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CAMBIOS ECOLÓGICOS EN ARRECIFES CORALINOS, DENTRO DEL PARQUE NACIONAL ARRECIFE DE PUERTO MORELOS ENTRE 1985-2016.

TESIS

QUE PARA OPTAR POR EL GRADO DE:
MAESTRA EN CIENCIAS
(BIOLOGÍA MARINA)

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RESUMEN

La alta integridad funcional en los arrecifes depende de la capacidad de los corales para mantener la acreción de estructuras tridimensionales. Sin embargo, crecientes presiones ambientales y antropogénicas están promoviendo una pérdida neta en la cobertura de corales constructores y cambiando la abundancia de las especies de coral hacia la dominancia de taxones mejor adaptados al estrés. En este contexto, conocer a detalle cómo los cambios en la composición de la comunidad coralina están influyendo en el potencial de función, en términos de producción de carbonato, de los arrecifes, se vuelve una prioridad de conservación y manejo. Por ello, en esta investigación se evaluó cómo han cambiado las comunidades coralinas en Puerto Morelos dentro del Caribe Mexicano, así como las implicaciones funcionales en arrecifes posteriores y frontales entre 1985 y 2016. Los resultados muestran que en un periodo de 31 años ha ocurrido un proceso de homogenización ecológica y funcional entre zonas arrecifales. En los arrecifes posteriores el único género ramificado encontrado, *Acropora*, disminuyó notablemente en abundancia, mientras que en el arrecife frontal la cobertura de especies no-constructoras aumentó significativamente. De igual manera, se observó una disminución significativa en la contribución de la cobertura, rugosidad y calcificación de las especies de coral entre años. Actualmente, las zonas posterior y frontal del arrecife se encuentran en un presupuesto negativo de producción de carbonato. Estas grandes reducciones en la producción de carbonato de las especies ponen en peligro la habilidad para sostener la acreción arrecifal, comprometiendo la estructura tridimensional existente, y con ello la capacidad actual y futura de proveer hábitat y brindar servicios ambientales.

ABSTRACT

The functional integrity of coral reefs depends on the capacity of the corals to maintain the accretion of the three-dimensional structures. However, increasing environmental and anthropogenic pressures are promoting a net loss in the quantity of corals and changing the abundance of coral species towards the dominance of taxa better adapted to stress. In this context, knowing in detail how changes in the composition of the coral community are influencing the reef's functional potential, in terms of coral carbonate production, becomes a priority for conservation and management. Therefore, it was evaluated how the coral communities in Puerto Morelos, within the Mexican Caribbean, have changed, as well as the functional implications in back and fore reefs between 1985 and 2016. The results show that in 31-year period a process of ecological and functional homogenization between reef areas has occurred. In the back-reefs the only branching genus found, Acropora, decreased significantly, while in the fore-reef the cover of non-framework species increased significantly. Similarly, there was a significant decrease in the contribution of cover, rugosity and calcification of coral species between years. Currently, the back and fore zones of the reef are in a negative carbonate production budget. These large reductions in the carbonate production of the species, endanger the ability to sustain reef accretion, compromising the existing three-dimensional structure, and with it the current and future capacity to provide habitat and provide environmental services.

INTRODUCCIÓN GENERAL

Los arrecifes de coral se desarrollan en aguas tropicales someras, oligotróficas y son el ecosistema marino con mayor diversidad biológica. Estos ecosistemas están estructuralmente determinados por los corales pétreos o escleractínios, los cuales, mediante la secreción de carbonato de calcio, van formando colonias que conforman la estructura tridimensional característica de un arrecife, misma que sirve como refugio y sitio de reproducción y alimentación para una gran cantidad de organismos, (Knowlton, 2001; Graham & Nash, 2013). De igual forma, los arrecifes también brindan diversos servicios ecosistémicos, como la protección de la línea de costa contra huracanes y generación de arena; el mantenimiento de la biodiversidad y la exportación de larvas y plancton a la red alimenticia, son una excelente fuente para el registro de cambio climático y cuentan con una gran valor estético y cultural (Moberg & Folke, 1999). Así mismo, desempeñan un papel importante para la economía, a través del ingreso económico que se genera del turismo y la pesca. Desafortunadamente, en los últimos 40 años la cobertura de coral en los arrecifes tropicales ha disminuido significativamente, en especial en el Mar Caribe, el cual ha experimentado los mayores cambios desde la década de 1970 (Gardner et al., 2003; Jackson et al., 2014).

De acuerdo con Burke et al. (2011), 75% de los arrecifes del Caribe están amenazados por diversas presiones ambientales incluidas la disminución de la calidad del agua, la contaminación, la sobrepesca y el desarrollo costero excesivo en áreas cercanas a los arrecifes. En su estudio, establecieron que entre las áreas con mayor degradación se encuentran la costa de la Península de Yucatán y el Caribe occidental. Debido al deterioro en la calidad del ambiente (aumento de la temperatura del agua y de nutrientes), los corales se vuelven más susceptibles al blanqueamiento y a las enfermedades coralinas (Bruno et al., 2003; Weil & Rogers, 2011; Mera & Bourne, 2018). Los corales tienen una relación simbiótica con dinoflagelados fotosintéticos, llamados zooxantelas, esta simbiosis le provee la energía necesaria para su desarrollo en aguas oligotróficas y contribuye enormemente en el proceso de calcificación de los corales (Muscatine & Porter, 1977; Pearse & Muscatine, 2007). Esta relación se puede ver interrumpida como respuesta a una variedad de estresores ambientales (p.ej. estrés térmico). Dichos cambios en el ambiente producen la expulsión del simbionte, ocasionando que los corales se vean blancos ya que el esqueleto calcáreo se hace visible a través del tejido transparente de los corales, este evento se conoce como blanqueamiento (Baker, Glynn & Riegl, 2008; Lough & Van Oppen, 2009). Es importante mencionar que si estos eventos son de larga duración pueden ocasionar una alta mortandad coralina. Los eventos de blanqueamiento han sido causados principalmente por aumentos en la temperatura del mar, los mayores eventos de blanqueamiento que en el Caribe han sido en 1997-1998, 2005, 2010 2014-2017 (Hernández-Arana, López-Adame & Vega-Zepeda, 2014; Eakin et al., 2016; Hughes et al., 2018), afectando a diversas especies de coral, contribuyendo al declive general de la cobertura coralina. Sin embargo, en esta región la prevalencia de enfermedades ha aumentado en las últimas décadas, impactando fuertemente las poblaciones de coral duros.

Un suceso que impactó severamente a los arrecifes del Caribe fue la banda blanca en la década de 1980, la cual disminuyó significativamente las poblaciones de acropóridos (Gladfelter, 1982; Patterson et al., 2002). En los años subsiguientes, la banda amarilla ha causado una alta mortalidad para las especies constructoras de arrecife del género *Orbicella* (Weil, Smith & Gil-Agudelo, 2006; Harvell et al., 2007). Desafortunadamente desde 2014 se detectó una nueva epizootia que aparentemente comenzó en Florida. Esta se ha denominado Stony Coral Tissue Loss Disease ("enfermedad de pérdida de tejido coralino") y se caracteriza por la rápida pérdida de tejido coralino, es un tipo de síndrome blanco que está afectando a distintas especies de coral, las cuales contribuyen a formar la estructura del arrecife (Precht et al., 2016; Walton, Hayes & Gilliam, 2018). A la fecha, eventos similares se han registrado en el Caribe mexicano perturbando un gran número de especies (p.ej. *Pseudodiploria strigosa, Meandrina meandrites, Dendrogyra cylindrus, Orbicella annularis* y *Montastraea cavernosa*). En conjunto, la aparición de distintas epizootias en las últimas décadas parece no tener precedentes dentro del registro geológico (Weil & Rogers, 2011), y esto ha contribuido al declive en la cobertura coralina de los últimos años.

Una consecuencia del declive en la cobertura de las especies coralinas formadoras de arrecife, es que los arrecifes de coral están experimentando un cambio en la dominancia de las especies coralinas, donde las especies no constructoras, de pequeño tamaño están dominando los arrecifes, ocasionando una pérdida de la complejidad arrecifal (Alvarez-Filip et al., 2011a; Perry et al., 2014). Estos cambios en la comunidad coralina están asociados con las historias de vida y los rasgos de cada especie de coral los cuales indican cómo se relacionan los organismos con el ambiente. En 2012 Darling y colaboradores realizaron un análisis para clasificar las especies de coral del Atlántico y del Pacífico de acuerdo a sus rasgos de vida, obteniendo tres grupos principales: (a) las especies *competitivas,* las cuales tienen un rápido crecimiento y debido a la eficiencia para utilizar los recursos del medio pueden dominar las comunidades aunque son susceptibles a altas temperaturas y a romperse; (b) las especies *oportunistas*, también llamadas no constructoras (Perry et al., 2014), tienen una rápida reproducción y pueden colonizar ambientes perturbados; y (c) las especies masivas *tolerantes al estrés* las cuales tienen un crecimiento lento y se reproducen mediante el desove a gran escala. Al tomar en cuenta los rasgos de vida de los corales, junto con las distintas variables ambientales que los pueden influenciar, podría ser posible predecir cambios futuros en la composición de la comunidad coralina y su repercusión en el funcionamiento arrecifal (Rachello-Dolmen & Cleary, 2007; McClanahan et al., 2014).

La pérdida de las especies constructoras pone en riesgo el funcionamiento arrecifal, definiéndolo en términos de cuánta acreción y complejidad aportan los corales al arrecife. Es decir, que la producción de carbonato aportada por los corales sea mayor que la bioerosión producida por los peces loro, erizos y esponjas incrustantes del género *Cliona* (Perry, Spencer & Kench, 2008; Perry et al., 2012). Por lo tanto, al perder a los grandes constructores, como lo son los corales del género *Acropora* y *Orbicella*, y en su lugar tener una mayor abundancia de especies no constructoras, como *Porites astreoides* y *Agaricia agaricites*, la estructura arrecifal se vería comprometida y por ende la función, ya que estas contribuyen en menor proporción a dicha función (Perry et al., 2014; González-Barrios & Alvarez-Filip, 2018). La alteración del balance entre la producción de carbonato de calcio y la bioerosión, debido al declive en las condiciones ambientales, puede ocasionar que los procesos erosionadores se vuelvan dominantes, ocasionando una reducción en los servicios que provee el arrecife (Ferrario et al., 2014; Newman et al., 2015)

Para entender la problemática actual de los cambios en la comunidad coralina, las bases de datos históricas son una gran herramienta para comprender estas trayectorias de cambio. Cuando se evalúa el estado de salud de un arrecife en una serie de tiempo, se utiliza una comparación entre un estado actual de la comunidad contra un estado pasado ya estudiado. El uso de series de tiempo ayuda al entendimiento de las dinámicas temporales, a partir de las cuales se podrían hacer una predicción de valores para poder visualizar el efecto de la variación a gran escala en el futuro.

JUSTIFICACIÓN E IMPORTANCIA

En México el desarrollo arrecifal más representativo se encuentra en el mar Caribe, el cual forma parte del Sistema Arrecifal Mesoamericano (SAM) que se extiende 1,000 km a lo largo de la costa, desde el norte de la Península de Yucatán, en México hasta el Golfo de Honduras. A pesar de que diversas partes del SAM se encuentran bajo algún tipo de protección, también está sujeto a diversos factores de estrés, incluyendo la sobrepesca, el desarrollo costero (i.e. infraestructura para el turismo masivo), las enfermedades coralinas y el cambio climático (Paddack et al., 2009; Eakin et al., 2010; Walton, Hayes & Gilliam, 2018). Debido a estos factores la cobertura de coral ha experimentado pérdidas significativas en los últimos 40 años (Jackson et al., 2014). Pero el deterioro no sólo ha influido en la disminución de la cobertura coralina, sino que los arrecifes están experimentando cambios en la dominancia de las especies, teniendo un declive en la cobertura de especies constructoras (p.ej. *Acropora* sp. y *Orbicella* sp.) y por ende una reducción en la complejidad estructural (Green, Edmunds & Carpenter, 2008; Graham & Nash, 2013).

En el Caribe mexicano, el desarrollo costero desmedido se ha incrementado exponencialmente desde 1970, amenazando los arrecifes circundantes, en especial el desarrollo enfocado al sector turismo. A pesar de que los arrecifes de esta región han sido ampliamente estudiados por su biodiversidad, el estado de salud (Jordán-Dahlgren, 1978; Rodríguez-Martínez et al., 2014; Rodríguez-Zaragoza & Arias-González, 2015) y enfermedades coralinas (Jordán-Dahlgren, Maldonado & Rodríguez-Martínez, 2005; Navarro-Espinoza, 2015; Rioja-Nieto & Alvarez-Filip, 2018), el entendimiento respecto a los cambios en la composición de la comunidad coralina y su influencia en la función arrecifal no ha sido explorada, debido a que cada zona arrecifal cuenta con una composición de la comunidad específica, es necesario realizar una evaluación del cambio que ha ocurrido en las comunidades coralinas en las últimas décadas y si dicho cambio ocurrió de la misma manera para las dos zonas arrecifales. La comprensión de los cambios en la función del arrecife podría brindar información necesaria para el desarrollo de mejores estrategias de manejo y conservación de estos ecosistemas.

PREGUNTAS DE INVESTIGACIÓN

A partir de lo anterior, surgieron dos preguntas sobre el cambio en la composición de la comunidad coralina en los arrecifes del norte del Caribe mexicano, en torno a la variación entre la zona posterior y frontal del arrecife: ¿Cómo ha cambiado la dominancia de especies coralinas entre 1985 y 2016? y, a partir de este cambio, ¿Cuál es el efecto de la pérdida de los principales constructores sobre la función arrecifal, en términos de la producción de carbonatos?

OBJETIVOS

Objetivo General

Realizar un estudio comparativo de los patrones históricos de cambio ecológico en arrecifes de Puerto Morelos entre 1985 y 2016 para dos zonas arrecifales y su influencia en la función arrecifal.

Objetivos específicos

- Recabar y sistematizar información disponible de la cobertura coralina a nivel de especie para 1985 y 2016 en los arrecifes de Puerto Morelos.
- Analizar el cambio de cobertura coralina para cuatro grupos de corales: corales ramificados, foliosos-digitiformes, masivos y no-constructores.
- Analizar el cambio en la composición de especies a nivel de zona arrecifal para ambos años.
- Determinar el cambio en el índice funcional del arrecife de acuerdo con la composición de las especies coralinas.
- Determinar el cambio en la producción neta de carbonato de calcio.

FUNCTIONAL CONSEQUENCES OF THE LONG-TERM DECLINE OF REEF-BUILDING CORALS IN THE CARIBBEAN

Abstract:

Functional integrity in coral reefs is strongly dependent upon coral cover and the presence of three-dimensional structures. Environmental and anthropogenic pressures have reduced the cover of key reef building species producing a shift towards the dominance of more stress tolerant taxa, leading to a reduction in the physical reef function (e. Understanding how changes in coral community composition influence the potential of reefs to maintain their function is a priority for their conservation and management. Here we evaluate how coral communities have changed in the northern sector of the Mexican Caribbean between 1985 and 2016, and the implications for the maintenance of physical reef functions in the back and fore-reef zones. In this period ecological homogenization occurred between the two zones mostly due to a reduction (from 14.1% to 0.07 %) in the cover of branching (*Acropora* spp) species in the back-reef, and to an increase of non-framework species (from 2% to 5%) in the fore-reef. This resulted in a significant decrease in substrate rugosity and calcification rates in the back-reef. At present both reef zones have negative carbonate budgets, and thus limited capacity to sustain reef accretion, compromising the existing reef-structure and its future capacity to provide habitat and environmental services.

Key words: Homogenization, carbonate production, reef function, coral reefs, reef zones

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Introduction

The three-dimensional structures provided by reef-building corals sustain one of the most biodiverse and socio-economically important ecosystems on the planet (Knowlton, 2001; Graham & Nash, 2013). However, over the last 40 years the average live coral cover on tropical reefs has declined significantly, with the Caribbean being among the regions that has experienced the most severe changes since the 1970s (Gardner et al., 2003; Jackson et al., 2014). The causes of coral cover decline include a combination of local and global anthropogenic impacts including overfishing, coastal development and associated pollution and rising sea temperatures. This decline has resulted in the loss of the ecological performance of reefs and compromising their future capacity to sustain their structural complexity (and hence diversity), to maintain many ecosystem services and to keep up with sea level rise (Graham & Nash, 2013; Perry et al., 2013, 2018). These changes can occur either when vertical coral reef growth is halted or inhibited (i.a., reef "turn-off"; Buddemeier and Hopley, 1988), when high rates of biological, chemical and physical processes drive net erosion of the underlying reef structure, or in response to direct impacts such as hurricanes through the breakage of coral skeletons (Gardner et al., 2005; Hoegh-Guldberg et al., 2007; Silverman et al., 2009; Yates et al., 2017). The resultant loss of reef three-dimensional structures has serious implications for the local economy, such as fishing and tourism, and since wave attenuation functions are reduced (Harris et al., 2018), it can also result in higher beach erosion (Moberg & Folke, 1999; Nyström, Folke & Moberg, 2000; Perry, Spencer & Kench, 2008; Elliff & Silva, 2017; Perry et al., 2018).

Ecological and geological records of reef-building corals in the Caribbean show that *Acropora* was historically one of the dominant coral genera and a major shallow-water reef-builder since the Pleistocene (Aronson & Precht, 2001; Pandolfi & Jackson, 2006; Jackson et al., 2014). However, populations of acroporids declined considerably between the 1980s and 1990s due to the white-band disease (Aronson & Precht, 2001; Porter et al., 2001; Patterson et al., 2002), and since then, very little recovery has been reported (McField et al., 2008; Rodríguez-Martínez et al., 2014). After the acroporid die-off, massive corals of the genera *Orbicella* remained as major Caribbean reef builders, however their populations have decreased in the last two decades mainly to disease impacts (Bruckner & Bruckner, 2006; Edmunds & Elahi, 2007; Harvell et al., 2007; Weil, Cróquer & Urreiztieta, 2009). What is most concerning is that remnant populations of reef-building corals are being affected by new emerging diseases (Precht et al., 2016; Van Woesik & Randall, 2017; Walton, Hayes & Gilliam, 2018) and thermal stress events (Loya et al., 2001; McClanahan, Weil & Baird, 2018).

The resultant decline of the major reef-building coral species across the Caribbean has led to a relative increase in the abundance of non-framework coral species, such as *Agaricia* spp. and *Porites astreoides* (Green, Edmunds & Carpenter, 2008; Buglass, Donner & Alemui I, 2016; Williams et al., 2017). This group of new dominant species is characterized by small size colonies that do not contribute importantly to the reef framework (Perry et al., 2014; González-Barrios & Alvarez-Filip, 2018). The shift in the dominance patterns of Caribbean coral communities is strongly linked to the life history strategies of corals and how they cope with rapidly changing environmental conditions (Darling et al., 2012; Mouillot et al., 2013). By taking into account these attributes, alongside environmental variables, it should therefore be possible to predict future changes in coral assemblages and how this will affect reef functioning, especially the potential of corals to accrete three-dimensional structures and provide habitat (Rachello-Dolmen & Cleary, 2007; McClanahan, Graham & Darling, 2014; Darling et al., 2017). The ultimate consequence of a reduced abundance of important reef-building species will reduced reef-carbonate budgets, with rates of bioerosion becoming increasingly important controls on overall budget states (Perry et al., 2012, 2014). Indeed, if coral carbonate production rates are sufficiently suppressed, carbonate budget will transition to increasingly net negative states compromising future reef accretion potential and endangering current reef structure.

Key to understanding changes in coral communities are long-term studies, but this remains a challenging issue, partly because community shifts may occur slowly and most measures of assessment rely upon the comparison of present status to a defined past reference condition (Gatti et al., 2015). Furthermore, robust datasets that can support historical timescale assessments are not numerous because past reference baselines are sparse or difficult to construct.

Despite this, the use of historical records can be especially important for understanding contemporary ecological transitions, and to aid predicting future changes (Côté et al., 2005; Mcclenachan, Ferretti & Baum, 2012). In this study, we use data collected in 1985 and 2016 from back- and fore-reef sites in the northern Mexican Caribbean, in order to assess changes in the community structure of reef-building corals and to determine the implications for reef functioning. We explore decadal-scale changes in community composition and track the trajectories of the main coral groups that influence the reef-structure with respect to colony shape (branching, foliose-digitiform, massive and non-framework). We also evaluate changes in physical reef function by using species identity and composition to estimate changes in calcification rates and reef-carbonate budgets through time.

Materials and methods

Study area

Puerto Morelos is located in the northern part of the Mexican Caribbean; its coast is characterized by a fringing reef system (located between 1 and 3 km offshore), which runs parallel to the coast in a semi-continuous barrier. This reef system has an identifiable zonation with a back-reef, reef crest and fore-reef (Jordán-Dahlgren & Rodríguez-Martínez, 2003) that is mostly associated with wave exposure and light penetration. Historically it has a well-developed back-reef and reef-crest that were dominated by *Acropora palmata*, while the fore-reef is relatively flat, with no significant reef framework development that descends gradually to a depth of ~20-25m (Jordán-Dahlgren, 1993). The area was affected by 13 hurricanes between 1985 and 2016, the strongest were Gilbert in 1988 and Wilma in 2005 (National Hurricane Center, 2018), which impacted the coral community mainly by fragmenting branching and digitiform coral species. Until the early 1980s, coastal developments exerted a minimal impact on these reefs but, at present, the accelerated expansion of the urban and tourist infrastructure in the coast has become an important threat, mostly due to untreated sewage discharges that seep into the underground water system which flows from the land to the sea (Hernández-Terrones et al., 2011, 2015; Suchley & Alvarez-Filip, 2018).

Data collection

This study compares data obtained in 1985 and in 2016. Data for 1985 were obtained by Jordan-Dahlgren (1993) which conducted an assessment of the coral reefs along the Mexican Caribbean across the main reef-zones, down to 30m depth, and generated detailed maps of their distribution. The data obtained from this historical dataset for the northern part of the Mexican Caribbean was compared to recent estimates of reef condition. The methodology used to estimate coral cover at species level was slightly different in 1985 and 2016 but, despite these differences, the two methods employed are known to produce relatively similar estimates of benthic cover (Facon et al., 2016). In 1985, surveys were conducted by means of line intercept transects (Loya, 1972) at three zones on each reef site: back-reef, reef-crest and fore-reef (Jordán-Dahlgren, 1993). In the fore-reef, surveys were conducted at four depths (5, 10, 15 and 20 m). On each zone or depth, five 20 m long transects were placed haphazardly, perpendicular to the coast, separated from each other by 5-25 m. The transects were delimited by plastic chains, with a 2.73 cm size chain link, that followed the contour of the bottom. All scleractinian corals below the chain were counted using the chain link as the measurement unit. In 2016, surveys were conducted in the back-reef and part of the reef crest (between 2-5 m deep) and in the fore-reef (between 6-13 m deep) zones following the AGRRA protocol V 5.5.(Lang et al., 2012). At each zone between six and eight 10 m long transects were placed haphazardly parallel to the coast on each reef site and surveyed using the point intercept method to determine benthic cover, including hard coral percentage cover identified at species level; transects were separated from each other by 5-25 m.

In 1985, the geographical coordinates of each reef site were not obtained as this pre-dated GPS, but to try to ensure realistic site comparisons we only selected sites in 1985 and 2016 where geographical location could be accurately constrained based on the original maps that indicated surveying locations, depth and distinct geomorphological structures (Jordán-Dahlgren, 1993). For the present study we compared only data from the back-reef zone and the ~10 m strata of the fore-reef zone. For the back-reef, we also include the reef crest, because the transects surveyed in 2016 covered both the back and part of the reef crest. After the reef site screening, the selected sites for study in the back-reef were Bonanza, Bocana, Petempich and Puerto Morelos and in the fore-reef zone were Bonanza, Nizuc and Punta Maroma (Fig. 1). For analysis, transect level data from each site were integrated into the reef zone level, and used for comparison between years. The total number of transects surveyed on the back-reef zone were 29 in 1985 and 39 in 2016, and on the fore-reef zone were 14 and 24 respectively.

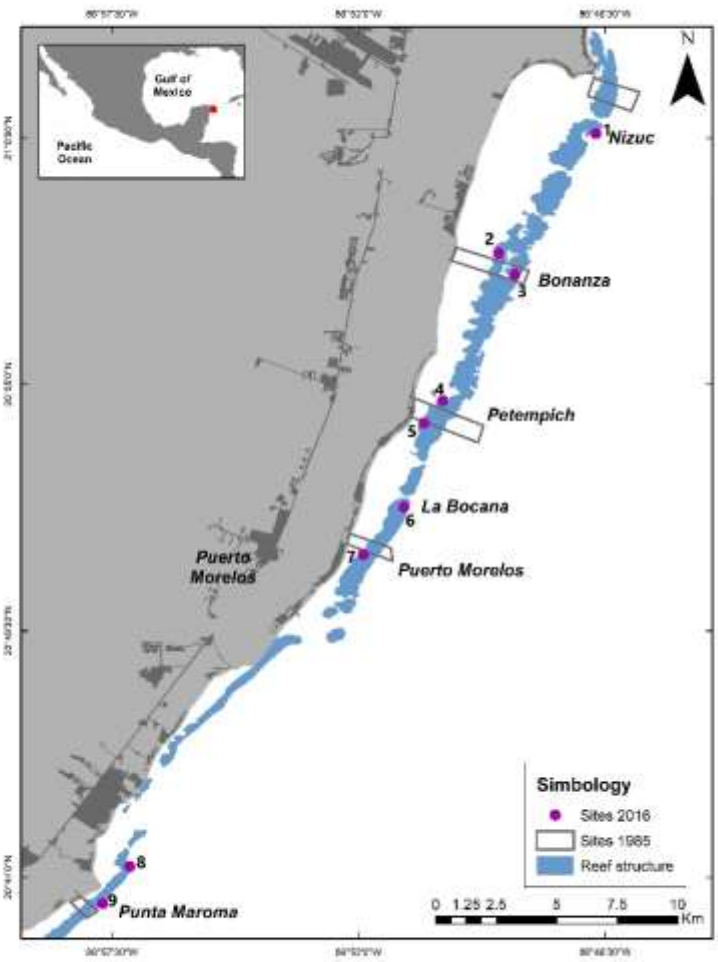

Figure. 1. Reef sites studied in the northern sector of the Mexican Caribbean to determine changes in coral composition from 1985 to 2016. The rectangles are an approximation of the study area of the sites surveyed in 1985: Nizuc, Bonanza, Petempich, Puerto Morelos and Maroma, this was taken from Jordán-Dahlgren (1993). The purple circles and the numbers represent the reef sites surveyed in 2016: 1. Nizuc, 2. Bonanza, 3. Bonanza Profundo, 4. Tanchacte Norte, 5. Tanchacte Sur, 6. La Bocana, 7. Radio Pirata, 8. Punta Maroma Norte and 9. Punta Maroma Sur. The coral reefs layer is from Millennium Coral reef Mapping Project (UNEP-WCMC).

Coral community changes

To explore changes in coral community composition between 1985 and 2016 we used two complementary approaches. First, we classified the coral species, in an attempt to establish the groups that are likely to be more persistent across time. Secondly, we assessed broader changes in coral species composition among years and reef zones.

We distinguished four main groups of corals based on colony morphology and their contribution to reef framework (Perry et al., 2014; González-Barrios & Alvarez-Filip, 2018): (a) branching corals - specifically the historically important reef framework building *Acropora* species; (b) foliose-digitiform species (*Agaricia tenuifolia* and *Porites porites)*, which contribute to reef three-dimensional structure at lower scales, create important microhabitats and are susceptible to breakage (thus generating rubble); (c) massive species that form the second important group of reef-framework species (e.g., *Orbicella*); and (d) small non-framework builder species, which some authors define as opportunistic (Darling et al., 2012) (Table S1). The mean percentage cover was estimated for each reef zone and year, both for each coral group and for the total cover.

Variation in coral species composition among years and reef zones was investigated with non-metric multi-dimensional scaling (nMDS) based on Bray-Curtis similarities of square root transformed coral cover species data in Primer v6 (Clarke & Gorley, 2006). The matrix was created with the mean coral cover by species for 1985 and 2016 at the selected sites. The cover of each coral species was used as the variable, the sites as the samples, and the years and the reef zones as factors. A two-way crossed Analysis of Similarities (ANOSIM) was used to test the significance of these groupings (9999 permutations), with years (1985 and 2016) and reef zones as factors.

To estimate the size of the coral community space between reefs zones and years, we used the nMDS resemblance similarity data to infer the *niche width* of each reef zone per year, by using the total area (TA) index; this is a measure of the area of a polygon drawn through the most extreme data points of the population in the coral community space (i.e., convex hull), and the standard ellipse area (SEA), which measures the width area of the mean coral community and contains approximately 40% of the data (Jackson et al., 2011). To compare the total area for each reef zone (i.e. back-reef, fore-reef) between years, we used the Bayesian standard ellipse area corrected for sample size (SEAc) estimated and plotted using the SIBER routine for the SIAR package in R (Parnell & Jackson, 2015) and the reef zones overlap was calculated as the proportion of SEAc overlapping (Jackson et al., 2011).

Reef functional changes

To assess changes in the functional capacity of studied reefs we first estimated coral community carbonate production (kg $CaCO_3 m^{-2} yr^{-1}$) by summing the estimated $CaCO_3$ production of each species. We then computed the Reef Functional Index (González-Barrios & Alvarez-Filip, 2018) that, in addition to the carbonate production, considers the morpho-functional attributes of each species. Finally, the net carbonate budget was calculated by subtracting an estimate of erosion to the coral production (kg$CaCO_3 m^{-2} yr^{-1}$).

Coral calcification is generally described by the product of extension rate (cm yr^{-1}) and the skeletal density (g cm^{-3}) of the coral skeleton (Dodge & Brass, 1984; Carricart-Ganivet et al., 2000). However, because the deposition of calcium carbonate varies according to different coral morphologies, we estimated calcification rates taking into account the morphological attributes of each species following González-Barrios and Alvarez-Filip (2018). A morphometric equation was used to estimate the calcification rate of each coral species, by accounting for the morphology (cylindrical growth, octahedron, paraboloid and hemispheric), growth, extension rate (cm yr^{-1}) and skeletal density (g cm^{-3}) for each coral species. By considering the characteristics of each species (morphology and growth), potential overestimations of calcium carbonate production are avoided, and thus represent the contribution of habitat forming species to carbonate accumulation. Coral calcification rates were estimated in units of kg $CaCO_3 m^{-2} yr^{-1}$. To evaluate the coral carbonate production, coral cover of each species by transect was multiplied by the calcification rate of each coral species for each reef zone and each sampling year (González-Barrios & Alvarez-Filip, 2018). Data on crustose coralline algae were not available for the 1985 surveys', however, they are typically minor components (Perry et al., 2012; pers. observation) and therefore were omitted.

The Reef Functional Index, in addition to calcification rate, integrates the rugosity and size of species. The data of each variable was first standardized because of their different scales, and then the three standardized variables were averaged to obtain a species-specific functional coefficient (Fc). The RFI values range from 0 to 1, where the value close to 1 represents an absolute dominance of one or several species with the highest calcification rates and the highest values of structural complexity (González-Barrios & Alvarez-Filip, 2018). The RFI is obtained through the fourth root of the summation of the product between live coral cover and the Fc of each species by transect for each reef zone and each sampling year (González-Barrios & Alvarez-Filip, 2018).

Net carbonate production was determined as the balance between the coral carbonate production and bioerosion rates. Due to the absence of historical data on bioeroders (*i.e*., from 1985), we assumed that bioerosion rates were similar in both periods of time. The rationale for this is that populations of *Diadema antillarum* and bioeroder parrotfishes have change little during the timespan of this period, an assumption supported by several observations. First, our historical data (1985) was collected soon after the Caribbean-wide die-off of *Diadema antillarum* (1983-1984) (Lessios, Robertson & Cubit, 1984; Lessios, 1988; Carpenter, 1990). This suggests that bioerosion rates were minimal at that time (Perry et al., 2014a), because *D. antillarum* commonly accounted for up to 75% of the total bioerosion on many reefs in the region (Bak, 1994). Since 1983, there has been very limited recovery of *D. antillarum* in the Caribbean (Hughes et al., 2010; Lessios, 2016) and thus current erosion from urchins is considered a reasonable proxy for 1985 rates. Second, although it is uncertain whether parrotfish populations have declined over the study period, populations were clearly low before the 1980s due to longstanding issues of overfishing since at least the middle 20th century (Hughes, 1994; Hughes et al., 2007; Jackson et al., 2014). Whilst recent evidence shows that parrotfish populations in the Mexican Caribbean have undergone a slight recovery due to management regulations (Suchley, McField & Alvarez-Filip, 2016; Rioja-Nieto & Alvarez-Filip, 2018), population increases have probably not been sufficient to markedly change erosion rates because small-bodied fish are more abundant that large sized fish (Hernández-Landa et al., 2015; Molina-Hernández, Garza-Pérez & Aranda-Fragoso, 2018). In summary, available evidence suggests that bioerosion rates from fish and urchins may presently be similar to those in 1985 or even slightly higher, but since these cannot be well constrained, we have used similar rates for both periods. At worst this would imply that our estimates of past (1985) net carbonate budget are conservative (*i.e.*, slightly underestimating net carbonate production).

Rates of bioerosion for 2016 were based on assessments undertaken at the same study sites in 2017/2018 using the ReefBudget methodology (Perry et al., 2012) for the back-reef and fore-reef. Briefly, the method consisted of estimating rates of erosion by different bioeroder groups: macroborers (clinoid sponges), sea urchins, parrotfish and microborers. The area covered by individual colonies of bioeroding sponges (cm^2), was determined by using a transparent 5 x 5 cm grid, within an area encompassing 0.5 m^2 either side of belt-transects of 10 x 1 m. From this, percentage surface area covered by different sponge species can be determined. To estimate sponge bioerosion rates from census data, the methodology utilized published datasets to derive a relationship between sponge tissue cover and bioerosion rate whereby bioerosion rate = % surface area of sponge tissue/papillae x 0.0231 (Perry et al., 2012; Murphy et al., 2016). For the sea-urchins the number and size class of urchins (to species) was collected in 10 x 2 m belt transects. To determine erosion rates by different species, ReefBudget uses published data on test size and erosion rate relationship, and since the bioerosion rates of *D. antillarum* and *Echinometra* spp. differs from other species, separate equations are used to calculate bioerosion rates (kg $m^{-2}yr^{-1}$) for *D. antillarum*, *Echinometra* and all 'other urchins'. Parrotfish were identified to species, phase and class size and the abundance was surveyed on 30 x 2 m belt transects. To calculate bioerosion rates, ReefBudget uses a model based on fork length as a predictor of bite rate (bites/hour) derived from two parrotfish species (*Sparisoma viride* and *Scarus vetula*) at different life-phase stages, that can be extrapolated within genera. Due to the difficulties in establishing microborer rates, the ReefBudget used the Caribbean rate data of Vogel (2000) for sites between 0 and 10 m depth at a rate of 0.27 kg $CaCO_3m^{-2}yr^{-1}$.

Data analysis

Differences between years and reef zones among all variables (coral cover of the species groups, coral carbonate production, reef functional index and net carbonate production) were tested by means of non-parametric Mann-Whitney U-tests as the data were not normally distributed, this was verified using the Shapiro-Wilk test using the package *stats* version 3.5 from R (Team, 2018).

Results

Coral community changes

From 1985 to 2016, mean coral cover in the back-reef zone showed a significant decrease from 32.90±9.39% to 16.71±3.55% (mean ± confidence intervals (CI); Mann-Whitney U test, p<0.05, value tests are in Supplementary table S2). Conversely, coral cover on the fore-reef did not change significantly (1985: 13.28±6.31%; 2016: 16.79±3.99%; Mann-Whitney U test, p>0.05, Fig. S1, Supplementary table S3). The proportion of cover by the four coral groups did change in both zones but did so in different ways. In the back-reef the cover of branching corals decreased significantly from 14.16±9.96% to 0.07±0.15% (Mann-Whitney U test, p= <0.01; Fig. 2a). The mean cover of foliose-digitiform species decreased significantly from 5.77±3.37 to 0.84±0.86% (Mann-Whitney U test, p<0.01). However, cover of massive species did not change significant during the last 31 years in the back-reef (8.93±3.32% to 13.12±3.72%; Mann-Whitney U test, p>0.05), and nor did cover of non-framework builder species (4.03±1.74 to 2.66±1.11; Mann-Whitney U test, p>0.05). In the fore-reef zone, the cover of branching species (0.85±0.94% to 0.45±0.42%), foliose-digitiform species (0.16±0.19% to 1.29±1.02%) and massive species (9.69±5.20% to 10±3.46%) did not change over time (Mann-Whitney U test, p>0.05), only the cover non-framework species increased from 2.57±1.20% to 5.04±1.46% (Fig. 2b), being statistically significant between years (Mann-Whitney U test, p<0.05).

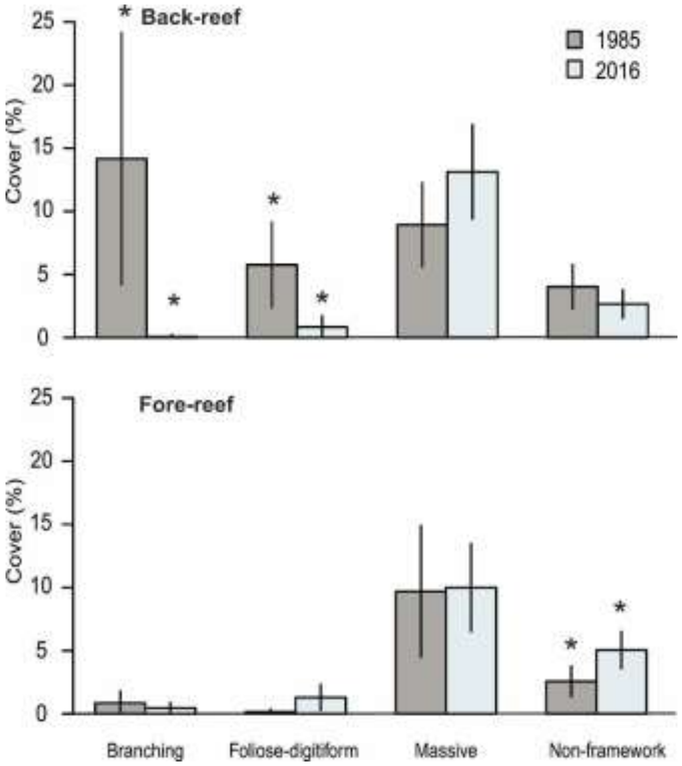

Figure 2. Coral cover of the different coral groups for the studied reef-zones during two sampling periods (1985 and 2016): a) back-reef and b) fore-reef zone. The error bars are the confidence intervals at 95% from the mean.

Coral community composition in the back- and fore-reefs zones in 1985 displayed a more scattered distribution, while that in 2016 is more tightly grouped, indicating a more similar composition between reef zones in 2016 (Fig. 3). A two-way crossed ANOSIM, showed significant differences between sampling years across reef zone groups (R= 0.624, p=0.001). The same for differences between groups across years (R=0.34, p= 0.05) although with some overlap. The total area of the coral community for each reef zone was compared between years and between reef zones from the same year. The back-reef zone in 1985 had the largest standard ellipse area (SEAc) of all the reef zones, in contrast to the fore-reef zone of 2016 which has the smaller SEAc (Table 1). Within reef zones across years, the only overlap between SEAc was in the reef zones of 2016, with much less overlap (17%) between the SEAc of the back-reef and the SEAc fore-reef in 2016, than the other way around (39%) (Table 1, Fig. 3). This overlapping between reef zones in 2016 suggests that their coral community composition is more similar than in 1985. In addition, the SEAc of the communities between reef zones is getting smaller as the coral communities become more homogeneous.

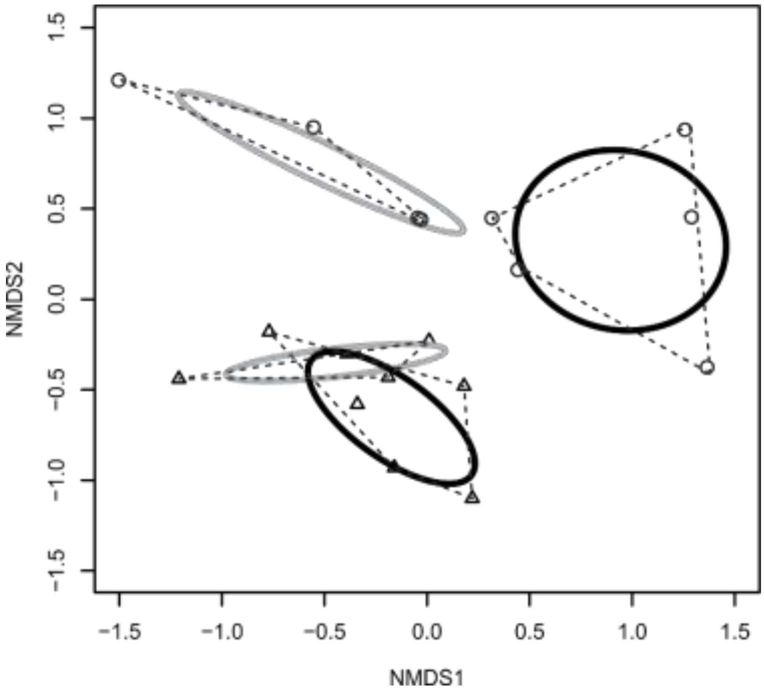

Figure 3. Coral community composition of the back- and fore-reef zones for the studied sites between sampling years. Multi-Dimensional Scaling (MDS) analysis displaying degree of similarity across 18 sites in the northern part of the MBRS for the coral cover by species. The circles represent the sites from 1985 and the triangles the ones from 2016. The black colour stands for the back-reef zone and the grey one for the fore-reef. Dotted lines: convex hull area (TA). Solid lines: standard ellipse area corrected for small sample sizes (SEAc).

Table 1. Convex hull total area (TA), Bayesian standard ellipse area (SEA), Bayesian-corrected estimate of the standard ellipse area (SEAc), overlap in SEAc between reef zones for each year, and percentage of overlap with SEAc of the reef zone between years and within the same year.

Year	**Reef Zones**	**TA units^2**	**SEA units^2**	**SEAc units^2**	**SEAc overlap units^2 (%)**
1985	Back-reef	0.77	0.80	1.07	0 (0%)
2016		0.38	0.34	0.45	0 (0%)
1985	Fore-reef	0.18	0.26	0.39	0 (0%)
2016		0.10	0.13	0.20	0 (0%)
1985	Back-reef vs. Fore-reef	0.77	0.80	1.07	0 (0%)

	Fore-reef vs. Back-reef	0.18	0.26	0.39	0 (0%)
2016	Back-reef vs. Fore-reef	0.38	0.34	0.45	0.8 (17%)
	Fore-reef vs. Back-reef	0.10	0.13	0.20	0.8 (39%)

Reef functional changes

Coral carbonate production decreased significantly (Mann-Whitney U test, p=0.01, value tests are in Supplementary table S4) in the back-reef zone between 1985 (Mean= 3.51 CI=1.66 G=kg $CaCO_3m^{-2}yr^{-1}$) and 2016 (1.38±0.38 G) (Fig. 4a). Conversely, in the fore-reef zone no significant differences (Mann-Whitney U test, p= 0.37) were recorded in coral carbonate production rates between years (1985: 0.97±0.51 G; 2016: 1.19±0.33 G).

The Functional Reef Index for the back-reef indicates a loss in the contribution of cover, rugosity and calcification of actual coral species across the study period, declining from 0.57± 0.66 (mean±CI) to 0.44±0.04, and the drop between years was statistically significant (Mann-Whitney U test, p= <0.01) (Fig. 4b). In contrast no significant changes occurred in the fore-reef zone between years (1985: 0.40±0.06; 2016: 0.45±0.03, Mann-Whitney U, p= 0.19).

Using the assumption that current rates of coral bioerosion are presently the same as in 1985, in 2016 the reefs had negative carbonate budgets, especially the shallow back-reef zone, where net carbonate production dropped significantly (Mann-Whitney U, p=0.01) from 1985 (-0.16±1.66 G) to 2016 (-2.30±0.38 G) (Fig. 4c). Although in 1985 net carbonate production was negative, the variation between transects is very large given that some transects had positive budgets. The same is true in 2016 where some transects still have a positive carbonate budget. In the fore-reef the mean net carbonate budget was negative in 1985 (-0.58±0.51 G), and in 2016 it is still negative (-0.36±0.33 G), but differences were not statistically significant (Mann-Whitney U, p=0.37).

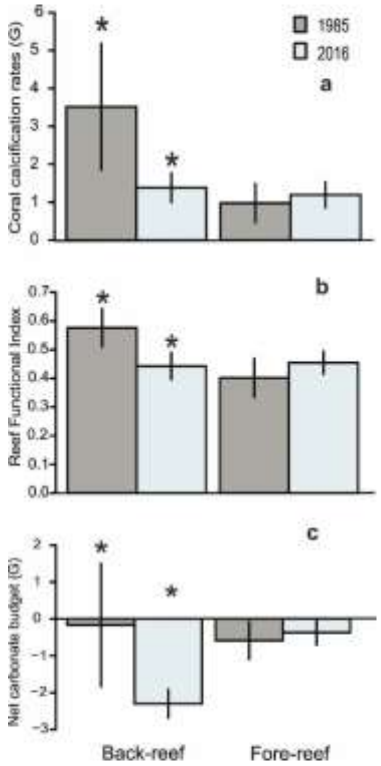

Figure 4. Reef function results for the back-reef and fore-reef for the studied sites between sampling years. **a)** Rates of coral carbonate production (G) b) The Functional Reef Index considers the morpho-functional attributes of each species by integrating the averages of calcification rates, rugosity, and height. c) Net carbonate production (G) estimated for both reef zones. The error bars are the confidence intervals from the mean.

Discussion

Coral communities in the northern Mexican Caribbean have changed rapidly over the last three decades, leading to a structural and functional convergence of the back-reef to the and fore-reef zone. In the back-reef coral cover declined by almost 50%, largely driven by the significant loss of branching, foliose and digitiform coral species; coral cover in the fore-reef remained relatively stable despite the significant increase of non-framework building coral species (*Agaricia agaricites* and *Porites astreoides*). The increase of these non-framework species had no measurable effect on the functional potential of the fore-reefs as these species contribute very little to the reef structure and carbonate production (González-Barrios & Alvarez-Filip, 2018). This ecological convergence towards the dominance of low-relief species will increasingly compromise the maintenance of reef-structure and the functional potential of the reef systems in the northern part of the Mexican Caribbean; reefs in this region are now defined by negative net carbonate budgets largely determined by the presence of bioeroding organisms rather than the contribution of carbonate producers.

Environmental gradients determine the distribution and dominance patterns of coral species across the reef profiles (Huston, 1985; Jordán-Dahlgren, 1989; Rodríguez-Zaragoza & Arias-González, 2015), and in many occasions the identity of those species defined the structural integrity and ecological complexity of the zones. For example, many reef crests across the Caribbean were historically shaped by the complex branching structures of *A. palmata* (Goreau, 1959; Gladfelter, 1982; Jordán-Dahlgren & Rodríguez-Martínez, 2003). In 1985, the back and fore-reef zones in the Mexican Caribbean were defined by distinct coral communities largely determined by the high cover of *Acropora* sp. in shallow areas and massive species on the fore-reef (~10m depth; Fig. 2). But what happens when, within a region, the coral assemblages are changing? Our study suggests that coral communities in the different reef zones changed in a non-random fashion. Specifically, major declines occurred in the important framework-building coral taxa that were the most important in delineating the back-reef zone. Conversely, an increase of non-framework species defined the main changes observed in the fore-reef zone. This modification of coral communities has led to a biologically homogenization between reef zones, whereby instead of a dominance of reef-builder coral species (a situation which was both historically and geologically the norm in the Caribbean; (Budd, 2000; Pandolfi & Jackson, 2006; Reyes-Bonilla & Jordán-Dahlgren, 2017), there are more non-framework species that cannot fulfill the same functions as reef-builders, leaving an important space vacant. This type of homogenization has also been observed in southern Florida, were the loss of massive-framework species led to a biotic homogenization within different locations, across depths and zones (Burman, Aronson & Woesik, 2012). Along with the loss of massive-framework species, climatic factors are changing the coral community assemblages, by favoring species to expand their ranges to higher latitudes. *Acropora cervicornis* has, for example, moved northwards of its previously known extant range along the Florida reef tract, and this has been associated with decadal-scale increases in annual sea-surface temperatures (Precht & Aronson, 2004). Besides the homogenization observed across depths and zones, there has also been a homogenization along a latitudinal gradient, where, contrary to our case, the loss of rare coral species and a potential distributional shift northwards of coral species have contributed to the homogenization in response to major disturbances, including bleaching events and predation by the crown-of-thorns-starfish (Riegl et al., 2012).

The increase in spatial similarity of coral communities reported here, also results in the net loss of potential to accumulate $CaCO_3$ and the capacity to sustain future structural complexity on these reefs, especially in the back-reef, which was previously the best developed zone in the north section of the Mexican Caribbean (Jordán-Dahlgren & Rodríguez-Martínez, 2003; Rioja-Nieto & Alvarez-Filip, 2018). Gross carbonate production estimates from shallow water Caribbean reefs, before recent changes in reef ecology, are reported to have been between 10-17 G (Vecsei, 2001); coral carbonate production on the back-reef in 1985 is calculated as having already been well below this, but similar to levels from some of the better sites in the Caribbean measured in recent studies (i.e. >4 kg; Fig. 4; Perry et al., 2013, 2014). This suggests that the reefs had already shifted towards net negative (and thus potentially net erosional) states before the start of our study period – a transition also suggested in recent work from Florida (Yates et al., 2017). By 2016, coral carbonate production was close to neutral, resembling the pathway being followed by the large majority of Caribbean reefs (Perry et al., 2014). In contrast, fore-reefs sites in our study historically did not have a proper reef development, therefore the carbonate production has remained low since the 1980s. Generally shallow reefs have higher accretion rates, compared with deep reef environments (Perry et al., 2013). However, if the loss of important structural species continues, the functionality of these environments could become more alike, especially in terms of their budget states. This idea has recently been discussed (Perry & Alvarez-Filip, 2018), and the data presented here would provide strong support for the notion that progressive depth-homogenization is occurring as a consequence of the shifting patterns of coral dominance. An addition issue of great concern is that the maintenance of carbonate budget states on many reefs in the Caribbean is dependent upon the massive taxa *Orbicella* sp. (Perry et al., 2013, 2014a; Kuffner & Toth, 2016), which is also rapidly succumbing to a recent emergent disease outbreak. If a demise of this species populations occurs, the implications for reef budget states will be profound (Walton, Hayes & Gilliam, 2018).

Current negative net carbonate budgets in both the back- and fore-reef zones will also compromise the ability of coral reefs to sustain high rates of reef accretion (Perry et al., 2015; Januchowski-Hartley et al., 2017); and compromise the export of rubble and sediments that can contribute to the formation of reef structures in nearby reef zones or habitats (Blanchon et al., 2017). With progressive shifts from communities dominated by reef-framework corals to slower calcifying taxa, many shallower reefs have transitioned to negative budgetary states and in some cases states of net erosion, a trend that increasingly threatens reef growth to a point where reefs will be unable to track sea level rise (Perry et al., 2018). In addition, such net erosion states could lead to a progressive breakdown of reef structural complexity (Perry & Alvarez-Filip, 2018), and loss of reef three-dimensional complexity, with implications for many reef-associated species such as fish (Alvarez-Filip, Gill & Dulvy, 2011; Darling et al., 2017). Although in many shallower Caribbean reefs, carbonate production rates have declined over the last 40 years, there are sites where carbonate production is greater than estimated bioerosion, and these could function as buffer sites within the accretionary crisis, as long as it remains in this condition for long enough. This is the case with *Limones reef* (see Fig. 1) which is located within the study area but was not part of the study because of the lack of historical data; this site has a high cover of *A. palmata* (>30%; 23), and a current estimated net production rate of 9.9 G.

The increase of non-framework species, especially in the fore-reef zone, is also transforming habitat configuration (Alvarez-Filip et al., 2013). This Caribbean-wide shift in coral assemblages has reduced the abundance and diversity of certain species traits that facilitate key ecological functions. In addition, and with the increasing anthropogenic and natural pressures, these novel assemblages are unlikely to return to historical conditions(Graham et al., 2014), because their environment has already changed (Hughes et al., 2003; Hoegh-Guldberg et al., 2007). These novel reef assemblages, with simplified reef communities, can alter ecosystem functioning and productivity, are defined by low coral carbonate production rates, and tend to have overall negative carbonate budgets. Although within these assemblages, some species have rapid calcification rates, they cannot be considered as important framework-builders capable of compensating for the loss of a robust structural complexity. Similar observations have been made on shallow fore-reef sites (10 m depth) in Bonaire and Curacao, where the relative importance of *Madracis mirabilis has* increased over 40 years and compensated for the reduction in production observed on the reefs (De Bakker et al., 2016); these new assemblages could continue functioning in a highly altered system.

The changes observed in the back-reef sites are a result of ecological decline driven both by various regional-scale factors, like coral disease and bleaching and exacerbated by local factors such as coastal development. Thus, and despite the fact that the sites are in a marine protected area, coral cover has diminished. The coastal development along the northern part of the Mexican Caribbean has been increasing in the last years, constructions often lack adequate wastewater treatment facilities and due to the karstic properties of the soil the filtration to the aquifer mantle is of great concern (Murray, 2007; Bauer-Gottwein et al., 2011). Such local land-based threats can be synergistic with other stressors, like nutrient enrichment that increases coral susceptibility to bleaching (Wiedenmann et al., 2013). As nutrient levels increase, macroalgae begins to proliferate, overwhelming the available space that will eventually overgrow corals (Bozec et al., 2008). As eutrophication increases, it is also likely that the capacity of reefs to recover will be increasingly inhibited and may become regime-shifted due to the increasing frequency of disturbance and the lack of reef resilience (Perry & Alvarez-Filip, 2018).

The dominance patterns of coral assemblages seems to be the most important driver of the functioning of coral reefs, therefore maintaining keystone coral species could enhance the future of coral reefs (Perry & Alvarez-Filip, 2018). If current deterioration continues, it may be expected that in the long term non-framework coral species could also disappear since no coral species appear to be effectively insensitive to anthropogenic impact (McClanahan, Graham & Darling, 2014). This new condition could favor the growth of other types of fauna (e.g. macroalgae, sponges, cyanobacteria), that in the future could replace coral assemblages (De Bakker et al., 2016). In a rapidly changing climate, where environmental conditions are constantly modifying, reefs with intermediate health and dominated by non-framework corals, may thus become the new norm on coral reefs (Mumby, 2017) increasing the transition away from high historical carbonate budget states to states of low net positive or negative production. Actions to address these transitions are thus urgently needed to facilitate maintenance of the key functions that reefs provide (Kuffner & Toth, 2016), such as sand supply, vertical reef accretion and maintenance of the macro- and micro-scale framework structures that create diverse habitat space and which support many of the key reef ecosystem services provided to society.

Supplemental information

Table S1. Classification of the coral species according to their form and contribution to the reef-structure.

Coral species	Coral type
Agaricia agaricites	Non-framework
Acropora cervicornis	Branching
Agaricia grahamae	Non-framework
Acropora palmata	Branching
Acropora prolifera	Branching
Agaricia humilis	Non-framework
Agaricia lamarcki	Non-framework
Agaricia tenuifolia	Foliose-digitiform
Colpophyllia natans	Massive
Dendrogyra cylindrus	Massive
Diploria labyrinthiformis	Massive
Dichocoenia stokesii	Non-framework
Eusmilia fastigiata	Non-framework
Favia fragum	Non-framework
Helioseris cucullata	Non-framework
Isophyllia rigida	Non-framework
Isophyllia sinuosa	Non-framework
Madracis aurentenra	Non-framework
Madracis decactis	Non-framework
Meandrina meandrites	Massive
Manicia areolata	Non-framework
Montastraea cavernosa	Massive
Mycetophyllia lamarckiana	Non-framework
Mussa angulosa	Non-framework
Orbicella annularis	Massive
Orbicella faveolata	Massive

Orbicella franksi	Massive
Porites astreoides	Non-framework
Pseudodiploria clivosa	Massive
Porites divaricata	Non-framework
Porites furcata	Non-framework
Porites porites	Foliose-digitiform
Pseudodiploria strigosa	Massive
Solenastrea bournoni	Non-framework
Stephanocoenia intersepta	Non-framework
Siderastrea radians	Non-framework
Siderastrea siderea	Massive

Table S2. Mann-Whitney U-test values

Years	Reef zone	Variable	U-value	P-value	Confidence interval
1985 vs. 2016	Back-reef	Coral cover	334	0.004	y1=-19.833291 y2=-3.333358
1985 vs. 2016	Fore-reef	Coral cover	200	0.3402	y1= -3.499965 y2= 11.833350
1985 vs. 2016	Back-reef	Branching	847.5	0.0000026	y1=1.529743e-05 y2=4.499947e+00
1985 vs. 2016	Back-reef	Foliose-digitiform	799	0.00005067	y1=7.190187e-05 y2=2.000051e+00
1985 vs. 2016	Back-reef	Massive	452.5	0.1627	y1=-7.500005 y2=0.833340
1985 vs. 2016	Back-reef	Non-framework	600	0.2399	y1=-7.500005 y2=0.833340
1985 vs. 2016	Fore-reef	Branching	183	0.556	y1= -8.784154e-06 y2= 3.985645e-05
1985 vs. 2016	Fore-reef	Foliose-digitiform	154	0.5837	y1= -3.027599e-05 y2= 3.782326e-05
1985 vs. 2016	Fore-reef	Massive	156	0.7274	y1= -6.500027 y2= 6.499931
1985 vs. 2016	Fore-reef	Non-framework	90	0.01857	y1= -4.3333978 y2= -0.4999497

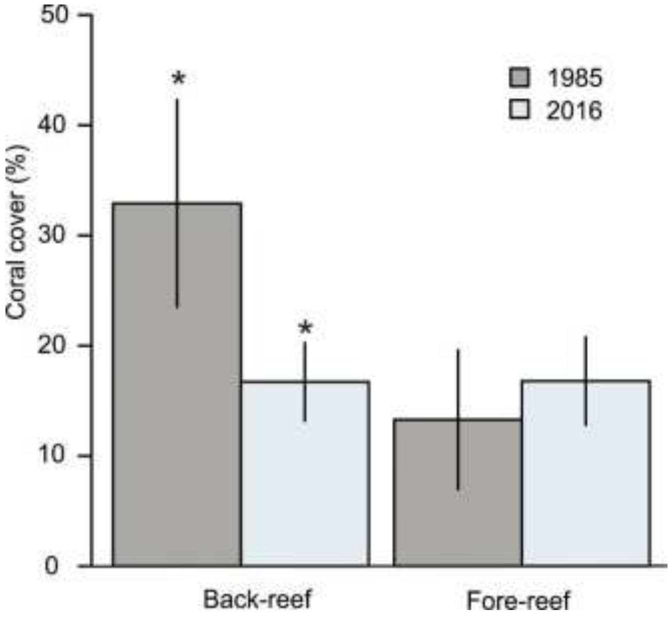

Figure S1. Average coral cover for the studied sites for the back- and fore-reef zones. The error bars are the confidence intervals from the mean

Table S3. Coral cover on the surveyed sites (n = 16) with their respective reef-zone for each year.

Site	Year	Reef zone	Coral cover (%)
Bocana	1985	Back	35.5
Bonanza	1985	Back	16.8
Bonanza	1985	Fore	4
Maroma	1985	Fore	28.5
Nizuc	1985	Fore	20.1
Petempich	1985	Fore	37.4
Puerto Morelos	1985	Back	33.8
Bonanza Profundo	2016	Fore	15.5
Bonanza	2016	Back	7.3
La Bocana	2016	Back	20.8
MX1062	2016	Fore	5.7
Punta Maroma Norte	2016	Fore	24.7
Punta Maroma Sur	2016	Fore	21.3
Radio Pirata	2016	Back	20.8

Tanchacté Norte	2016	Back	16.6
Tanchacté Sur	2016	Back	18.6

Table S4. Mann-Whitney U-test values of the reef function parameters

Years	Reef zone	Variable	W-value	P-value	Confidence interval
1985 vs. 2016	Back-reef	Coral carbonate production	755	0.01909	y1=0.1212755 y2=1.6372102
1985 vs. 2016	Back-reef	Functional Reef Index	795	0.004515	y1= 0.02737289 y2= 0.18858781
1985 vs. 2016	Back-reef	Net carbonate production	755	0.01909	y1=0.1212755 y2=1.6372102
1985 vs. 2016	Fore-reef	Coral carbonate production	124	0.3767	y1=-0.8126667 y2=0.2479000
1985 vs. 2016	Fore-reef	Functional Reef Index	124	0.1906	y1=-0.16145356 y2=0.02694995
1985 vs. 2016	Fore-reef	Net carbonate production	138	0. 3767	y1=-0.8126667 y2=0.2479000

DISCUSIÓN GENERAL

Las comunidades coralinas en los arrecifes del norte de Quintana Roo han sufrido un deterioro ecológico y funcional en las últimas décadas. Esto se evidencia notablemente en la homogeneización presentada entre las zonas arrecifales, debido a la pérdida de especies clave para el desarrollo del arrecife en la zona posterior y al aumento de especies no-constructoras en la zona frontal. Este cambio pone en riesgo la acreción arrecifal futura, ya que actualmente los presupuestos de carbonato están en estado negativo, es decir, la bioerosión sobrepasa la calcificación de la comunidad coralina. Este fenómeno es de suma importancia debido a las repercusiones ecológicas que puede traer consigo, debido a que el mantenimiento futuro de la estructura arrecifal se verá seriamente comprometido y con ello el hábitat de diversas comunidades de organismos. De igual forma se ve comprometida la capacidad de seguir el ritmo del cambio en el nivel del mar (Perry et al., 2018). Estos resultados coinciden con el panorama actual general del Caribe (Perry et al., 2014; Januchowski-Hartley et al., 2017), donde muchos arrecifes presentan presupuestos neutros o negativos de carbonato, y sólo aquellos con un alta cobertura de especies constructoras (p.ej. *Orbicella* spp. y *Acropora* spp.) siguen presentando presupuestos positivos de carbonato.

Para conocer el estado de un sitio, es esencial conocer qué especies estaban presentes en un momento determinado, a partir de ello se pueden evaluar las funciones ecológicas que desempeñan dentro del sistema. Para evaluar el cambio en dicho sitio, es importante contar con una serie de tiempo o en su defecto, tener un estado pasado y un estado actual para efectuar la comparación. En el caso de los arrecifes de coral del Caribe existen bases de datos continuas, a partir de las cuales se han evaluado las trayectorias de cambio ecológico (p.ej., Gardner et al., 2003, 2005; Alvarez-Filip et al., 2011b; Jackson et al., 2014), en cambio, para los arrecifes del norte de Quintana Roo la información disponible no es continua, especialmente entre 1970-1990 , por lo tanto, para este estudio se decidió comparar un tiempo pasado y un tiempo presente. En este sentido, una de las limitaciones presentadas en el estudio fue que los datos utilizados para la comparación entre años fueron tomados con distintas metodologías (transectos de línea y de punto de intersección), lo que genera un ligero sesgo para analizar los datos, sin embargo, diversos estudios han comparado la eficacia y precisión de ambos métodos para medir la cobertura coralina, realizados en diferentes regiones y hábitats, y encontraron que hay una correlación positiva entre estos, lo cual hace comparable los resultados obtenidos (Beenaerts & Vanden Berghe, 2005; Facon et al., 2016; Darling et al., 2017). Otro punto importante fue la falta de datos para cuantificar la bioerosión en 1985, en México no se cuenta con datos sobre abundancia de peces loro o erizos, ni sobre esponjas excavadoras (p.ej. *Cliona* sp.), por lo tanto, se asumió que la bioerosión actual es la misma que en el pasado. Esto debe de tratarse con cuidado, ya que existen diversos factores que podrían contribuir a que la bioerosión del tiempo anterior sea menor a la considerada actualmente. Por ejemplo, la mortandad del mayor bioerosionador *D. antillarum* ya se había presentado desde principios de la década de 1980 (1983-1984; Lessios, 1988). En una revisión treinta años después, Lessios (2016) señala que la recuperación de este erizo ha sido muy pausada y localizada, por lo que en determinado momento se podría haber presentado una ligera recuperación en los sitios monitoreados. Algo similar sucede con los peces loro, a pesar de que en México no ha existido una pesca dirigida hacia estas especies, de acuerdo a observaciones personales de algunos autores, los peces loro son víctimas de la pesca incidental (Hernández-Landa et al., 2015). Aunado a ello, en 1985 no existía el Parque Nacional Arrecife de Puerto Morelos que actualmente protege los sitios estudiados, por lo tanto en el pasado podrían haber estado sometidos a algún tipo de presión, resultando en una menor abundancia de peces loro y en consecuencia la presión por bioerosión sería menor, teniendo presupuestos de acreción arrecifal mayormente positivos.

Agentes de cambio en los arrecifes del Caribe mexicano

El declive en la cobertura y por ende en la función arrecifal es resultado de una sinergia de distintos factores, de los cuales los derivados por actividades antropogénicas son los de mayor daño. Por ejemplo el aumento en la temperatura media del mar ha ocasionado que los eventos masivos de blanqueamiento (p.ej. el ocurrido en 1998), sean cada vez más frecuentes, el último evento prolongado ocurrió entre 2014-2016, ocasionando una alta pérdida de la cobertura coralina a nivel mundial, pero se prevé que en las próximas décadas estos episodios sean más frecuentes (Levas et al., 2018). Además del blanqueamiento, las enfermedades han contribuido a la pérdida de especies constructoras de arrecife, por ejemplo, entre 1980-1990 las enfermedades de la banda blanca y viruela blanca diezmaron las poblaciones de los constructores arrecifales *Acropora palmata* y *A. cervicornis*, de los cuales hasta la fecha sus poblaciones no se han recuperado (Rodríguez-Martínez et al., 2014). Junto con el aumento en los eventos de blanqueamiento, también se prevé un aumento en la prevalencia y gravedad de las enfermedades coralinas (Maynard et al., 2015). Actualmente la epizootia del síndrome blanco letal está afectando severamente a poblaciones de múltiples especies de coral (p.ej. *Pseudodiploria strigosa*, *Diploria labyrinthiformis*, *Siderastrea siderea, Colpophyllia natans, Mendrina meandrites*). Este síndrome se caracteriza por generar lesiones en forma de banda o parches irregulares, los cuales se van expandiendo hasta matar la colonia entera en un corto período de tiempo. Se reportó primeramente en 2014, en los arrecifes de Florida, a lo largo de cuatro años fue extendiéndose hasta llegar a los cayos del sur en 2018 (Precht et al., 2016; Walton, Hayes & Gilliam, 2018). Para México, esta enfermedad se empezó a registrar en el verano de 2018 dentro del Parque Nacional Arrecife de Puerto Morelos, al norte de Quintana Roo, extendiéndose rápidamente por todo el Caribe Mexicano en un período de seis meses (julio-diciembre de 2018), pero en el transcurso de 2019 la enfermedad continúa afectando a las distintas especies. El impacto que esta epizootia puede tener en la función arrecifal, aún no ha sido medido, pero puede ser mayor al causado por la banda blanca en la década de 1980, que ocasionó la pérdida de *Acropora palmata.* El número de especies afectadas es mayor, alrededor de 20 especies, dentro de las cuales se encuentran importantes constructores arrecifales, contribuyendo considerablemente a la función arrecifal (Perry et al., 2014; González-Barrios & Alvarez-Filip, 2018).

En el estado de Quintana Roo el desarrollo turístico masivo representa un importante estresor para los arrecifes circundantes. Desde 1970 el número de construcciones hoteleras, campos de golf y plazas comerciales, ha ido creciendo exponencialmente para satisfacer la demanda turística (Mata-Lara et al., 2018). Este desarrollo desmedido, ha traído consigo la deforestación de selva y manglar, así como la contaminación de las aguas tanto del manto freático como del mar. El mal manejo de los residuos y la falta de plantas de tratamiento para el agua ha provocado que los niveles de nutrientes aumenten en aguas costeras (Murray, 2007; Hernández-Terrones et al., 2015). Bozec y colaboradores (2008) observaron que el desarrollo costero ha afectado la resiliencia de los arrecifes de Quintana Roo, en especial los arrecifes del norte, los cuales tendrían un menor potencial de recuperación después de un disturbio (p.ej. huracanes). De acuerdo a un modelo realizado por Suchley y Alvarez-Filip (2018) para evaluar la efectividad de las áreas marinas protegidas, las actividades costeras tienen una influencia negativa sobre la cobertura coralina, por lo tanto, para mejorar la efectividad de las AMPs, es necesario regular adecuadamente el manejo costero. Aunado al mal manejo de los residuos, el arribo masivo de sargazo que ha afectado los arrecifes del Caribe mexicano desde 2014 a la fecha (Rodríguez-Martínez & Van Tussenbroek, 2016), ha generado la mortandad de diversos organismos, como pastos marinos y colonias de coral, debido a la reducción de luz, oxígeno y pH causada por la marea marrón producto de la descomposición del sargazo que se encuentra en la costa, lo que también provoca un incremento en los nutrientes (van Tussenbroek et al., 2017).

Este trabajo hace una comparación entre un estado pasado (1985) y un estado actual (2016), donde vemos que la pérdida de corales constructores ha llevado a una homogenización estructural y funcional entre las zonas arrecifales. Esta pérdida fue ocasionada por distintos factores (p.ej. enfermedades coralinas, eventos de blanqueamiento, incremento de los nutrientes). De no mejorar las condiciones ambientales actuales, la tendencia de homogenización entre las zonas arrecifales encontrada en los arrecifes del norte de Quintana Roo, podría encontrarse en el resto del Caribe mexicano. Teniendo arrecifes corales que calcifiquen poco y una bioerosión alta.

El contar con datos de distintos tiempos para una comunidad en un sitio de interés nos permite hacer una comparación de cómo ha cambiado dicha comunidad y ayuda a identificar ciertos sucesos que pudieron haber propiciado dicho cambio. Por lo tanto es recomendable el tener monitoreos continuos, esto resulta de importancia, en especial para los manejadores de Áreas Naturales Protegidas ya que al tener una base de datos con información en distintos años, se puede realizar un análisis para identificar si ha ocurrido algún cambio en la comunidad coralina, por ejemplo un declive de la cobertura de especies clave. También se pueden identificar sitios clave que necesiten de protección especial debido al tipo de especies que los compongan, por ejemplo el proteger un sitio con alta cobertura de corales constructores resulta de importancia para mantener las funciones estructurales del arrecife. En conjunto está información les podría ayudar a modificar el uso que se les da a ciertos sitios, para resguardar la funcionalidad del arrecife.

CONCLUSIONES

- La homogeneización biológica y funcional observada entre las zonas arrecifales (posterior y frontal), no había sido reportada anteriormente para los arrecifes del norte de Quintana Roo.
- Actualmente la zona posterior del arrecife se encuentra en un estado negativo de acreción, por lo que la estructura arrecifal futura está seriamente comprometida.
- En la zona frontal del arrecife no se observó algún cambio significativo, posiblemente a que el arrecife no tiene una estructura propiamente desarrollada.
- A pesar de que la mayoría de los arrecifes se encuentran dentro de un Área Natural Protegida, la protección no contempla actividades terrestres.
- Se recomienda generar planes de manejo para regular el desarrollo costero, el tratamiento de aguas residuales y para el levantamiento y tratamiento del sargazo que arriba a las costas de Quintana Roo.

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