hurricane's path, receives 80 to ~60% of the maximum wind speed. Risk 3 areas between 50 and 100 kilometres, in which the wind speed range is ~60 to 40% of the maximum wind speed. These risk regions were defined from the model generated by Mrowiec et al. (2016), in which they simulate the evolution of a hurricane and its internal dynamics. The simulated storm reaches a maximum speed of 80 m/s, equivalent to 5 in the Saffir-Simpson category, and also has a radius greater than 300 km (Figure S2.2)

The reef ecological data sampling period was also taken as a variable to reference the frequency of the sampling sites receiving hurricane events (Figure S2.3).

We used the following formula once each other of the variables was obtained:

$$I_H = \frac{\sum \frac{h}{r}}{\Delta t}$$

$I_H = Hurracane\ Index$
$h = Hurricane\ scale\ Saffir - Simpson$
$r = Risk\ regions\ 1, 2\ o\ 3$
$\Delta t = Monitoring\ years\ of\ the\ reef\ sites$

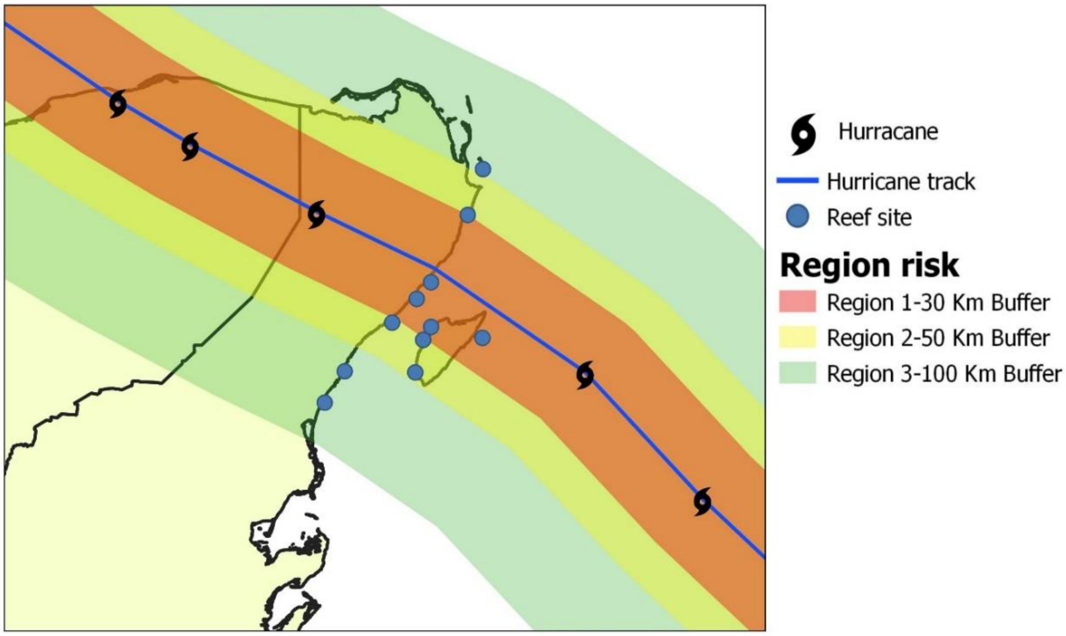

Figure S3.2 *Hurricane risk categories.*

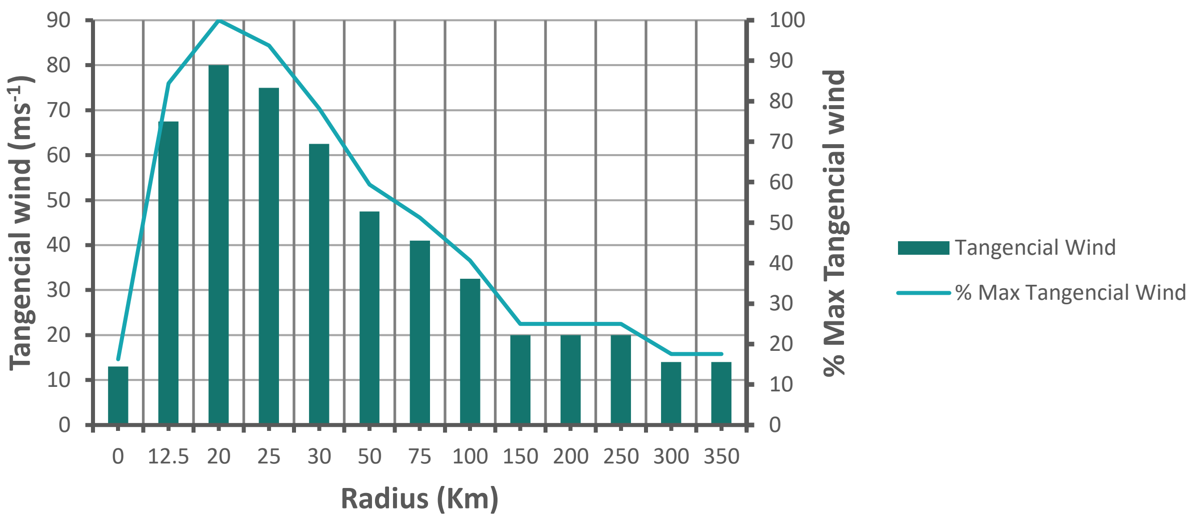

Figure S3.3 *Tangential wind speeds as a function of the distance from the eye of the hurricane, and the secondary axis shows the percentage of the maximum wind speed tangential to the eye of the hurricane (Mod. From Mrowiec et al., 2016).*

Literature

Mrowiec, A. A., Pauluis, O. M., & Zhang, F. (2016). Isentropic analysis of a simulated hurricane. Journal of the Atmospheric Sciences, 73(5), 1857–1870. https://doi.org/10.1175/JAS-D-15-0063.1

Hurricanes [https://www.ncei.noaa.gov/data/]

Mangrove change index

Mangrove forests are among the most biodiverse and among the world's most threatened tropical ecosystems, with a global reduction to 135,870 km2 (1996-2016) (Worthington et al., 2020). Existing mangrove deforestation rates have negative consequences for the ecosystem function, fisheries productivity and reefs resilience (Mumby et al., 2004). Mangrove loss in the Mexican Caribbean has been exhaustive since late 1970. Deforestation took place, especially in the Northern area, with Cancun's construction as an international tourist destination. Urban growth in this region has modified the landscape and caused the loss of the original vegetation through the opening of roads and the establishment of population centres for people who found a source of employment in the tourist centres (Calmé et al., 2011). This process is now reaching the south of the state, the Xcalak-Mahahual area, with a mangrove deforestation rate of -0.85%, being the direct cause urban and infrastructure expansion driven by tourism development (Hirales-Cota et al., 2010).

The mangrove clearing in the Mexican Caribbean has impacted the adjacent ecosystems, i.e., coral reefs. However, an indirect measure of its impact on coral reefs has not been quantified for the whole region. Thus, we developed an improved mangrove index of change in a single map with the most critical mangrove changes on the Mexican Caribbean coast. This index was based on a mangrove change map between 2005 and 2015; we then reclassified the resulting changes based on the adaptive cycle and cross-scale effects concept defined by Walker et al. (2004).

According to the adaptive cycle concept, the ecosystem can be subject to a series of changes; however, the changes do not infer static systematic cycling (Walker et al., 2004). In Figure S3.1, we present the adaptive mangrove cycle. Class 0 corresponds to an unperturbed mangrove, where the system maintains its structure and function. The complete cycle in Figure S3.1 shows intermediate changes (which can or cannot occur) until complete anthropization. Based on the adaptive cycle concept, the processes are constructed on observed system changes; the system can move back or forward.

We explain the value of the changes in the mangrove index of change with Figure S3.1. Here, the change class 2) Mangrove change to another wetland type moves back to class 0) Mangrove; in this case, the index value for this change would be -2. In the second example, the change moves from class 1) Mangrove change to species composition toward class 6) Mangrove change to agriculture; in this case, the index's value will be 6. Using ARC GIS, we reclassified the mangrove map of changes 2005-2015 to generate a holistic index of mangrove change according to the assessment mangrove status

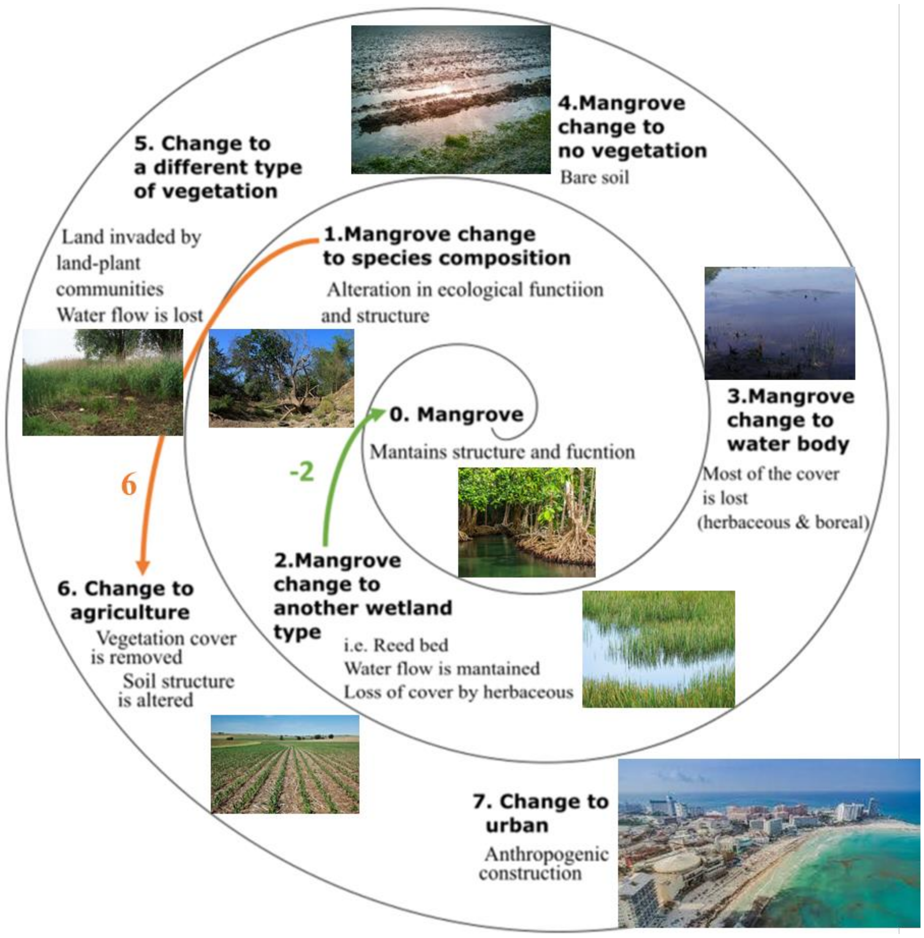

Figure S3.4 *Assessment of mangrove status. Arrows indicate change value in the index of mangrove change.*

References

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Hirales-Cota, M., Espinoza-Avalos, J., Schmock, B., Ruiz-Luna, A., & Ramos-Reyes, R. (2010). Drivers of mangrove deforestation in Mahahual-Xcalak, Quintana Roo, southeast Mexico. Ciencias Marinas, 36(2), 147–159.

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Anthropogenic index

Anthropogenic activities' indirect and direct effects continue increasing progressively in coastal areas. According to the literature, the term of anthropization derives from the hemeroby concept: "the measure of the human influence on ecosystems" (Kowarik, 2014). Martínez-Dueñas (2010) takes this approximation to generate the relative integrated anthropogenic index (INRA) within a spatial and land cover analysis framework used to measure: "the degree of modification of an ecosystem due to anthropogenic effects." The relative integrated anthropogenic index used in this work encompasses different processes defined in Velazquez-Salazar et al. (2019). The base cartography used to create the index was derived from the mangrove distribution map from CONABIO. The 'anthropic development' category was then subclassified to evaluate coastal anthropogenic impacts in the Mexican Caribbean (Table S4.1). The subclassification was an adaptation of the CORINE Land Cover Programme from the European Environmental Agency (2004) complemented with data from the Mexican National Institute of Statistics and Geography (INEGI by its Spanish acronym).

A summary of the index generation is presented in Figure S3.5 The first step is to define the units of analysis (UA) of 100 subunits of analysis (SUA) in the area of interest. As a second step, the minimum mapping unit of the base cartography (1 ha = 100 × 100 m) was used, and the SUA was established with 50 m per side. Therefore, the UA measured 500 m2. Once the UA were defined within the study area, the land cover to which each SUA belonged was established (Table S4.1). The third step encompasses estimating the relative values for each land cover and land use in the study area to assign each SUA to a relative partial anthropization value. The values of the categories and subcategories used in this study are described in Velazquez-Salazar et al., (2019). In the fourth step, the relative anthropization value by SUA was calculated by weighting areas with different subcategories in cases where the UA contained more than one activity. This method (Eq. 1) considers the proportion of the relative anthropization value assigned to each land cover and subcategories of analysis.

$$R_{SUA}V = \left(\frac{A_1 \cdot VR_1}{2500}\right) + \left(\frac{A_2 \cdot VR_2}{2500}\right) + \cdots \left(\frac{A_n \cdot VR_n}{2500}\right) \quad \text{Eq. 1}$$

Where:

$R_{SUA}V$ = Relative anthropization value of the SUA

A_1, A_2 … A_n = Surface in m2 of the different activities within an area

VR_1, VR_1 … VR_n = Relative value of the different activities

2500 = The surface in m2 of each SUA

Finally, the anthropogenic index for each UA can be calculated (Eq. 2)

$$INRA = \left(\frac{\sum SUA}{n}\right) 100 \quad \text{Eq. 2}$$

Where:

$\sum SUA$ = Sum of partial anthropization value of the SUA

n = Number of SUA

The anthropization index was expressed as a percentage because not all the UA had the same number of SUA. The index was calculated using ArcToolBox (ModelBuilder in ArcGis 10.3) as an automated process replicated for the two dates (2005 and 2015). Once the anthropogenic index was calculated, an analysis of change was performed, taking the index differences for 2005 and 2015.

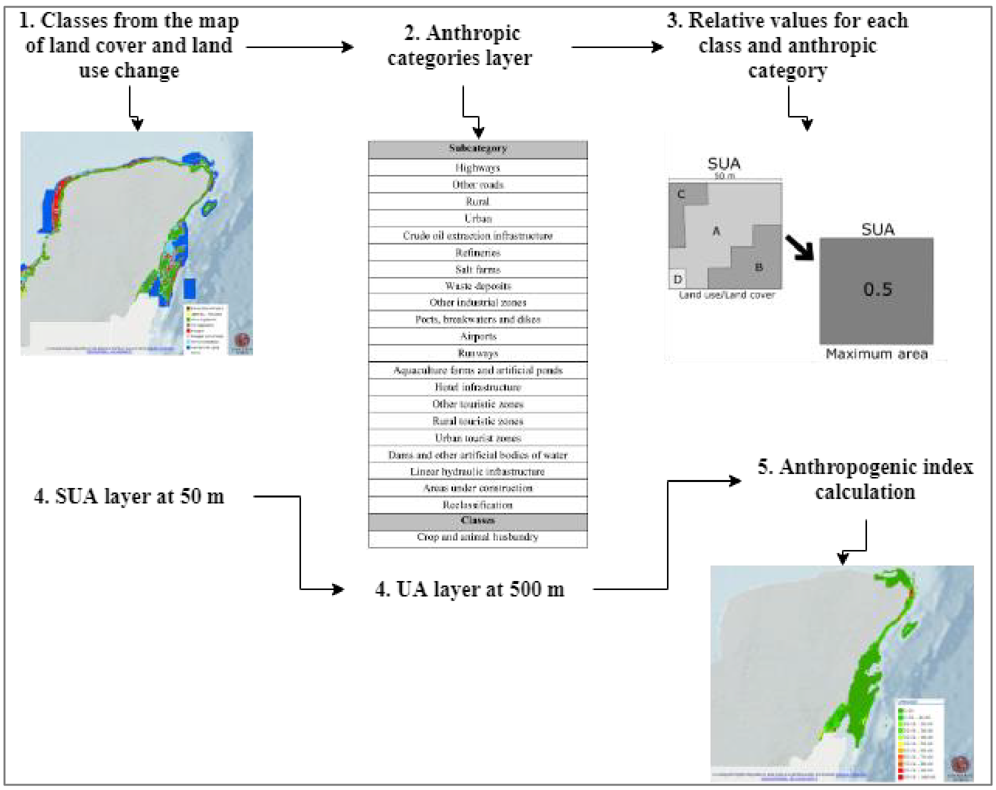

Figure S3.5 *Summary of the anthropogenic index calculation.*

Table S3.1 *Anthropogenic classification and subclassification categories*

Category	Subcategory	Category	Subcategory
Transport	Highways Roads	Airports and runways	Airports Runways
Settlements	Rural	Aquaculture farms and artificial ponds	Aquaculture farms

	Urban		Artificial ponds
Industrial zones	Crude oil extraction infrastructure	Touristic zones	Hotel infrastructure
	Refineries		Other touristic zones
	Salt farms		Rural touristic zones
	Waste deposits		Urban touristic zones
	Other industrial zones	Hydraulic infrastructure	Dams and other artificial bodies of water
Port zones	Ports		Linear hydraulic infrastructure
	Breakwaters	Building zones	Areas under construction
	Dikes	Reclassification zones	Reclassification zones

References

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Land-Sea Model algorithm to extract the data

We used GRASS GIS 7.8.3 to apply the different steps of the model wrapped into a single algorithm (Figure S3.6).

The set of steps and instructions in the algorithm for the model are as follows:

1. Importation of each single reef site.
2. One extra column will be added to the attribute table named "buffer10."
3. We consider the 10 km buffer of interest in the coastal area; therefore, we measure the distance from the reef site to the coast and add this distance to the buffer to actualize the new column generated in step 2.
4. A new vector is created with the sum of the 10 km vector and the distance to the coast over the reef site.
5. The vector generated in step 4 is converted to raster.
6. The raster of interest (anthropization index change or mangrove change index) is intersected with the buffer in step 5.
7. The total buffer area is calculated in meters.
8. The reef site is converted to raster.
9. Generation of a distance matrix from the reef site to each pixel centroid.
10. Extraction of the pixel value within the buffer of interest and is divided by the distance's cube root.
11. The index value is divided by the total area of the influence buffer.

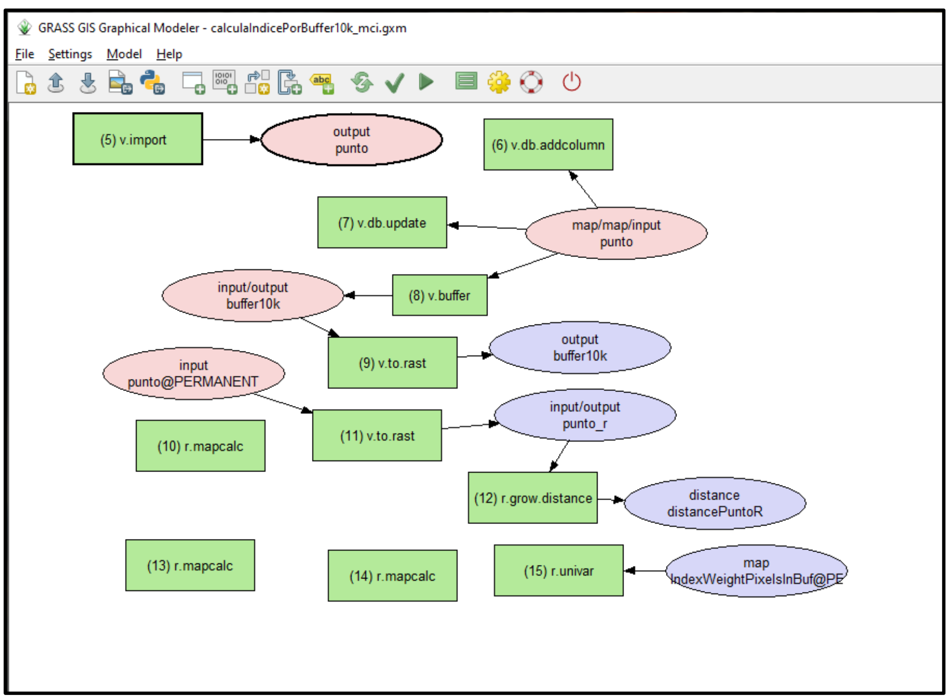

Figure S3.6 *Visual scheme of the land-sea model algorithm.*

Land-sea influence model script

```
#!/usr/bin/env python3
#
#####################################################################
##########
#
# MODULE:      Land-sea_influence_model
#
# AUTHOR(S):    usuario
#
# PURPOSE:      Scrip generado por el Modelador Gráfico wxGUI.
#
# DATE:       Wed Oct 28 14:48:17 2020
#
#####################################################################
##########

#%module
#% description: Scrip generado por el Modelador Gráfico wxGUI.
#%end
#%option
#% key: vimport5_input
#% description: Name of OGR datasource to be imported
#% required: yes
#% type: string
#% answer: C:\Grass\Ameris\Indcoralsites\ID_X75.gpkg
#%end
import sys
import os
import atexit
from grass.script import parser, run_command
def cleanup():
    pass

def main(options, flags):
    run_command("v.import",
                overwrite = True,
                input=options["vimport5_input"],
                output="punto",
                extent="input",
                snap=-1)
    run_command("v.db.addcolumn",
                map="punto",
                layer="1",
                columns="buffer10 DOUBLE")
    run_command("v.db.update",
                map="punto",
                layer="1",
                column="buffer10",
```

```
            query_column="Distance_s + 10000")
    run_command("v.buffer",
            flags='t',
            overwrite = True,
            input="punto",
            layer="1",
            type="point,line,area",
            output="buffer10k",
            angle=0,
            column="buffer10",
            scale=1.0)
    run_command("v.to.rast",
            overwrite = True,
            input="buffer10k",
            layer="1",
            type="point,line,area",
            output="buffer10k",
            use="cat",
            value=1,
            memory=300)
    run_command("r.mapcalc",
            overwrite = True,
            expression="IndexInBuff = if (!isnull(cmi@PERMANENT) &&
!isnull(buffer10k@PERMANENT),cmi@PERMANENT,null())",
            region="current")
    run_command("v.to.rast",
            overwrite = True,
            input="punto@PERMANENT",
            layer="1",
            type="point,line,area",
            output="punto_r",
            use="attr",
            attribute_column="cat",
            value=1,
            memory=300)
    run_command("r.grow.distance",
            overwrite = True,
            input="punto_r",
            distance="distancePuntoR",
            metric="euclidean")

    run_command("r.mapcalc",
            overwrite = True,
            expression="WeightsPuntoIndex = if
(!isnull(IndexInBuff@PERMANENT),1/distancePuntoR@PERMANENT^.5,null())",
            region="current")
    run_command("r.mapcalc",
            overwrite = True,
```

```
            expression="IndexWeightPixelsInBuf = if
(!isnull(IndexInBuff@PERMANENT),IndexInBuff@PERMANENT*WeightsPuntoIndex@PERMANEN
T,null())",
            region="current")
   run_command("r.univar",
            overwrite = True,
            map="IndexWeightPixelsInBuf@PERMANENT",

output="C:\Grass\Ameris\OutputCmimodel_coral\valorSumatoriadeIndicesMultiplicadosPorPeso.t
xt",
            percentile=90,
            separator="pipe")

   return 0
if __name__ == "__main__":
   options, flags = parser()
   atexit.register(cleanup)
   sys.exit(main(options, flags))
```

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

Table S3.2 *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
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

Table S3.3. *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

Appendix C Curriculum Vitae

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“Impact evaluation on forest coverage and level of rural development revenue in Biological Corridors in Southern Mexico”

2012

“Design of a system visualization software as tool prioritization of Climate Change adaptation measures”

2011

“Networks development for the territorial management of the Mesoamerican Biological Corridor - Mexico”

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“Course for Mexico City public servants to guarantee the applications of the environmental regulations in the water forest region in Mexico City”

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“Use of Remote Sensing for evaporation calculation in the Lerma-Chapala Basin”

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Certificate “Introduction to the Theory and Practice of GIS and Remote Sensing with emphasis on open-source Software” – Lab Assistant Metropolitan Autonomous University (UAM), Mexico City

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PROFFESIONAL AFFILIATIONS

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GLOMAR – Bremen International Graduate School for Marine Sciences

CEIBA – Interdisciplinary Center of Biodiversity and Environment (Centro Interdisciplinario de Biodiversidad y Ambiente)

RedRUM – Network of researchers from Mexico's Usumacinta Region (Red de Investigadores de la Región Usumacinta en México)

PUBLICATIONS

JOURNALS

Contreras-Silva, A.I., Tilstra, A., Migani, V., et al. A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean. Sci Rep 10, 8897 (2020). https://doi.org/10.1038/s41598-020-65801-8

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ORAL & POSTER PRESENTATIONS

CONFERENCES & PRESENTATIONS

2022 "15TH INTERNATIONAL CORAL REEF SYMPOSIUM "

Bremen, Germany

"Effects of coastal anthropisation and hurricane impacts in the Mexican Caribbean coral reefs"

2018 "International conference on marine science"

Medellín, Colombia

"Spatiotemporal benthic changes in Mexican Mesoamerican Coral Reefs over the last 4 decades"

2014 "XVIII CONGRESO NACIONAL DE OCEANOGRAFÍA"

"Análisis multitemporal en los fondos bénticos de Banco Chinchorro, México"

La Paz, Baja California Sur, México

2011 "VI CONGRESO INTERNACIONAL DE ORDENAMIENTO TERRITORIAL Y ECOLÓGICO: RETOS SOCIALES, ECONÓMICOS Y CULTURALES"

"Ciudad de México: Instrumentos de gestión territorial orientada a preservar servicios ecosistémicos"

Ensenada, Baja California, México

2010 “XVI CONGRESO NACIONAL DE OCEANOGRAFÍA”

“Caracterización de las comunidades bénticas en Banco Chinchorro, México, a través de percepción remota como herramienta clave para su manejo y conservación” Ensenada, Baja California, México

2009 “SPIE REMOTE SENSING FOR AGRICULTURE, ECOSYSTEMS, AND HYDROLOGY XI”

Coralline reefs classification in Banco Chinchorro, Mexico Berlin, Germany

POSTER PRESENTATION

2016 “13th INTERNATIONAL CORAL REEF SYMPOSIUM”

“Developing a conceptual model for coral reef monitoring in the Mexican Mesoamerican barrier reef system” HAWAI'I, 19-24 June

2011 “II CONGRESO NACIONAL DE ESTUDIANTES DE CIENCIAS DE LA TIERRA”

“Clasificación de fondos bénticos en arrecifes de coral mediante imágenes satelitales. Banco Chinchorro, México”

Juriquilla, Querétaro, México Poster presentación

SKILLS

LANGUAGES

Spanish – Mother tongue
English – Advanced
Deutsch – Advanced

OTHER SKILLS

- Analysis & Problem solving
- Leadership & Collaboration
- Critical thinking
- Project Management & Organization
- Research & Written communication
- SCUBA Diving

SOFTWARES

- R Statistical analysis
- GRASS – GIS software
- QGIS – GIS software
- PCI Geomatics
- ERDAS Imagine

Appendix D Versicherung an Eides Statt

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Versicherung an Eides Statt

Name, Vorname	Contreras Silva, Ameris Ixchel
Matrikel-Nr.	3059738

Ich, **Contreras Silva, Ameris Ixchel** versichere an Eides Statt durch meine Unterschrift, dass ich die vorstehende Arbeit selbständig und ohne fremde Hilfe angefertigt und alle Stellen, die ich wörtlich dem Sinne nach aus Veröffentlichungen entnommen habe, als solche kenntlich gemacht habe, mich auch keiner anderen als der angegebenen Literatur oder sonstiger Hilfsmittel bedient habe.
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