UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS DEL MAR Y LIMNOLOGÍA

¿Cuál es el efecto de la herbivoria y la protección en el Arrecife Mesoamericano?

TESIS

QUE PARA OPTAR POR EL GRADO ACADÉMICO DE:
DOCTOR EN CIENCIAS

PRESENTA:
ADAM WILLIAM SUCHLEY

TUTOR PRINCIPAL:
DR. LORENZO ALVAREZ FILIP, Investigador Asociado C, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, UNAM

COMITÉ TUTOR:
DR. ROBERTO IGLESIAS PRIETO, Investigador Titular B, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, UNAM
DR. JOAQUÍN RODRIGO GARZA PÉREZ, Profesor de Carrera Titular A, Unidad Multidisciplinaria de Docencia e Investigación, Sisal, Facultad de Ciencias, UNAM
DRA. MAITÉ MASCARÓ MIQUELAJAUREGUI, Profesor de Carrera Titular B, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, UNAM
DR. JUAN PABLO CARRICART GANIVET, Investigador Titular B, Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, UNAM

MÉXICO, CD. MX., FEBRERO, 2018

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To my family and friends for putting up with me

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ÍNDICE GENERAL

RESUMEN

Los ecosistemas marinos han experimentado pérdida de hábitat, biodiversidad y función globalmente en respuesta a la creciente población y actividad humana, siendo los arrecifes coralinos uno de los ecosistemas más amenazados. Los arrecifes del Caribe se han degradado dramáticamente en las últimas décadas, mostrando una disminución en la cobertura de coral vivo y el deterioro de los servicios ecosistémicos asociados. La pérdida de los corales suele provocar un aumento rápido de las macroalgas, a la vez que disminuye la capacidad de recuperación de las comunidades de corales. Tales cambios de fase son particularmente evidentes en el Caribe, donde la capacidad herbívora se ha reducido sustancialmente debido a la sobrepesca y brotes de enfermedades masivas a través del tiempo.

El establecimiento de Áreas Marinas Protegidas (AMP) ha sido ampliamente adoptado para limitar actividades extractivas, así como de mejorar la resiliencia ecosistémica de los arrecifes coralinos. Si bien es cierto que la protección tiene un impacto generalmente positivo en las poblaciones de peces, los beneficios para las comunidades de coral siguen siendo inciertos. La protección marina podría beneficiar a los corales directamente e indirectamente a través de la protección de los peces herbívoros. En consecuencia, la evaluación de la capacidad de los peces herbívoros para consumir las algas y beneficiar a los corales ayuda a entender la eficacia de la protección para los arrecifes. De esta manera, en esta investigación se hace uso de técnicas para investigar el efecto de la herbivoria y la protección marina en las comunidades coralinas sobre tres escalas espaciales: (1) el Arrecife Mesoamericano de

México, Belice, Guatemala y Honduras; (2) el Caribe Mexicano; (3) un arrecife protegido del Parque Nacional Arrecife de Puerto Morelos, México.

Encuentro que la herbivoria y la protección marina juegan papeles importantes en el Arrecife Mesoamericano. El efecto de la herbivoria por peces sobre la condición bentónica del arrecife varía espacialmente y temporalmente. Mediante un estudio experimental de exclusión de herbívoros en Puerto Morelos, muestro que a escala fina los peces herbívoros pueden controlar las macroalgas y su ausencia resulta en la proliferación de macroalgas y la supresión de crecimiento coralino. Además, mediante censos de 48 sitios, revelo que la cobertura de coral actual en el Caribe Mexicano está correlacionada positivamente con la biomasa de peces herbívoros y negativamente con la cobertura de macroalgas. Sin embargo, a través de un análisis de datos de monitoreo de largo plazo muestro que a nivel de todo el Arrecife Mesoamericano hubo un patrón claro de aumento en la cobertura de corales y macroalgas entre 2005 y 2014 mientras la biomasa de peces herbívoros no cambiaba.

Además encuentro que el efecto de la protección marina en las comunidades coralinas es más consistente que la herbivoria por peces. Muestro que la protección tiene un efecto positivo en la cobertura coralina actual en el Caribe Mexicano, además en el cambio (aumento) de la cobertura coralina del Arrecife Mesoamericano entre 2005 y 2014. Sin embargo, la cobertura coralina es significativamente menor en sitios del Caribe Mexicano con altos niveles de amenaza de desarrollo costero, contaminación y daño marino. Este hallazgo, además de la falta de relación entre los peces herbívoros y el aumento de macroalgas en el Arrecife Mesoamericano, sugiere que factores externos como los nutrientes y la sedimentación terrígenos juegan un papel importante en la dinámica arrecifal. Esta tesis tiene implicaciones importantes para el manejo de los arrecifes de la región y sugiere que, además de la protección marina, los políticos y administradores locales correspondientes deberían aplicar controles más estrictos sobre el desarrollo costero y el tratamiento de aguas residuales si se quiere mantener o mejorar la condición de las comunidades de coral.

ABSTRACT

Marine ecosystems globally have experienced loss of habitat, biodiversity and function in response to growing human activity, and coral reefs have been particularly affected. Caribbean reefs have deteriorated dramatically in recent decades with declines in live coral cover and associated ecosystem services. The loss of corals often causes a rapid increase in macroalgae which in turn reduces coral community resilience. Such phase shifts are particularly evident in the Caribbean, where herbivore capacity has been reduced substantially from historical levels due to overfishing and disease outbreaks.

The establishment of Marine Protected Areas (MPAs) has been widely adopted to limit extractive activities and improve coral reef ecosystem resilience. While protection has a generally positive impact on fish populations, the benefits for coral communities remain uncertain. Marine protection may benefit corals directly and indirectly via the protection of herbivorous fish. Therefore, assessing the ability of herbivorous fishes to consume algae and benefit corals helps elucidate protection effectiveness. In this thesis, I use a combination of techniques to investigate the effect of herbivory and marine protection on coral communities at three spatial scales: (1) the Mesoamerican Reef of Mexico, Belize, Guatemala and Honduras; (2) the Mexican Caribbean; (3) a protected reef of Parque Nacional Arrecife de Puerto Morelos, Mexico.

I find that herbivory and marine protection play important roles on the Mesoamerican Reef. The effect of fish herbivory on reef benthic condition varies spatially and temporally. By means of an experimental herbivore exclusion study in Puerto Morelos, I show that at small scales herbivorous fish can control macroalgae, and their absence results in the proliferation of macroalgae and the suppression of coral growth. In addition, through surveys of 48 sites, I reveal that current coral cover in the Mexican Caribbean is positively correlated with herbivorous fish biomass and negatively correlated with macroalgae coverage. However, via an analysis of long-term monitoring data I show that on the Mesoamerican Reef overall there was a clear pattern of increasing coral and macroalgal cover between 2005 and 2014 while herbivorous fish biomass remained unchanged.

Furthermore, I find that the effect of marine protection on coral communities is more consistent than the effect of fish herbivory. I show that protection has a positive effect on current coral cover in the Mexican Caribbean, as well as on the change (increase) in coral cover on the Mesoamerican Reef between 2005 and 2014. However, coral cover is significantly lower at Mexican Caribbean sites with high levels of coastal development, pollution and marine damage threat. This finding, in addition to the lack of relationship between herbivorous fish and increasing macroalgae on the Mesoamerican Reef, suggests that external factors such as nutrients and terrestrial sedimentation play an important role in reef dynamics. This thesis has important implications for reef management in the region and suggests that, in addition to marine protection, policy makers and local administrators must apply stricter controls on coastal development and wastewater treatment if coral community condition is to be maintained or improved.

INTRODUCCIÓN GENERAL

Los arrecifes coralinos son ecosistemas diversos que nutren, sirven de sustento y protegen a las poblaciones humanas de las costas tropicales. Sin embargo, en las últimas décadas los arrecifes coralinos han sido particularmente afectados por una combinación de impactos humanos globales y locales (Hughes et al. 2017a). La sobrepesca y la eutrofización han interrumpido las redes tróficas, reduciendo función ecosistémica y resiliencia al cambio climático y otros factores de estrés (Hughes et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004; Melbourne-Thomas et al. 2011a). Como resultado, muchos arrecifes han sufrido transiciones hacia la dominancia de macroalgas, amenazando la provisión de bienes y servicios que provienen de la acreción arrecifal (Done 1992; Hughes 1994; Moberg & Folke 1999).

El manejo marino espacial a través del establecimiento de Áreas Marinas Protegidas (AMP) ha sido adoptado frecuentemente para abordar directamente ciertas amenazas y mantener o mejorar la resiliencia ecosistémica frente a otras (Jennings & Kaiser 1998; Bellwood et al. 2004). La regulación de prácticas pesqueras destructivas y otras actividades como el buceo recreativo busca reducir el daño directo al hábitat que provoca la pérdida de la complejidad de los fondos marinos y la mortalidad de los organismos bentónicos (Jennings & Kaiser 1998; Russ 2002). Asimismo al limitar o prevenir las actividades de extracción en las Zonas de Exclusión Pesquera (NTZ, por sus siglas en inglés), la protección marina busca restaurar las poblaciones de peces e invertebrados (Halpern 2003; Costello & Ballantine 2015). De esta manera, se han establecido AMP en los arrecifes de coral a nivel mundial, debido a la sobrepesca y el deterioro de la condición bentónica en los ecosistemas arrecifales (Mora et al. 2006). En los lugares donde existe protección, especialmente en las NTZ, las poblaciones de peces generalmente responden positivamente en términos de densidad, biomasa, tamaño individual y riqueza de especies (Halpern 2003; Lester et al. 2009; Gill et al. 2017). Sin embargo, sólo el 21.7% de las especies de peces y el 5.7% de las especies de coral cumplen con los objetivos de protección geográfica (Mouillot et al. 2016).

La protección marina, particularmente el establecimiento de Zonas de Exclusión Pesquera, tiene un impacto generalmente positivo en las poblaciones de peces; sin embargo, los beneficios para las comunidades de corales son inciertos (Halpern 2003; Lester et al. 2009; Gill et al. 2017). La protección marina puede proteger o promover la recuperación de las comunidades de coral mediante dos mecanismos principalmente. El primer mecanismo consiste en regular las actividades que causan daños físicos a los corales, tales como el uso de anclas, prácticas de pesca destructivas y el buceo recreativo no controlado (Davis & Tisdell 1995; McManus 1997). El segundo mecanismo es indirecto: se espera que las poblaciones de herbívoros restauradas beneficien indirectamente a las comunidades de corales al controlar las macroalgas bentónicas (Williams & Polunin 2001; Mumby et al. 2006a). Sin embargo, varios estudios reportan efectos poco significativos en la protección de los corales (Graham et al. 2003; Jones et al. 2004; Coelho & Manfrino 2007; Stockwell et al. 2009; Huntington et al. 2011; Noble et al. 2013; Toth et al. 2014; Russ et al. 2015a) y ocasionalmente se han observado aumentos en la cobertura de coral en las NTZ (Mumby & Harborne 2010; Guarderas et al. 2011; Magdaong et al. 2014).

La protección marina podría beneficiar a los corales directamente e indirectamente a través de la protección de los peces herbívoros. En consecuencia, la evaluación de la capacidad de los peces herbívoros para consumir las algas y beneficiar a los corales ayuda a entender la eficacia de la protección. Esto es particularmente importante en el Caribe donde la capacidad de herbivoria se ha disminuido sustancialmente en las últimas décadas y los arrecifes han experimentado cambios de fase que van desde la dominancia por corales hacia macroalgas (Jackson et al. 2001; Gardner et al. 2003; Paddack et al. 2009). Las macroalgas tienden a superar a los corales, ocasionando la reducción de la fecundidad y el crecimiento coralino, inhibiendo el asentamiento de las larvas de coral y provocando un aumento en la mortalidad de los corales (Tanner 1995; Lirman 2001; Diaz-Pulido et al. 2010). Un herbívoro caribeño previamente importante, el erizo *Diadema antillarum*, experimentó un evento de mortalidad masiva entre 1983-84, y desde entonces sólo se ha recuperado parcialmente en algunos sitios (Jackson et al. 2001; Idjadi et al. 2010; Lessios 2016). Por otro lado, los peces loro y peces cirujanos son considerados actualmente los herbívoros dominantes en los arrecifes del Caribe (Carpenter 1986; Hughes et al. 2010); sin embargo, la sobrepesca ha reducido considerablemente sus poblaciones (Jackson et al. 2001; Paddack et al. 2009).

El declive de la capacidad de herbivoria en los arrecifes del Caribe ha provocado que un gran número de estudios, observacionales y experimentales, evalúen el control de algas por herbívoros. Estudios observacionales correlativos cubren una amplia gama de escalas espaciales y temporales, y la evidencia de estos trabajos revela resultados a favor (Newman et al. 2006; Jackson et al. 2014) y en contra (Russ et al. 2015b; Cox et al. 2017) en la capacidad de los herbívoros en controlar las algas bentónicas.

Estudios a escala fina buscan evaluar la regulación de las algas por los peces herbívoros al estimar tasas de consumo (basado en contenidos de estómagos, mordidas o biomasa) y de producción algal (Hatcher 1981; Paddack et al. 2006; Kopp et al. 2010). Otros estudios se caracterizan por la exclusión de herbívoros para evaluar experimentalmente la capacidad de los peces e invertebrados en el pastoreo de algas y esta técnica ha sido adoptada por muchos investigadores (Burkepile & Hay 2006). En contraste con estudios correlativos, estudios experimentales a escala fina registran un impacto significativo de los herbívoros sobre la proliferación del césped algal y macroalgas, y además reportan que otros factores como niveles de nutrientes desempeñan un papel secundario (Burkepile & Hay 2006, 2009; Sotka & Hay 2009).

Factores externos como el aporte de nutrientes y el cambio climático pueden limitar el éxito de la protección de los arrecifes coralinos (Mora 2008; Edgar et al. 2014). Mientras que la protección marina trata de abordar las amenazas humanas dentro de los límites de las AMP, no impide eventos de blanqueamiento coralino causados por el calentamiento global, observado tanto en sitios protegidos, como no protegidos (Allison et al. 1998; Jameson et al. 2002; Hughes et al. 2003; Selig et al. 2012). Las actividades humanas terrestres locales también tienen un impacto sustancial en el medio ambiente marino e ignorar las interacciones entra tierra y mar puede resultar en que las AMP costeras no cumplan sus objetivos de conservación (Stoms et al. 2005; Richmond et al. 2007; Halpern et al. 2009; Álvarez-Romero et al. 2011). Si no se gestiona adecuadamente, la agricultura y el desarrollo costero pueden ocasionar niveles elevados de nutrientes y sedimentación, causando impactos perjudiciales en las comunidades de corales cercanas, independientemente de la protección marina (De'ath & Fabricius 2010; Kroon et al. 2014).

La sedimentación terrígena que llega a los arrecifes aumenta con la pérdida de cobertura de vegetación como resultado del cambio de uso de suelo, el dragado costero y la construcción costera (Fabricius 2005; Erftemeijer et al. 2012). Los sedimentos sofocan los corales y aumentan la turbidez del agua, reduciendo la actividad fotosintética, las reservas de energía y el crecimiento de los corales (Fabricius 2005; Wear & Thurber 2015). Además, los sedimentos se han relacionado con una elevada prevalencia de enfermedades de los corales, reducción de la fecundidad y el reclutamiento coralino (Fabricius 2005; Pollock et al. 2014; Wear & Thurber 2015). Las fuentes de nutrientes antropogénicas incluyen fosas sépticas, desagües de aguas residuales, fertilizantes agrícolas y ganadería (Lapointe et al. 1990, 2010). Los nutrientes que llegan a los arrecifes afectan a las comunidades de coral por mecanismos directos e indirectos. Directamente, los nutrientes aumentan la prevalencia y gravedad de las enfermedades de los corales y pueden tener un efecto sinérgico con el estrés térmico (Wooldridge & Done 2009; Vega Thurber et al. 2014). Indirectamente, los nutrientes promueven el crecimiento de macroalgas que compiten con los corales (McCook et al. 2001; Chadwick & Morrow 2011).

En el Caribe, las actividades humanas relacionadas con el uso de suelo y el desarrollo costero han desempeñado un papel importante en el deterioro de los arrecifes en las últimas décadas (Gardner et al. 2003; Mora 2008). La degradación arrecifal se ha relacionado con la sedimentación en sitios como Barbados (Tomascik & Sander 1987), Bermuda (Flood et al. 2005), Costa Rica (Cortés & Risk 1985), Curaçao (Bak 1978), Florida (Marszalek 1981), Puerto Rico (Loya 1976; Acevedo et al. 1989; Ryan et al. 2008), y Saint Lucía (Bégin et al. 2016), y con niveles elevados de nutrientes en Barbados (Tomascik & Sander 1985; Wittenberg & Hunte 1987), Florida (Lapointe 1997; Wagner et al. 2010), Jamaica (Goreau et al. 1997; Lapointe 1997), Martinica (Littler et al. 1993) y Tobago (Lapointe et al. 2010). Además, se reconoce que la sedimentación y la eutrofización son factores claves que disminuyen la resiliencia del Arrecife Mesoamericano ante el cambio climático (Melbourne-Thomas et al. 2011a).

Evidencia reciente muestra que el aporte de nutrientes y sedimentos terrígenos es un problema creciente para el Arrecife Mesoamericano (Burke & Sugg 2006; Carilli et al. 2009; Soto et al. 2009; Baker et al. 2013; Hernández-Terrones et al. 2015). El Arrecife Mesoamericano abarca más de 1,000 km de las costas caribeñas de México, Belice, Guatemala y Honduras donde prevalece el deterioro de la condición arrecifal (Bozec et al. 2008; García-Salgado et al. 2008; Rodríguez-Martínez et al. 2014; Martínez-Rendis et al. 2016; Arias-González et al. 2017; Cox et al. 2017). Muchos de los arrecifes mesoamericanos se encuentran dentro de Áreas Marinas Protegidas y la eficacia de su protección cobra particular importancia debido a los declives en la condición arrecifal en las últimas décadas (García-Salgado et al. 2008; Kramer et al. 2015). La protección de los peces es un objetivo principal de las AMP y la evaluación de la capacidad de los peces herbívoros en el consumo de algas y el consecuente beneficio a las poblaciones coralinas puede determinar la eficacia de la protección para los arrecifes.

JUSTIFICACIÓN E IMPORTANCIA

El Arrecife Mesoamericano está sujeto a un amplio rango de factores de estrés incluyendo la sobrepesca, el desarrollo costero, la enfermedad y el cambio climático (Ward et al. 2006; Mora 2008; Paddack et al. 2009; Eakin et al. 2010). Debido a estos estresores los arrecifes coralinos de la región han experimentado pérdidas dramáticas en la cobertura de coral vivo en las últimas décadas (Gardner et al. 2003; Schutte et al. 2010; Jackson et al. 2014). Además, los arrecifes del Caribe han experimentado transiciones a especies de coral que contribuyen menos a la acreción y complejidad arrecifal, reduciendo el hábitat disponible para la fauna arrecifal y amenazando la provisión de los servicios ecosistémicos asociados como la protección costera (Graham & Nash 2013; Perry et al. 2015b).

Las AMP son unas de las pocas herramientas que se puede usar para combatir ciertas amenazas y mantener o mejorar resiliencia ecosistémica frente a otras amenazas (Selig & Bruno 2010; Selig et al. 2012). Sin embargo, los beneficios de las AMP para las comunidades coralinas son inciertos y estudios de AMP especificas muestran la heterogeneidad en el efecto de la protección (Mumby & Harborne 2010; Guarderas et al. 2011; Huntington et al. 2011; Noble et al. 2013; Toth et al. 2014). La protección marina puede beneficiar a los corales a través de la protección de los peces herbívoros que consumen las algas que compiten con los corales. En consecuencia, una evaluación de la capacidad de los peces herbívoros para consumir las algas es importante para entender la eficacia de la protección para las comunidades coralinas. Estudios previos presentan evidencia a favor (Burkepile & Hay 2006; Newman et al.

2006; Jackson et al. 2014) y en contra (Russ et al. 2015b; Cox et al. 2017) la capacidad de los herbívoros en controlar las algas bentónicas. Debido a la variabilidad en la eficacia de la protección marina y la capacidad de los herbívoros en controlar las algas bentónicas es necesario realizar una evaluación de estos factores para cada región de interés.

PREGUNTAS DE INVESTIGACIÓN

En esta tesis, se integran técnicas de investigación para responder a tres preguntas principales: (1) ¿Cuál es la relación a gran escala y largo plazo entre los peces herbívoros, las macroalgas y los corales; (2) cual es el efecto de la protección marina en la condición actual de los arrecifes del Caribe Mexicano; (3) cuál es el efecto de la herbivoria en el crecimiento coralino? Abordo estas tres preguntas sobre tres escalas espaciales: el Arrecife Mesoamericano de México, Belice, Guatemala y Honduras (escala regional); el Caribe Mexicano (escala nacional); la escala fina de un arrecife dentro del Parque Nacional Arrecife de Puerto Morelos, México (escala local).

OBJETIVOS

Esta tesis tiene el objetivo general de explorar el efecto de la herbivoria y la protección en las comunidades coralinas del Arrecife Mesoamericano. En el **Capítulo 1** realizo un análisis de datos de monitoreo a largo plazo del Arrecife Mesoamericano para relacionar los cambios en las macroalgas y los corales y entender el efecto de los peces herbívoros y la protección marina. El **Capítulo 2** se basa en datos de campo sobre la condición de los arrecifes adentro y afuera de Áreas Marinas Protegidas del Caribe Mexicano para entender el efecto de la protección marina en los arrecifes de la región. En el **Capítulo 3,** realizo un estudio experimental de exclusión de herbívoros a escala fina para entender cuál es el efecto de la herbivoria en el crecimiento de un coral constructor importante.

CAPÍTULO 1: El aumento rápido de la cobertura de macroalgas no está relacionada con peces herbívoros en los arrecifes Mesoamericanos

Abstract

Long-term phase shifts from coral to macroalgal dominated reef systems are well documented in the Caribbean. Although the impact of coral diseases, climate change and other factors is acknowledged, major herbivore loss through disease and overfishing is often assigned a primary role. However, direct evidence for the link between herbivore abundance, macroalgal and coral cover is sparse, particularly over broad spatial scales. In this study we use a database of coral reef surveys performed at 85 sites along the Mesoamerican Reef of Mexico, Belize, Guatemala and Honduras, to examine potential ecological links by tracking site trajectories over the period 2005–2014. Despite the long-term reduction of herbivory capacity reported across the Caribbean, the Mesoamerican Reef region displayed relatively low macroalgal cover at the onset of the study. Subsequently, increasing fleshy macroalgal cover was pervasive. Herbivorous fish populations were not responsible for this trend as fleshy macroalgal cover change was not correlated with initial herbivorous fish biomass or change, and the majority of sites experienced increases in macroalgae browser biomass. This contrasts the coral reef top-down herbivore control paradigm and suggests the role of external factors in making environmental conditions more favourable for algae.

Increasing macroalgal cover typically suppresses ecosystem services and leads to degraded reef systems. Consequently, policy makers and local coral reef managers should reassess the focus on herbivorous fish protection and consider complementary measures such as watershed management in order to arrest this trend.

Keywords: Coral reefs, top-down control, Marine Protected Areas, macroalgae, Mesoamerican Reef, phase shifts, herbivory, Caribbean

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Introduction

Caribbean coral reefs have experienced major declines over recent decades, with substantial reductions in live coral cover accompanied by concomitant losses in reef accretion and structural complexity (Schutte et al. 2010; Alvarez-Filip et al. 2011a; Perry et al. 2015b). Although a wide array of factors have contributed to reef deterioration including coral diseases, coastal development and climate change, the loss of key herbivores is thought to be a leading driver of ecosystem transition towards macroalgal domination at many reef sites in the region (Hughes 1994; Jackson et al. 2014). Macroalgae compete with corals, reducing coral fecundity, recruitment and survival via various mechanisms including overgrowth, shading and allelopathy (McCook et al. 2001; Hughes et al. 2007b; Bruno et al. 2009; Rasher et al. 2011). Today, populations of key herbivore taxa are diminished on many Caribbean reefs. The sea urchin *Diadema antillarum* was previously an important grazer in the Caribbean (Jackson et al. 2001). In 1983/4 *Diadema* suffered mass mortality across the Caribbean due to putative disease and populations have subsequently shown only limited recovery (Lessios et al. 1984; Kramer 2003; Hughes et al. 2010). Furthermore, long-term overfishing has resulted in marked reductions in herbivorous fish populations at many sites across the region (Jackson et al. 2001; Paddack et al. 2009).

Given the pivotal role of herbivores in controlling macroalgal growth (Mumby et al. 2006a), it is widely accepted that restoring populations of key herbivores enhances reef resilience by controlling algal communities and facilitating coral recovery by freeing space for coral recruits (Nyström et al. 2000; McCook et al. 2001; McManus & Polsenberg 2004; Bruno et al. 2009). Consequently, coral reefs with high herbivore abundance are expected to have lower macroalgal cover and greater coral cover (Jackson et al. 2014; Kramer et al. 2015). This paradigm has encouraged global awareness campaigns promoting conservation and fisheries management strategies to protect and restore populations of key herbivorous fishes, particularly parrotfishes (Jackson et al. 2014). In the Mesoamerican region, for example, Belize and Guatemala have banned the capture and possession of herbivorous fishes (Kramer et al. 2015).

Direct evidence of herbivores' ability to facilitate the maintenance and recovery of resilient coral reefs is limited. Experimental herbivore exclusion studies demonstrate the action of *Diadema* and herbivorous fish grazing on macroalgal cover, although evidence for the impact on corals is limited by the short-term nature and restricted spatial extent of the experiments (Lirman 2001; Burkepile & Hay 2006, 2009; Hughes et al. 2007b). Observational studies tend to focus on inter-site comparisons without an explicit temporal dimension, rather than tracking long-term reef change trajectories to provide a more in-depth understanding of drivers of ecosystem dynamics (Karr et al. 2015). Little consensus exists between studies, which exhibit contrasting patterns between herbivorous fish populations and macroalgal cover. In a Caribbean-wide point-in-time study, Newman et al. (2006) found a significant negative correlation between herbivorous fish biomass and fleshy algal biomass, whereas (Loh et al. 2015) observed that overfished Caribbean sites had lower macroalgal cover than protected sites. For the Northern Mesoamerican Reef of Mexico, Bozec et al. (2008) did not observe a relationship between herbivore biomass and macroalgal cover. In a long-term study, Ilves et al. (2011) observed increases in both herbivorous fish abundance and algal cover in the Bahamas. On the Northern Florida Reef Tract, Lirman & Biber (2000) observed no correlation between algal biomass and cover and fish grazer abundance and consumption rates. Jackson et al. (2014) found a significant negative correlation between parrotfish biomass and macroalgal cover in 16 Caribbean locations; however, no such relationship was observed for a broader data set covering 46 locations. The lack of relationship between herbivorous fish and macroalgal cover is evident for other regions: Carassou et al. (2013), for example, found that macroalgal cover was not correlated with the biomass, density and diversity of macroalgae feeders in the South Pacific. To further understand the relationship between herbivory pressure and changes in macroalgal cover we propose a simple conceptual framework (Fig. 1). Here, reefs may experience one of four scenarios of temporal changes in fleshy macroalgal cover and herbivorous fish biomass, a widely used proxy for herbivory intensity (Graham et al. 2015). Principal ecological drivers are presented for each idealised scenario, although in reality a number of drivers act in conjunction to varying extents. A phase shift from coral to algae domination due to herbivore loss is represented by the scenario in the upper-left quadrant. Here, decreasing herbivory leads to increasing macroalgal cover. Conversely, in the bottom-right quadrant, increases in herbivorous fishes result in reduced macroalgal cover. This quadrant represents the scenario sought by management measures and fisheries regulations restricting extraction, particularly of herbivorous fishes (Halpern 2003; Lester et al. 2009; Selig & Bruno 2010; Guarderas et al. 2011).

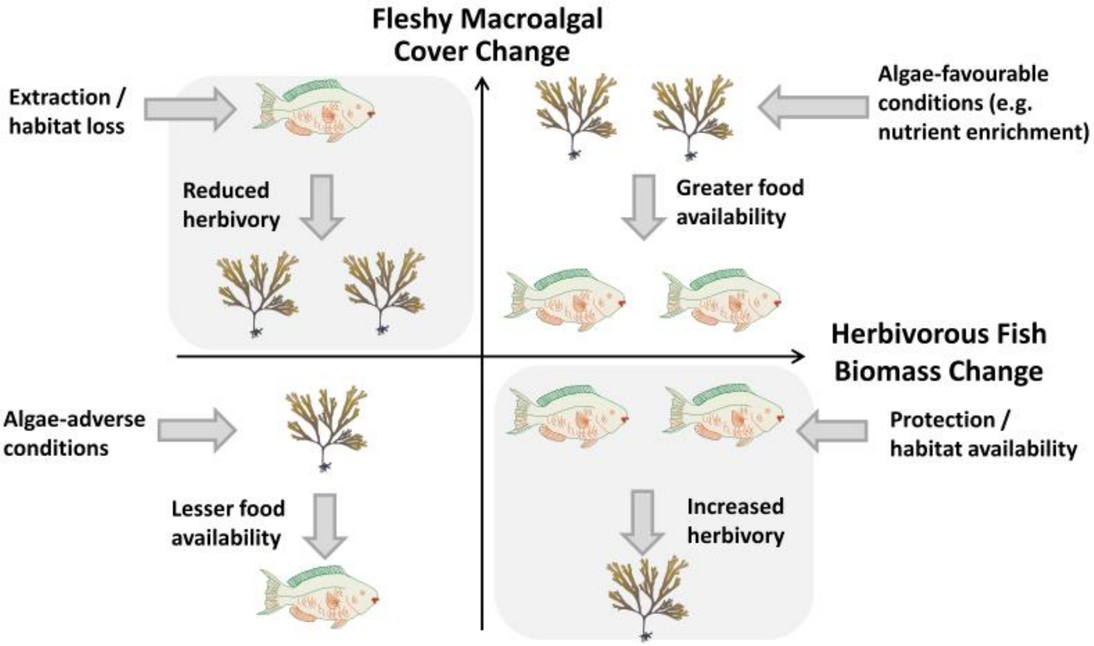

Figure 1. Relationship between changes in herbivorous fish biomass and benthic fleshy macroalgal cover. Possible cause-and-effect scenarios with external drivers are postulated for each quadrant. Fish and algae graphics by Diana Kleine and Tracey Saxby (IAN Image Library, Integration and Application Network, University of Maryland Center for Environmental Science, http://ian.umces.edu/imagelibrary).

Alternatively, a *positive* relationship may exist between macroalgal cover and herbivorous fish biomass, as represented by the scenarios of the upper-right and bottom-left quadrants of Fig. 1. This may occur when herbivores are food limited, as evidenced by increases in herbivore abundance and biomass following algal growth and by resource competition between *Diadema* and herbivorous fishes (Hay & Taylor 1985; Carpenter 1990; Adam et al. 2011). In these scenarios, predominantly external drivers such as nutrient availability, temperature and solar irradiance determine macroalgal cover and herbivorous fish biomass responds according to food availability (Burkepile & Hay 2006; Ferrari et al. 2012).Numerous experimental manipulation studies have reported the significant positive impact of nutrient enhancement on primary producer abundance, although herbivory has generally been found to play a greater role (Burkepile & Hay 2006). Contrastingly, few studies have addressed the importance of macroalgal productivity potential relating to environmental factors such as light availability and temperature (Steneck & Dethier 1994; Ferrari et al. 2012).

Herbivore and algal community composition also play an important role in herbivore-algal dynamics. Subsequent to the *Diadema* mass mortality event of the early 1980's, herbivorous fishes of the Scaridae and Acanthuridae families are recognised as the primary herbivores on many Caribbean reefs (Jackson et al. 2014; Adam et al. 2015a). While common Acanthurus surgeonfishes have a broad diet feeding on a combination of turf algae, macroalgae and detritus, *Sparisoma* and *Scarus* parrotfishes are more selective (Burkepile & Hay 2011; Adam et al. 2015a). *Sparisoma* parrotfishes, with the exception of the excavating *S. viride*, are macroalgae browsers, while *Scarus* spp. primarily graze algal turfs (Bonaldo et al. 2014; Adam et al. 2015b). Consequently, a suitable mix of herbivores are required in order to both graze turf algae to facilitate coral recruitment and to crop down macroalgal stands to reduce competition with adult coral colonies (McCook et al. 2001; Hughes et al. 2007b; Burkepile & Hay 2008). However, herbivores' ability to effectively moderate macroalgal cover is mediated by macroalgal predation defences (Rasher et al. 2013). Such defences are species specific and include morphological, structural, mineral and chemical traits that deter herbivores, with several genera (e.g. *Lobophora*, *Peyssonnelia* and *Codium*) being unpalatable (Hay 1997; Smith et al. 2010). These defences likely influence herbivore feeding preferences and conversely algal community structure is often influenced by herbivore mix, resulting in a complex interaction between the two communities (Adam et al. 2015a).

Here, by following individual site trajectories, we examine the prevalence of the four herbivorous fish and macroalgae change scenarios across 85 sites surveyed from 2005 to 2014 along the Mesoamerican Reef. We also consider herbivore functional group composition and trajectories, and compare these with overall trends. Subsequently, we evaluate the potential effects of herbivorous fish biomass, fleshy macroalgal cover and other factors such as degree of protection, on changes in coral cover during the same timeframe. Our hypothesis is that for sites where herbivory increased, fleshy macroalgal cover decreased, and that herbivore biomass and the decline in macroalgal cover are among the main factors explaining coral cover on today's reefs.

Materials & Methods

We used data produced by the Healthy Reefs Initiative (HRI) and the Atlantic and Gulf Rapid Reef Assessment (AGRRA) programs, which include ecological censuses for 398 sites along the Mesoamerican Reef in Mexico, Belize, Guatemala and Honduras from 2005 to 2014. Site selection was based on benthic habitat maps produced by the Millennium Reef Mapping Program, with 200 × 200 m sites randomly selected following stratification by geomorphological characteristics and depth (Andréfouët et al. 2003; Kramer 2003). The database contains 85 long-term monitoring sites that were surveyed in 2005/2006 and 2013/2014 over a 7, 8 or 9-year period, a timeframe sufficient to observe ecologically meaningful changes (Babcock et al. 2010). Of these sites, 43 were repeatedly surveyed in four time periods (2005/2006, 2009/2010, 2011/2012 and 2013/2014). Sites were located primarily on the fore reef and reef crest at a mean (± Standard Error s.e.m.) depth of 6.9 ± 0.2 m.

Benthic cover and reef fish surveys were performed according to AGRRA protocol, with transects located haphazardly, parallel to the coast (Lang et al. 2010). The majority of sites were surveyed at similar times during the summer year-on-year in order to minimise seasonal effects. At each site an average of five to six 10 m-transects were surveyed using point intercept methodology to determine benthic cover including hard coral percentage cover and fleshy macroalgal percentage cover. The abundance and total length (TL) of 81 key reef fish species, including herbivorous fishes of the Scaridae and Acanthuridae families, was recorded in ten 30 m-long, 2 m-wide transects. Reef fish abundance was subsequently converted to biomass density using standard allometric length-weight conversions.

The data analyses focussed on the relation between three ecological indicators for each reef site: herbivorous fish (Scaridae and Acanthuridae) biomass, fleshy macroalgal (excluding turf and calcareous algae) cover and hard coral (scleractinians and *Millepora* spp.) cover. Very few *Diadema* spp. were observed and therefore we focussed on reef fishes as the principal herbivores. For all three ecological indicators, a number of metrics were calculated to evaluate and examine temporal trends: absolute annual change, annual relative rate of change and geometric rate of change. The metrics for each ecological indicator (I) were determined as follows:

$$I_{\text{Absolute Annual Change}} = \frac{\left(I_{t_f} - I_{t_0}\right)}{\Delta t} \quad (1)$$

$$I_{\text{Annual Relative Rate of Change}} = \frac{\left(I_{t_f} - I_{t_0}\right)}{I_{t_0} \times \Delta t} \quad (2)$$

$$I_{\text{Annual Geometric Rate of Change}} = \left(\frac{I_{t_f}}{I_{t_0}}\right)^{\frac{1}{\Delta t}} - 1 \quad (3)$$

where I_{t_f} is the value of the ecological indicator at the end of the period, I_{t_0} is the initial value and Δt is the length of the period (in years). The former two metrics provide complementary information, for example: if an ecological indicator such as coral cover increases from 10 % to 15 %, the absolute change (equation (1)) is 5 %, while the relative rate of change (equation (2)) indicates that coral cover has increased by 50 % relative to its initial value. Geometric rate of change (equation (3)) was utilised in order to assess and compensate for non-linearity in the relative rate of change, while still providing an interpretable value (Côté et al. 2005).

Univariate comparison of ecological indicators was performed using ANOVA, t-tests or non-parametric equivalents (Mann-Whitney U or Wilcoxon Signed Rank tests), based on an assessment of normality and homogeneity of variance using Shapiro-Wilk and Levene tests. To test our first hypothesis, herbivorous fish biomass was compared with fleshy macroalgal cover using Spearman rank-order correlation due to non-normality. Herbivorous fishes were further categorised according to feeding preferences as macroalgae browsers (*Sparisoma* spp., with the exception of *S. viride*), turf grazers/ scrapers (*Scarus* spp. and *Acanthurus* spp.) or bioeroders (*Sparisoma viride*) (Bellwood et al. 2004; Burkepile & Hay 2011; Bonaldo et al. 2014; Adam et al. 2015a, 2015b). Change in functional group biomass was compared with overall change in herbivorous fish biomass using Spearman rank-order correlation. Furthermore, change in macroalgal cover was compared with absolute levels of overall herbivorous fish and macroalgae browser biomass both graphically by categorising sites by initial fish biomass (based on deciles) and by using Spearman rank-order correlation.

To test our second hypothesis, change in absolute coral cover from 2005/6 to 2013/4 for long-term monitoring sites was modelled using multiple linear regressions as model assumptions were satisfied. To address the common problem of spatial autocorrelation in multi-site studies we performed a Moran's I test on coral cover change by site location which reported no spatial autocorrelation present (Moran's I = 0.070, P = 0.08). The optimum regression model was selected based on Akaike Information Criterion (AIC). Candidate independent variables were selected based on ecological relevance and data availability (Supplemental Information, Table S1.1). Potential collinearity among predictor variables was examined using Pearson correlations and variance inflation factors, and outliers were removed on the basis of Cook's D. All statistical analyses were performed using R (R Core Team 2016).

Results

Here we present herbivorous fish biomass and fleshy macroalgal cover average trends for repeatedly surveyed sites and assess changes in these variables for long-term monitoring sites. Subsequently we examine herbivorous fish feeding guilds and geographic trends for long-term monitoring sites, and assess the effect of protection on site trajectories. Finally we present the ecological drivers of long-term coral cover change.

Herbivorous fish biomass and macroalgal cover trends

During the time period 2005–2014, regional averages showed a clear trend of increasing fleshy macroalgal cover on the Mesoamerican Reef, while herbivorous fish biomass remained relatively constant. Across 43 sites surveyed repeatedly in four time periods (Fig. 2), mean herbivorous fish biomass did not change significantly (Wilcoxon Signed Rank, $Z = 0$, $P = 1$), while mean macroalgal cover doubled during the same period (Wilcoxon Signed Rank, $Z = -5.02$, $P < 0.001$). Between 2005/2006 and 2009/2010 mean herbivorous fish biomass decreased and mean fleshy macroalgal cover increased significantly (Wilcoxon Signed Rank, $Z = 3.36$, $P < 0.001$ and $Z = -3.86$, $P < 0.001$, respectively). From 2009/10 to 2011/12 the trend appeared to be reversed, although the changes were not significant for macroalgae (Wilcoxon Signed Rank, $Z = -2.95$, $P = 0.003$ and $Z = 0.59$, $P = 0.55$, respectively; Fig. 2). From 2011/2012 to 2013/2014 macroalgal cover increased significantly, while herbivorous fish biomass remained unchanged (Wilcoxon Signed Rank, $Z = -3.81$, $P < 0.001$ and $Z = -0.35$, $P = 0.73$, respectively; Fig. 2).

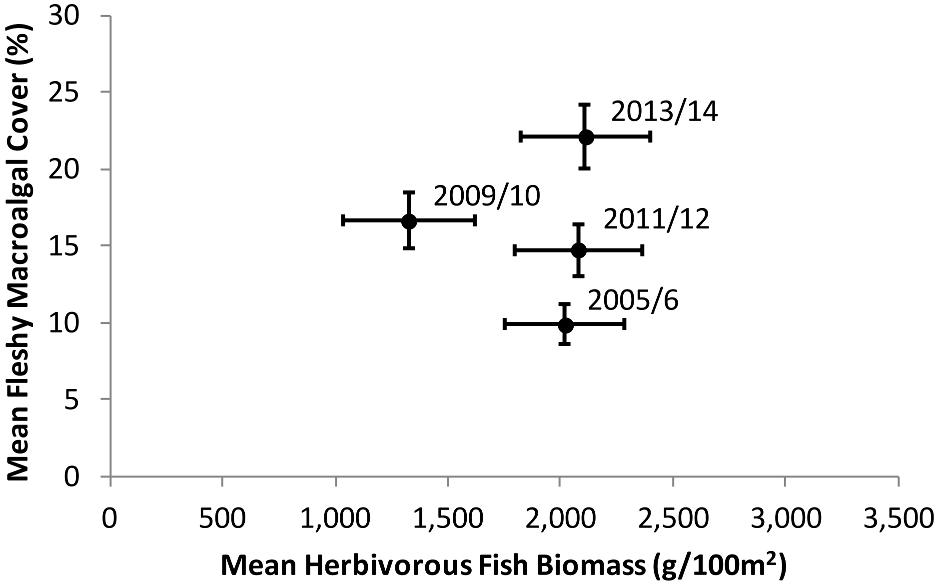

Figure 2. Temporal trend in mean herbivorous fish biomass and benthic fleshy macroalgal cover on the Mesoamerican Reef. Mean (± s.e.m.) values are shown for all 43 sites surveyed repeatedly in each monitoring period (2005/2006, 2009/2010, 2011/2012 and 2013/2014). Similar trends were observed for all sites surveyed in consecutive monitoring periods (Supplemental Information, Fig. S1.1).

Tracking individual trajectories of the 85 long-term monitoring sites surveyed over a 7, 8 or 9-year period permitted a more detailed investigation of the relation between the temporal changes in herbivorous fish biomass and fleshy macroalgal cover. Herbivorous fish biomass ranged from approximately 50–14,000 g/100m^2 and fleshy macroalgal cover ranged from 0–57.5%. There was no correlation between the changes in herbivorous fish biomass and fleshy macroalgal cover for long-term monitoring sites (Spearman, $r_s = -0.11$, $P = 0.35$). Only 7% of sites exhibited increased herbivorous fish biomass and decreased macroalgal cover; 35% of sites displayed decreases in fish biomass and increases in macroalgal cover; almost half of the sites (48%) exhibited increases in both herbivorous fish biomass and macroalgal cover; and 10% displayed decreased fish biomass and macroalgal cover (Fig. 3). Across all sites macroalgal cover increased irrespective of initial conditions of herbivorous fish biomass (Spearman, rs = -0.12, P = 0.3; Fig. 4A) and macroalgae browser biomass (Spearman, rs = -0.21, P = 0.3; Fig. 4B). Furthermore, there was no relationship between herbivorous fish and macroalgal cover when dividing the data by reef zone (crest versus reef front) or structural complexity (Fig. S1.6).

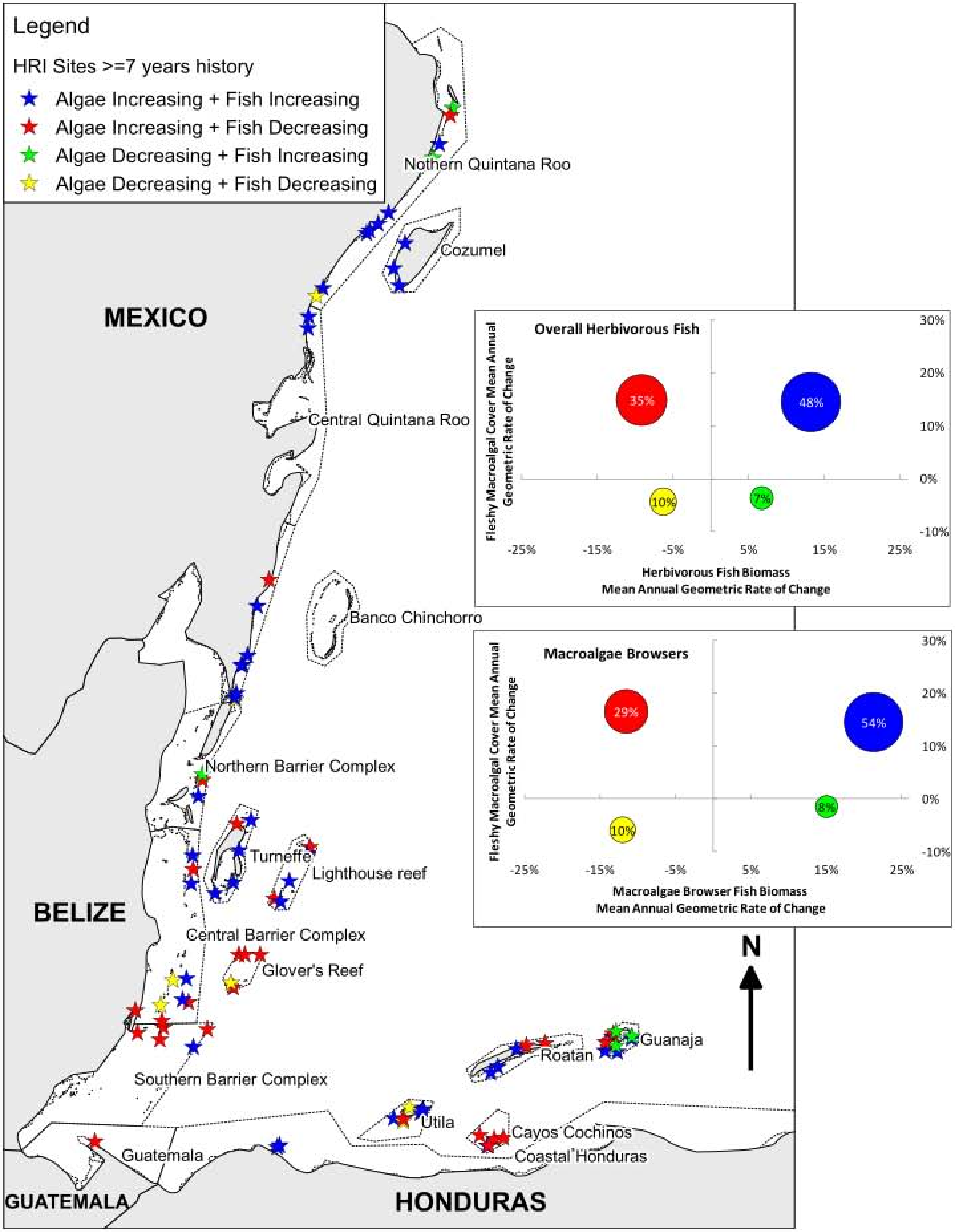
Legend
HRI Sites >=7 years history
★ Algae Increasing + Fish Increasing
★ Algae Increasing + Fish Decreasing
★ Algae Decreasing + Fish Increasing
★ Algae Decreasing + Fish Decreasing
Nothern Quintana Roo
Cozumel
MEXICO
Central Quintana Roo
Banco Chinchorro
Northern Barrier Complex
Turneffe
Lighthouse reef
BELIZE
Central Barrier Complex
Glover's Reef
Southern Barrier Complex
Guanaja
Roatan
Utila
Cayos Cochinos
Coastal Honduras
Guatemala
GUATEMALA
HONDURAS
N
Overall Herbivorous Fish
Fleshy Macroalgal Cover Mean Annual Geometric Rate of Change
35%
48%
10%
7%
30%
20%
10%
0%
-10%
-25%
-15%
-5%
5%
15%
25%
Herbivorous Fish Biomass
Mean Annual Geometric Rate of Change
Macroalgae Browsers
Fleshy Macroalgal Cover Mean Annual Geometric Rate of Change
29%
54%
8%
10%
30%
20%
10%
0%
-10%
-25%
-15%
-5%
5%
15%
25%
Macroalgae Browser Fish Biomass
Mean Annual Geometric Rate of Change

Figure 3. Long-term herbivorous fish and benthic fleshy macroalgal cover trends on the Mesoamerican Reef. Map and graphs indicating relationship between changes in overall and macroalgae browsing herbivorous fish biomass and fleshy macroalgal cover from first (2005 or 2006) to last (2013 or 2014) year for all (85) long-term monitoring sites with ≥ 7 years' history. Map indicates Healthy Reef Initiative regions within countries and locates sites by the relationship between changes in herbivorous fish biomass and fleshy macroalgal cover (Kramer et al. 2015). Inset graphs separately indicate relationship between changes in herbivorous fish biomass and fleshy macroalgal cover, and macroalgae browsing herbivorous fish biomass and fleshy macroalgal cover. For inset graphs, each circle represents the sites for that quadrant and circle position reflects mean site-level annual geometric rates of change. Circle area represents proportion of sites in that quadrant (also labelled). All (85) sites with ≥ 7 years' of history are plotted in order to provide long-term trends, although the equivalent analysis for sites with ≥ 8 years' of history produced similar results (Supplemental Information, Fig. S1.2).

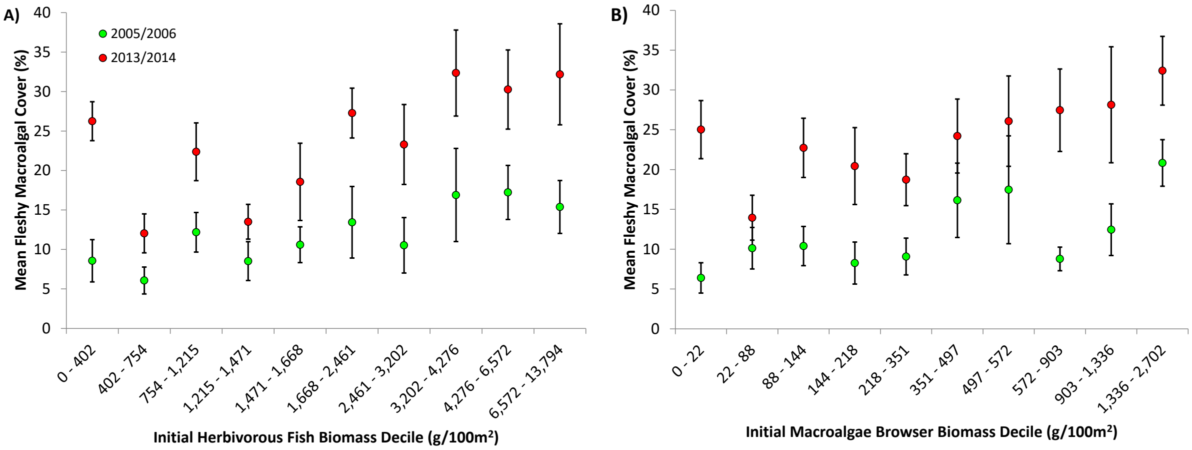

Figure 4. Effect of initial herbivorous fish biomass on fleshy macroalgal cover on the Mesoamerican Reef. A) Mean (± s.e.m.) benthic macroalgal cover in 2005/6 (green symbols) and 2013/14 (red symbols) by initial level of overall herbivorous fish biomass, for all (85) long-term monitoring sites. Sites divided into 10 categories based on initial overall herbivorous fish biomass deciles. B) Mean (± s.e.m.) benthic macroalgal cover in 2005/6 (green symbols) and 2013/14 (red symbols) by initial macroalgae browser biomass, for all (85) long-term monitoring sites. Sites divided into 10 categories based on initial macroalgae browser biomass deciles.

Considering herbivorous fish feeding preferences based on Bellwood et al. (2004), communities of the Mesoamerican Reef present a mixture of guilds with 24.3% macroalgae browsers by biomass in 2013/14 (19.4% in 2005/6), 48.4% (57.3%) turf grazers/scrapers and 27.3% (23.3%) bioeroders. Herbivorous fish biomass and macroalgal cover change were broadly similar between macroalgae browsers and overall results (Fig. 3). Macroalgae browser biomass displayed a slightly greater tendency for increase than overall herbivorous fish biomass, as observed for 61% of sites compared with 55%, and site-level changes in these were correlated (Spearman, $r_s = 0.70$, $P < 0.001$).

Geographically, the principal trend was for increasing fleshy macroalgal cover and herbivorous fish biomass in Mexico and northern Belize, including the atolls of Turneffe and Lighthouse Reef, but for increasing fleshy macroalgal cover and decreasing herbivorous fish biomass to the south in south-central and southern Belize, Glover's Reef, Guatemala and Cayos Cochinos, Honduras (Fig. 3). However, the Bay Islands of Honduras were exceptions to this broad north-to-south trend with Guanaja island displaying the highest proportion of sites with increasing herbivorous fish biomass and decreasing macroalgal cover. The only other three sites that experienced increasing herbivorous fish biomass and decreasing macroalgal cover were located at Isla Mujeres and Puerto Morelos in Mexico, and San Pedro in Belize.

Of the 85 long-term monitoring sites, 12 sites were located within No Take Zones (NTZs) where all extractive practices are prohibited, 47 were within Marine Protected Areas (MPAs) but not NTZs where reefs benefit from regulation but some extractive practices are permitted, and the remaining 26 were unprotected. The level of protection was observed to affect the initial levels of fleshy macroalgal cover and herbivorous fish biomass, in addition to changes in these over time. In 2005/6, sites within NTZs exhibited similar herbivorous fish biomass and fleshy macroalgal cover to sites located elsewhere within MPAs (Mann-Whitney, U=197, Z=-1.60, P=0.11; and U=297, Z=0.28, P=0.78 respectively; Fig. 5). Protected sites (both MPAs and NTZs) displayed significantly higher initial macroalgal cover than unprotected sites (Mann-Whitney, both $U \geq 247$, $Z \geq 2.85$, $P \leq 0.003$; Fig. 5), but only protected sites outside of NTZs exhibited significantly higher initial herbivorous fish biomass than unprotected sites (Mann-Whitney, MPA vs unprotected, U=819, Z=2.40, P=0.016; NTZ vs unprotected, U=161, Z=0.16, P=0.89; Fig. 5). Along the protection gradient (from unprotected, through MPA to no-take protection), sites appeared to experience a greater increase in herbivorous fish biomass and a lesser increase in macroalgal cover, although the differences were not statistically significant (ANOVA, annual geometric rate of change in fish biomass, $F_{2,82} = 0.04$, P = 0.97; annual geometric rate of change in macroalgal cover, $F_{2,80} = 1.01$, P = 0.37).

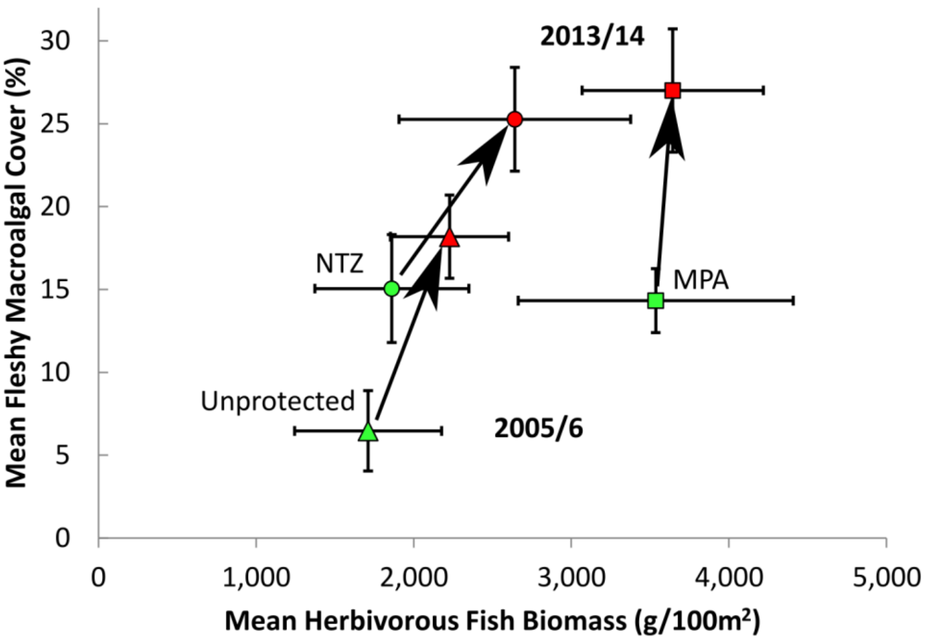

Figure 5. Effect of protection on herbivorous fish biomass and fleshy macroalgal cover on the Mesoamerican Reef. Mean (± s.e.m.) herbivorous fish biomass and benthic macroalgal cover in 2005/6 (green symbols) and 2013/14 (red symbols) by level of protection, for all (85) long-term monitoring sites. Unprotected = sites outside Marine Protected Areas (n = 26), MPA = sites inside Marine Protected Areas but not within No Take Zones (n = 47), NTZ = sites inside No Take Zones within Marine Protected Areas (n = 12).

Predicting coral cover change

Across all 85 long-term monitoring sites, mean (± s.e.m.) hard coral cover increased significantly from 12.2 ± 0.8% in 2005/6 to 15.0 ± 0.8% in 2013/14 (Wilcoxon Signed Rank, Z = -3.81, P < 0.001). Individual sites displayed varying trajectories with annual changes in coral cover ranging from -3.1 to +2.7%. The optimum linear regression model for the annual absolute change in hard coral cover displayed a modest but significant fit (Adjusted $R^2 = 0.18$, $F_{7,74} = 3.57$, $P = 0.002$). The model included seven predictor variables (Supplemental Information, Table S1.1), of which four were significant: MPA, country (Honduras), annual logarithmic change in herbivorous fish biomass and initial hard coral cover (Fig. 6). Interpreting these significant variables, sites within MPAs experienced greater increases in coral cover than unprotected sites; Honduran sites experienced lesser increases in coral cover than other countries; and increases in herbivorous fish biomass corresponded with increases in coral cover. Initial coral cover was the most significant predictor of coral cover change and therefore in order to further understand its impact, sites were categorised as low (< 10%), medium (10–20%) or high (≥ 20%) initial coral cover. For the 12 long-term monitoring sites with high initial coral cover, mean coral cover decreased over time (mean ± s.e.m. annual change in coral cover of -0.6 ± 0.4%), while coral cover increased for sites with lower levels of initial cover (low initial coral cover, +0.6 ± 0.1%; medium initial coral cover, +0.4 ± 0.2%).

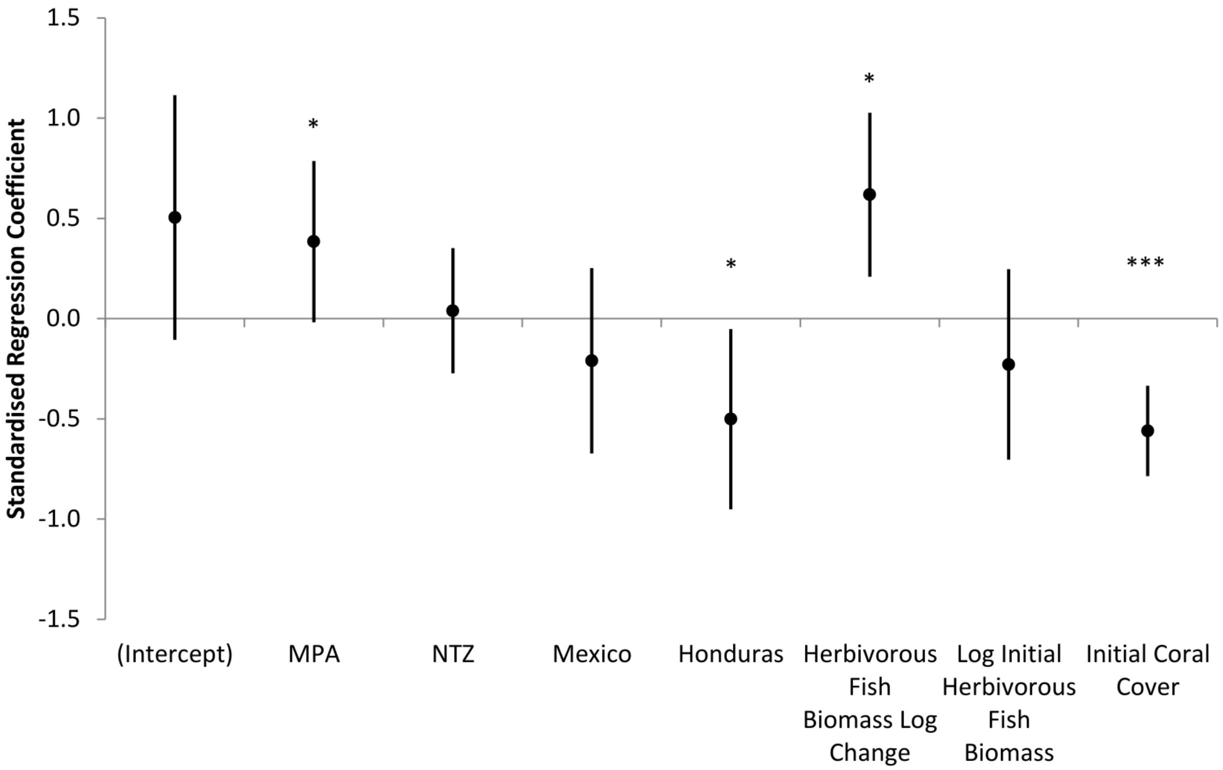

Figure 6. Prediction of coral cover change on the Mesoamerican Reef. Standardised regression coefficients for independent variables in AIC-selected optimum model of annual absolute change in hard coral cover from 2005/6 to 2013/14 for all long-term monitoring sites. MPA and NTZ are binary indicators of the location of sites within a Marine Protected Area or No Take Zone, respectively. Mexico and Honduras are binary indicators of the location of sites within those countries. Coefficients reflect the number of standard deviations change in the dependent variable for a one standard deviation increase in each independent variable, while controlling for all other independent variables. Error bars are coefficient standard errors. Significant variables (in non-standardised regression) are highlighted (*** 0.001 level, * 0.05 level).

Despite not being selected in the optimum regression model, we further explored the relationship between coral and macroalgal cover due to the long-term ecological shifts reported on many Caribbean reefs. Across all 85 long-term monitoring sites, mean (± s.e.m.) macroalgal cover increased significantly from 12.0 ± 1.1% in 2005/6 to 24.1 ±

1.5% in 2013/14 (Wilcoxon Signed Rank, $Z = -7.07$, $P < 0.001$). We observed little or no relationship between coral and macroalgal cover since macroalgal cover consistently increased irrespective of changes in coral cover (Supplemental Information, Fig. S1.3). All initial coral cover categories (low (< 10%), medium (10–20%), and high (≥ 20%)) experienced increases in fleshy macroalgal cover, and initial macroalgal cover, similarly categorised, did not impact coral cover changes over time (ANOVA, $F_{2,82} = 1.10$, $P = 0.34$).

Discussion

Substantial changes in the ecological composition of the Mesoamerican Reef were evident in a time span of only nine years. The principal trend is for increasing fleshy macroalgal cover, as observed at 83% of long-term monitoring sites (Fig. 3). Mean absolute cover of fleshy macroalgal cover increased by approximately 12% in the region between 2005 and 2014 (Fig. 2). Mean herbivorous fish biomass remained relatively stable (Fig. 2), although displaying substantial site variation, with 55% of sites showing an increase in herbivorous fish biomass between 2005 and 2014 (Fig. 3). The scenario of both increasing fleshy macroalgal cover and herbivorous fish biomass was observed at 48% of the 85 sites while the ‘desirable’ scenario of increasing herbivorous fish biomass and decreasing macroalgal cover was the least frequent of all four scenarios (Fig. 3). Similar trends were observed for the macroalgae-browsing fish guild (Fig. 3), with site-level macroalgae browser biomass change correlating with overall herbivorous fish biomass change. This suggests that fish herbivory was not a major driver of fleshy macroalgal cover change on the majority of surveyed sites across the Mesoamerican Reef (Fig. 3).

The clear pattern of increasing macroalgal cover and stable herbivorous fish biomass on Mesoamerican reefs contrasts with the widely accepted coral reef top-down herbivore control paradigm and management recommendations that advocate increasing herbivory to control fleshy macroalgal cover (Nyström et al. 2000; McCook et al. 2001). This result is consistent with a multi-decadal study reporting that macroalgal cover was not related to long-term parrotfish losses due to fishing in the Philippines (Russ et al. 2015b). Furthermore, we found that coral cover on the Mesoamerican Reef was low and unrelated to macroalgal cover. Since both coral cover and reduced herbivory were not responsible for increasing macroalgal cover, external factors may have played a role. For the Mesoamerican Reef region a growing body of evidence shows that rising nutrient levels is a worsening problem that may be accelerating macroalgal increase. In the Mexican Caribbean, previous studies have observed elevated nutrient input to coral reefs due to coastal development (Baker et al. 2013; Hernández-Terrones et al. 2015) and the subsequent degradation of reef systems (Bozec et al. 2008). In southern Belize and Honduras, riverine discharge and escalating reef sediment and nutrient loads associated with urban and agricultural run-off may have played a role in increasing macroalgal cover (Burke & Sugg 2006; Carilli et al. 2009; Soto et al. 2009). Our finding that fish herbivory is not responsible for macroalgal cover trends contrasts the results of herbivore exclusion studies, which emphasize the relative importance of herbivory over nutrient availability (McClanahan et al. 2002; Burkepile & Hay 2006, 2009; Sotka & Hay 2009). However, contrary to the present study, such experiments tend to be conducted on restricted spatial and temporal scales. Unfortunately, site nutrient data are not widely available for the Mesoamerican Reef, impeding a quantitative exploration of this effect in our analyses.

One alternative that could partially explain the rapid increases in fleshy macroalgae across the Mesoamerican Reef is that reef ecosystems passed critical thresholds beyond which herbivorous fishes are unable to control macroalgae due to either excessive algal production and/or insufficient herbivory (Mumby et al. 2007). This is particularly relevant given that Caribbean reefs may suffer from insufficient herbivory due to both the limited population recovery of *Diadema antillarum* subsequent to previous mass mortality and the inability of herbivorous fish to adequately compensate for this loss (McClenachan 2009; Paddack et al. 2009; Hughes et al. 2010). However, excessive algal production is unlikely on the Mesoamerican Reef as regional average macroalgal cover increased from only 10% in 2005/6 to 22% in 2013/14 (Fig. 2), values that are likely considerably below ecosystem thresholds for Caribbean reefs (Bruno et al. 2009). Furthermore, an examination of macroalgal change by absolute levels of herbivorous fish biomass revealed increasing fleshy macroalgal cover even for those sites with the highest initial fish biomass (the uppermost deciles possessed average overall herbivorous fish biomass and macroalgae-browsing fish biomass of 9,065 g/100 m^2 and 1,762 g/100 m^2 respectively; Fig. 4). Although there is little consensus on Caribbean reef herbivorous fish thresholds, a global assessment of the status of coral reef herbivorous fishes identified only 9 of 132 localities as having herbivorous fish biomass greater than 9,000 g/100 m^2, suggesting this to be a high benchmark (Mumby et al. 2007; Edwards et al. 2014). In addition, a negative correlation between Caribbean reef herbivorous fish biomass and fleshy algal biomass has been previously observed with a site maximum of only 7,000 g/100 m^2 approximately (Newman et al. 2006). The threshold hypothesis would be particularly relevant if the decline in average herbivorous fish biomass between 2005/6 and 2009/10 resulted in changes in the relative proportion of key functional groups, favouring non-macroalgae-browsing species (Adam et al., 2015b; Fig. 2). However, the relative proportions of the three main herbivorous fish functional groups remained stable during the study period (Supplemental Information, Fig. S1.4). Additionally, a close examination of those sites that suffered the greatest herbivorous fish biomass losses between 2005 and 2009 revealed that these sites experienced similar macroalgal growth from 2009 to 2014 compared with other sites (Supplemental Information, Fig. S1.5). This suggests that the observed rapid increases in fleshy macroalgae are not due to Mesoamerican reefs passing critical thresholds of excessive algal production and/or insufficient herbivory.

Fish populations may impact benthic communities indirectly through mediation of benthic competition. Sponges are a major component of Caribbean coral reef benthos that compete for space with corals and macroalgae (Loh et al. 2015). Sponges' competitive superiority over corals is well documented and likely due to a number of mechanisms including shading, smothering and allelopathy (Porter & Targett 1988; Loh et al. 2015). Overfishing of spongivorous parrotfishes and angelfishes has been shown to alter ecosystem dynamics through the alleviation of predation pressure on sponges (Loh & Pawlik 2014; Loh et al. 2015). Therefore, it is likely that at sites with high parrotfish biomass, spongivory will control benthic sponge cover, indirectly benefiting macroalgal and coral communities via reduced benthic competition. Unfortunately we could not further explore the role of sponges in shaping benthic interactions as the survey protocol does not focus on producing reliable sponge cover information (Lang et al. 2010).

Coral recovery on the Mesoamerican Reef was related to MPA protection and increasing biomass of herbivorous fish, but not via the expected mechanism of macroalgal declines through fish herbivory. Alternative mechanisms for the effect of protection on reef corals are less well studied, but may include reduced disease prevalence, and diminished physical reef damage through regulation of fishing and recreational diving practices (Hasler & Ott 2008; Lamb et al. 2015). Replenished fish communities inside marine reserves can also drive coral recovery through ecological processes not necessarily linked with herbivory. For example, trophically diverse fish communities inside marine reserves have been shown to ameliorate coral disease prevalence, although the pathways through which this takes place remain unclear (Raymundo et al. 2009). Alternatively, coral cover and complexity may influence herbivorous fish populations, rather than vice-versa, or the relationship may be purely correlative with both indicators being driven by marine protection (Halpern 2003; Selig & Bruno 2010; Alvarez-Filip et al. 2011b).

Reef protection has a positive impact on herbivorous fish biomass and coral cover, although fleshy macroalgal cover continued to increase at most sites. Although protection impacted herbivorous fish biomass and macroalgal cover trajectories (Fig. 5), initial differences between protected and unprotected sites tend to persist, with unprotected sites continuing to display lower macroalgal cover. This may be attributable to reserve age, as protected sites were located within reserves designated in 2003 (± 1 year) on average, and studies have shown that protection influence may be subject to a lag effect (Babcock et al. 2010; Selig & Bruno 2010). Furthermore, the use of protection categories (No Take Zones (NTZs), MPAs but not NTZs, and unprotected) is a coarse measure of the actual range of protection and fishing pressure experienced at sites. Additionally, local conditions and reserve regulations often obfuscate protection impact due to variability of internal factors such as reef community structure and enforcement level, and external impacts including local stressors and global climate change (McClanahan et al. 2006; Mora et al. 2006; Selig et al. 2012). Finally, trophic effects may play a role since trophic cascades are expected when populations of large predators are enhanced due to protection (Estes et al. 2011). The protection of piscivores, for example, may result in herbivore reduction and consequently elevated macroalgal growth inside marine reserves. However, studies that explored this question have found that changes in predator populations do not discernibly influence or are even positively correlated with the density, size, and biomass of herbivorous fishes, suggesting that top-down forces may not play a strong role in regulating large-bodied herbivorous fish on coral reefs (Mumby et al. 2006a; Houk & Musburger 2013; Rizzari et al. 2015).

Conclusions

Despite the long-term reduction of herbivory capacity reported across the Caribbean, the Mesoamerican Reef displayed relatively low macroalgal cover at the onset of this study. Subsequently, during the last decade, fleshy macroalgal cover increased rapidly on Mesoamerican reefs. Herbivorous fish populations were not responsible for this trend, contrasting the coral reef top-down herbivore control paradigm and implicating the role of external factors in making environmental conditions more favourable for algae. Increasing macroalgal cover typically suppresses ecosystem services and leads to degraded reef systems. Consequently, policy makers and local managers should consider complementary protection measures such as watershed management, in addition to herbivorous fish protection, in order to arrest this trend.

Supplemental Information

Table S1.1. Candidate predictor variables of coral cover change on the Mesoamerican Reef. Site country classification was split into three binary variables. All sites in Northern Quintana Roo, Mexico are considered to have been impacted by hurricanes in 2005. Some sites were surveyed in August and September 2005 after Hurricane Emily (17/7/2005), although this was not considered to have a sizeable effect on the results as Wilma (21-24/10/2005) was the strongest hurricane registered in the Caribbean (Álvarez-Filip & Gil 2006).

Variable	Type	Description
MEX	Binary	Binary indicator of location of site within Mexico
BEL	Binary	Binary indicator of location of site within Belize
HON	Binary	Binary indicator of location of site within Honduras
Island	Binary	Binary indicator of island or continental (mainland) site
Hurricane	Binary	Binary indicator of sites affected by 2005 hurricanes
Log_{10}(Fish_Initial)	Continuous	Logarithm of initial herbivorous fish biomass. Log values used to modify scale
Fish_Log_Diff	Continuous	Annual logarithmic change in herbivorous fish biomass
Algae_Initial	Continuous	Initial benthic cover by fleshy macroalgae. Decimal values from 0 to 1 representing 0 % to 100 %
Algae_Diff	Continuous	Absolute annual percentage change in fleshy macroalgal cover (decimal values)
Coral_Initial	Continuous	Initial benthic cover by hard coral. Decimal values from 0 to 1 representing 0 % to 100 %
NTZ	Binary	Binary indicator of location of site within a No Take Zone
MPA	Binary	Binary indicator of location of site within a Marine Protected Area

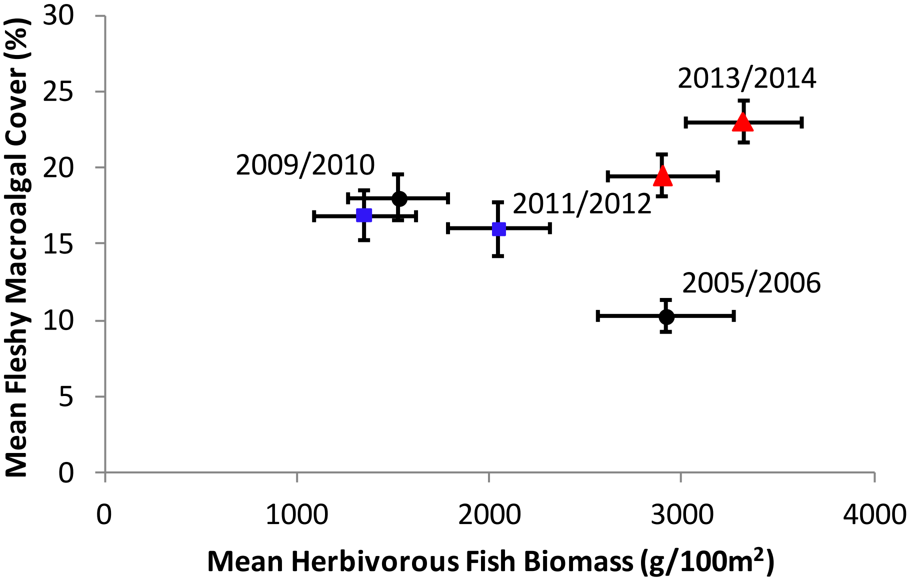

Figure S1.1. Temporal trend in mean herbivorous fish biomass and benthic fleshy macroalgal cover on the Mesoamerican Reef. Mean (± s.e.m.) values are shown for all sites surveyed repeatedly in consecutive monitoring periods. 62 sites were surveyed in both 2005/2006 and 2009/2010 (black circles), 50 sites in 2009/2010 and 2011/2012 (blue squares), and 90 sites in 2011/2012 and 2013/2014 (red triangles).

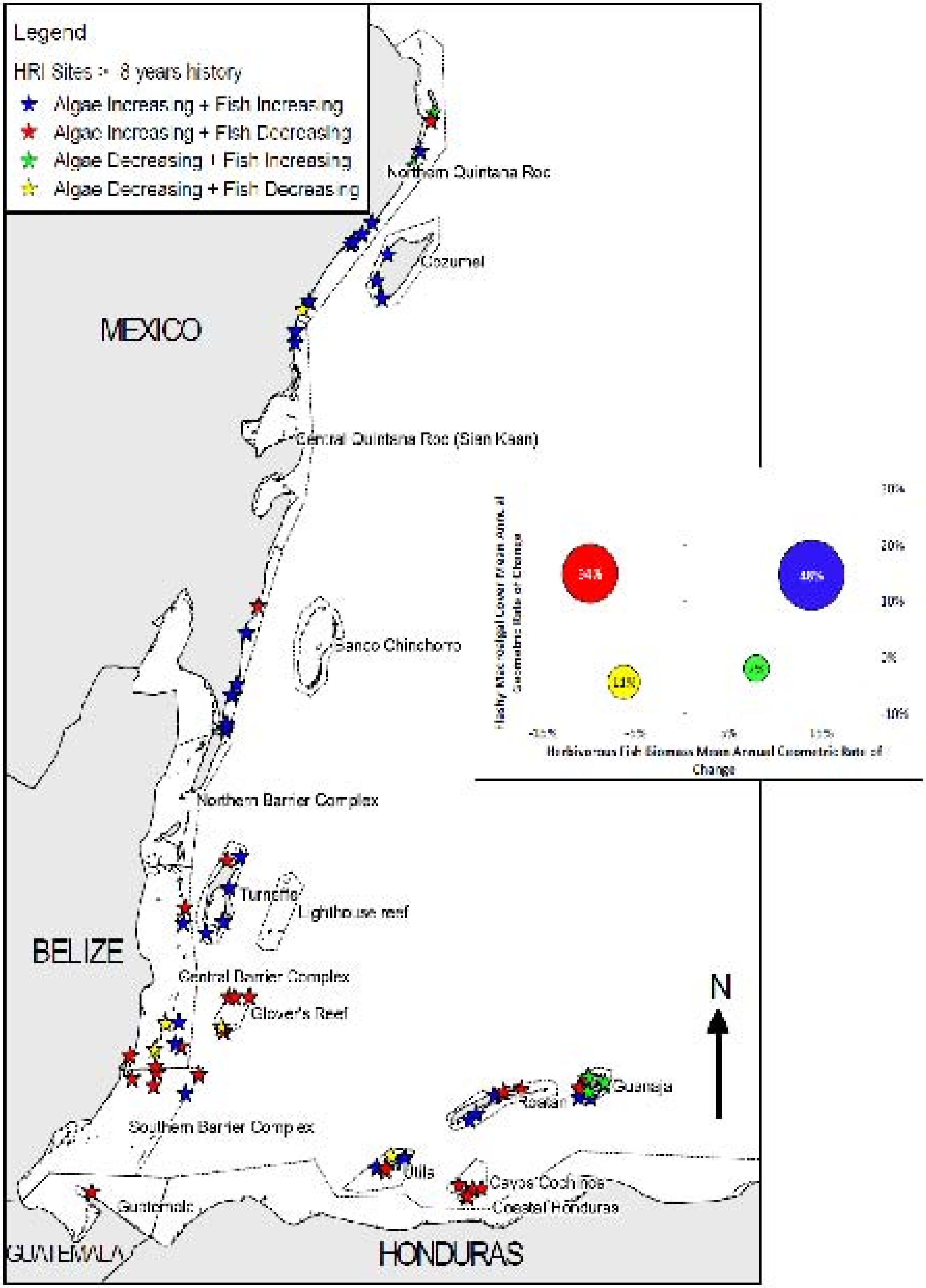
Legend
HRI Sites > 8 years history
★ Algae Increasing + Fish Increasing
★ Algae Increasing + Fish Decreasing
★ Algae Decreasing + Fish Increasing
★ Algae Decreasing + Fish Decreasing
Northern Quintana Roo
Cozumel
MEXICO
Central Quintana Roo (Sian Kaan)
Banco Chinchorro
Northern Barrier Complex
Turneffe
Lighthouse reef
BELIZE
Central Barrier Complex
Glover's Reef
Southern Barrier Complex
Roatan
Guanaja
Utila
Cayos Cochinos
Coastal Honduras
Guatemala
GUATEMALA
HONDURAS
N
Fleshy Macroalgal Cover Mean Annual Geometric Rate of Change
Herbivorous Fish Biomass Mean Annual Geometric Rate of Change
30%
20%
10%
0%
-10%
-10%
-5%
0%
5%
34%
48%
11%

Figure S1.2. Long-term herbivorous fish and benthic fleshy macroalgal cover trends on the Mesoamerican Reef. Map and inset graph indicating relationship between changes in herbivorous fish biomass and fleshy macroalgal cover from first (2005 or 2006) to last (2013 or 2014) year for all (73) long-term monitoring sites with ≥ 8 years' history. For inset graph, each circle represents the sites for that quadrant and circle position reflects mean annual geometric rates of change. Circle area represents proportion of sites in that quadrant (also labelled).

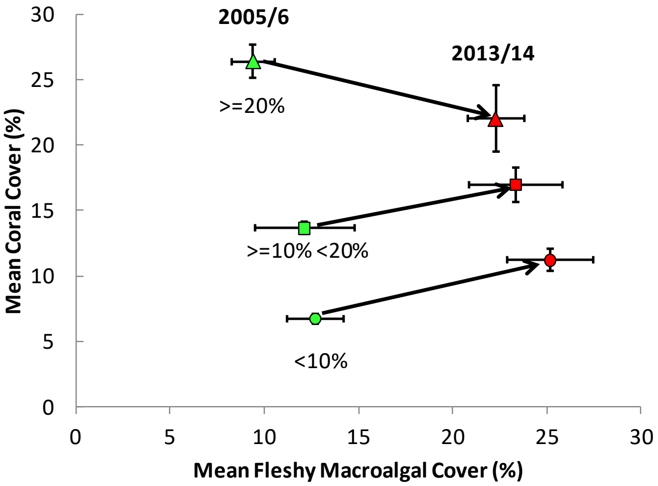

Figure S1.3. Effect of initial coral cover on change in fleshy macroalgal and coral cover over time on the Mesoamerican Reef. Mean (± s.e.m.) benthic macroalgal and coral cover for first (2005/6) and last years (2013/14) by initial level of coral cover, for all (85) long-term monitoring sites. Initial level of coral cover categories are < 10 % (n = 40); ≥ 10% and < 20 % (n = 33); and ≥ 20 % (n = 12) benthic cover.

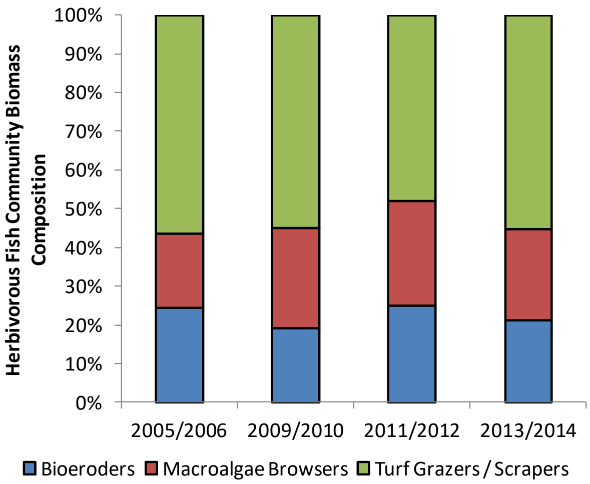

Figure S1.4. Mesoamerican Reef herbivorous fish community biomass composition by feeding guild between 2005/2006 and 2013/2014. Percentage composition of herbivorous fish community biomass by feeding guild (bioeroders, macroalgae browsers and turf grazers / scrapers) for sites surveyed repeatedly in each monitoring period (2005/2006, 2009/2010, 2011/2012 and 2013/2014).

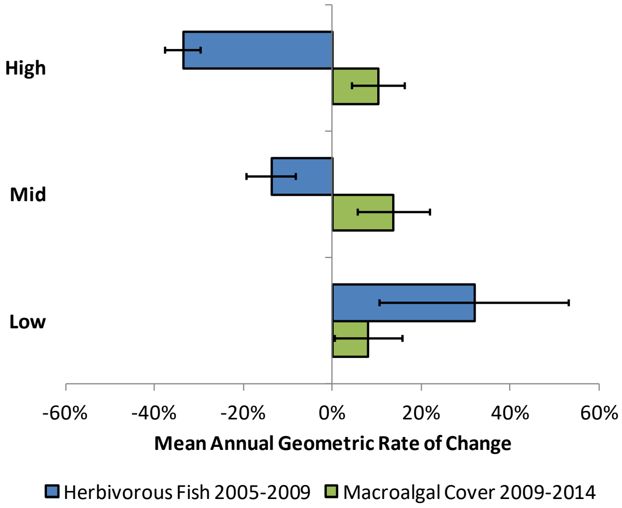

Figure S1.5. Comparison between herbivorous fish biomass change 2005/6-2009/10 and subsequent benthic fleshy macroalgal cover change 2009/10-2013/14 on the Mesoamerican Reef. Mean (± s.e.m.) annual geometric rates of change for herbivorous fish biomass and fleshy macroalgal cover for sites surveyed repeatedly in each monitoring period (2005/2006, 2009/2010, 2011/2012 and 2013/2014). Sites are grouped into terciles (Low, Mid, High) by initial (2005/2006) herbivorous fish biomass.

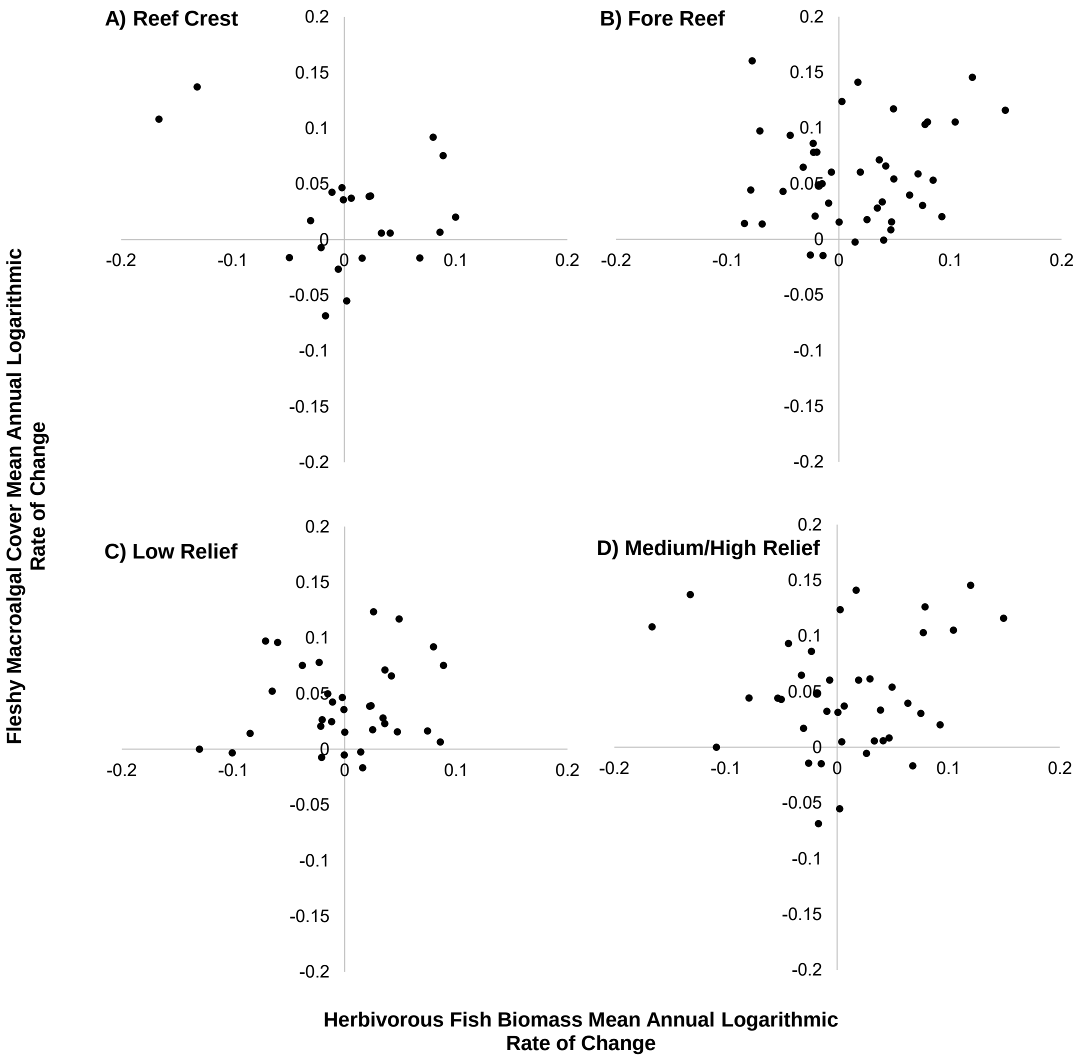

Figure S1.6. Long-term herbivorous fish and benthic fleshy macroalgal cover trends on the Mesoamerican Reef by reef zone and structural complexity. Graphs indicate relationship between changes in herbivorous fish biomass and fleshy macroalgal cover from first (2005 or 2006) to last (2013 or 2014) year for all (85) long-term monitoring sites with ≥ 7 years' history. Trends plotted separately for A) reef crest and B) fore reef sites, and sites with C) low and D) medium, high or very high structural complexity.

CAPÍTULO 2: Las actividades humanas locales limitan la eficacia de la protección marina en los arrecifes de coral del Caribe

Abstract

Marine ecosystems globally have suffered habitat, biodiversity and function loss in response to human activity. Marine Protected Areas (MPAs) can limit extractive activities and enhance ecosystem resilience, but do not directly address such external stressors. We surveyed forty-eight sites within seven MPAs and nearby unprotected areas to evaluate drivers of coral reef condition in the Mexican Caribbean. We found that local human activity limits protection effectiveness. Coral cover was positively related to protection characteristics, but was significantly lower at sites with elevated local human activity. Furthermore, we predict ongoing coastal development will reduce coral cover despite expanded protection within a regionwide MPA if an effective integrated coastal zone management strategy is not implemented. Policy makers must acknowledge the detrimental impact of uncontrolled coastal development and apply stringent construction and wastewater regulations in addition to marine protection.

Keywords: Coastal development, effectiveness, eutrophication, local human threats, management, Mesoamerican Reef, protected area network

Submitted:

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Introduction

Marine ecosystems globally have suffered habitat, biodiversity and function loss in response to rising human population and activity (Sanderson et al. 2002; Dirzo et al. 2014; McCauley et al. 2015). Coral reefs are particularly sensitive to perturbations as they persist within a narrow range of physicochemical conditions (Hughes et al. 2017a). Reefs worldwide have experienced declines in condition and function since the 1970s, attributed to coral disease, overfishing and herbivore loss, eutrophication, sedimentation and global climate change (Mora 2008; Hughes et al. 2017a). However, management actions have primarily targeted overfishing and direct physical threats through the establishment of Marine Protected Areas (MPAs), while external stressors such as climate change and land-use change are frequently unaddressed (Mora et al. 2006; Mora 2008; Hughes et al. 2017a). Recent research has highlighted that such external stressors can reduce MPA efficacy (Bégin et al. 2016; Lamb et al. 2016; Wenger et al. 2016). On the Great Barrier Reef, no take reserves are ineffective in mitigating coral loss and disease due to elevated terrestrial run-off (Lamb et al. 2016; Wenger et al. 2016). In the Caribbean, benthic composition has been linked with land-use change, rather than marine protection (Bégin et al. 2016). Consequently, in order to develop effective reef management strategies it is critical to understand the performance of marine protection in the context of external stressors and evaluate their impact on benthic condition.

Spatial management through the establishment of MPAs has been widely adopted to directly limit extractive activities and enhance ecosystem resilience (Jennings & Kaiser 1998; Bellwood et al. 2004). Where protection is in place, particularly within complete

No Take Zones (NTZs), fish populations generally respond positively in terms of density, biomass, individual size and species richness (Lester et al. 2009; Gill et al. 2017). Coral communities can benefit from marine protection by two principal mechanisms. First, MPAs may regulate activities that cause physical damage to corals, such as careless anchor use, destructive fishing practices and uncontrolled snorkelling and diving tourism (Dinsdale & Harriott 2004; Lamb et al. 2015). Second, the positive effect of protection on herbivorous fish populations is expected to control benthic macroalgae and indirectly benefit corals by reducing competition and freeing space for recruitment and growth (Mumby et al. 2006a). Yet, conservation outcomes are highly variable, depending not only on MPA design and management effectiveness, but also on biological and external factors (Mora et al. 2006; Maina et al. 2013). Increases in coral cover have rarely been observed in MPAs (Mumby & Harborne 2010), while a number of studies report no significant effect of protection on coral condition (Huntington et al. 2011; Noble et al. 2013; Toth et al. 2014).

Ignoring land-sea interactions often result in coastal MPAs failing to meet their conservation objectives (Álvarez-Romero et al. 2011). Reef degradation has been linked with anthropogenic eutrophication, sedimentation and local contamination of coastal waters at numerous sites globally including the Great Barrier Reef, Indonesia, Jamaica, and Florida (Lapointe 1997; Edinger et al. 1998; Fabricius & De’ath 2004). If not properly managed, agriculture and coastal development can lead to elevated sediment and nutrient run-off, with detrimental impacts on nearby reefs, irrespective of marine protection (Mora 2008; Bégin et al. 2016; Lamb et al. 2016; Wenger et al. 2016). Sedimentation increases with loss of vegetative cover as a result of land-use change to agricultural or urban use, coastal dredging for beach replenishment and navigation, and coastal construction (Fabricius 2005; Erftemeijer et al. 2012). Sediments smother corals, raise water turbidity, reducing coral photosynthetic activity, energy reserves and growth, and have been linked with elevated coral disease prevalence, reduced fecundity and recruitment (Fabricius 2005; Pollock et al. 2014). Anthropogenic nutrient sources include septic tanks, sewage outfalls, agricultural fertilizers and livestock (Lapointe et al. 1990, 2010; Drucker & Latacz-Lohmann 2003). Directly, nutrients increase the prevalence and severity of coral diseases (Vega Thurber et al. 2014). Indirectly, nutrients promote the growth of macroalgae, which compete with corals, reducing their fecundity, recruitment, growth and survival through various mechanisms such as excessive growth, shading and allelopathy (Chadwick & Morrow 2011). Furthermore, local-land based threats can be synergistic with other stressors (Wiedenmann et al. 2013; Wooldridge & Brodie 2015). For example, nutrient enrichment increases coral susceptibility to bleaching and improving water quality can ameliorate the effects of climate change on corals (Wooldridge & Done 2009; Wiedenmann et al. 2013).

The Mexican Caribbean coast has experienced dramatic coastal development over the last 30-40 years. Over 10 million tourists visit the region annually and the local population has grown rapidly from 88,000 in 1970 to 1.5 million in 2015 (INEGI 2010). As a result, coastal waters of the region have experienced eutrophication and increased sedimentation levels (Baker et al. 2013; Arias-González et al. 2017). Coastal dredging, construction, and marine port construction have contributed sedimentation and have been associated with nearby reef degradation (Martínez-Rendis et al. 2016; Arias-González et al. 2017). Hotels and residences are often constructed without adequate wastewater treatment facilities and due to the karstic nature of the sub-surface terrain, seepage is of particular concern (Murray 2007; Bauer-Gottwein et al. 2011). Loss of forest and mangrove vegetation owing to hotel construction and urbanisation has reduced groundwater filtration, further increasing nutrient concentrations reaching the ocean (Ellis et al. 2017). Consequently, eutrophication resulting from inadequate wastewater treatment is considered a principal driver of declining reef condition in the region (Bozec et al. 2008; Martínez-Rendis et al. 2016; Suchley et al. 2016; Arias-González et al. 2017).

Coastal development in the Mexican Caribbean has taken place despite an extensive marine protection network consisting of eight coral reef MPAs protecting over 260 km of reef. These MPAs exert little influence over land-based human activities and are generally not complemented by terrestrial protected areas as part of integrated coastal zone management (CONANP 2017). Here, we evaluate the impact of protection status, local human threats and other factors on Mexican Caribbean coral reef condition. This region provides an ideal model as many reefs are protected within MPAs of varying characteristics while declining reef condition has been linked to burgeoning coastal development (Bozec et al. 2008; Baker et al. 2013). As elsewhere, MPA establishment and design is often driven by political and socioeconomic concerns in addition to ecosystem considerations (Marinesque et al. 2012). In December 2016, after this study was conducted, the entire Mexican Caribbean was declared a biosphere reserve and consequently marine protection effectiveness considerations are particularly timely. Although the reserve will protect almost all Mexican Caribbean coral reef habitats, the adjacent coastline, which is planned for extensive further development, will continue to be outside protected area limits (Fig. 1; Supplemental Information, Fig. S2.1). To critically evaluate the capacity of expanded MPA networks to protect reefs confronted with ongoing coastal development we forecast regionwide coral cover under varying management scenarios.

Materials and methods

Forty-eight reef sites were surveyed in the Mexican Caribbean over the period April-November 2016 (Fig. 1). Sites were located within seven MPAs and nearby unprotected areas on the reef front at a mean (± s.e.m.) depth of 11.3 ± 0.5 m. Of the 48 sites, 33 were located within MPAs, of which 12 were located within complete No Take Zones (NTZs) where extractive practices are not permitted, and the remaining 15 sites were unprotected. Between 3 and 11 sites were surveyed in each MPA according to MPA size and reef area, known geomorphological heterogeneity and logistical considerations. Sites were selected to be representative of the locality based on national park monitoring and conservation programs, prior research and local knowledge, and hardground sites were avoided.

At each site, reef benthos was surveyed using 10 videotransects of 25 m length at a swimming speed of approximately 10 m/min. Videotransects were performed using a GoPro Hero 4 Silver action camera with a red filter at a resolution of 1080 HD, recording at 60 frames per second with a narrow field of view. The camera was maintained 50 cm from the reef substrate using a plumb-line, resulting in video capturing approximately 60 cm × 40 cm of substrate. Videotransects were each sampled using 10 frame stills as photo-quadrats, which in turn were point-sampled with 50 points using the software Coral Point Count (CPCe; Kohler & Gill 2006). Points were classified as hard coral, fleshy macroalgae, calcareous algae, turf algae, turf algae sediment mat, crustose coralline algae (CCA), sponge, gorgonian, cyanobacteria or bare reef substrate. Coral bleaching incidence was recorded, but was generally low and no bleaching-induced mortality was observed.

A preliminary study was conducted to determinate the appropriate number of quadrats and points needed to accurately estimate coral cover, the principal metric used to assess reef condition. Manchones reef, Puerto Morelos, was oversampled using 250 photo-quadrats and 200 points for each photo-quadrat (50,000 points in total). Increasing quantities of photo-quadrats and points were randomly resampled 100 times each, and mean coral cover was determined for combinations of photo-quadrats and points. Estimates of coral cover were observed to stabilise at around 100 photo-quadrats and 50 points per photo-quadrat, hence 5,000 points in total were used to sample each of the 48 surveyed sites as in Aronson & Swanson (1997). To sample the 10 videotransects for each site, 10 non-overlapping frame stills were randomly taken for each transect, yielding the required 100 photo-quadrats per site.

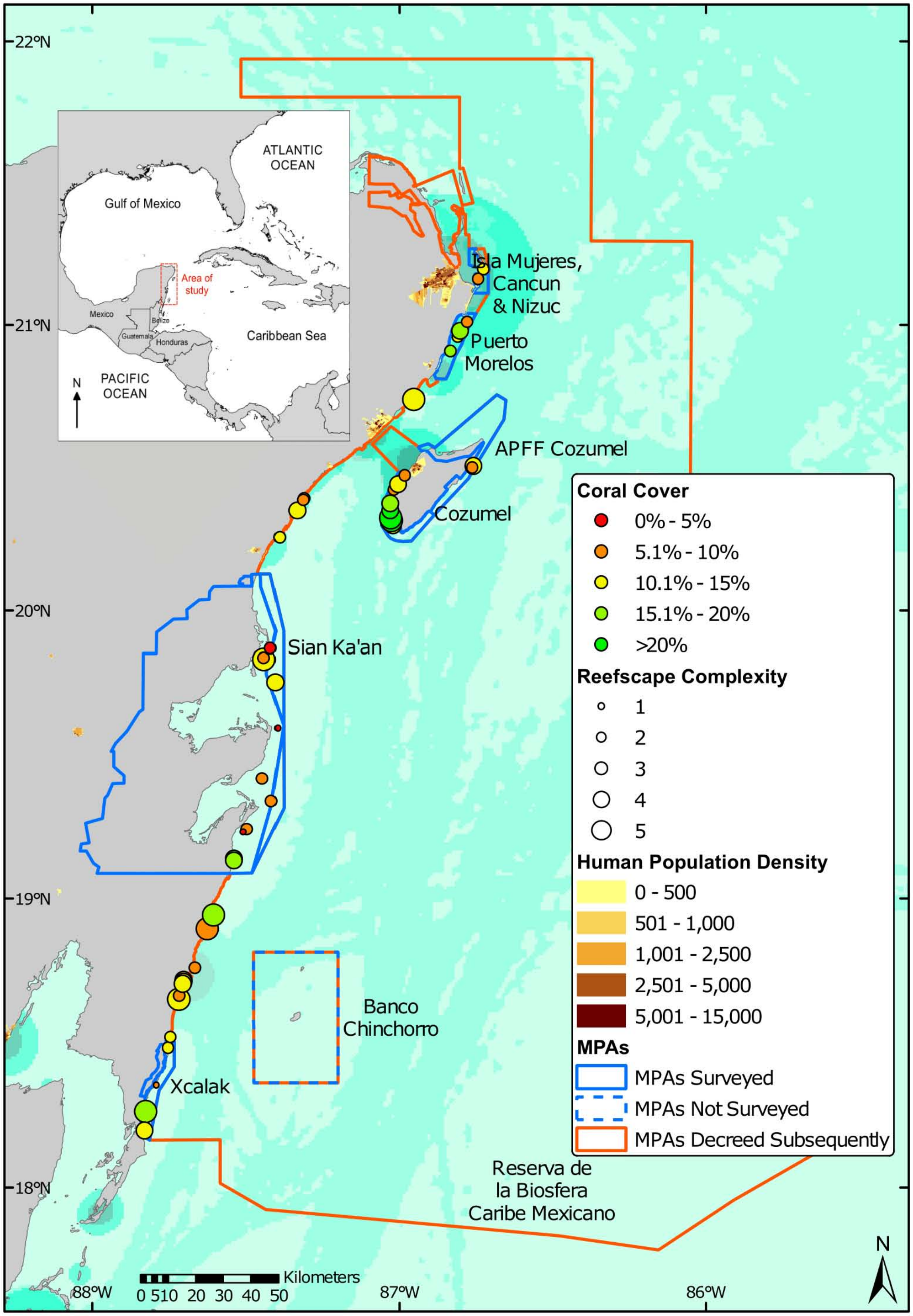
22ºN
21ºN
20ºN
19ºN
18ºN
88ºW
87ºW
86ºW
ATLANTIC OCEAN
Gulf of Mexico
Area of study
Mexico
Belize
Guatemala
Honduras
Caribbean Sea
PACIFIC OCEAN
N
Isla Mujeres, Cancun & Nizuc
Puerto Morelos
APFF Cozumel
Cozumel
Sian Ka'an
Banco Chinchorro
Xcalak
Reserva de la Biosfera Caribe Mexicano
Kilometers
0 5 10 20 30 40 50
N
Coral Cover
0% - 5%
5.1% - 10%
10.1% - 15%
15.1% - 20%
>20%
Reefscape Complexity
1
2
3
4
5
Human Population Density
0 - 500
501 - 1,000
1,001 - 2,500
2,501 - 5,000
5,001 - 15,000
MPAs
MPAs Surveyed
MPAs Not Surveyed
MPAs Decreed Subsequently

Figure 1. Study site location in the Mexican Caribbean. 48 sites were surveyed in total. 33 sites were located within 7 MPAs (blue shaded areas), of which 12 were located within complete No Take Zones (NTZs) where extractive practices are not permitted, and the remaining 15 sites were unprotected. Sites are identified by circles whose colour reflect mean site coral cover and size reflect reef structural complexity. Urban area human population density shown by basic geostatistical area for 2010 (INEGI 2010). Marine background shade represents local human threat level (darker for higher threat) based on combined coastal development and marine pollution & damage threat from the World Resources Institute (WRI; Burke et al., 2011).

At each site, reefscape structural complexity was visually estimated on a 0 to 5 scale by a single observer and reef rugosity was evaluated using the chain method (Wilson et al. 2007). A 2 m fine-link aluminium chain was carefully draped over the reef in random locations along the path of the videotransects an average (± s.e.m.) of 19 ± 0.5 times per site. The linear distance between chain ends was measured and rugosity determined as the ratio of total and linear chain lengths. Mean rugosity values were then calculated per site. Herbivorous fish (Scaridae and Acanthuridae) abundance and total length (TL) and *Diadema antillarum* sea urchin abundance were recorded in 30 m-long and 2 m-wide transects. We attempted to perform eight transects per site; however, given site conditions and time availability this was occasionally not achievable and at some sites we were able to perform more (range from 5 to 11). Fish abundance was converted to biomass density using standard allometric length-weight conversions. Very few sea urchins were present and were only observed at 26 of 48 sites.

We tested the effect of protection status (full No Take Zone / general use MPA / unprotected); MPA age, time since publication of management plan, size and effectiveness; herbivorous fish biomass; *Diadema* density; fleshy macroalgal cover;

reefscape structural complexity and rugosity; local human threat; wave exposure, hurricane frequency and other abiotic variables on coral cover (Supplemental Information, Table S2.1). Water temperature trends were not included as remote sensing data do not capture local variations at the resolution available (4 km; Chollett et al. 2012). Furthermore, previous studies have shown that temperature is a poor predictor of spatial variation in coral reef condition in this ecoregion (Cox et al. 2017). Local human threat index and MPA protection variables were key to the analysis and are explained further.

The level of local human threats not related to extractive activities was estimated by integrating two component indices developed at a global scale by the World Resources Institute (WRI; Burke et al. 2011). The advantage of using a global data source is that this approach can be replicated for any region or reef site worldwide. The component indices were: 1) coastal development and 2) marine-based pollution and damage threats. Watershed-based pollution threat, also available from WRI, was not considered reliable as the Yucatan peninsula has very little surface drainage due to its karstic nature (Bauer-Gottwein et al. 2011). Coastal development threat is determined based on the location and size of cities, ports, and airports, population density within 10 km of the coast, coastal population growth, and tourism growth (Burke et al. 2011). Marine-based pollution and damage threat is evaluated principally based on the distance to commercial and cruise ports scaled by shipping and passenger volumes (Burke et al. 2011). We integrated these two threat levels to generate a combined local human threat index on a five-point scale (Low, Low/Medium, Medium, Medium/High, High).

MPA age was determined as the time since formal decree, and the time since publication of management plan was also obtained (CONANP 2017). MPA size is the total marine area protected in km^2 (CONANP 2017). We characterised MPA effectiveness in terms of enforcement and compliance based on the 2016 Mesoamerican Reef Eco-Audit performed by the Healthy Reefs Initiative and partner organizations (Healthy Reefs Initiative 2016). The Eco-Audit draws on input from NGOs, governmental agencies, and the private sector to classify MPAs according to three criteria: 1) the existence of an updated management plan; 2) the adequacy of personnel and equipment; and 3) the level of enforcement. The scores for the three criteria were combined to determine overall MPA effectiveness on a seven-point scale.

To model coral cover we adopted generalised linear mixed models (GLMMs) with site as a random effect. A binomial error distribution with a logit link function was adopted to account for non-normal error distribution resulting from modelling percent cover data. Model assumptions were validated with residual plots and multicollinearity was eliminated by removing predictors with the highest variance inflation factors (VIFs) until all VIFs (degrees-of-freedom-adjusted GVIFs) were less than 2 (Graham 2003). Least significant predictors were sequentially removed backwards and models compared pairwise with chi-square tests of significant differences in residual deviance. The more parsimonious model was preferred until the chi-square test revealed a significant difference and the prior model retained as the minimum adequate model. Spline spatial correlograms were plotted to check that residuals were not spatially autocorrelated. MPA predictor variables were collinear and thus only one remained in the candidate model. In order to assess the importance of MPA characteristics, alternative GLMMs were fitted retaining different MPA predictor variables during multicollinearity assessment.

The final fitted model was utilised to forecast regional coral cover in 20 years' time. The entire Mexican Caribbean was recently decreed a biosphere reserve. We assumed that this will function similarly to existing MPAs and thus forecasts were performed assuming all sites will be protected and current MPA age was increased by 20 years. Extensive urban and tourism development is planned for the Mexican Caribbean coastline and its impact on regional coral cover must be considered. Based on an assessment of current threat levels and planned development, local human threat was increased to the highest category for all mainland sites north of Sian Ka'an Biosphere Reserve and those located in central Mahahual (Fig 1; Supplemental Methods). We then ran three forecast scenarios based on varying assumptions concerning protected area management strategy (Table 1). All statistical analyses were performed in R version 3.3.2 using packages including *tidyverse*, *reshape2*, *plyr* and *boot* for data manipulation, *lme4* for GLMMs, *car* for VIF assessment, *coefplot* for coefficient plotting, *effects* for partial effect plots and *ncf* for spline correlograms.

Table 1: Protected area management scenarios for the Mexican Caribbean. Passive, coastal zone and comprehensive management scenarios adopted to predict regional coral cover in 20 years' time. Under each strategy, existing or improved strategies are assumed for coastal zone and herbivorous fish management, with consequences for local human threat levels and herbivorous fish biomass. We assumed that the Mexican Caribbean Biosphere Reserve will protect all surveyed sites not already protected in 2016 and thus current MPA age was increased by 20 years for all sites. All other model predictor variables were maintained constant.

Scenario	Coastal Zone Management Strategy	Herbivorous Fish Management Strategy	Assumptions
Passive management	Existing	Existing	Current strategy continues and adopted by the Mexican Caribbean Biosphere Reserve.
Coastal zone management	Improved	Existing	Active coastal zone management strategy to reduce the impact of local human activities. For example, improved wastewater treatment services at new hotel and residential developments, and retrofitting existing installations, would reduce nutrient run-off reaching the reefs (Murray 2007). Prevention of mangrove destruction and sedimentation mitigation strategies for coastal construction would reduce the amount of terrestrial and coastal sediments in the water column (Ellis et al. 2017). Furthermore, marine traffic management, engine and fuel regulations would reduce local contamination. These combined actions are assumed to reduce local human threat level (after increases due to planned development) by two categories (e.g. High to

			Medium, Medium to Low etc.) over the 20-year forecast period.
Comprehensive management	Improved	Improved	Active strategy to reduce the impact of local human activities as per coastal zone management scenario. Herbivorous fish extraction banned as in other locations in the ecoregion (Kramer et al. 2015). Herbivorous fish ban assumed to increase biomass at non-NTZ sites by ratio of mean biomass at NTZ and non-NTZ sites (203%; Supplemental Information, Fig. S2.4C), a plausible level over the 20-year forecast period given no-take protection results elsewhere (McClanahan et al. 2007; Williams et al. 2016).

Results

Mexican Caribbean reefs were dominated by fleshy macroalgae and turf algae / turf algal sediment mats. Mean (± s.e.m.) site fleshy macroalgal cover was 27.2 ± 2.0% (with cover ranging from 1.8% to 59.6%) and mean turf cover was 20.5 ± 1.0% (range: 5.5% to 37.5%), while mean coral cover was only 11.9 ± 0.8% (range: 2.2% to 33.2%; Supplemental Information, Fig. S2.2). Coral cover was found to be significantly related to local human threat, MPA age, herbivorous fish biomass, fleshy macroalgal cover, reef structural complexity and hurricane frequency (Fig. 2). Coral cover was positively correlated with MPA age, herbivorous fish biomass, reef structural complexity and hurricane frequency, and exhibited a negative relationship with fleshy macroalgal cover (Fig. 3). Medium/high and high levels of local human threat were associated with lower coral cover, and these levels displayed a stronger (negative) relationship with coral cover than that between fleshy macroalgal cover and coral cover or the (positive) relationship between MPA Age and coral cover (Fig. 2). *Diadema* sea urchin density was not a significant predictor of coral cover. To fully assess the importance of MPA characteristics (MPA size, effectiveness, protection status and the time between formal decree and management plan publication), four alternative models were fitted, each retaining different MPA predictor variables during multicollinearity assessment. For all four alternatives, MPA variables were significant in the resulting models (Supplemental Information, Fig. S2.3).

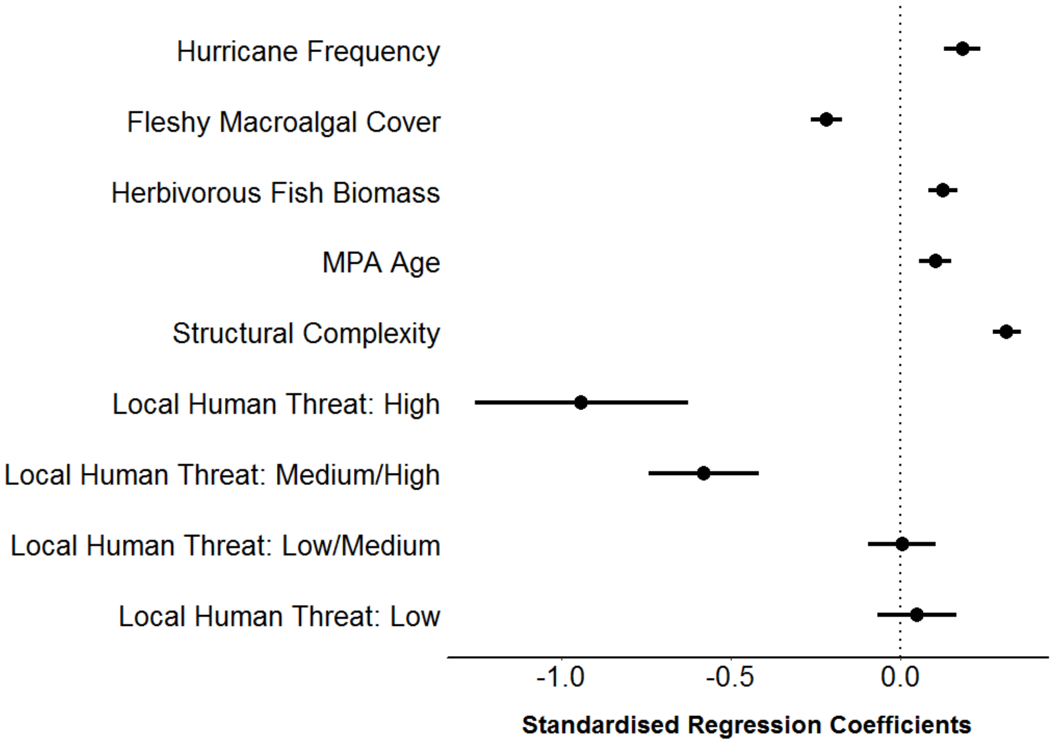

Figure 2. Coral cover predictors in the Mexican Caribbean. Standardised regression coefficients for predictor variables in minimum adequate binomial logit GLMM model of coral cover. The minimum adequate GLMM was refitted using z-scores for numerical predictor variables (calculated by subtracting

the mean from each raw data point and then dividing by the standard deviation) to enable a comparison of predictor weights. Coefficients reflect the number of standard deviations change in the log odds of the dependent variable $\left(ln\left(\frac{Coral\ Cover\ \%}{1-Coral\ Cover\ \%}\right)\right)$ for a one standard deviation increase in each predictor variable, while controlling for all other independent variables. Error bars represent one standard deviation in coefficient estimates. As Local Human Threat is a categorical variable, coefficients are not standardised but shown by category, with Medium selected as the base level and therefore not shown. There was no significant difference in model fit between the minimum adequate model and an alternative developed with separate local human threat components (coastal development and marine pollution & damage) as candidate predictor variables (chi-square test, X^2= 1.99, 2 d.f., P = 0.37) and the combined model was retained as was more parsimonious.

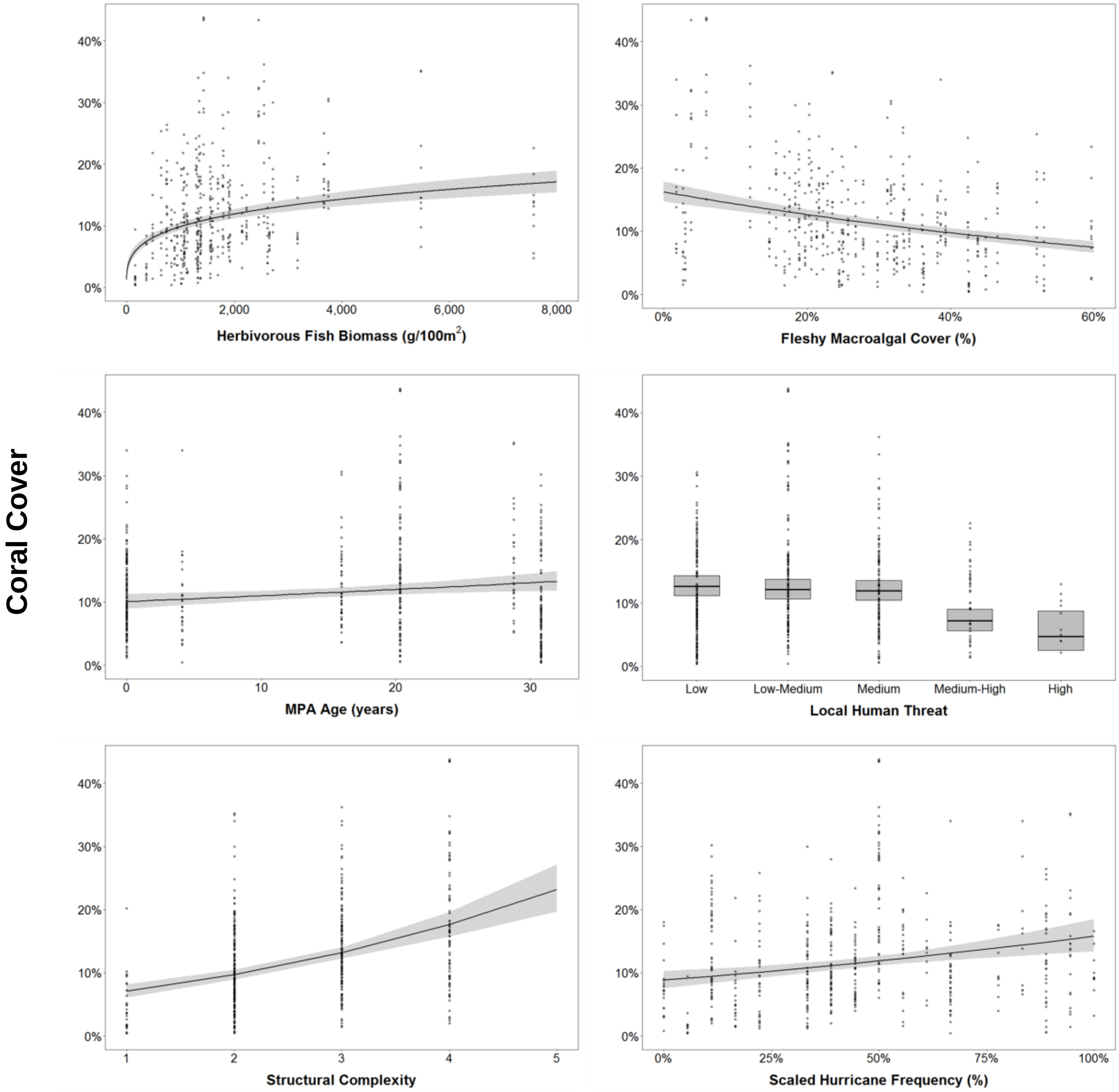

Figure 3. Coral cover predictor partial effects. GLMM model-predicted coral cover and actual mean transect coral cover by minimum adequate model predictor variables. Actual coral cover shown as points. Model partial effects shown as lines (with 95% confidence intervals) and determined for each predictor variable by holding all other fixed effect predictors at mean value. Structural complexity was assessed on a 0 to 5 scale. Sites with zero complexity were excluded as were not considered reefs. A single site was assigned a complexity of five, but was excluded from the analyses as fish data were not recorded.

Hurricane frequency in years scaled by maximum and minimum observed values to give values between 0 and 100% for ease of interpretation.

The final fitted model was utilised to forecast regional coral cover in 20 years' time (Table 1). The model predicted that if planned coastal development takes place but management strategy remains unaltered then the proportion of degraded sites with coral cover below 5% will increase substantially (Fig. 4). However, if a coastal zone management strategy were implemented to reduce the impact of local human activity, then reef condition would improve beyond the current state (Fig. 4). If complemented with regionwide herbivorous fish protection as part of a comprehensive management strategy then reef condition is expected to improve further with a large proportion of sites reaching 20% coral cover or greater (Fig. 4).

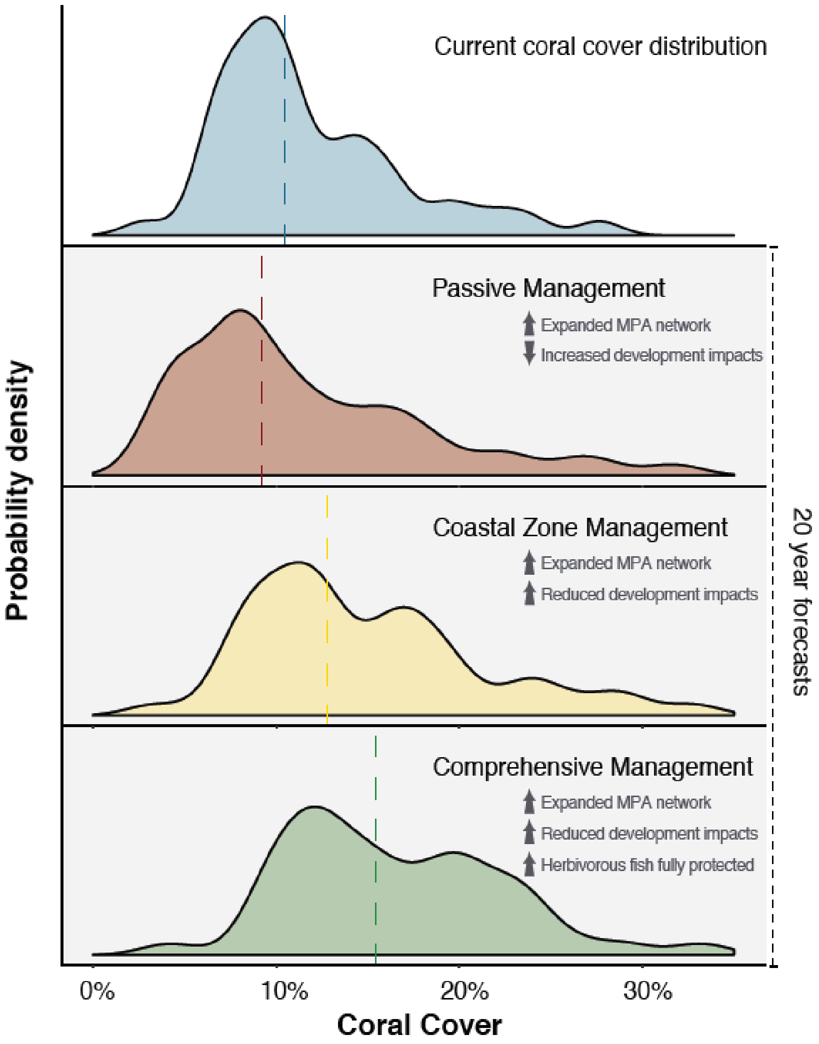

Figure 4. Mexican Caribbean coral cover forecasts. Three future coral cover forecast scenarios are contrasted with the current coral cover distribution. Scenarios are for 20 years in the future based on expanded marine protection in the Mexican Caribbean Biosphere Reserve and expected population and tourism growth. Three protected area management strategies are considered: 1) existing passive management with little mitigation of the impact of coastal development, 2) coastal zone management with an active strategy to reduce the impact of local human activities, 3) comprehensive management of the coastal zone and regionwide herbivorous fish protection (Table 1). Coral cover calculated using fitted GLMM model (Fig. 2) for current and future scenarios. Vertical dashed lines indicate median values.

Discussion

Local human activities outweigh the effect of marine protection on coral communities in the Mexican Caribbean (Fig. 2; Fig. 4). Coral cover is positively related to marine protection characteristics including protection time, effectiveness and MPA size, but is significantly reduced at sites with elevated coastal development and marine pollution and damage threat levels (Fig. 1; Fig. 2; Fig. 3). This finding agrees with recent research reporting the detrimental impact of external stressors on MPA efficacy and extends it geographically (Bégin et al. 2016; Lamb et al. 2016; Wenger et al. 2016). Further, we forecasted that, despite increasing MPA coverage, highly degraded sites with very low coral cover are likely to become increasingly common if current management strategy continues (Table 1; Fig. 4). However, integrated coastal zone management, particularly if combined with a regionwide ban on herbivorous fish extraction, could mitigate the negative impacts of planned developments and improve benthic condition beyond current levels (Fig. 4).

While coral reef protection seeks to address human threats within MPA limits, it frequently does not address external threats such as climate change and local land-based human activities (Mora 2008; De'ath & Fabricius 2010; Hughes et al. 2017b). In recent decades, reef benthic condition has deteriorated at many sites despite marine protection (Huntington et al. 2011; Noble et al. 2013; Toth et al. 2014). MPA efficacy has been compromised by terrestrial sedimentation and flood run-off in both the Indo-Pacific and Caribbean basins (Bégin et al. 2016; Lamb et al. 2016; Wenger et al. 2016). The current study took place in a region with one of the highest rates of coastal development globally (Baker et al. 2013). The northern coast of the Mexican Caribbean is highly developed, with major ports located across the region, and is set to develop even further (Fig. 1; Supplemental Information, Fig. S2.1; Baker et al. 2013). Here we found that despite the positive effect of the MPA network, coral cover has declined in response to coastal development and marine activities (Fig. 3; Supplemental Information, Fig. S2.3). We hypothesize that coastal dredging, construction, and marine ports contribute sedimentation and pollution locally while coastal development and urbanisation has resulted in widescale eutrophication of coastal waters of the region. While this reasoning is in agreement with a growing body of evidence (Bozec et al. 2008; Martínez-Rendis et al. 2016; Suchley et al. 2016; Arias-González et al. 2017), it is often not possible to identify causal factors of reef degradation due to limited and inconsistent nutrient and sediment data for many Caribbean reefs (Risk 2014; Bland et al. 2017).

In the Mexican Caribbean, we observed that coral cover is positively related to protection time (Fig. 2). This corresponds with other studies; however, it is important to consider selection bias as managers may preferentially protect reefs with higher coral cover (Graham et al. 2008; Selig & Bruno 2010). Nevertheless, our finding that coral cover is related to MPA size and effectiveness (management planning, personnel and equipment, and enforcement), in addition to protection time, provides evidence for the value of MPA protection for coral communities (Supplemental Information, Fig. S2.3; Mora et al. 2006; Gill et al. 2017). In addition to marine protection and local human threats, we found other factors also influence coral reef condition. Both herbivorous fish biomass and fleshy macroalgal cover were significant predictors of coral cover (Fig. 2), suggesting that macroalgal-coral competition is important (Chadwick & Morrow 2011).

Enhanced herbivorous fish biomass was related to no-take protection and although herbivorous fishes (parrotfishes and surgeonfishes) are not commercially targeted in Mexico, banning extractive practices can benefit populations through reduced by-catch (Supplemental Information, Fig. S2.4C; Allison et al. 1998). No-take protection was also associated with lower macroalgal cover (Supplemental Information, Fig. S2.4B); however, coral cover was not significantly correlated with no-take protection itself (Fig. 2; Supplemental Information, Table S2.1). Given that coral cover was significantly (positively) related to overall MPA protection (Fig. 2; Supplemental Information, Fig. S2.3), both direct (overall MPA protection) and indirect mechanisms (related to herbivorous fish protection) may be necessary to benefit coral communities.

Coral cover was also related to reefscape structural complexity and historical hurricane frequency (Fig. 2). Structural complexity influences the abundance, diversity, and trophic structure of reef fish assemblages, which in turn may benefit benthic condition due to food web integrity and enhanced resilience (Graham & Nash 2013). Although major hurricanes can have extensive immediate effects on reefs, less severe hurricanes and storms may be beneficial. For example, moderate hurricanes remove abundant fleshy macroalgae while not affecting robust standing corals (Harmelin-Vivien 1994; Mumby et al. 2006b). Hurricanes can also serve to promote asexual coral recruitment through the creation and dispersal of coral fragments (Fong & Lirman 1995; Lirman 2003). Furthermore, hurricanes have not driven Caribbean-wide declines of coral cover historically. Both impacted and non-impacted sites suffered similar declines in the 1990s due to the prior disease-driven loss of the predominant coral, *Acropora palmata* (Harmelin-Vivien 1994; Aronson & Precht 2001; Gardner et al. 2005).

We found that local human threats act to reduce the efficacy of protection for Mexican Caribbean coral reefs. Given that few protected areas studied have sizeable terrestrial components in areas with human activities (Fig. 1), the protected area network currently provides insufficient protection from land-based threats. Indeed, we predict that ongoing coastal development will reduce regionwide coral cover despite extended protection within the newly decreed Mexican Caribbean Biosphere Reserve (Fig. 1; Fig. 4). Although MPA efficacy should not be determined by the ability to mitigate threats originating outside MPA boundaries, these rising threats need to be considered by embedding MPAs in broader management frameworks such as coastal zone management or ridge to reef management (Table 1; Cicin-Sain & Belfiore 2005; Richmond et al. 2007). These are not new concepts, yet have been implemented in relatively few coral reef regions (Keller et al. 2009). Policy makers and managers globally must acknowledge the detrimental impact of uncontrolled coastal development on coral reefs. In addition to improved implementation and enforcement of herbivorous fish protection, authorities must apply more stringent controls on coastal development and wastewater treatment in order to improve coral condition and ecosystem resilience.

Supplemental Information

Supplemental Methods: *Local human threat forecasts*

The final fitted model was utilised to forecast regional coral cover in 20 years' time. Extensive urban and tourism development is planned for the Mexican Caribbean coastline and its impact on regional coral cover must be taken into consideration (Gobierno de México 2016). Based on an assessment of current threat levels and planned development, local human threat was increased to the highest category for the 20 year forecasts for all mainland sites north of Sian Ka'an Biosphere Reserve and those located in central Mahahual. Mexican government forecasts are available for human population and tourism growth (Fig. S2.1). Northern municipalities and the southern resort town of Mahahual are expected to experience far greater population and tourism growth than the rest of the coastline (Fig. S2.1). Our model includes a composite local human threat index and both coastal development and marine pollution & damage components will be impacted by forecast growth; the former directly and the latter indirectly as cruise ship traffic and recreational marine activities increase with greater tourism. Although relative growth in Cancún is expected to be lower than other northern localities, as current threat levels in Cancún are already predominantly medium/high increasing local human threat to the highest category for all northern mainland sites is justified. For the island of Cozumel growth is expected primarily in the principal settlement to the north-west of the island, where sites have already been affected by human activity. Sites further south are not expected to be impacted further and consequently local human threat was not modified for Cozumel.

Table S2.1: Candidate predictor variables of coral cover in the Mexican Caribbean. Candidate predictor variables in coral cover model are listed with variable type, description and justification for inclusion.

Predictor	Type	Description	Justification
Location	Categorical	Site location. Continental, island leeward or island windward.	Reef geomorphology, coral abundance and community composition have been observed to vary between leeward and windward locations in this region (Fenner 1988; Reyes-Bonilla et al. 2014).
Depth	Continuous	Site depth (m).	Depth is a key driver of coral reef zonation due to gradients of environmental variables and biological interactions (Sheppard 1982; Done 1983; Jackson 1991).
Reef Structural Complexity	Ordinal	Reef structural complexity visually estimated on a 0-5 scale by a single observer (Polunin & Roberts 1993).	Reef structural complexity influences coral reef fish assemblages (Roberts & Ormond 1987; Grigg 1994; Graham & Nash 2013), which in turn may have a positive impact on benthic condition (Bellwood et al. 2004; Raymundo et al. 2009; Thibaut et al. 2012). Corals are responsible for creating reef complexity, resulting in a potentially collinear relationship between coral cover and structural complexity (Graham & Nash 2013). However, dead corals, sponges and other benthic components are increasingly responsible for structural complexity on Caribbean reefs. Furthermore, reef complexity provides refugia from algal contact and coral predators and therefore promotes coral recovery post disturbance (Colgan 1987; Mumby & Steneck 2008; Graham & Nash 2013; Doropoulos et al. 2016). Including structural complexity can account for reef geomorphological heterogeneity between sites.

Predictor	Type	Description	Justification
Rugosity	Continuous	Fine-scale reef rugosity evaluated using the chain method (Risk 1972; Luckhurst & Luckhurst 1978; McCormick 1994).	Same as Reef Structural Complexity.
Local Human Threat	Categorical	Combined coastal development and marine pollution & damage threat from WRI (Burke et al. 2011). Combined to give 5 threat categories. Coastal development includes coastal engineering, land filling, runoff from coastal construction, sewage discharge, and impacts from unsustainable tourism, and is determined from the location of cities and coastal population density. Marine pollution and damage threat includes solid waste, nutrients, toxins from oil and gas installations and shipping, and physical damage from anchors and ship groundings, and is determined from the size of cruise ship & commercial shipping ports, and intensity of shipping traffic. Watershed-based pollution threat also available from WRI is not useful as the Yucatan peninsula has very little surface drainage. Overfishing and destructive fishing threat not incorporated as the effect of fishing is taken into account by Herbivorous Fish Biomass (as destructive fishing practices are not generally adopted in the region).	Mora et al. (2006) recognise external risks in an index of coral reef MPA conservation status. Elevated sediment and nutrient levels from nearby human activities are detrimental for coral communities (Rogers 1990; Edinger et al. 1998; Fabricius 2005; Stoms et al. 2005).

Predictor	Type	Description	Justification
Fleshy Macroalgal Cover	Continuous	Mean fleshy macroalgal cover (percentage proportion expressed as decimal).	Fleshy macroalgae compete with corals reducing fecundity, recruitment and survival (McCook et al. 2001; Hughes et al. 2007b; Bruno et al. 2009; Chadwick & Morrow 2011).
Herbivorous Fish Biomass	Continuous	Mean biomass density of fishes of Scaridae and Acanthuridae families (g/100m^2). Values were log-transformed due to right-skewed data.	Herbivorous fish control algal abundance and as a result maintain the balance between algae and corals (Bellwood et al. 2004; Mumby et al. 2006a).
Diadema Density	Continuous	Mean density of *Diadema* sea urchins per 100m^2. Values were log-transformed due to skewed data.	*Diadema* was a key herbivore historically in the Caribbean before a mass mortality event in the 1980s, although it has since only partially recovered at a few sites across the region (Jackson et al. 2001; Lessios 2016).
NTZ	Binary	Binary indicator of location within a No Take Zone.	By limiting extractive practices, the decline of fish stocks can be halted or reversed in NTZs (Lubchenco et al. 2003; Hughes et al. 2007a; Lester et al. 2009). This can benefit coral communities indirectly through the protection of herbivorous fishes which control algal proliferation (Williams & Polunin 2001; Mumby et al. 2006a; Mumby & Harborne 2010).
MPA	Binary	Binary indicator of location within a Marine Protected Area.	Selig & Bruno (2010) in a meta-analysis of 310 MPAs observed that marine protection has a small positive impact on coral cover. MPAs are expected to regulate activities that cause physical damage to reefs, such as anchor use, destructive fishing practices and uncontrolled snorkelling and diving tourism (Davis & Tisdell 1995; McManus 1997). MPA fishing regulations including gear restrictions, catch and size limits, in addition to temporary and permanent closures, seek to maintain fish populations (with subsequent benefits for coral communities) and reduce direct reef damage (Lamb et al. 2015).

Predictor	**Type**	**Description**	**Justification**
Recreational Use	Categorical	Low/Medium/High recreational use determined qualitatively based on interviews with local stakeholders.	Tourism can cause damage to coral reefs through snorkeler and diver contact with corals and careless anchor use (Allison 1996; Zakai & Chadwick-Furman 2002; Hasler & Ott 2008; Roche et al. 2016). Considered in addition to MPA indicator since as a result of MPA establishment recreational use may not change or can even increase (Davis & Tisdell 1995; Thurstan et al. 2012).
MPA Age	Continuous	Time since formal decree of Marine Protected Area (CONANP 2017). Zero for unprotected sites. Reserva de la Biosfera Sian Ka'an and Reserva de la Biosfera Arrecifes de Sian Ka'an MPAs merged as are managed jointly and age taken as oldest value.	A global study that evaluated 87 MPAs identified 5 key criteria which determine fish protection success: no take, well enforced, old (>10 years), large (>100 km^2), and isolated (Edgar et al. 2014). Selig & Bruno (2010) in a meta-analysis of 310 MPAs globally observed that coral cover increases with time protected. Babcock *et al.* (2010) found that for MPAs in Australia, the Philippines and Kenya the indirect effects of protection on coral abundance take longer (up to 13 years) to be detected compared with direct effects on target fish taxa.
MPA Plan Time	Continuous	Time with published MPA management plan (CONANP 2017). Zero for unprotected sites. Plan time taken as longest value for Sian Ka'an MPAs.	Same as MPA Age.
MPA Size	Continuous	MPA marine area (km^2) (CONANP 2017). Zero for unprotected sites. Log-transformed due to right-skewed distribution resulting from the large size of Sian Ka'an (principally Reserva de la Biosfera Sian Ka'an).	Studies suggest that protection efficacy is related to MPA size due to mobile species home ranges and sedentary species larval dispersal distance (Botsford et al. 2001, 2003; Shanks et al. 2003; Gaines et al. 2010). Furthermore, Mora et al. (2006) recognises the importance of MPA size in an index of coral reef MPA conservation status.

Predictor	**Type**	**Description**	**Justification**
MPA Effectiveness	Ordinal	MPA effectiveness evaluated on a 7-point scale using the 2016 Eco-Audit performed by Healthy Reefs Initiative which considers the MPA management plan, personnel/equipment and MPA enforcement (Healthy Reefs Initiative 2016).	Effectiveness of marine reserve protection in terms of enforcement/compliance is expected to have a direct benefit on protected species (Roberts 2000). A global study that evaluated 87 MPAs identified 5 key criteria which determine fish protection success: no take, well enforced, old (>10 years), large (>100 km^2), and isolated (Edgar et al. 2014). Mora et al. (2006) also recognises the importance of poaching (due to ineffective enforcement) in an index of coral reef MPA conservation status.
Wave Exposure	Continuous	Average wind driven wave exposure (J m^{-3}, log scale) extracted from the wave stress map for the Caribbean built by Chollett et al. (2012).	Wave exposure is a key driver of coral reef zonation (Geister 1977; Jackson 1991). Furthermore, wave exposure has been linked with spatial variation in herbivory (Bejarano et al. 2017) and reef-building corals (Chollett & Mumby 2012).
Hurricane Frequency	Continuous	Frequency of occurrence of Category 1-5 hurricanes during the period 1851-2008 from Chollett et al. (2012).	Hurricanes are an integral part of coral reef ecology (Connell 1978) and historically average coral cover is reduced by 17% following a hurricane (Gardner et al. 2005).

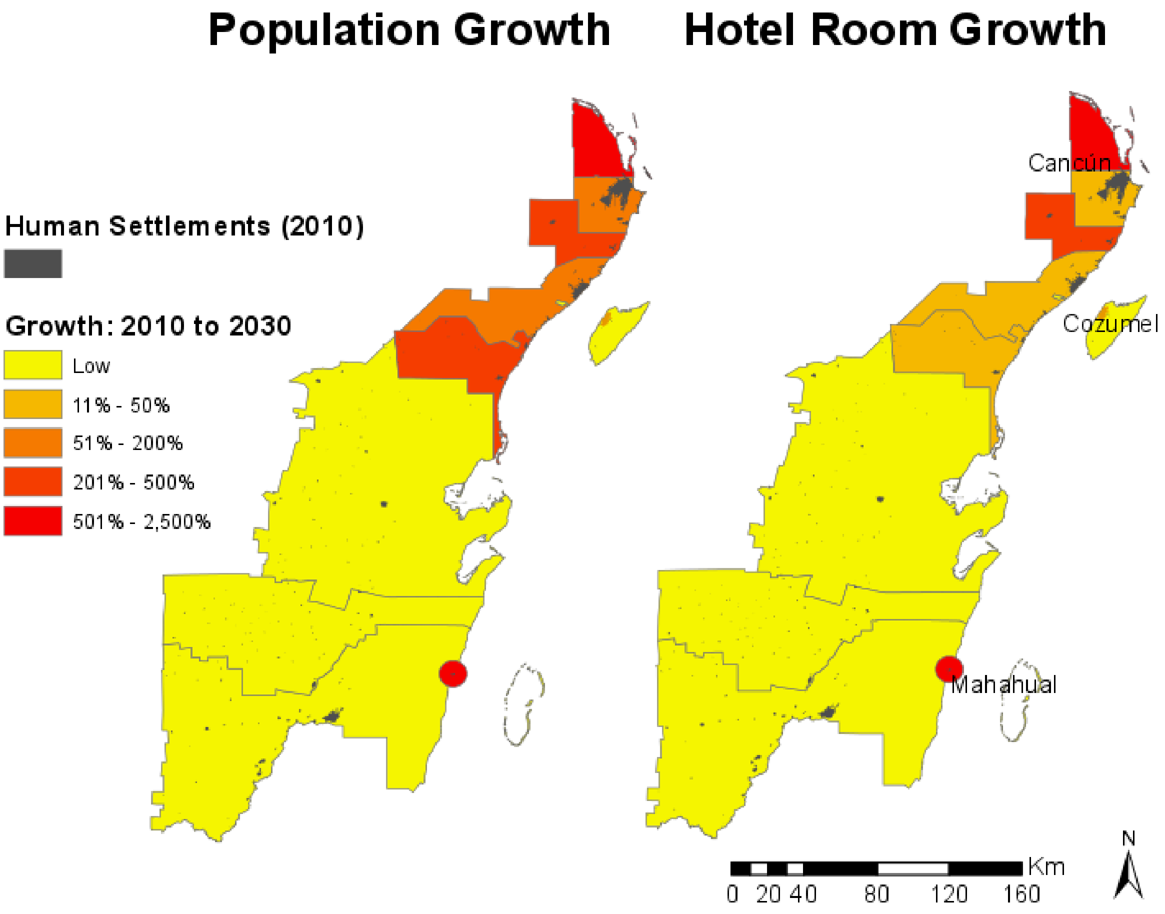

Figure S2.1. Human population and tourism growth forecasts for the Mexican Caribbean. Growth forecasts are shown by municipality. Population and hotel room data for northern states were sourced from Gobierno del Estado de Quintana Roo (2010). Population data for southern municipalities were sourced from central government forecasts (Consejo Nacional de Población 2014). Coastal population and tourism growth in southern municipalities is planned principally for Mahahual (Palafox-Muñoz et al. 2007). To represent coastal growth for southern municipalities, inland growth was not included in the municipality-level data and growth rates are shown separately for Mahahual (Municipio de Othon P. Blanco 2004, 2007). Note that hotel room forecasts for Mahahual are for 2025. For the island of Cozumel growth is expected primarily in the principal settlement to the north-west of the island and consequently growth rates are shown separately for the town and the rest of the island. Delimitations of current human settlements sourced from INEGI (2010).

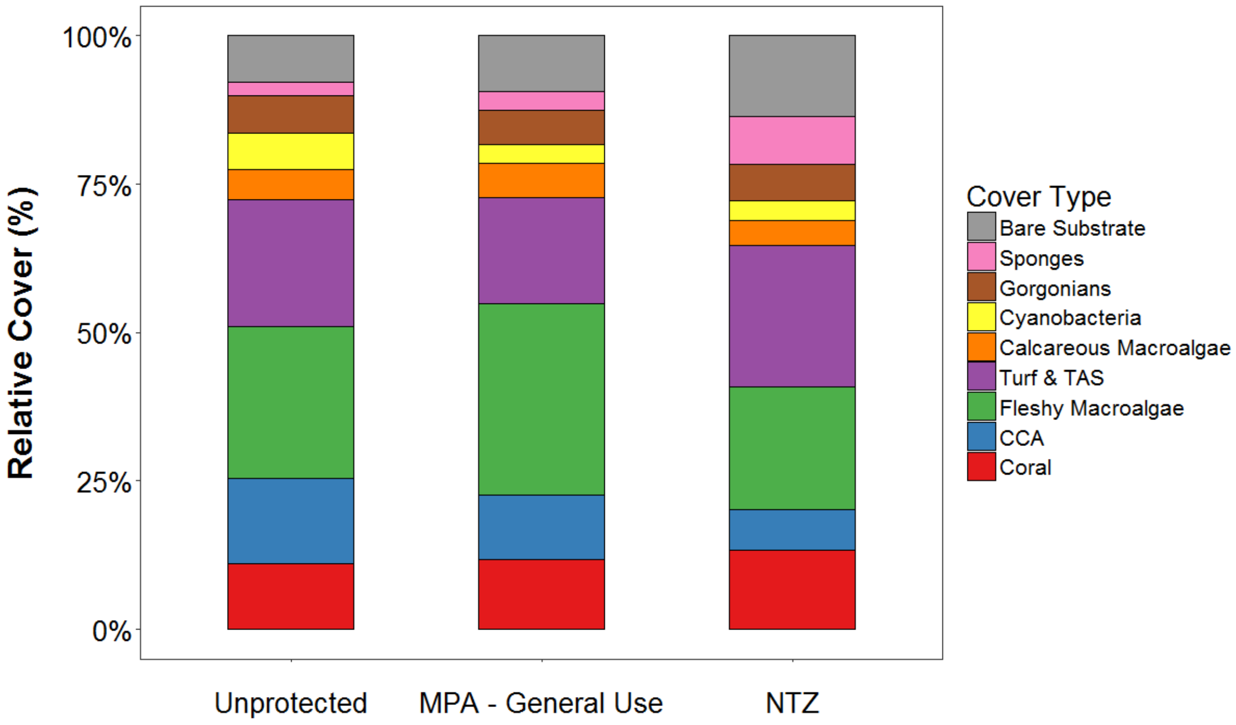

Figure S2.2. Benthic composition by protection status in the Mexican Caribbean. Relative cover of key benthic components by protection status. Sites are split by those located in No Take Zones (NTZ, n= 12), those located elsewhere in Marine Protected Areas (MPA – General Use, n = 21) and unprotected sites (n = 15). CCA is crustose coralline algae and TAS is turf algae sediment mats.

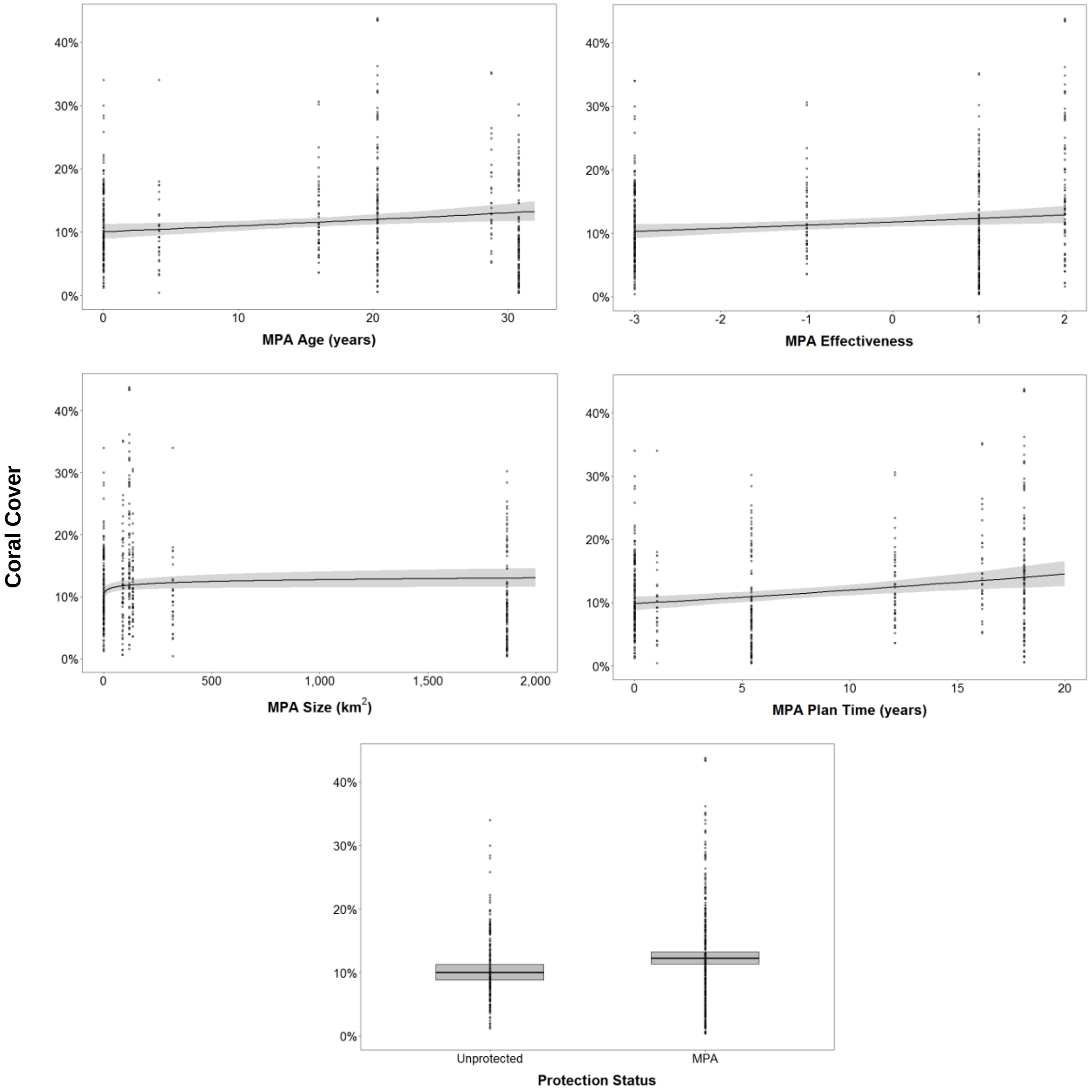

Figure S2.3. Alternative coral cover model MPA predictor variable partial effects. Model-predicted coral cover and actual mean transect coral cover by alternative minimum adequate model MPA predictor variables. Each panel shows the MPA variable in a different model. Actual coral cover shown as points. Model partial effects shown as lines (with 95% confidence intervals) and determined for each predictor variable by holding all other fixed effect predictors at mean value.

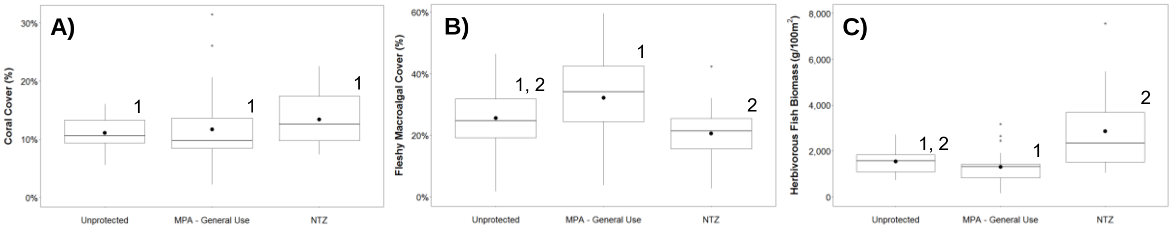

Figure S2.4. Reef condition by protection status in the Mexican Caribbean. Mean coral cover (A), fleshy macroalgal cover (B) and herbivorous fish biomass (C) by protection status. Sites are split by those located in No Take Zones (NTZ, n= 12), those located elsewhere in Marine Protected Areas (MPA – General Use, n = 21) and unprotected sites (n = 15). Plots are standard box plots with the addition of mean values (filled circles). Numbered indices indicate significant differences identified by pairwise post-hoc tests (Tukey HSD or Mann-Whitney U tests).

CAPÍTULO 3: La herbivoria facilita el crecimiento de un coral constructor de arrecifes caribeños importante

Abstract

The decline of reef-building corals in conjunction with shifts to short-lived opportunistic species has prompted concerns that Caribbean reef framework-building capacity has substantially diminished. Restoring herbivore populations may be a potential driver of coral recovery; however, the impact of herbivores on coral calcification has been little studied. We performed an exclusion experiment to evaluate the impact of herbivory on *Orbicella faveolata* coral growth over 14 months. The experiment consisted of three treatments: full exclusion cages; half cage procedural controls; and uncaged control plates, each with small *O. faveolata* colonies. We found that herbivorous fish exclusion had a substantial impact on both macroalgal cover and coral growth. Fleshy macroalgae reached 50% cover within some exclusion cages, but were almost absent from uncaged control plates. Critically, *O. faveolata* calcification rates were suppressed by almost half within exclusion cages, with monthly coral growth negatively related to overgrowth by fleshy macroalgae. These findings highlight the importance of herbivorous fishes for coral growth and the detrimental impact of macroalgal proliferation in the Caribbean. Policy makers and local managers should consider measures to protect herbivorous fishes and reduce macroalgal proliferation to enable coral communities to continue to grow and function.

Keywords: Calcification, coral reefs, coral–macroalgal competition, *Dictyota*, herbivory, *Orbicella*

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Suchley A. & Alvarez-Filip L. 2017. Herbivory facilitates growth of a key reef-building Caribbean coral. Ecology and Evolution 7:11246–11256.

Introduction

On coral reefs, scleractinian corals perform an extensive ecosystem engineering role through the calcification of structurally complex physical structures (Jones et al. 1994; Graham & Nash 2013). Corals provide habitat for diverse fauna including herbivorous fishes, which are key organisms as they control the abundance and community structure of macroalgae which compete with corals (Hughes 1994; Paddack et al. 2009; Jackson et al. 2014). Although the impact of herbivory on algae has been well studied, facilitation of coral growth and calcification is poorly understood (McCook et al. 2001; Burkepile & Hay 2006; Fong & Paul 2011). Explaining the role of herbivores in facilitating coral ecosystem engineering is of fundamental ecological interest and can inform reef conservation strategies seeking to maintain ecosystem function.

In recent decades coral reefs have experienced major declines in live coral cover resulting from climate change, coral diseases, herbivore decline and coastal development (Aronson & Precht 2001; Hoegh-Guldberg et al. 2007; Mora 2008; Jackson et al. 2014). Furthermore, Caribbean reefs have undergone shifts in coral community composition to dominance by short-lived and slower growing species that contribute less to community calcification (Bruckner & Bruckner 2006; Edmunds & Elahi 2007; Alvarez-Filip et al. 2013). Coral declines are often accompanied by rapid increases in macroalgae that impair the capacity of coral communities to recover (Hughes et al. 1987; Done 1992; Birrell et al. 2008). Such phase shifts have been particularly evident in the Caribbean where herbivory has been substantially reduced from historical baselines (Jackson et al. 2001; Paddack et al. 2009). A previously key Caribbean herbivore, the sea urchin *Diadema antillarum*, experienced a mass mortality event in 1983/4, and has recovered at few sites across the region (Jackson et al. 2001; Idjadi et al. 2010; Lessios 2016). Parrotfishes, surgeonfishes and sea urchins are considered the dominant herbivores on today's Caribbean reefs (Hughes et al. 2010; Sangil & Guzman 2016; Kuempel & Altieri 2017); however, overfishing has considerably diminished reef fish populations (Jackson et al. 2001; Paddack et al. 2009).

Diminished grazing capacity on Caribbean reefs has prompted extensive evaluation of the role of herbivores in algal control by both observational and experimental studies. Observational studies cover a broad range of spatial and temporal scales and provide evidence for (Newman et al. 2006; Jackson et al. 2014) and against (Russ et al. 2015b; Cox et al. 2017) the ability of grazers to control benthic algae. Herbivore exclusion has become a standard technique to experimentally assess the ability of both fishes and invertebrates to graze algae, and has been adopted by many studies. These small-scale experimental studies generally involve the exclusion of herbivores via caging of experimental plots or artificial substrate units over time periods ranging from days to years. In contrast to observational studies, experimental studies consistently tend to report a significant effect of herbivores on turf and macroalgal proliferation, with other factors such as nutrient levels and seasonality playing secondary roles (Burkepile & Hay 2006, 2009; Sotka & Hay 2009; Ferrari et al. 2012).

Phase shifts from coral to algal dominance experienced by many Caribbean reefs have underlined the importance of the interaction between algae and scleractinian corals (Hughes 1989; Done 1992; Arias-González et al. 2017). However, despite the importance of the herbivore-algal-coral interaction, experimental evidence of the impact of herbivory on coral calcification is limited. In the Caribbean, *Acropora* spp. were major reef framework builders historically, but subsequent to a wide-spread epizootic event in the 1970/80s populations remain severely diminished (Gladfelter 1982; Aronson & Precht 2001; Alvarez-Filip et al. 2011a). Following the loss of *Acropora*, species of the genus *Orbicella* are the major framework builders on many of today's Caribbean reefs (McClanahan & Muthiga 1998; Perry et al. 2012; Porto-Hannes et al. 2015). Although the effect of herbivory on *Orbicella* spp. has been considered (Lirman 2001; Foster et al. 2008; Vermeij et al. 2010), the impact of herbivory on coral calcification has seldom been assessed (Vu et al. 2009). To address this knowledge gap, we performed a 14-month herbivore-exclusion experiment to determine the effect of fish herbivory on *Orbicella faveolata* calcification. Our hypothesis is that herbivorous fishes restrict algal growth and that algal interaction has a negative impact on coral growth and calcification.

Materials and Methods

This study was conducted over a 14-month period from August 2015 to October 2016 in the 'La Bocana' back reef located in the Parque Nacional Arrecife de Puerto Morelos, Mexico (20° 52' 26" N, 86° 51' 5" W). We reviewed national park monitoring data from the previous three years and preliminary surveys were performed at three sites within the park to evaluate the abundance of sea urchins and the biomass of fishes of the Scaridae and Acanthuridae families. Sea urchins were not observed at any site. Consequently, 'La Bocana' back reef patch was selected as it displayed among the highest herbivorous fish biomass (average of 3,600 g/100 m^2 from national park monitoring and preliminary survey data). La Bocana reef patch is at a depth of 4 m and is characterised by large *Orbicella faveolata* colonies, *Agaricia* spp., dead *Acropora palmata* framework, gorgonians, and an algal community dominated by brown macroalgae, turf algae, green calcareous *Halimeda* spp. and red calcareous *Amphiroa* spp. Preliminary surveys and national park monitoring revealed reef patch coral cover of approximately 17% and fleshy macroalgal cover of 17%.

To test the effect of fish herbivory on coral growth, fishes were excluded from experimental units containing small *O. faveolata* colonies. Half-ellipsoid *O. faveolata* colonies (approximately 5 cm maximum diameter) were collected prior to 2011 from the same site by removing fragments from large colonies, and were left in the reef lagoon for later use. The experimental design constituted three treatments with replicate numbers limited by coral colony availability: (1) full cages excluded herbivorous fishes (n = 6); (2) half cages with caging at sides but no top panel acted as procedural controls testing for caging effects by allowing fish access (n = 6); (3) plates with no caging acted as full controls (n = 6). Cages were built upon 36 cm-square concrete plates, with 30-cm vertical steel reinforcing bars and thin 3 cm x 2 cm polyethylene mesh (Supplemental Information, Fig. S3.1). Concrete is commonly used as an artificial substrate in herbivore exclusion experiments (Burkepile & Hay 2009, 2010; Rasher et al. 2012). In late August 2015 coral colonies were retrieved and wet-weighed in the laboratory. Cages and plates were randomly located in the reef patch over an area of approximately 400 m^2, with a minimum separation of 2 m, and coral colonies were affixed to plate centres using underwater epoxy plasticine (Supplemental Information, Fig. S3.1). At the end of the observation period, coral colonies were removed from plates and re-weighed in order to determine net calcification rates (in g cm^{-2} y^{-1}, based on average colony area over the observation period). Underwater Hobo data loggers tracked *in situ* water temperature at cage depth during the experiment, and the impact of caging on light levels was evaluated using three underwater Hobo data loggers in a cage, a half cage and on a control plate during a sunny day at the end of June 2016. Light levels were converted from Lux to µmol quanta m^{-2} s^{-1} by applying a conversion factor of 54 (Sager & McFarlane 1997). Light levels were compared between treatments using a Friedman test for repeated measures due to non-normality.

Cages were monitored at the beginning of every month for 14 months and the mesh cleaned of algae and other fouling organisms with brushes every 1 to 2 weeks during this period. Every month top-down photographs of the plates were taken in order to assess algal cover. The software photoQuad v1.4 was used to determine percentage cover by area of a 30-cm quadrat contained within cages and on control plates by tracing algal mini-patch perimeters (Trygonis & Sini 2012). Plate cover components were classified as short (< 0.5 cm) or long (≥ 0.5 cm) filamentous turf algae; brown, green or red fleshy macroalgae (to species or genus level); crustose coralline algae (CCA); calcareous algae; cyanobacteria; or gorgonian.

To identify which herbivorous fishes were browsing plate algae, *in situ* feeding was recorded by static GoPro video cameras. Observations were performed over 1-hour intervals for a total of three hours for full cages, three hours for half cages, and eight hours for uncaged control plates, between May and August 2016 between 11 am and 4 pm. For each 1-hour interval, feeding fish bite counts were recorded by species, total length (size categories estimated based on plate size), and bite target. Individual bites were defined as those involving a rapid movement of the head toward and away from the plate (Bellwood & Fulton 2008). Fish biomass was determined using standard allometric length-weight conversions. Bite counts were subsequently converted to estimates of herbivory pressure by standardising (multiplying) by herbivore biomass following Bellwood et al. (2006). Herbivory pressure was compared between treatments based on the first three hours of concurrent observation to standardise for temporal variation in fish activity. Herbivore identity evaluation was performed for control plates only (based on 8 hours of observation) due to low levels of consumption within exclusion cages.

Every month close-up photographs of coral colonies (with a ruler for scale) were taken in order to evaluate coral planar area (substrate area occupied by colonies), perform polyp counts using the software ImageJ, and count occurrences of algal overgrowth (Rasband 2014). Photos were taken with consistent orientation to minimize variation in coral area and polyp counts due to camera angle. Corals were overgrown *Dictyota* spp. and/or turf algae/sediment mix (also known as the ‘epilithic algal matrix’). Each month overgrowth was assessed and corals classified as overgrown if any partial overgrowth was evident. As colony perimeters were obscured by algal overgrowth it was not possible to quantify interactions by coral area affected. Incidence of disease, coral bleaching, mortality and algal overgrowth were recorded.

Mixed effect models were fitted to evaluate the influence of experimental treatment and water temperature on monthly total, fleshy macroalgal and turf algal cover, with month and replicate included as random effects. Algal cover was evaluated at the beginning of each month and consequently the mean water temperature for the prior month was utilised. The algal cover time series were truncated to begin in December 2015 to account for initial algal growth after cage installation (Fig. 1). Linear model assumptions were assessed using residual diagnostic plots. All algal percent cover variables were arcsin-sqrt transformed due to non-normality of residuals. Interaction terms between treatment and temperature were tested and subsequently removed if found not to be significant. ANOVAs were applied to the fitted models to determine variable-level significance and Tukey post-hoc testing was performed to compare effects between treatments.

Comparison of coral calcification between treatments was performed using Welch's t-tests or non-parametric Mann-Whitney U tests, based on an assessment of normality using Shapiro-Wilk tests. Initial coral colony planar area, polyp count and mass were compared between treatments using ANOVAs, with assumptions checked using residual diagnostic plots. To determine the drivers of coral growth over time, coral polyp count was preferred to coral planar area as it was observed to be a more consistent measure of individual colony growth. Mixed effect models were fitted to evaluate the drivers of month-on-month coral polyp count change. Experimental treatment, water temperature, plate fleshy macroalgal and turf algal cover, fleshy macroalgal and turf algal overgrowth of coral colonies were included as fixed effects, with month and replicate included as random effects. One-month lagged versions of algal cover and overgrowth were also included as candidate predictor variables. The time series was truncated to begin in November 2015 as October 2015 was used as the baseline for polyp counts. Linear model assumptions were assessed using residual diagnostic plots. Multicollinearity among predictor variables was tested using variance inflation factors (VIFs), but no evidence of multicollinearity was observed (Graham 2003). Least significant predictors were sequentially removed backwards and models compared pairwise with partial F-tests of significant differences in error sum-of-squares. The more parsimonious model was preferred until the partial F-test revealed a significant difference and the prior model retained as the minimum adequate model. All statistical analyses were performed using R version 3.3.2 (R Core Team 2016) using packages including *lme4* and *nlme* for mixed effect modelling, *car* for VIF assessment, *multcomp* for Tukey post-hoc testing and *r2glmm* for mixed effect model partial R-squared.

Results

Effect of herbivore exclusion on macroalgal cover

Experimental units were installed in late August 2015 and were subsequently rapidly colonized by turf algae and macroalgae (Fig. 1). Averaging across all monthly observation periods and plates, mean plate turf algal cover was 5.7%; fleshy macroalgae, 4.1%; cyanobacteria, 1.0%; CCA, 0.1%; and calcareous algae, 0.01%. Cyanobacteria were subject to short-term blooms such as in July 2016 which resulted in sudden increases in cover to over 20% in some cages. Fleshy macroalgal cover was dominated by *Dictyota* spp. (82% mean cover relative to total fleshy macroalgae) and showed substantial variation over time reaching above 50% total cover within some cages (Fig. 1B), while turf algal cover appeared more stable over time (Fig. 1C).

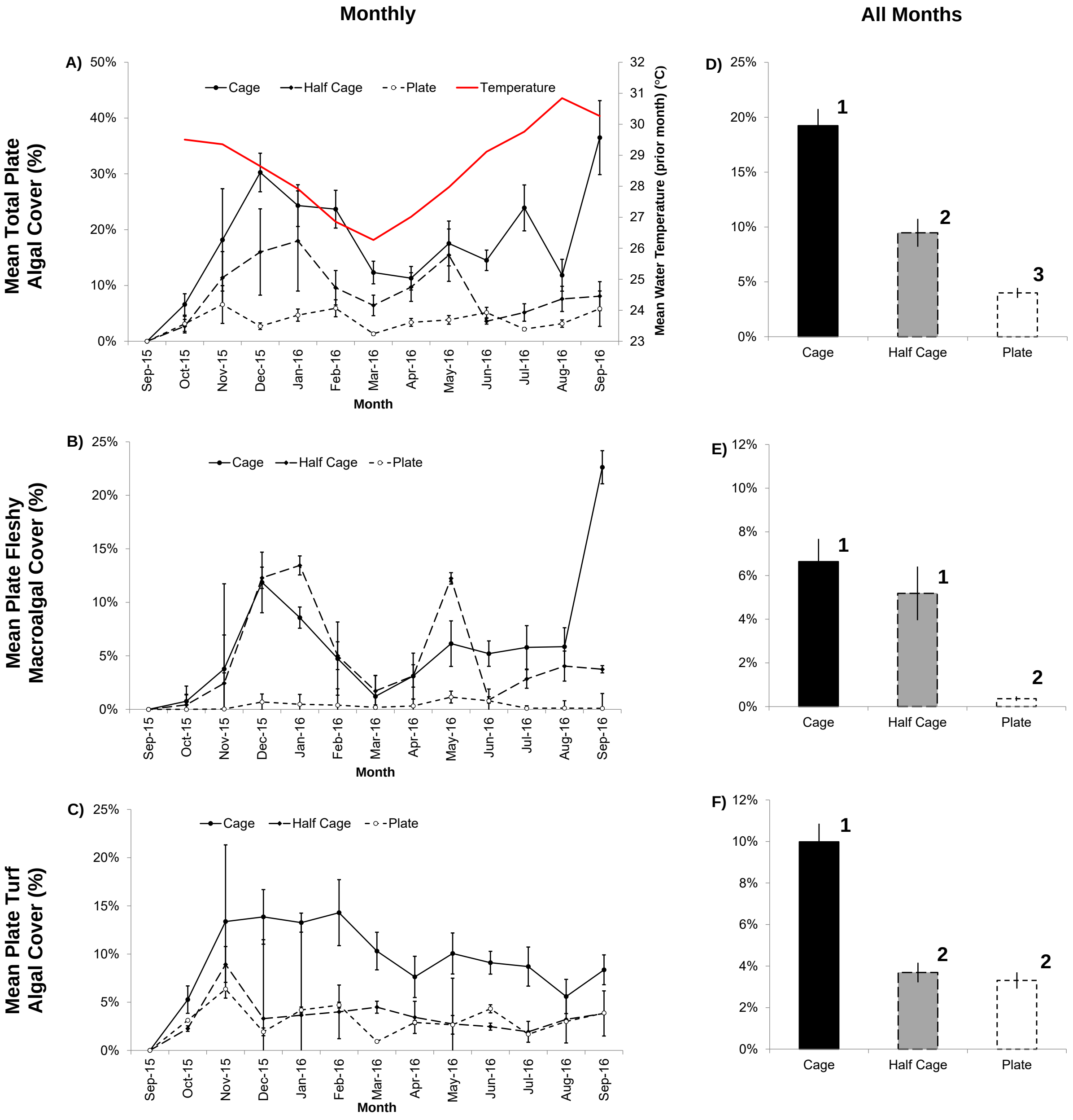

Figure 1. Total algal, fleshy macroalgal and turf algal plate mean cover and temporal trends. (A-C) Mean (± s.e.m.) monthly total plate algal cover (A), fleshy macroalgal cover (B), and turf algal cover (C) for full exclusion cages (n = 6), half cage controls (n = 6) and uncaged control plates (n = 6). Algal cover monitoring was performed at the beginning of each month. Mean water temperature for the prior month measured by Hobo data loggers is also shown. (D-F) Mean (± s.e.m.) total plate algal cover (D), fleshy macroalgal cover (E), and turf algal cover (F) over the observation period for full cages (n = 6), half cages (n = 6) and uncaged control plates (n = 6). Numbers represent significant differences indicated by mixed

model Tukey post-hoc testing (Table 2). Note the difference in scale between panels A and D and other panels.

Total algal cover, fleshy macroalgal cover and turf algal cover varied significantly by experimental treatment (Fig. 1; Table 1). Algal cover was consistently significantly higher in full exclusion cages than on uncaged control plates (Fig. 1D, E, F; Table 2). On average, macroalgal cover was 1731% relatively higher and turf algal cover was 202% higher in full exclusion cages than on uncaged control plates (Fig. 1E, F). While there was no significant difference in fleshy macroalgal cover between full and half cages (Fig. 1E; Table 2), turf algal cover was significantly (171%) higher in full cages than half cages (Fig. 1F; Table 2). Mean short (< 0.5 cm) and long (≥ 0.5 cm) algal turf cover displayed similar relative levels between treatments (Supplemental Information, Fig. S3.2). The interaction of water temperature and cage type had a significant effect on fleshy macroalgal cover (Fig. 1B; Table 1).

Table 1. Monthly algal cover mixed modelling. Plate monthly total algal cover, fleshy macroalgal cover and turf algal cover between December 2015 and September 2016 were modelled as a function of treatment (cage type) and water temperature (mean temperature for the prior month), with month and replicate as random effects. Table shows ANOVA model summaries. The time series were truncated to December 2015 to account for initial algal growth after cage installation (Fig. 1). Interaction terms were removed from the models if non-significant for all variable categories. Asterisks denote level of significance (* denotes $P < 0.05$ and ** denotes $P < 0.01$).

Dependent Variable	Predictor	F-value	df	P
Total Algal Cover	(Intercept)	342.59	1	<0.001**
	Cage Type	22.11	2	<0.001**
	Temperature	0.37	1	0.545
Fleshy Macroalgal Cover	(Intercept)	48.07	1	<0.001**
	Cage Type	7.36	2	0.006**
	Temperature	2.60	1	0.109
	Cage Type × Temperature	6.06	2	0.003**
Turf Algal Cover	(Intercept)	944.28	1	<0.001**
	Cage Type	47.65	2	<0.001**
	Temperature	2.67	1	0.104
	Cage Type × Temperature	2.64	2	0.075

Table 2. Effect of experimental treatment on monthly algal cover. Plate monthly total algal cover, fleshy macroalgal cover and turf algal cover compared between experimental treatments by applying Tukey post-hoc tests to fitted mixed models (Table 1). Experimental treatments are full exclusion cages (n = 6), half cage controls (n = 6) and uncaged control plates (n = 6). Asterisks denote level of significance (* denotes $P < 0.05$ and ** denotes $P < 0.01$).

Dependent Variable	Comparison	P
Total Algal Cover	Cage vs Control Plate	<0.001**
	Cage vs Half Cage	<0.001**
	Half Cage vs Control Plate	0.023*
Fleshy Macroalgal Cover	Cage vs Control Plate	<0.001**
	Cage vs Half Cage	0.479
	Half Cage vs Control Plate	0.026*
Turf Algal Cover	Cage vs Control Plate	<0.001**
	Cage vs Half Cage	<0.001**
	Half Cage vs Control Plate	0.831

Herbivorous fish identity

In situ herbivore feeding observations revealed grazing on plates by herbivorous fishes. Uncaged control plates experienced an average of 87 bites / hour, and both full and half cages were subject to 63 bites / hour, with the majority (87%) directed at turf algae. Fishes up to 10 cm total length (TL) were observed to enter full cages through the 3 cm x 2 cm mesh. *Acanthurus* spp. larger than 10 cm TL entered half cages from above, although these did not feed on half cage plate algae. Consequently, less herbivory pressure was observed within full and half cages (64 and 520 bites g hr^{-1} $plate^{-1}$ respectively) compared with control plates (6,874 bites g hr^{-1} $plate^{-1}$; Supplemental Information, Fig. S3.3). The majority (62.4%) of turf algal consumption on control plates was performed by *Acanthurus bahianus* surgeonfish, with juvenile *Scarus iseri* parrotfish (25.5%), *A. coeruleus* surgeonfish (9.1%) and juvenile *Sparisoma aurofrenatum* parrotfish (2.9%) carrying out lesser roles. Control plates displayed very low fleshy macroalgal cover and so an equivalent analysis for macroalgae consumers, in addition to feeding electivity estimation (sensu Adam, Kelley, et al. 2015), was not possible.

Effect of herbivore exclusion on coral growth and calcification

Initial *Orbicella faveolata* colony planar area, polyp count and mass were not significantly different between treatments (ANOVA, coral area, $F_{2,14} = 0.44$, $P = 0.65$; polyp count, $F_{2,14} = 0.95$, $P = 0.41$; mass, $F_{2,14} = 1.05$, $P = 0.38$; Supplemental Information, Fig. S3.4). At the end of the observation period, coral calcification was significantly (43%) lower for colonies enclosed by full and half cages than those located on uncaged control plates subject to herbivory (Welch's t-test, control plate vs full cage, $t = 2.68$, d.f. = 8.1, $P = 0.03$; control plate vs half cage, $t = 2.34$, d.f. = 7.4, $P = 0.05$; Fig. 2D). Calcification was not significantly different between colonies located in full cages and those in half cages (Welch's t-test, $t = 0.03$, d.f. = 9.8, $P = 0.98$; Fig. 2D).

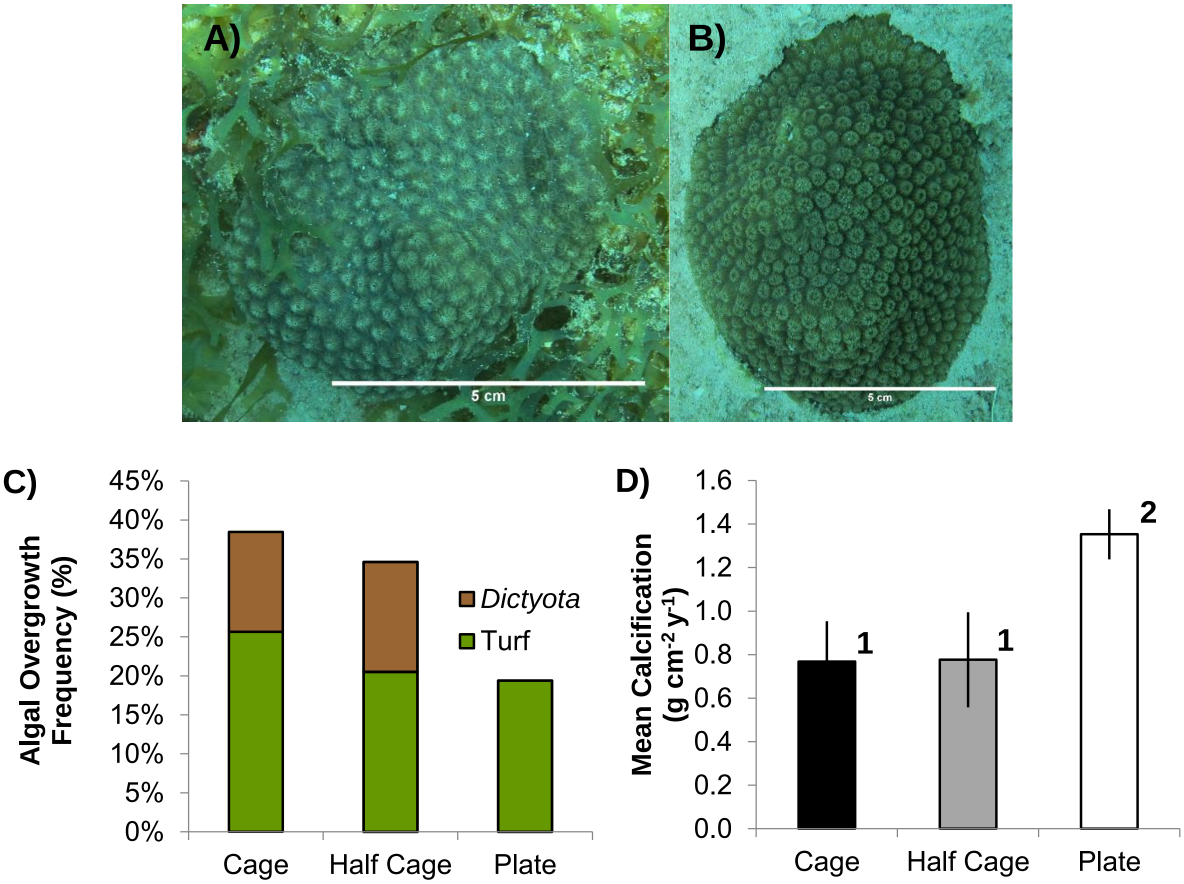

Figure 2. Coral-algal interactions and *Orbicella faveolata* colony calcification rates. (A) *O. faveolata* colony within a herbivore exclusion cage overgrown by the fleshy macroalgae *Dictyota* spp. (B) *O. faveolata* colony on an uncaged control plate partially covered by the surrounding turf algae / sediment mix along colony perimeter. (C) Percentage of monthly coral observations recording partial algal overgrowth. Algal overgrowth is classified as partial overgrowth by *Dictyota* or turf algae/sediment mix. (D) Mean (± s.e.m.) net calcification rates calculated as annualised change in colony mass by average colony planar area over the study period from August 2015 to October 2016 for full exclusion cages (n = 6), half cage controls (n = 6) and uncaged control plates (n = 5, as one colony was lost after two months). Numbers represent significant differences in calcification indicated by Welch's t-tests.

Interactions between *Orbicella faveolata* colonies and surrounding algae were commonly observed (Fig. 2). Within cages, coral colonies were often partially overgrown by *Dictyota* spp. and/or the surrounding turf algae/sediment mix (Fig. 2A, C). *Dictyota* spp. were the only fleshy macroalgae observed overgrowing corals. All instances of overgrowth by *Dictyota* also involved turf algae/sediment mix to some extent. For uncaged control plates, overgrowth by *Dictyota* was not observed, and only coral colony perimeters were partially covered by the surrounding turf algae/sediment mix (Fig. 2B, C). Coral polyp counts and planar area were assessed on a monthly basis and show generally linear increases over time (Fig. 3). Cage type and overgrowth by *Dictyota* had a significant effect on monthly polyp count change while other candidate predictor variables (water temperature, plate fleshy macroalgal and turf algal cover, turf algal overgrowth, and one-month lagged versions of algal cover and overgrowth) were not significant and were removed from the model (Table 3). The interaction of cage type and *Dictyota* overgrowth was tested and found not to be significant. Further interaction term testing was limited by model degrees of freedom.

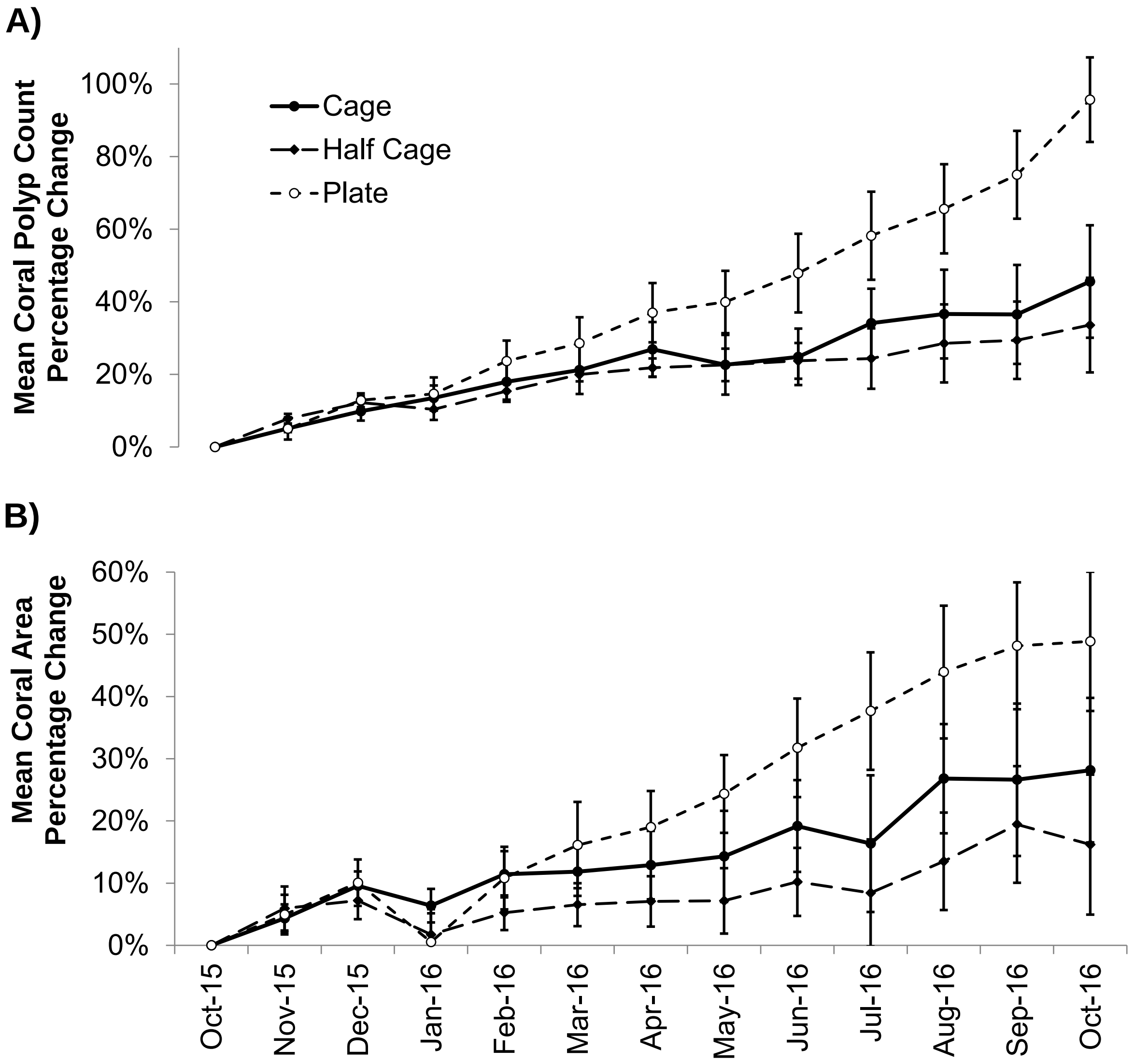

Figure 3. *Orbicella faveolata* colony growth temporal trend. (A) Mean (± s.e.m.) coral polyp count percentage change over the study period. (B) Mean (± s.e.m.) coral planar area percentage change over the study period. Colony growth was determined at the beginning of each month for full exclusion cages (n = 6), half cage controls (n = 6) and uncaged control plates (n = 5, as one colony was lost after two months).

Table 3. Coral colony polyp count change mixed model coefficient estimates. Month-on-month coral colony polyp count change between October 2015 and September 2016 was modelled as a function of treatment (cage type), temperature, plate fleshy macroalgal and turf algal cover, fleshy macroalgal (*Dictyota* spp.) and turf algal overgrowth of coral colonies, with month and replicate as random effects. Uncaged control plates were selected as the base level for the cage type variable. Non-significant predictor variables were removed from the model. The time series was truncated to use October 2015 as a baseline for polyp counts. Asterisks denote level of significance (* denotes P < 0.05 and ** denotes P < 0.01).

Predictor	**Estimate**	**P**	**Partial R-Squared**
Intercept	16.309	<0.001**	
Cage Type: Half Cage	-8.614	0.030*	0.093
Cage Type: Full Cage	-7.852	0.045*	0.077
Dictyota Overgrowth	-9.957	0.007**	0.062

Over the study period no coral mortality (except for colony perimeter tissue loss) occurred and few disease symptoms were observed. Coral bleaching in late summer 2016 was limited to two polyps on one *Orbicella faveolata* colony. Caging was observed to have an effect on light intensity (Friedman test, chi-squared = 722, d.f. = 2, P < 0.001). On a sunny day at the end of June 2016 mean daylight incident at uncaged control plates (408.6 µmol quanta m^{-2} s^{-1}) was slightly (4.7%) higher than within half cage procedural controls (390.3 µmol quanta m^{-2} s^{-1}), which in turn was (10.9%) greater than within full exclusion cages (352.0 µmol quanta m^{-2} s^{-1}).

Discussion

The substantial impact of reduced fish herbivory on algal cover mediates growth rates of the important reef-building coral, *Orbicella faveolata*. Over our 14-month study, macroalgal and turf algal cover were greater within herbivore exclusion cages than on uncaged control plates (Fig. 1; Table 2). *In situ* observations revealed negligible herbivory pressure within exclusion cages (Supplemental Information, Fig. S3.3). Fleshy macroalgae were almost always absent from uncaged control plates while cover reached over 50% within some herbivore exclusion cages. Coral-algal interactions were common within cages and caged coral colonies experienced significantly lower growth than those on control plates (Fig. 2; Fig. 3; Table 3). Net annual calcification rates on uncaged control plates were comparable with benchmark values, while in both full and half cages calcification was reduced by over 40% (Fig. 2; Perry et al. 2012).

Our findings suggest that herbivorous fishes are critical to the maintenance of coral calcification rates. *Orbicella* spp. are major framework builders on Caribbean reefs and *O. faveolata* exhibit relatively high mean calcification rates of 1.17 g cm^{-2} y^{-1} (Perry et al. 2012). Variation in *Orbicella* calcification rates has previously been associated with variability in environmental factors such as temperature and thermal stress, nutrient levels, aragonite saturation state, and light availability (Carricart-Ganivet & Merino 2001; Carricart-Ganivet et al. 2012; Dunn et al. 2012; Manzello et al. 2015). For uncaged colonies we observed *O. faveolata* calcification rates (mean 1.35 ± 0.11 g cm^{-2} y^{-1}) similar to the Caribbean average, while in both full and half cages these were reduced by 43% to 0.77 ± 0.19 g cm^{-2} y^{-1} (Fig. 2D). These findings imply that coral calcification is strongly mediated by macroalgal overgrowth (Fig. 2) compared with other factors. For example, Carricart-Ganivet et al. (2012) predict that sea surface temperature increase will not have a similar impact on *Orbicella* spp. calcification rates until the year 2100. Recently, Cramer et al. (2017) reported a positive causal effect of parrotfishes on reef accretion at millennial timescales. Linking our findings with processes occurring at geological scales, and investigating the interaction of herbivore loss with global climate change and other anthropogenic stressors should be a priority in order to conserve community calcification in the mid and long term (Kuffner & Toth 2016).

Ecosystem processes are often scale-dependent (Levin 1992; Hewitt et al. 2010). External drivers and internal feedbacks affecting coral-algal dynamics in reef systems vary over both temporal and spatial scales (Adam et al. 2015a). Our finding that fish herbivory has a significant impact on algal proliferation is consistent with previous small-scale exclusion experiments (Fig. 1; Burkepile & Hay 2006), but contrasts with large-scale correlational studies that show no evidence of herbivore control of algae on Caribbean reefs (Russ et al. 2015b; Suchley et al. 2016; Cox et al. 2017). On small spatial and temporal scales herbivorous fishes may control algal growth while at larger and longer scales nutrient input, herbivore depletion below critical thresholds and other ecological processes may promote algal proliferation (Mumby et al. 2007; Paddack et al. 2009).

In this study, *in situ* herbivore feeding observations suggest that turf grazing was primarily performed by the surgeonfish *Acanthurus bahianus* and juvenile *Scarus iseri* parrotfishes. *Acanthurus* spp. have a mixed diet (Burkepile & Hay 2011; Adam et al. 2015a) and may also have been responsible for (unobservable) macroalgal propagule removal from uncaged control plates; however, longer observation periods would be required to detect this effect. *Scarus* parrotfishes are primarily turf grazers (Burkepile & Hay 2010; Adam et al. 2015b) and small-bodied *S. iseri* have been shown to exert substantial grazing pressure on certain Caribbean reefs (Kuempel & Altieri 2017). Herbivore exclusion encouraged growth of *Dictyota* spp., brown fleshy macroalgae common to Caribbean reefs (Quan-Young et al. 2004; Littler et al. 2006; Renken et al. 2010). *Dictyota* spp. domination may result from their ability to grow and colonize substrata faster than many other benthic components as their branching form facilitates overgrowth and fragmentation enables rapid dispersal (Beach et al. 2003; Herren et al. 2006; Ferrari et al. 2012). These results agree with previous studies that suggest a mix of herbivorous fishes are required in order to both prevent algal colonisation, graze turf algae and crop existing macroalgal stands (Burkepile & Hay 2008; Rasher et al. 2013). This has important implications for coral communities as turf grazing liberates substrate space for coral recruits and cropping of macroalgal stands reduces competition with adult coral colonies enhancing coral fecundity, growth and survival (McCook et al. 2001; Kuffner et al. 2006; Box & Mumby 2007).

Increased macroalgal (specifically *Dictyota*) overgrowth in herbivore exclusion cages suppressed *Orbicella faveolata* growth rates (Fig. 2; Fig.3; Table 3). However, it is unclear which competitive mechanism - smothering, shading, abrasion, allelopathic or enhanced microbial activity - is responsible for diminished coral growth and tissue mortality (McCook et al. 2001; Chadwick & Morrow 2011). Recent studies suggest that abrasion may have a limited impact as a mechanism for coral-algal interaction (Diaz-Pulido et al. 2010; Rasher & Hay 2010). We observed that coral growth was unrelated to overall plate algal cover and consequently direct contact may be necessary for other coral-algal interaction mechanisms such as allelopathy, microbial transmission and local hypoxia to take effect (Nugues et al. 2004; Rasher & Hay 2010; Barott et al. 2012; Wolf et al. 2012). The negative effects of turf algal overgrowth were negligible in this study potentially due to the low severity of interactions or the inconsistent nature of hypoxia generated at the coral-algal interface (Wangpraseurt et al. 2012).

While some herbivore exclusion studies have found evidence of coral growth suppression, other studies report no impact of reduced herbivory levels on coral growth. This is likely a result of the specific nature of the interaction between corals and macroalgae that proliferate as a result of reduced herbivory (McCook et al. 2001). Coral-algal interaction outcomes depend upon coral growth form (branching, massive, encrusting, digitate), condition and life stage; algal morpho-functional group (foliose, filamentous, calcareous, crustose); species identity; and environmental factors such as nutrient and light levels (McCook et al. 2001; Fong & Paul 2011). For example, canopy-forming algae (e.g. *Sargassum* spp.), foliose macroalgae (e.g. *Dictyota* spp. or *Lobophora* spp.) or filamentous turf algae, generate distinct physical coral interactions due to their varying morphologies (River & Edmunds 2001; Box & Mumby 2007; Titlyanov et al. 2007). Exclusion studies typically employ small, short-lived, ‘weedy’ species such as Caribbean *Porites* spp. (Miller & Hay 1998; McClanahan et al. 2003; Sotka & Hay 2009; Burkepile & Hay 2010) which may be more susceptible to algal overgrowth and contribute little to reef framework (Tanner 1995; Alvarez-Filip et al. 2013). In one of the few studies of important reef-building corals, Lirman (2001) explored the impact of herbivore exclusion on large (> 1 m diameter) *O. faveolata* colony perimeters. In the absence of herbivores, Lirman (2001) observed increases in filamentous algae, corticated red macroalgae and *Dictyota* along coral perimeters; resulting in greater live tissue margin retreat and mortality rates. For *O. faveolata* fragments, our findings contrast Vu et al. (2009) who report no significant impact of macroalgae on coral growth. However, this may be because calcification rates were determined after only 21 days in that study.

Herbivore exclusion has become a standard technique to experimentally assess herbivores' ability to graze reef algae. However, by definition such studies involve manipulation and consequently are susceptible to confounding factors (McCook et al. 2001). Accordingly, these studies often include procedural controls in an attempt to control for experimental manipulation. In this study, we adopted the common procedural control of half exclusion cages to allow fish access from above, but retain the manipulation and barrier and shading effects of side panels. However, we observed that half cage procedural controls allowed an intermediate level of herbivory (Fig. 1D), similarly to other studies (Diaz-Pulido & McCook 2003; Ferrari et al. 2012; Castro-Sanguino et al. 2016). The effectiveness of the procedural control varied with algal type. Turf algal cover was significantly higher in full cages than half cages (Fig. 1F) whereas *Dictyota* macroalgae grew in both full exclusion cages and half cage procedural controls (Fig. 1E). Supported by *in situ* observations, it is likely that larger macroalgae-browsing *Sparisoma* parrotfishes were either unable or unwilling to enter half cages (Diaz-Pulido & McCook 2003). Consequently, similar levels of macroalgal-coral overgrowth and coral growth rates were observed in full and half cages (Fig. 2C; Fig. 2D; Table 3), suggesting that half cages may have limited efficacy as procedural controls. Two further options for procedural controls were cages with top panels only to test the effect of side panels and plates with steel reinforcing bars only to test for any effect of the bars themselves; however, insufficient coral colonies were available for these.

Few studies have evaluated the effect of caging on the enclosed environment. Water movement has been assessed using different techniques and found not to be significantly affected within exclusion cages (Lewis 1986; Vermeij et al. 2010; Castro-Sanguino et al. 2016). Studies report differing effects of caging on incident light levels, potentially due to cage construction, ambient light levels, other environmental conditions or measurement procedure (Vermeij et al. 2010; Ferrari et al. 2012; Castro-Sanguino et al. 2016). In this study, we used Hobo data loggers to observe that mean light intensity incident at uncaged control plates on a particular day was slightly (4.7%) higher than within half cages, which in turn was (10.9%) greater than within full cages. However, coral calcification rates are relatively insensitive to such minor reductions in light intensity and consequently cage effects could only account for a small fraction of the differences in calcification between herbivore treatments (Venti et al. 2014).

Nutrient enrichment of coastal waters and overfishing have promoted macroalgal proliferation on Caribbean reefs (Lapointe et al. 2005, 2010; Jackson et al. 2014). Macroalgae compete with corals, reducing fitness and suppressing growth (McCook et al. 2001; Chadwick & Morrow 2011; Fong & Paul 2011). In this study we have shown that fish herbivory combats macroalgal growth and facilitates *Orbicella* coral calcification, a major contributor to Caribbean reef framework. However, in recent decades, Caribbean reefs have lost both overall coral cover and suffered shifts to more short-lived coral species which contribute less to reef framework. Consequently, herbivorous fishes and macroalgal control are increasingly important for today's

Caribbean reefs. Policy makers and local managers should consider measures to protect herbivorous fishes and reduce macroalgal proliferation in order for reefs to continue to grow, function and survive anthropogenic sea-level rise. Fisheries management strategies including quotas, size limits, and gear restrictions can serve to protect fish populations. Spatial management such as the implementation of marine protected areas and no-take zones are also useful tools if well enforced. However, these measures must be combined with watershed management strategies to address uncontrolled coastal development and inadequate wastewater treatment which have caused large-scale nutrient enrichment of coastal Caribbean waters (Risk 2014).

Supplemental Information

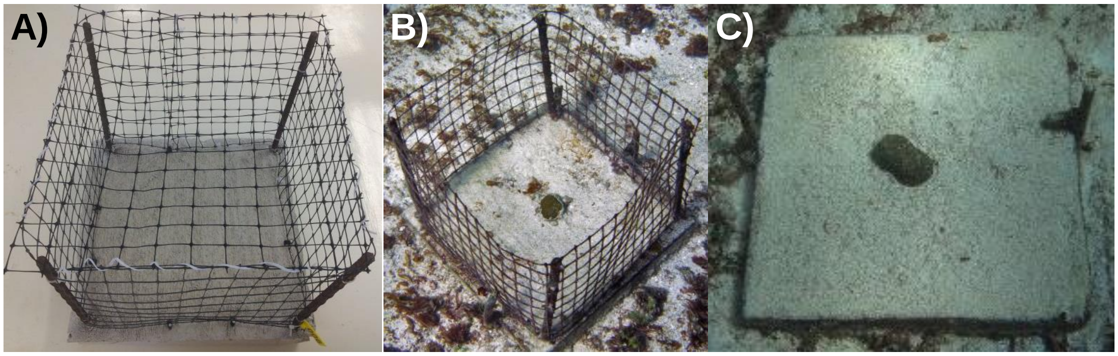

Figure S3.1. Herbivorous fish exclusion cages. (A) A full exclusion cage. Cages were built upon 36 cm-square concrete plates, with 30 cm vertical rebars and 3 cm x 2 cm polyethylene mesh. The top panel was attached to cage sides using twist ties to allow access for mesh cleaning and plate monitoring. Small (approximately 5 cm maximum diameter) *O. faveolata* coral colonies were affixed to plate centres using underwater epoxy plasticine. (B) A half exclusion cage *in situ* with an *Orbicella faveolata* coral colony. Half cages acted as procedural controls and were identical to full cages without a top panel to allow fish access. (C) An uncaged control plate *in situ* with an *Orbicella faveolata* coral colony. Controls were merely concrete plates without any caging or rebars.

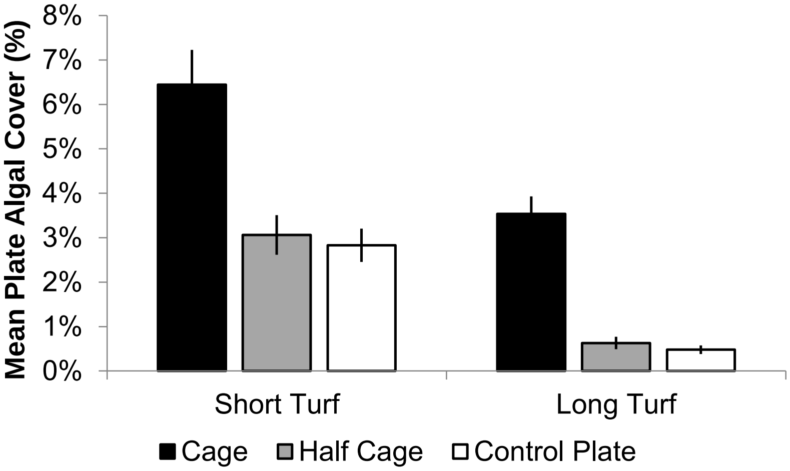

Figure S3.2. Mean plate short and long turf algal cover. Mean (± s.e.m.) short (< 0.5 cm) and long (≥ 0.5 cm) algal turf cover over the observation period for full exclusion cages (n = 6), half cages (n = 6) and uncaged control plates (n = 6).

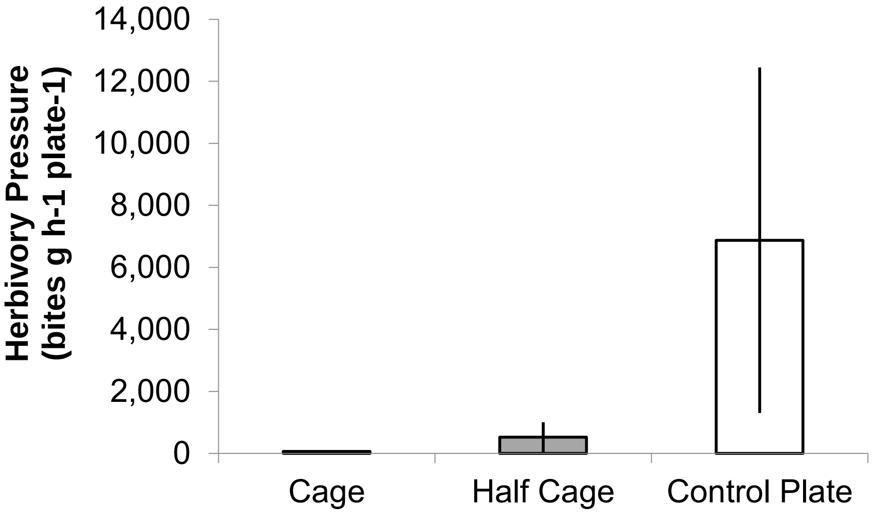

Figure S3.3. Herbivory pressure. Mean (± s.e.m.) herbivory pressure for full exclusion cages (n = 3), half cages (n = 3) and uncaged control plates (n = 3) based on *in situ* observations. Herbivory pressure expressed as bite rate per hour per plate standardised (multiplied) by grazing herbivorous fish biomass.

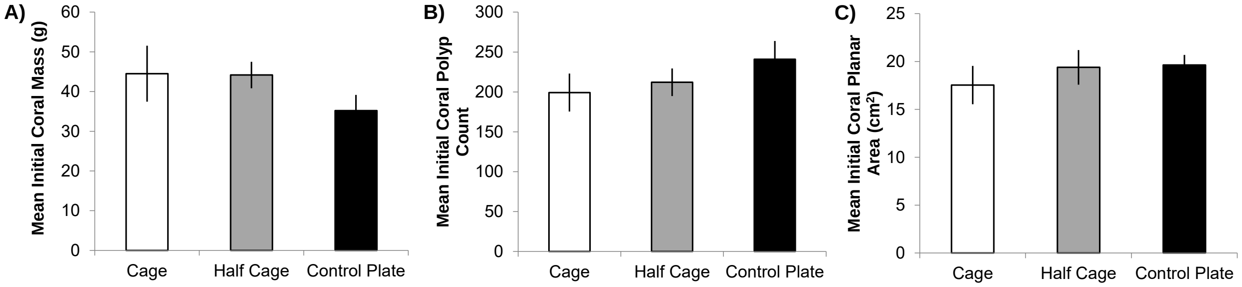

Figure S3.4. Initial *Orbicella faveolata* colony size. (A) Mean (± s.e.m.) initial coral colony mass. (B) Mean (± s.e.m.) initial coral colony polyp count. (C) Mean (± s.e.m.) initial coral colony planar area. All shown for full exclusion cages (n = 6), half cages (n = 6) and uncaged control plates (n = 5, as one colony was lost after two months and is therefore not included in the coral growth calculations).

DISCUSIÓN GENERAL

La herbivoria y la protección marina juegan un papel importante en la condición bentónica de los arrecifes coralinos del Arrecife Mesoamericano. En una escala fina en el Caribe Mexicano, se encontró que los peces herbívoros pueden controlar las poblaciones de macroalgas y su ausencia resulta en la proliferación de macroalgas y la supresión de crecimiento coralino durante un año (Capítulo 3). Además, se observó que la cobertura coralina actual en el Caribe Mexicano está correlacionada positivamente con la biomasa de peces herbívoros y negativamente con la cobertura de macroalgas (Capítulo 2). Sin embargo, a nivel de todo el Arrecife Mesoamericano se encontró un claro patrón en el aumento de la cobertura de corales y macroalgas entre 2005 y 2014, mientras que la biomasa de peces herbívoros no mostró cambios en el mismo periodo de tiempo (Capítulo 1). Además, se observó el efecto positivo de la protección en la cobertura coralina actual (Capítulo 2) en el Caribe Mexicano, el cual es consistente con el aumento de la cobertura coralina del Arrecife Mesoamericano entre 2005 y 2014 (Capítulo 1).

Dado el papel fundamental de los herbívoros en el control del crecimiento de las macroalgas (Mumby et al. 2006a), generalmente se acepta que restaurar poblaciones de herbívoros claves mejora la resistencia del arrecife al controlar las algas y facilitar la recuperación de los corales (Nyström et al. 2000; McCook et al. 2001; McManus & Polsenberg 2004; Bruno et al. 2009). En consecuencia, se espera que los arrecifes de coral con alta abundancia de herbívoros tengan menor cobertura de macroalgas y mayor cobertura coralina (Jackson et al. 2014; Kramer et al. 2015). Este paradigma ha servido de base para campañas de conciencia global que promueven estrategias de conservación y manejo de la pesca para proteger y restaurar las poblaciones de peces herbívoros claves, en particular los peces loro (Jackson et al. 2014). Sin embargo, se ha demostrado que el impacto de la protección de peces sobre la condición bentónica arrecifal varía espacialmente y temporalmente, y por lo tanto es necesaria una evaluación a un nivel apropiado dado los objetivos de conservación del arrecife (Guarderas et al. 2011; Toth et al. 2014; Russ et al. 2015a; Gill et al. 2017).

En el Arrecife Mesoamericano se encontró un patrón claro de aumento en la cobertura de macroalgas, mientras la biomasa de peces herbívoros no muestra cambios, contrastando el paradigma de control herbívoro ‘top-down’ (Capítulo 1). Una probable explicación del rápido aumento en la cobertura de macroalgas carnosas en los arrecifes mesoamericanos es que los ecosistemas pasaron los umbrales críticos más allá de los cuales los peces herbívoros son incapaces de controlar las macroalgas debido a la excesiva producción de algas y / o insuficiente herbivoria (Mumby et al. 2007). Sin embargo, la producción excesiva de algas no es probable ya que las macroalgas exhiben niveles que están considerablemente por debajo de los umbrales conocidos para los arrecifes del Caribe (Bruno et al. 2009). De igual manera, se experimentó un aumento de la cobertura de macroalgas carnosas incluso para los sitios que mostraron globalmente alta biomasa de peces inicialmente.

Aunque los peces herbívoros no tuvieron impacto en el aumento de las macroalgas del Arrecife Mesoamericano, se encontró que la recuperación de los corales estaba relacionada con los peces herbívoros y la protección por AMP (Capítulo 1 y 3). De manera similar, en los arrecifes del Caribe Mexicano, se observó que la cobertura coralina actual estuvo relacionada con los peces herbívoros y las AMP (Capítulo 2). Sin embargo, estos hallazgos sugieren que el mecanismo por el cual los peces herbívoros benefician a las comunidades de coral puede variar. En el Capítulo 2, encontré que la protección dentro de Zonas de Exclusión Pesquera aumentó la biomasa de peces herbívoros y disminuyó la cobertura de macroalgas carnosas, que a su vez benefició a los corales. En el Capítulo 1, debido a la falta de evidencia de la interacción herbívora-alga-coral, se postuló que los peces herbívoros pueden beneficiar a las comunidades de corales a través de mecanismos alternativos, en lugar del control de macroalgas. Por ejemplo, se ha demostrado que las comunidades de peces tróficamente diversas dentro de las AMP reducen la prevalencia de las enfermedades de los corales (Raymundo et al. 2009). Se observó el efecto positivo de la duración de la protección en la condición de los arrecifes del Caribe (Capítulo 2) y se propone que la persistencia de las diferencias iniciales (de cobertura de macroalgas) entre los arrecifes mesoamericanos protegidos y no protegidos puede deberse a un tiempo de protección relativamente corto (Capítulo 1). Además, el tamaño y la eficacia de las AMP mexicanas (en términos de recursos disponibles y cumplimiento) también tuvieron un impacto positivo en la cobertura de los corales, un hallazgo que tiene implicaciones importantes para la planificación de la protección marina (Capítulo 2).

Los procesos ecosistémicos a menudo dependen de la escala (Levin 1992; Hewitt et al. 2010). Los mecanismos de control externos y las retroalimentaciones internas que afectan a la dinámica coral-alga en los arrecifes varían tanto en escala temporal como espacial (Adam et al. 2015a; van de Leemput et al. 2016). El hallazgo en el Capítulo 3 donde la herbivoria por peces tiene un impacto significativo en la proliferación de algas es consistente con los experimentos previos de exclusión a pequeña escala (Burkepile & Hay 2006), pero contrasta con algunos estudios correlativos a gran escala que proporcionan evidencia contra el control herbívoro de las algas (Loh et al., 2015; Russ et al., 2015b; Cox et al., 2017; Capítulo 1). Una posible explicación puede ser que en escalas espaciales y temporales finas, los peces herbívoros pueden controlar el crecimiento de las algas (Capítulo 3), mientras que a escalas mayores los nutrientes (Capítulos 1 y 2) y la pérdida de herbívoros por debajo de umbrales críticos promueven la proliferación de algas (Mumby et al. 2007; Paddack et al. 2009). La productividad de algas varía en pequeñas escalas espaciales a nivel de la zona de arrecife (Carpenter 1985; Klumpp & McKinnon 1992; Russ 2003). Aunque la presión de la herbivoria tiende a seguir la producción de algas, las diferencias locales como la complejidad del hábitat, depredación y tasas de reclutamiento pueden variar los procesos de retroalimentación ecosistémicos provocando la proliferación de macroalgas a escala de arrecife (Russ 2003; Fox & Bellwood 2007; van de Leemput et al. 2016).

Varios estudios han intentado evaluar el impacto de las amenazas humanas locales sobre la condición de los arrecifes de coral (e.g. Mora 2008; Bruno & Valdivia 2016; Cox et al. 2017). Sin embargo, pocos estudios han abordado el impacto de las amenazas terrestres humanas locales sobre la eficacia de la protección de los arrecifes de coral (Bégin et al. 2016; Lamb et al. 2016; Wenger et al. 2016). En el Capítulo 2, se observó el beneficio de la protección marina para las comunidades de corales del Caribe Mexicano, mientras que los niveles elevados de amenaza humana local redujeron la cobertura coralina. Se encontró que la combinación de las amenazas del desarrollo costero, la contaminación y el daño directo actúa para reducir la cobertura de coral. En el Caribe Mexicano, el desarrollo costero provoca niveles elevados de nutrientes en aguas costeras (Murray 2007; Baker et al. 2013; Hernández-Terrones et al. 2015), así como las actividades marinas pueden causar sedimentación y contaminación local que son perjudiciales para las comunidades coralinas (Rogers 1990; Edinger et al. 1998; Fabricius 2005; Stoms et al. 2005). Los efectos externos como estos pueden explicar por qué, a escala de todo el Arrecife Mesoamericano, los peces herbívoros no fueron capaces de prevenir el aumento de la cobertura de macroalgas observada en el Capítulo 1.

Es importante reconocer las limitaciones inherentes a las metodologías empleadas en esta tesis. Primero, en el Capítulo 1, se utilizó una base de datos externa producida por los programas de Iniciativa Arrecifes Saludables (HRI) y Atlantic and Gulf Rapid Reef Assessment (AGRRA), que incluía censos ecológicos para 398 sitios durante un período de 9 años. Aunque la metodología de los censos fue estandarizada (Lang et al. 2010), la geomorfología del sitio varía sustancialmente y puede ser importante en la definición de patrones de diversidad y abundancia de especies asociadas a los arrecifes (Karlson et al. 2004; Graham & Nash 2013). Sin embargo, se observó que no existe relación entre los peces herbívoros y la cobertura de macroalgas cuando se dividen los datos por zona arrecifal (cresta contra frontal) o complejidad estructural (Capitulo 1, Fig. S1.6). Segundo, los estudios correlativos como el Capítulo 1 (y el Capítulo 2 en menor medida) están intrínsecamente limitados ya que la causalidad sólo se infiere. En el Capítulo 1, por ejemplo, observamos que el aumento de la biomasa de peces herbívoros incrementó la cobertura de coral. Una explicación alternativa es que la cobertura coralina y la complejidad arrecifal influyen en las poblaciones de peces herbívoros contrariamente a lo que se ha planteado o que la relación puede ser correlativa con ambos indicadores impulsados por la protección marina (Halpern 2003; Selig & Bruno 2010; Alvarez-Filip et al. 2011b). Tercero, en el Capítulo 2 encontramos que el desarrollo costero y la contaminación marina actúan para reducir la cobertura coralina y en el Capítulo 1 postulamos que los niveles de nutrientes son un factor clave de la degradación de los arrecifes mesoamericanos. Sin embargo, datos de nutrientes en la región no están ampliamente disponibles, por lo tanto no se realizó una exploración cuantitativa del efecto de este factor (Melbourne-Thomas et al. 2011b; Bland et al. 2017). Finalmente, por definición los experimentos de exclusión de herbívoros (Capítulo 3) implican manipulación; por lo tanto son susceptibles a factores de confusión (McCook et al. 2001). Al utilizar medias jaulas como controles del procedimiento experimental nuestros resultados sugieren que éste tratamiento puede presentar una eficacia limitada, como se ha observado en otros estudios (Diaz-Pulido & McCook 2003; Ferrari et al. 2012; Castro-Sanguino et al. 2016). Adicionalmente, las jaulas influyen en el ambiente físico enjaulado, incluyendo la hidrodinámica y la intensidad de la luz. Por ejemplo, se observó que la intensidad de la luz incidente en las placas de control sin jaula fue ligeramente superior al tratamiento de las medias jaulas, que a su vez fue mayor que en jaulas completas. Sin embargo, las tasas de calcificación de los corales son relativamente insensibles a tales cambios menores en la intensidad de la luz (Venti et al. 2014).

CONCLUSIONES

Los hallazgos de este trabajo tienen implicaciones importantes para el manejo de los arrecifes del Arrecife Mesoamericano. Los peces herbívoros tienen un efecto positivo en la cobertura (Capítulos 1 y 2) y la calcificación (Capítulo 3) coralina. La calcificación crea la estructura tridimensional que proporciona hábitat a diversas comunidades de peces, invertebrados y plantas. A escala de arrecife, la acreción permite que los arrecifes sigan el ritmo del cambio del nivel del mar y eviten que se ahoguen a profundidades con poca luz (Blanchon & Shaw 1995; Perry et al. 2008, 2015a). Dado que los arrecifes del Caribe han perdido cobertura de coral y han sufrido cambios a especies que contribuyen menos a la acreción arrecifal, los peces herbívoros y el control de las macroalgas son cada vez más importantes para los arrecifes actuales.

De acuerdo con los resultados de este estudio, la protección marina beneficia a las comunidades de corales de la región (Capítulos 1 y 2). Por ende, en México la Comisión Nacional de Áreas Naturales Protegidas (CONANP) debería considerar ampliar las Zonas de Exclusión Pesquera en los arrecifes de la región y asignar recursos económicos y humanos adecuados para su vigilancia. Además del manejo espacial, es importante implementar nuevas estrategias de manejo pesquero. En México, por ejemplo, para proteger a las poblaciones de peces herbívoros, la Comisión Nacional de Acuacultura y Pesca (CONAPESCA) debería considerar establecer cuotas de captura, restricciones en las artes de pesca, y evaluar la prohibición de la extracción de éstos en el Caribe.

Desafortunadamente en los últimos 40 años el Caribe ha experimentado desarrollo costero extensivo que ha provocado el enriquecimiento de nutrientes de las aguas costeras y otros impactos humanos que amenazan la eficacia de la protección (Capítulo 2). Actualmente, la protección que provee la red de AMP del Arrecife Mesoamericano probablemente es insuficiente contra las amenazas terrestres ya que muy pocas incorporan componentes terrestres en sus estrategias de manejo. Por lo tanto, para lograr una protección adecuada de los arrecifes coralinos del Caribe mexicano es necesario que los tres niveles de gobierno (Federal, Estatal y Municipal) reconozcan el impacto perjudicial del desarrollo costero descontrolado que ocurre en la región, que desarrollen estrategias de manejo de las cuencas hidrográficas y que apliquen controles más estrictos sobre el desarrollo costero. Esto se puede lograr a través de la Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), de la Secretaría de Ecología y Medio Ambiente (SEMA) del Gobierno del Estado de Quintana Roo y de las direcciones de desarrollo urbano y ecología de los Municipios.

Es indispensable mejorar el tratamiento de las aguas residuales, tanto en los desarrollos urbanos y hoteleros (nuevos y existentes) para reducir el aporte de nutrientes y contaminantes al arrecife. Esto se puede dar con la implantación de un sistema de drenaje y una red de plantas de tratamiento que sean capaces de procesar contaminantes emergentes como son los nutrientes (nitratos y fosfatos), los metales pesados y el nitrógeno de origen antropogénico. Además, hay que prevenir la destrucción de los manglares y desarrollar estrategias de mitigación para que durante la construcción de desarrollos turísticos en la zona costera se reduzca la cantidad de sedimentos que llegan a la columna de agua. La SEMARNAT debería ampliar su

Programa de Playas Limpias en el estado de Quintana Roo y evaluar la calidad del agua en los arrecifes de manera continua. Además, de las bacterias que actualmente son monitoreadas en las playas, se deberían de monitorear los niveles de otros contaminantes emergentes ya mencionados. Sin estas acciones combinadas la condición bentónica de los arrecifes coralinos del Caribe Mexicano seguiría decayendo.

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