Habitat complexity in coral reefs: patterns of degradation and consequences for biodiversity

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A mi familia, esta tesis no es más que el resultado
del amor y apoyo que he recibido
de ustedes a lo largo de mi vida

A México, por sus colores, por su magia, por su gente

Nature is not fragile . . . what is fragile are the
ecosystems services on which humans depend
Levin, S.

Contents

Abstract

Habitat destruction and degradation are primary causes of loss of biodiversity and ecosystem services. In the marine realm, there is the overwhelming concern about the rates of decline of coral reefs, which sustain thousands of species and support millions of livelihoods. Although declines in reef-building corals have been reported across different regions of the world, the concomitant consequences for reef architectural complexity have not been quantified to date. This in part is because the true nature of the relationship between live coral cover and reef architecture has yet to be described in detail. In this thesis, I describe the patterns of change in architectural complexity and explore the relationships between reef complexity, coral cover and the identity of reef-building corals in the Caribbean, a region in which coral reefs are highly threatened and degraded.

Using an extensive database of studies reporting coral cover and reef rugosity over the last 40 years, I provide region-wide analyses of changes in reef architectural complexity. The results show that reef complexity has declined non-linearly with near disappearance of the most complex reefs over the last 40 years. The loss of coral cover is directly followed by reductions in complexity with little time-lag, and that there is little correspondence between the overall rates of change in coral cover and reef architecture, probably due to spatial variation in coral composition on reefs. Major drivers of coral mortality, such as coral bleaching, do not immediately influence architectural complexity, instead hurricane impacts and enhanced bioerosion inside protected areas appear to be important drivers of the widespread loss of architecturally complex reefs in the Caribbean.

Through detailed studies of coral reefs in Cozumel, Mexico, I then show that although reef architectural complexity increases with coral cover, the rate of increase is highly dependent on the identity of dominant corals, with important reef-building coral such as Montastrea providing the most complex reefs. that the most complex remaining reefs in Cozumel, particularly those dominated by robust *Montastrea* corals, support fish assemblages with higher mean trophic levels and larger abundances of small-bodied fishes. This highlights the importance of complex reefs for fish recruitment, and thus the need to protect and enhance complex reef structures in order to maintain reef fisheries and biodiversity in the Caribbean.

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General Introduction

Global ecosystems are changing at an unprecedented rate, largely as a consequence of several human-induced drivers of change (Pimm *et al*. 1995; Vitousek *et al*. 1997; Sala *et al*. 2000; Hoekstra *et al*. 2005). Although recent international efforts to halt rates of loss (Balmford & Bond 2005), most indicators of the state of biodiversity indicate ongoing declines, with no significant reductions in rate (Butchart *et al*. 2010). Habitat degradation has been shown to be one of the primary causes of species endangerment and ecosystem simplification (Pimm *et al*. 1995; Tilman *et al*. 2001), and habitat loss is considered to be a significant cause of increased risk of extinction in many terrestrial and marine species (Temple & Cary 1988; Owens & Bennett 2000; Dulvy *et al*. 2003; Costello *et al*. 2010). The degradation of habitat also has a considerable effect on the capacity of ecosystems to provide fundamental environmental services. For example, the loss of forest cover can reduce water flow and yield to agricultural and urban areas (Maass *et al*. 2005; Brauman *et al*. 2007), and degraded coastal ecosystems are associated with reduced fisheries yields and increasing social and economic costs following tropical storm impacts (Aburto-Oropeza *et al*. 2008; Costanza *et al*. 2008). The understanding of the trends, drivers and consequences of habitat loss may therefore help to prioritise the conservation efforts to restore the benefits that ecosystems provide to biodiversity and humans.

Coral reefs are highly heterogeneous marine environments. They make up only 0.2% in area of marine environments, and yet they harbour around one third of all described marine species (Reaka-Kudla 2001; Spalding *et al*. 2001). Unfortunately they are also among the most rapidly changing ecosystems in the world (Bryant *et al*. 1998; Halpern *et al*. 2007). Drivers of coral reefs degradation range from direct damage due to destructive human practices (McManus 1997; Barker & Roberts 2004; Saphier & Hoffmann 2005), to the loss of ecological resilience due to the harmful algal blooms resulting from the loss of herbivory and coastal eutrophication (Fabricius *et al*. 2005; Mumby 2006). More recently, climate change has emerged as an additional and serious threat to coral reefs, which can be manifest in at least three ways. Current rates of increases in sea temperatures have been associated with widespread bleaching events, in which temperature-induced stress results in the loss of symbiotic algae that live within coral tissue; (Hoegh-Guldberg 1999; Hoegh-Guldberg *et al*. 2007; Veron *et al*. 2009), and disease outbreaks (Harvell *et al*. 2002; Bruno *et al*. 2007). In addition, increasing CO_2 concentrations poses the threat of ocean acidification, which may result in the dissolution and/or reduced deposition of the calcium carbonate skeletons of reef building corals (Kleypas *et al*. 1999; Hoegh-Guldberg *et al*. 2007; Kleypas & Yates 2009). Finally, rising sea levels, primarily as a consequence of thermal expansion resulting from global warming, may potentially drown some reefs (Pittock 1999; Barnett & Adger 2003; Veron *et al*. 2009).

Reef deterioration may occur as a direct response to an individual stressor such as mass bleaching (Darling *et al*. 2010), but it more commonly occurs in response to combinations of different stressors acting simultaneously, and occasionally synergistically, to increase coral mortality or reduce coral growth and reproduction (Green & Bruckner 2000; Hughes *et al*. 2003; Crain *et al*. 2008; Darling & Côté 2008). After mass bleaching events, for example, coral growth may remain suppressed for considerable periods of time in sites with high anthropogenic stressors (Carilli *et al*. 2009; 2010). As result of this wide range of drivers of change and their interactions, the cover of reef-building corals has decreased rapidly on tropical reefs throughout the world (Gardner *et al*. 2003; Bellwood *et al*. 2004; Bruno & Selig 2007), which has resulted in the loss of a least 20% of the total cover of tropical reefs. Most of the remaining coral reefs are seriously perturbed and threatened (Wilkinson 2008).

The ecological degradation of coral reefs is likely to affect the associated ecosystem goods and services provided to humanity (Costanza *et al*. 1997; Adger *et al*. 2005; Balmford & Bond 2005). The world's coral reefs support the livelihood of well over 250 million people, especially in the developing world, providing protein in the form of fisheries resources and supporting a global tourism industry (Moberg & Folke 1999; Cinner *et al*. 2009; Hughes 2009). In addition, reef systems protect essential mangrove, seagrass and lagoon habitat that are support vulnerable life stages of a wide range of commercially exploited species (Nagelkerken *et al*. 2002; Mumby *et al*. 2004), and shield coastlines from wave erosion and tropical storms (Gourlay & Colleter 2005; Sheppard *et al*. 2005; Koch *et al*. 2009). The consequences of coral reef destruction would not be limited to the loss of the value of these goods and services, but the demise of reefs would also represent the lost of a large proportion of the world's marine biodiversity (Veron *et al*. 2009). For example, within reef-building corals alone, one third of species are currently facing increasing risks of extinction (Carpenter *et al*. 2008).

Because of the importance of hard coral cover in building and structuring the reef matrix, most of the interest in understanding and protecting against reef degradation has focused on exploring the trends, drivers and consequences of the loss of live coral cover (e.g. Gardner *et al*. 2003; Côté *et al*. 2006; Gill *et al*. 2006; Bruno & Selig 2007; Schutte *et al*. 2010). However, most of the ecological and socio-economic value of coral reefs is provided not just by the cover of live coral, but also by the intricate three-dimensional architecture that reef corals promote. Reef architectural complexity is therefore more likely to have substantial ecological, economical and social relevance. For instance, reef complexity is strongly related to the availability of shelter and refugia, and consequently to fish and invertebrate richness, abundance and biomass (e.g. Risk 1972; Dulvy *et al*. 2002; Gratwicke & Speight 2005; Idjadi & Edmunds 2006; Wilson *et al*. 2007). Reef architectural complexity also plays a key role in providing additional important environmental services to humans such as coastal protection. Wave energy transmitted over reefs is significantly dissipated by the friction exerted by bottom roughness (Lugo-Fernandez *et al*. 1998; Sheppard *et al*. 2005). A decreased architectural complexity would therefore be expected to offer less resistance to water flow, thus increasing the risks of coastal erosion and flooding of low-lying areas, with associated heightened economic and social costs for coastal communities. The consequences of reef-framework degradation for shoreline protection were apparent in Sri Lanka during the 2004 tsunami, when sections of coastline for which reef structure had been impacted by poaching and mining were unable to provide an effective buffer against the wave energy, and water inundation and wave heights were considerably more severe than in those areas protected by healthy reefs (Kunkel *et al*. 2006; Fernando *et al*. 2008).

Despite the importance of reef architectural complexity, little is known of how current losses in the cover of reef-building corals and associated components of benthic communities influence reef complexity. The Caribbean is unfortunately an exceptionally good model system in which to explore these issues, given the dramatic degradation that has been evident across the region in recent decades. Caribbean reefs have been intensively studied since the 1970s, enabling a detailed description of changes in biodiversity (live coral cover, macroalgae and fishes; Gardner *et al*. 2003;

Bruno *et al*. 2009; Paddack *et al*. 2009; Schutte *et al*. 2010), and the effects of the major drivers of change including hurricanes, diseases outbreaks, overfishing and human-induced climate change (Aronson & Precht 2001; Jackson *et al*. 2001; Gardner *et al*. 2005; McWilliams *et al*. 2005; Sheppard & Rioja-Nieto 2005; Aronson & Precht 2006). Declines in coral cover started in the late 1970s, when the major reef-formers *Acropora palmata* and *A. cervicornis* (Elkhorn and Staghorn corals) suffered dramatic population reductions as result of widespread infection with white-band disease (Aronson & Precht 2001, 2006; Schutte *et al*. 2010). Thereafter, the die-off of the black sea urchin (*Diadema antillarum*), a major consumer of macroalgae, combined with the long-term depletion of herbivorous fishes through over-fishing, facilitated the gradual increase in macroalgae on many reef sites (Carpenter 1988; Jackson *et al*. 2001; Bruno *et al*. 2009). More recently, reef-building corals in the Caribbean and elsewhere face new threats from the increase in atmospheric green house gases, as coral bleaching and mortality become progressively worse as thermal anomalies intensify and lengthen, and ocean acidification is compromising carbonate accretion and therefore the reef building process (Hughes *et al*. 2003; McWilliams *et al*. 2005; Hoegh-Guldberg *et al*. 2007).

Thesis outline

In this thesis, I use a combination of regional and local-scale analyses to investigate three major questions: (1) how has reef architectural complexity changed in the Caribbean, (2) how do coral cover and different drivers of change on reefs influence reef complexity, and (3) what are the consequences of the degradation of reef complexity for reef-associated fishes? As local differences in reef structure and composition can make it difficult to scale-up findings from small-scale studies (Levin 1992; Hughes & Connell 1999; Purvis & Hector 2000; Pandolfi *et al.* 2005) and thus identify the effects of different drivers (Aronson & Precht 2006; Bruno & Selig 2007; Halpern *et al.* 2007), in the first three chapters I use a large-scale approach to explore patterns of change at the region-wide level. Following on from these studies, I then carry out a detailed local-scale field study in order to identify the mechanisms that are likely to influence the large-scale patterns, and to explore the possible consequences for reef-associated biodiversity.

In ***Chapter 1***, I provide a region-wide analysis describing the trend in change of reef architectural complexity since the 1970s, and explore whether these trends vary between different sub-regions and depth strata. ***Chapter 2*** focuses on exploring the temporal and spatial covariation between live coral cover and reef architectural complexity, using a Caribbean-wide dataset of temporally-replicated measures of reef structure spanning four decades. In ***Chapter 3***, I use a meta-analysis to examine how annual rates of change in architectural complexity across the Caribbean are influenced by three key drivers of change on coral reefs: hurricanes, coral bleaching and fisheries. ***Chapter 4*** uses field data that I collected in Cozumel, Mexico to explore the contribution of different types of coral to reef architectural complexity. Specifically I explore the role of coral diversity, coral community composition and the taxonomic and functional attributes of coral dominance. ***Chapter 5*** examines the influence of the architectural complexity of reef-building corals on reef- associated fishes. In particular, I compare diversity, abundance, biomass and the trophic and size structure of reef fishes along a gradient of coral cover, species dominance and architectural complexity. Finally, in the ***Concluding remarks***, I synthesize the key findings of this research and discuss the implications for coral reef management, and future research

Chapter 1

Flattening of Caribbean coral reefs: region-wide declines in architectural complexity

Abstract

Coral reefs are rich in biodiversity, in large part because their highly complex architecture provides shelter and resources for a wide range of organisms. Recent rapid declines in hard coral cover have occurred across the Caribbean region, but the concomitant consequences for reef architecture have not been quantified on a large scale to date. We provide the first region-wide analysis of changes in reef architectural complexity, using nearly 500 surveys across 200 reefs, between 1969 and 2008. The architectural complexity of Caribbean reefs has declined non-linearly with near disappearance of the most complex reefs over the last 40 years. The flattening of Caribbean reefs was apparent by the early 1980s, followed by a period of stasis between 1985 and 1998 and then a resumption of the decline in complexity to the present. Rates of loss are similar on shallow (< 6 m), mid-water (6 - 20 m) and deep (> 20 m) reefs and are consistent across all five subregions. The temporal pattern of declining architecture coincides with key events in recent Caribbean ecological history: the loss of structurally-complex *Acropor*a corals, the mass mortality of the grazing urchin *Diadema antillarum*, and the 1998 ENSO-induced world-wide coral bleaching event. The consistently low estimates of current architectural complexity suggest regional-scale degradation and homogenisation of reef structure. The widespread loss of architectural complexity is likely to have serious consequences for reef biodiversity, ecosystem functioning and associated environmental services.

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Introduction

The physical structure of a habitat profoundly influences its associated biodiversity and ecosystem functioning (MacArthur & MacArthur 1961), with more complex habitats facilitating species coexistence through niche partitioning and the provision of refuges from predators and environmental stressors (Bruno & Bertness 2001; Willis *et al.* 2005). In tropical shallow waters, the calcium carbonate skeletons of stony corals contribute to reef frameworks that sustain the most diverse ecosystem in our seas (Spalding *et al.* 2001). However, coral reefs have been heavily impacted worldwide by a combination of local and global stressors, including overfishing, climate change-induced coral bleaching, eutrophication and diseases (Hughes *et al.* 2003). The marked declines in live hard coral cover documented over recent decades throughout the Caribbean and the Indo-Pacific regions (Gardner *et al.* 2003; Bruno & Selig 2007) exceed those reported for many other foundation species in terrestrial or marine ecosystems (Balmford *et al.* 2003). However, in contrast to other ecosystems where degradation usually indicates reductions in habitat area (e.g., deforestation), decreases in live coral cover on coral reefs do not immediately result in loss of available habitat because the reef framework can persist long after the death of corals.

In the Caribbean, declines in live coral cover began in the late 1970s, when substantial loss of the major reef-forming corals *Acropora palmata* and *A. cervicornis* occurred as a result of with white-band disease (Aronson & Precht 2001). Coral mortality, in combination with the mass mortality of the black sea urchin (*Diadema antillarum*), which was a major remover of algae, and the long-term depletion of herbivorous fishes through overfishing, facilitated phase-shifts to macroalgal dominance on many reefs (Carpenter 1988; Precht & Aronson 2006). In the Caribbean and elsewhere, reef-building corals now face new threats from climate change, particularly in the form of thermally-induced coral bleaching and mortality, which are becoming increasingly frequent and extensive as thermal anomalies intensify and lengthen (Hughes *et al.* 2003; McWilliams *et al.* 2005).

A potential consequence of the widespread reduction in Caribbean coral cover is a reversal of the historic net accretion of calcium carbonate, resulting in a decrease in calcification and erosion of the reef framework. At local scales, hard coral mortality is associated with the loss of architectural complexity and 'reef flattening' after direct impacts, such as hurricanes through the breakage of coral skeletons (e.g. Rogers *et al.* 1982). Reefs may also erode gradually owing to the natural activity of host organisms, such as herbivorous fishes and sea urchins, and by physical abrasion or geochemical shifts. However, widespread mortality of hard corals, for example after severe bleaching events moves the balance toward net reef erosion (Sheppard *et al.* 2002). These impacts could be exacerbated in the future by ocean acidification, which is expected to enhance calcium carbonate dissolution with negative consequences, initially for coral growth and eventually for the entire reef framework (Hoegh-Guldberg *et al.* 2007).

The ecological and socio-economic consequences of declining architectural complexity are likely to be substantial (Pratchett *et al.* 2008). For many reef organisms, risk of predation is influenced by access to refuges, and the densities of herbivores and grazing rates typically increase with architectural complexity (Beukers & Jones 1997; McClanahan 1999; Almany 2004; Lee 2006). Consequently the species richness, abundance and biomass of coral reef fishes and invertebrates are all influenced by architectural complexity (e.g. Gratwicke & Speight 2005; Idjadi & Edmunds 2006; Wilson *et al.* 2007). The loss of architectural complexity may therefore drive declines in diversity, particularly of habitat specialists, and compromise fisheries productivity through elevated post-settlement mortality (Beukers & Jones 1997; Graham *et al.* 2007). Reef architectural complexity also plays a key role in providing important environmental services to humans, including enhancing coastal protection through the dissipation of wave energy transmitted over reefs (Lugo-Fernandez *et al.* 1998).

While recent regional-scale analyses have revealed declines in hard coral cover (Gardner *et al.* 2003; Bruno & Selig 2007), the consequences for reef habitat complexity on a similar large scale have not been quantified. The capacity of reefs to continue to perform key functions of refuge provision and coastal protection will depend on whether reef architecture persists for a substantial period of time following the loss of live coral. Here we collate published and unpublished estimates of reef complexity spanning four decades from reefs across the Caribbean, a region with clear evidence of recent declines in coral cover. We explore the rate and timing of changes in reef architecture in relation to region-wide events, such as the demise of *Acropora* corals and grazing urchins. As the drivers of reef degradation are apparent throughout the Caribbean, we also examine whether the patterns are consistent throughout the entire region.

Material and methods

Estimating architectural complexity

Habitat complexity on coral reefs has been measured using a variety of methods which differ in the attributes measured, the scale of measurement and the degree of subjectivity (with attendant variation in inter-observer comparability). To determine which methods are commonly used by researchers to measure habitat complexity on coral reefs, we conducted a preliminary literature search using the ISI web of Knowledge in July 2007 for papers containing any of the following words in the title, abstract or keywords: “rugosity”, “spatial heterogeneity”, “spatial index”, “habitat structure”, “habitat complexity”, “structural complexity”, “substratum complexity”, “reef relief”, “coral complexity”, and “complexity index”. Additionally, the same words were searched in the entire text of the 1368 papers published in Volumes 1 (June 1982) to 26 (September 2007) of the journal Coral Reefs. We retained all papers that reported work carried out in the Caribbean and in which the methodology used to measure architectural complexity was clearly explained. A total of 49 papers met these two criteria. The description and frequency of use of the various methodologies used to describe habitat complexity in Caribbean coral reefs are presented in table 1.

The rugosity index is by far the most widely used method for measuring reef architectural complexity (table 1), and is generally highly correlated with other methods (Wilson *et al.* 2007). Studies reporting the rugosity index were therefore chosen to quantify spatial and temporal variation in the architectural complexity of reefs across the Caribbean.

The rugosity index is expressed as the ratio between the total length of a chain and the length of the same chain when moulded to a reef surface. A perfectly flat surface would have a rugosity index of one, with larger numbers indicating a greater degree of architectural complexity (figure 1). The index tends toward infinity with increasing architectural complexity; however, rugosity estimates greater than three are very rare.

Table 1. Description and percentage of use (% of studies) of methodologies used to measure reef structural complexity in the Caribbean.

Method	**%**
Rugosity index. A fine-link chain is laid over the contours of the substratum, and the ratio between the total length of the chain (a) to the planar distance between the ends of the chain (b) is calculated. The greater the ratio, the more complex the substratum. Some papers use a modified rugosity index: 1- (b / a).	59.2
Visual assessment. Semi-quantitative estimates of reef structural complexity on an arbitrary scale, e.g. scores 0–5 where 0 corresponds to a totally flat surface and 5 represents maximum reef complexity.	14.3
Maximum relief. The difference (usually in cm) between the lowest and highest points of the substratum along a transect or within a quadrat. Larger differences indicate greater complexity.	10.2
Remote sensing. Optical analyses of data obtained from aerial photographs or scanners (e.g., light detection and ranging altimeter).	10.2
Layers. An imaginary vertical line is placed through a transect or quadrat and the number of times it passes from coral to water to coral again represents structural complexity. A structural complexity value of 0 indicates a flat surface, while greater values represent a substratum with more layers and hence more complexity.	4.1
Number of holes. The number of holes of different sizes within an area or transect is counted, and complexity increases with increasing number of holes.	2.0

Data search

A database of quantitative surveys that measured reef rugosity within the wider Caribbean was compiled. We searched online ISI Web of Science, Google Scholar and other relevant databases (e.g. Reefbase) for peer-reviewed and grey literature using several search terms (see previous section for examples). We also searched for papers that used the rugosity index in all issues of the journals *Coral Reefs*, *Bulletin of Marine Sciences*, *Atoll Research Bulletin*, *Caribbean Journal of Science* and in all *Proceedings of the International Coral Reef Symposium*. Additionally, we contacted directly coral reef scientists, site managers and those responsible for reef monitoring programs throughout the Caribbean, asking for any available data pertaining to their study sites.

A total of 464 records from 200 reefs surveyed between 1969 and 2008 across the Caribbean were obtained (figure 2*a*,*b*). The database includes reefs that were surveyed only once (n = 214) and reefs where repeated measures of rugosity were collected over more than one year (n = 250). Both datasets provide highly consistent results (see table 2 and table A1.1 in Appendix 1). We therefore only present findings from the whole dataset, because it offers a wider spatial and temporal representation.

Figure 1. Examples of three different values of rugosity index of architectural complexity on Caribbean reefs. The value of the index is indicated in each photo. (Source for photos: L. Alvarez-Filip, M. Uyarra, W. Henry).

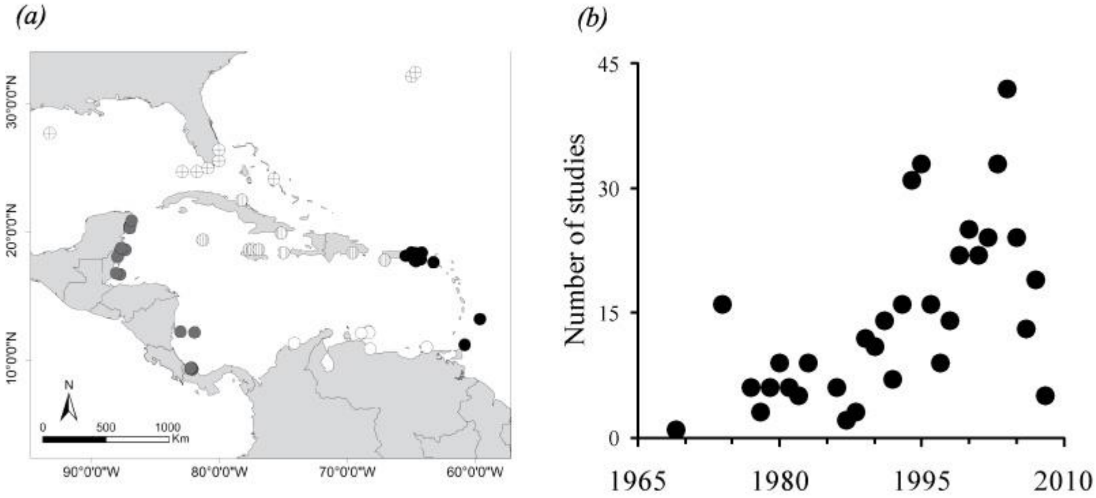

Figure 2. *(a)* Regional distribution of locations from which rugosity values were obtained; grey circles= Central America; white circles= South America; black circles= Lesser Antilles; circles with vertical lines= Greater Antilles; circles with crosses= SW North Atlantic. *(b)* Number of studies from which rugosity data were collated per year, from 1969 to 2008.

Analyses

To assess the temporal pattern of change in region-wide architectural complexity, we calculated annual estimates of rugosity averaged across all available sites for each year from 1969 to 2008. We fitted a range of linear and non-linear models to represent increasing degrees of complexity in the rate of change in rugosity over time, and used the small-sample adjusted Akaike Information Criterion AIC_c to evaluate the models

(Burnham & Anderson 2002). Linear models were fitted using both simple regressions and robust regression, to downweight the influence of outliers. We contrasted these linear models, which represent a hypothesis of constant change in rugosity over the whole time period, against segmented models that assumed piecewise linear relationships (i.e. two or more straight lines connected by breakpoints) and a General Additive Model (GAM) of an unspecified non-linear (spline) function, which assumed that the rate of change in rugosity varied over time (Venables & Ripley 2002; Muggeo 2003). In addition, because the number of sites contributing to each annual rugosity estimate varied, with more sites available toward the end of the time period, we ran all models with annual estimates unweighted and weighted by sample size. Weighted models consistently provided a significantly better fit (lower AIC and higher variance explained) than unweighted models. All analyses were implemented in R (R 2009).

We used randomisation techniques to evaluate whether the pattern and rate of change were sensitive to the inclusion of any particular site or year. For the best-supported model identified in the AIC_c analysis, we tested whether the rate of decline in rugosity was biased by the inclusion of any particular year, using a jackknife method to calculate the distribution of annual decline rates while sequentially removing each individual year. To evaluate any potential site selection bias, we used a bootstrap method to compare the annual decline rate to the range of possible decline rates for 10,000 random combinations of year, rugosity and weighting.

To explore if the trends of changing architectural complexity varied with depth and within the region, we aggregated the data by decade to maximise the signal relative to interannual variation while retaining sufficient power. To evaluate the change in rugosity at different depths, we divided the data into three zones: (i) < 6 m, which represents the optimal range of *Acropora palmata* (and therefore *Acropora* reefs); (ii) 6 - 20 m, to include the range other reef-building scleractinian corals, including *A. cervicornis*; and (iii) > 20 m, to reflect sites where hard corals are present but do not necessarily form complex three-dimensional structures. We also aggregated the data within five sub-regions to explore spatial variation in changes in rugosity within the Caribbean region (figure 2*a*).

A key question is if the regional change in reef structure has produced more structurally homogeneous habitats throughout the Caribbean. We classified each reef into one of five rugosity index categories (1.0-1.49, 1.5-1.99, 2.0-2.49, 2.5-2.99, >3.0) to explore the change in region-wide representation of complex (rugosity > 2.0) and flatter (rugosity ≤ 1.5) reefs for the four different decades.

Results

There has been a marked decline in the architectural complexity of Caribbean reefs over the past four decades (figure 3). The best-supported model of change in rugosity over time was a weighted segmented model (table 2), which suggests that the decline in rugosity has three distinct phases of change (figure 3). Architectural complexity declined steeply early in the time series (1969 – 1985), from reefs with indices ~2.5 to much flatter reefs with indices ~1.5. This period of decline ended in 1985 (± 2.4 years SE), and architectural complexity throughout the region then remained relatively stable until the late 1990s. However, since 1998 (± 2.8 years SE) the declining trend has resumed, with rugosity indices after the mid 2000s reaching the lowest levels recorded in the time-series (~1.2; see example in figure 1). The pattern of change is robust to the inclusion or exclusion of individual years (Jackknife) and individual sites (bootstrap) (Appendix 1, figure A1.1).

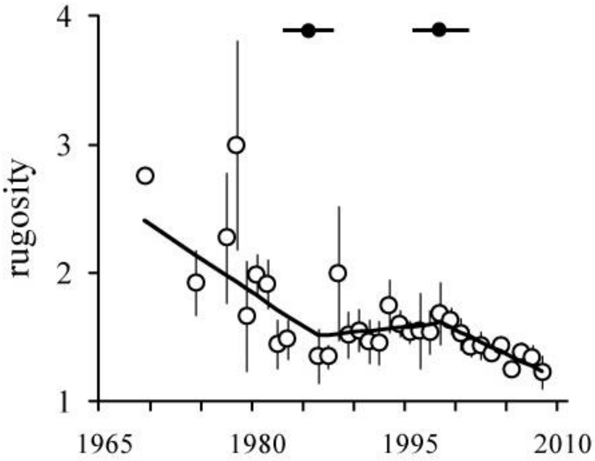

Figure 3. Changes in reef rugosity on reefs across the Caribbean from 1969 to 2008. Black line represents the best fitting model – a segmented regression weighted by the number of sites contributing to each annual rugosity estimate (mean ± 95% confidence intervals). Black dots at the top of the figure indicate the significant break-point in 1985 and 1998 (± 1 SE) for the segmented regression. Model slopes: 1969 to 1984= -0.054; 1985 to 1997= 0.008; 1998 to 2008= -0.038.

Table 2. Model structure and the temporal pattern of change in Caribbean architectural complexity**.** Summary of Akaike Information Criterion analysis of linear and non-linear models of change in yearly mean rugosity (derived from all 464 estimates), ordered by decreasing weight. Models in which annual rugosity estimates have been weighted by sample size are indicated (wt). df = degrees of freedom of the model (for GAM we use the estimated degrees of freedom). AIC$_c$ is the Akaike Information Criterion corrected for small sample size. Δ is the difference in AIC$_c$ between a given model and the best-supported model (indicated in bold). W is the Akaike weight, which represents the probability that a given model is the best of those models considered.

Model	**R^2**	**Slope**	**df**	**AIC$_c$**	**Δ AIC$_c$**	**AIC$_c$ W**
Segmented model (wt)	**0.64**	**-0.028***	**26**	**-25.8**	**0**	**0.8695**
Linear model (wt)	0.53	-0.019	30	-17.1	8.7	0.0112
Robust linear model (wt)	-	-0.018	30	-16.9	8.8	0.0107
Segmented model	0.65	-0.038*	26	-2.9	22.9	0.0000
Generalized additive model (wt)	0.99	-0.033*	3.6	0.1	25.8	0.0000
Linear model	0.49	-0.026	30	9.4	35.2	0.0000
Robust linear model	-	-0.021	30	11.2	37	0.0000
Generalized additive model	0.59	-0.044*	3.3	22.8	48.6	0.0000

*average slope of the different model segments

The decline in architectural complexity is widespread. The temporal pattern of change was consistent across all three depth intervals (figure 4*a*) and across the three sub-regions for which the available data spanned the whole time period, and the two regions with patchier data (Central America and SW North Atlantic; figure 4*b*).

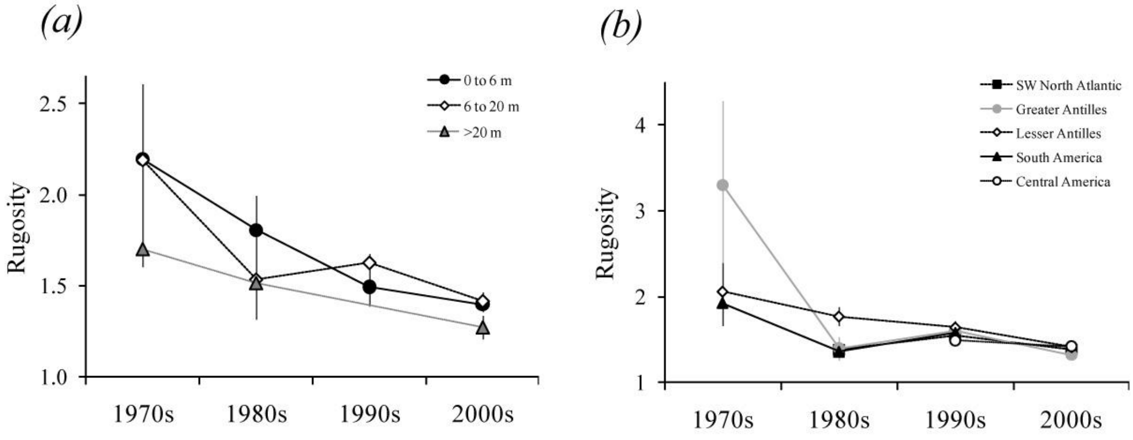

Figure 4. Change in Caribbean reef rugosity in four different decades *(a)* at three depth intervals and *(b)* in five subregions (mean index value ± 95% confidence intervals).

Caribbean reefs are becoming both flatter and more structurally homogeneous across the region. The proportion of complex reefs (rugosity > 2) has declined from ~45% of sites to ~2% in the past four decades (figure 5).

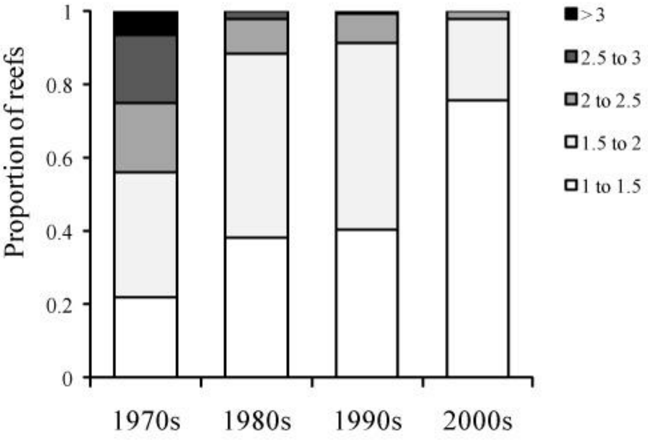

Figure 5. Proportion of reefs in five rugosity index categories across the Caribbean between 1969 and 2008. Number of studies for each decade: 1970s: n = 32; 1980s: n = 52; 1990s: n = 136 and 2000s: n = 167.

Discussion

The architectural complexity of coral reefs has declined drastically over the last 40 years throughout the Caribbean. Structurally complex reefs with a rugosity of >2 have been virtually lost from the entire region. Today, the flattest reefs (rugosity <1.5) comprise approximately 75% of the total compared to ~20% in the 1970s, with most of the increase in the proportion of flattest reefs occurring in the 2000s. The high proportion of complex reefs in the 1960s and 1970s is unlikely to result from researchers at this time tending to visit just the most pristine reefs, because less architecturally complex categories were also well represented during this period. The loss of architectural complexity is non-linear and has occurred over three distinct phases that coincide closely with large-scale events that have affected Caribbean reef ecosystems. The rate of decline was steepest prior to 1985. The sample sizes are small and variance high during the 1960s and 1970s, hence it is unclear whether the decline began prior to the early 1980s, when widespread loss of acroporid corals began (Precht & Aronson 2006). After this period, average architectural complexity changed little until the late 1990s, when a new episode of decline began. The pattern of decline is consistent across depth zones and sub-regions. The widespread occurrence of flatter reefs could have serious implications for reef-associated biodiversity and reef-based environmental services.

The non-linearity in the loss of architectural complexity suggests that different drivers operating at different times have influenced components of the reef community. Disturbances on reefs range in scale and intensity, from local tropical storms that can break and displace coral skeletons, to widespread events such as climate-induced bleaching and diseases that kill coral tissue without immediately compromising the reef structure (Pratchett *et al.* 2008). In the late 1970s, one key event is likely to have had a major role in the early, steep decline in Caribbean reef architecture. White band disease killed ~90% of the shallow-water, structurally dominant acroporid corals, exposing their fragile branching skeletons to erosion and hurricanes that likely led to their collapse in subsequent years (Aronson & Precht 2001). However, declines also occurred at depths greater than those at which acroporids were dominant, suggesting that the systematic loss of Caribbean reef corals was more widespread than previously thought during the 1970s and early 1980s.

After 1985, the main driver(s) of declining architectural complexity appear to cease; by this time, acroporids had disappeared almost entirely from the Caribbean, and the sea urchin *D. antillarum* had experienced a region-wide disease-induced mass mortality in 1983/4 (Carpenter 1988). The loss of this important source of bioerosion may have slowed the decline following the first phase of reef flattening. This intermediate stable period of architectural complexity in the region persisted in the face of several disturbance events including the first large-scale bleaching events and several major hurricanes (Gardner *et al.* 2005; McWilliams *et al.* 2005).

Around 1998, Caribbean reefs were tipped into a new phase of structural decline, following the most intense and widespread coral bleaching event to date (McWilliams *et al.* 2005). The coral mortality and reductions in growth rates that typically follow such bleaching events are likely to have precipitated the resumption of loss of architectural complexity. The low levels of coral cover, and presumably reef accretion, at this time (Gardner *et al.* 2003) may also have increased rates of erosion of underlying geological structures that were no longer shielded by actively growing hard corals. Since 1998, further mass bleaching events have occurred regularly (McWilliams *et al.* 2005), likely contributing to the continued decline in reef complexity.

All of the major events that are likely to have impacted reef complexity have occurred against a backdrop of changes not only in coral abundance but also in community composition. Following the disappearance of acroporids, massive species with slower growth rates, such as *Montastrea* spp, remained as the primary reef framework builders, and weedy corals, such as *Porites* spp and *Agaricia* spp, that form rapidly growing, small colonies that are short lived and quickly replaced, started to increase in abundance (Green *et al.* 2008). The shift from major reef-building species to weedy species that contribute less to maintenance of the reef framework, combined with increases in macroalgae (Côté *et al.* 2006) which compete for space with coral recruits (Mumby *et al.* 2007), likely reduced the rates of coral accretion on Caribbean reefs.

The loss of reef architecture is likely to have profound ecological, social and economic impacts. A growing body of evidence indicates severe repercussions for biodiversity of the loss of architectural complexity. On Indo-Pacific reefs, major changes in fish community composition have resulted from the long-term loss of structure following coral bleaching events (Pratchett *et al.* 2008 and references therein). The effects of bleaching are first manifest in obligate coral-dwelling species, followed by impacts on other small-bodied fishes (both small adults and juveniles of larger species) when the physical matrix of the reef collapses(Pratchett *et al.* 2008). In the Caribbean, the greatest impacts on biodiversity are expected to occur only with the breakdown of the reef matrix because no fish species feed exclusively on live coral, although many reef-associated species depend highly on rugose substrata to feed, recruit and hide (Gratwicke & Speight 2005). In this context, declining reef complexity may explain the onset of a decline in Caribbean reef fishes that has occurred since ~1996 (Paddack *et al.* 2009). Given that the loss of reef architecture began much earlier: our analysis supports the notion of a degradation debt for Caribbean reef fishes. Reduced recruitment resulting from a lack of settlement sites and refuges for species with commercial importance, such as lobsters and large fishes (Graham *et al.* 2007; Wynne & Côté 2007), may compromise the long-term sustainability of fisheries and fishing communities. Collapsing reef structures may also lead to the loss of important environmental services such as coastal protection. Simulation models predict that a reduction in reef surface roughness of ~50% could produce a doubling of the wave energy reaching the shores behind those reefs (Sheppard *et al.* 2005). The vulnerability of coastal human communities in the Caribbean to projected increases in the intensity of Atlantic Ocean hurricanes and sea levels (Hopkinson *et al.* 2008) will therefore likely be compounded by the reduced wave dissipation function of architecturally simpler reefs.

Reversing declines in reef architecture will be a major challenge for scientists and policy-makers concerned with maintaining reef ecosystems and the security and well-being of Caribbean coastal communities. Although recent evidence suggests increases in coral cover on some Caribbean reefs (e.g. Cho & Woodley 2000; Idjadi *et al.* 2006), the effect of coral recovery on architectural complexity is unknown. If weedy corals dominate this recovery in the long-term, future reef complexity is unlikely to mirror any improvement in coral condition. To regain the levels of architectural complexity that were prevalent prior to 1980, the recovery of large branching corals (i.e., *Acropora* spp.) and the maintenance of healthy populations of massive robust species (e.g., *Montastrea* spp.) are essential within the region. Not meeting these challenges will most probably result in a continued flattening of reefs throughout the region and seriously compromised biodiversity and environmental services.

Chapter 2

Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story?

Abstract

The complexity of coral reefs is largely generated by reef-building corals, yet the effects of current regional-scale declines in coral cover on habitat complexity are poorly understood. Here we explore temporal and spatial covariation between coral cover and reef architectural complexity using a Caribbean-wide dataset of temporally-replicated estimates spanning four decades. Although coral skeletons can remain after coral mortality, the loss of coral cover is directly followed by loss of complexity with little time-lag, However, there is little correspondence between the overall rates of change in coral cover and reef architecture, probably due to temporal and spatial variation in coral community composition. Across the Caribbean, sites with greater coral cover tend to also be more complex but the variance in architectural complexity also increases with increasing coral cover. Reef architectural complexity is therefore not a direct function of coral cover, but both are key attributes of coral reef health that need to be considered separately in reef ecology and management.

Submitted:

Alvarez-Filip L., Côté I.M., Gill J.A., Watkinson A.R. & Dulvy N.K. Region-wide temporal and spatial variation in Caribbean reef architecture: is coral cover the whole story? *Global Change Biology*.

Introduction

In some ecosystems, complex structural or functional attributes can be provided by a single taxon. Consequently, these foundation species can provide essential habitat for a wide variety of other species and underpin fundamental ecosystem processes such as productivity and nutrient cycling (Bruno & Bertness 2001; Ellison *et al.* 2005). In tropical shallow waters, hard corals increase the architectural heterogeneity of the seascape considerably, providing suitable habitat and microclimatic conditions for a myriad of species and contributing substantially to ecosystem dynamics (Hatcher 1997). Loss of hard corals on reefs is therefore likely to have severe repercussions for associated biodiversity, ecosystem structure, function and stability.

Hard corals are increasingly threatened worldwide by direct and indirect effects of human activities (Pandolfi *et al.* 2003; Carpenter *et al.* 2008; Mora 2008). As result, live coral cover has decreased rapidly on tropical reefs throughout the world (Gardner *et al.* 2003; Bruno & Selig 2007), but the effects of changing coral cover on habitat complexity are not yet clear. At large scales, direct relationships between changing coral cover and reef architecture have been suggested based on the aftermath of widespread coral mortality following mass bleaching events on some Indo-Pacific reefs (Wilson *et al.* 2006; Pratchett *et al.* 2008). Declines in architectural complexity appeared to lag bleaching-induced coral mortality by more than five years in ‘before-and-after’ comparisons (Graham *et al.* 2007; 2008). In contrast, for the Caribbean, turning points in the regional trajectory of declining architectural complexity coincide closely with the loss of structurally complex *Acropora* corals and El Niño Southern Oscillation-induced coral mortality, and there is little evidence of a region-wide lag in loss of habitat complexity following declines in coral cover (Aronson & Precht 2006; Chapter 1) Consequently, the exact nature of the relationship between coral cover and reef architecture, including the generality of a 5-year lagged response, has yet to be established.

Here we use a Caribbean-wide dataset of temporally replicated coral cover and reef architecture estimates that spans four decades to explore the regional covariance in coral cover and reef architectural complexity. First, we test whether the change in architectural complexity lags behind the change in live coral cover. Second, we test for a dose-response coral cover-architectural complexity relationship by quantifying changes in both coral cover and architectural complexity on a year-by-year basis. Finally, we test for a positive relationship between the spatial variance in live coral cover and reef architecture across the region.

Material and methods

Data collation

We collated all available site-specific data on the percentage cover of live hard coral and associated architectural complexity for reefs within the wider Caribbean Basin. We focused on studies that used the rugosity index to describe reef architecture, as this is the most commonly used method for measuring reef complexity in the region (Chapter 1). Reef rugosity is less frequently measured than coral cover, thus we first searched for studies reporting rugosity of specific sites, and then from this dataset we selected all studies that also reported information on coral cover.

The database was compiled by searching online ISI Web of Science, Google Scholar and other relevant databases (e.g. Reefbase) for peer-reviewed and grey literature. We searched for pertinent papers in all issues of the journals *Coral Reefs*, *Bulletin of Marine Sciences*, *Atoll Research Bulletin*, *Caribbean Journal of Science* and in all *Proceedings of the International Coral Reef Symposium*. Additionally, we directly contacted scientists and site managers asking for any available data pertaining to their study sites. The search resulted in a total of 81 studies that includes 312 records from 139 reefs surveyed between 1977 and 2008 across the Caribbean. From this larger database, we identified 24 studies with repeated measures (i.e. data collected over more than one year; figure 1). This subset included 96 records reporting information for 37 reef sites between 1978 and 2004 (table A2.1 in appendix 2), and ranging in duration from two to 12 years (mean = 5.01 ± 3.41 SD years).

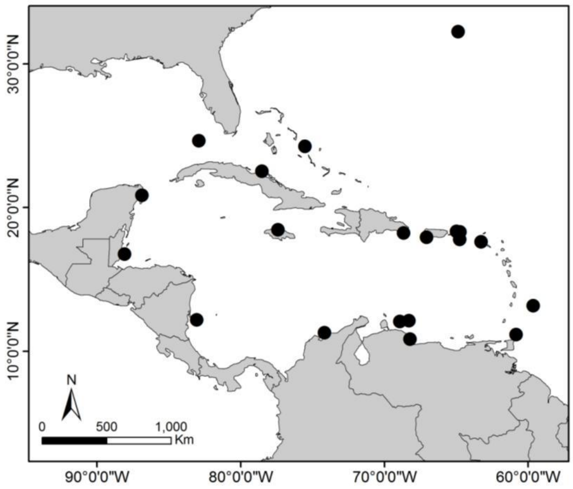

Figure 1. Regional distribution of reef sites with both live coral cover and rugosity data replicated over more than one year.

Statistical analyses

We tested for a delayed response in architectural complexity to changing coral cover using region-wide annual estimates of coral cover and architectural complexity. We first used all available information (repeated and unrepeated measures) to calculate regional annual averaged estimates of live coral cover and reef rugosity. We then calculated the correlation coefficient for the coral cover – architectural complexity relationship for lags of up to 15 years. This technique provides a broad view of the temporal correlations between coral cover and architectural complexity; however, each iteration includes data from different sites and thus spatial variation in either parameter could influence the strength of the correlation. We therefore also restricted the analyses to the repeated-measures dataset, in which both coral cover and architectural complexity measures were available for more than one year. In this analysis, architectural complexity on each site was lagged iteratively by one year, up to a maximum of six years (as sample size decreases rapidly with this technique). For each time lag, all sites for which estimates of both coral cover and architectural complexity were available were used to calculate a coefficient of correlation between coral cover and reef architecture. In both analyses, the largest significant coefficient of correlation is considered as the best estimate of the number of years required to detect the effects of declining coral cover on reef architecture. False discovery rates were used to correct for multiple tests (Benjamini & Hochberg 1995).

To investigate temporal variation in rates of change on coral cover and reef architecture, we examined how annual region-wide changes in coral cover were related to the corresponding annual change in architectural complexity between 1974 and 2004. We used a weighted meta-analytic approach to estimate annual rates of change in live coral cover and reef architecture in the temporally replicated studies (Rosenberg *et al.* 2000). The standardised effect size was the annual rate of change in coral cover and reef rugosity for each study, calculated as:

$$\text{annual rate of change} = (\log End - \log Start) / d$$

where *End* and *Start* represent the final and initial coral cover or reef rugosity of the time series, respectively, and *d* is the number of years elapsed between the two estimates. This metric has been previously used in studies of ecological change on coral reefs (Côté *et al.* 2005; Paddack *et al.* 2009) and its properties as an effect size have been thoroughly investigated (Côté *et al.* 2005). We weighted effect sizes using the natural logarithm of the total transect length surveyed (see also Mosqueira *et al.* 2000; Côté *et al.* 2001; Molloy *et al.* 2008). Statistically significant effect sizes were identified by 95% bias-corrected bootstrapped confidence intervals (generated from 9999 iterations) that did not encompass zero. The Q_M statistic was used to test for differences in rates of change in live coral cover and architectural complexity. A significant Q_M implies that there are differences in mean effect sizes among groups, but a non-significant Q_M does not preclude individual groups showing significant effect sizes (i.e. individual CIs that do not overlap zero). The meta-analyses were conducted in MetaWin Version 2.0 (Rosenberg *et al.* 2000). Annual rates of change and confidence intervals are presented back-transformed to percentages to facilitate their interpretation.

Finally, we explored the spatial relationship between live coral cover and reef architecture at the regional scale using (i) all available data (i.e. repeated and unrepeated measures) and (ii) a smaller dataset of unrepeated measures (which avoids including more than one estimate per site). As both datasets provide very similar results (see figure 4 and figure A2.1 in appendix 2), we only present findings for all the available data because of the wider spatial and temporal representation. Because preliminary analysis demonstrated that the variance in reef rugosity was unequal along the gradient of coral cover, we used quantile regression to obtain a detailed picture of the relationship between coral cover and architectural complexity (Koenker & Bassett 1978). Quantile regression differs from ordinary least squares regression in that it minimizes the sum of absolute values of residual errors around a specified quantile of the dependent variable, rather than just changes in the mean (Cade & Noon 2003). Exploring the full range of quantile responses provides a more complete view of the relationship between variables than those captured by individual (median) quantile regression functions (Knight & Ackerly 2002), hence we estimated the complete series of quantile regression functions from the 1st to the 99th quantile for the regional relationship between coral cover and reef architecture. Analyses were carried out in R and using the *Quantreg* package (R 2009).

Results

What is the time-lag between coral cover loss and reef structural decline?

At both region-wide and site scales, there was little evidence for a time-lag of more than two years between the onset of a change in coral cover and a subsequent change in architectural complexity (figure 2). In both analyses, the strongest correlation between architectural complexity and coral cover was found when the data were unlagged. After the correction for multiple tests, the only statistically significant (α = 0.05) lagged-relationship was the two-year lag in the regional analysis (tables 1 and 2).

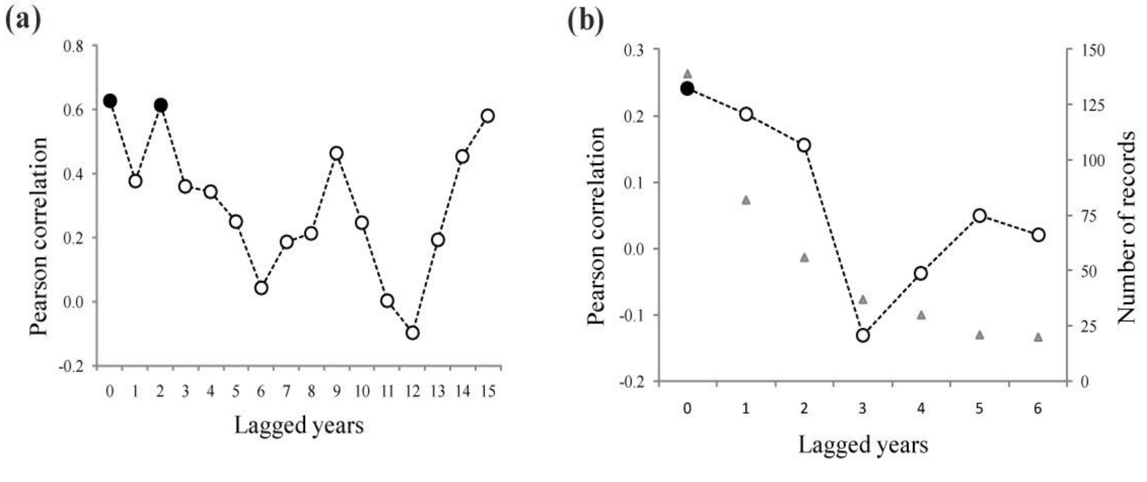

Figure 2. Changes in Pearson correlation coefficients for (a) lagged relationships between regional average live coral cover and reef rugosity from 1977 to 2008 and (b) lagged relationships between live coral cover and reef rugosity on the same sites, in which each time series was lagged by one additional year in each iteration. Significant correlations, corrected for false discovery rates, are indicated with filled circles; the grey triangles in (b) indicate the number of records used in each iteration.

Table 1. Unadjusted and corrected (using false discovery rates) P values of the correlations between the regional average live coral cover and reef rugosity from 1978 to 2008, with time-lags ranging from 0 to 15 years.

	P-value	Corrected P-value
no-lag	**0.001**	**0.011**
1 year lag	**0.070**	**0.224**
2 year lag	0.002	0.019
3 year lag	0.118	0.275
4 year lag	0.139	0.277
5 year lag	0.302	0.536
6 year lag	0.869	0.927
7 year lag	0.473	0.624
8 year lag	0.411	0.598
9 year lag	0.060	0.224
10 year lag	0.345	0.552
11 year lag	0.995	0.995
12 year lag	0.729	0.833
13 year lag	0.507	0.624
14 year lag	0.120	0.275
15 year lag	0.047	0.224

Table 2. Unadjusted and corrected (using false discovery rates) P values of regional correlation between site-lagged live coral cover and reef rugosity, withtime-lags ranging from 0 to 6 years.

	P-value	Corrected P-value
no-lag	**0.004**	**0.029**
1 year lag	0.068	0.237
2 year lag	0.254	0.592
3 year lag	0.441	0.772
4 year lag	0.842	0.932
5 year lag	0.830	0.932
6 year lag	0.932	0.932

Are the rates of change of coral cover and reef architecture similar?

There is no consistent relationship between the annual rates of change in coral cover and annual changes in reef rugosity across the 37 sites with repeated measures (figure 3), and the overall meta-analysis showed that both live coral cover and reef architecture have declined significantly (i.e. the confidence intervals do not encompass zero) but at different overall rates ($Q_M = 3.68$, $P = 0.054$). The annual rate of change in coral cover has been -8.6% (95% CI = -11.9% to -5.2%) while the annual change in rugosity has been -4.0% (95% CI = -7.8% to -1.3%).

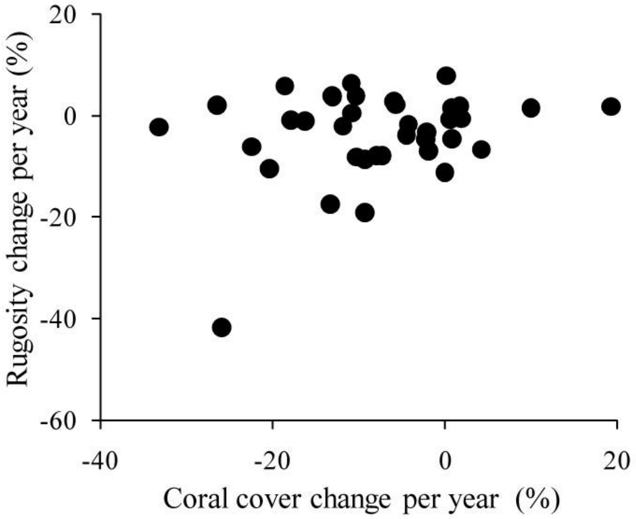

Figure 3. The absence of a relationship between annual rates of change in live coral cover and architectural complexity for 37 reef sites across the Caribbean region ($R^2 = 0.07$, $P = 0.12$).

Is reef architecture a function of coral cover?

Architectural complexity varies more widely with increasing hard coral cover, across 139 reef sites and 31 years throughout the Caribbean (figure 4a). For example, the rugosity indices of reefs with 10% coral cover vary from 1.05 (i.e. relatively flat) to ~2.0 (i.e. moderately complex reefs) while, at 40% coral cover, rugosity ranges from 1.05 to 3.5 (i.e. highly complex reefs; figure 3a). Quantile regression analyses indicated consistently positive relationships between coral cover and reef architecture, with steeper relationships for higher quantiles of architectural complexity (figure 4b). In the lower quantiles, rugosity is low across a wide range of coral cover estimates, indicating that reefs with relatively high coral cover may still be quite flat (figure 4b). By contrast, the steepest coral cover-architectural complexity relationships are associated with high rugosity even at the lowest levels of coral cover (figure 4b, c), with slopes of the highest quantiles lying far above the mean and 90% CI of the overall relationship (figure 4 a, b). Thus, some reefs with lower coral cover may still have some level of architectural complexity.

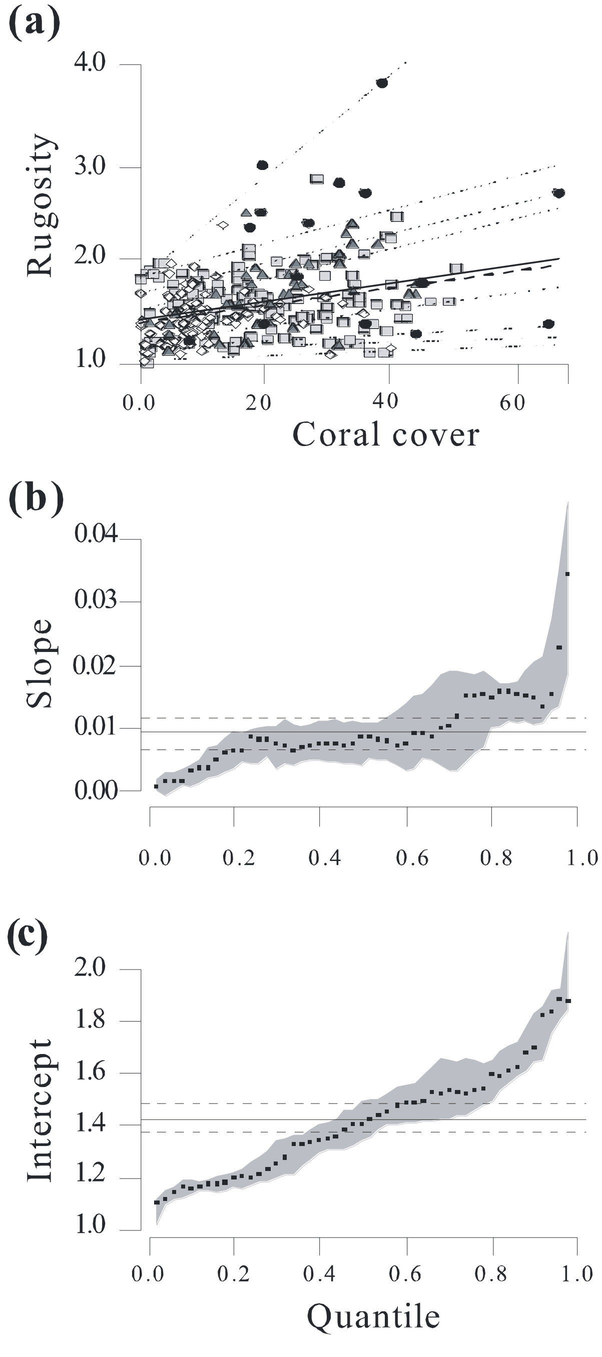

Figure 4. *(a)* Relationship between coral cover and reef rugosity on 139 reef sites (323 surveys from 1977 to 2008) throughout the Caribbean. The decade in which each study was conducted is indicated (circles= 1970s, triangles= 1980s, squares= 1990s, diamonds=2000s). Nine estimated quantile regression lines (0.01, 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 0.99 quantile) are superimposed on the scatterplot; the median (0.5 quantile) is indicated with a black dashed line and the others are indicated with grey dotted lines. The least square estimate of the mean function is indicated by the black solid line ($R^2 = 0.11$, Slope = 0.009, $P<0.001$). The (b) slopes and (c) intercepts of the quantile regressions are shown from the 0.01 quantile to the 0.99 quantile, with 90% confidence bands (grey shading), and the mean (solid line) ± 90% confidence intervals (dashed lines) from the ordinary least squares regression.

Discussion

The decline of coral cover represents both an absolute loss and a reduction in the quality of reef habitat. Although coral skeletons can persist after coral mortality, our findings show that the region-wide loss in Caribbean coral cover has been rapidly followed by the loss of architectural complexity with little evidence of a lag greater than two years. However, the inconsistent relationship between the annual rates of change in coral cover and in architectural complexity suggests a temporally complex and non-linear relationship between these components of reef function. In addition, the increase in variance in local architectural complexity with increasing coral cover suggests that architectural complexity is not a simple function of coral cover.

Time-lags may be expected when the drivers of coral mortality and those affecting structural complexity are separate and occur more or less sequentially. Examples of the former include disease and bleaching events, which can produce widespread coral mortality without immediately modifying the reef framework (beyond halting carbonate accretion; Glynn 1997; Aronson & Precht 2001; Sheppard *et al.* 2002); examples of the latter include persistent direct human impacts and recurrent physical disturbances such as hurricanes which degrade underlying reef structures (Hughes 1994; Hughes & Connell 1999; Gardner *et al.* 2005). In the Caribbean, drivers of both coral mortality and erosion have operated as virtually chronic pressures throughout the entire region in recent decades (Pandolfi *et al.* 2003; Gardner *et al.* 2005; Aronson & Precht 2006; Mora 2008), which may be why no evidence of a time-lag is apparent in our regional analysis.

The lack of a clear response of architectural complexity to changes in coral cover may also be partly a consequence of the relative susceptibility of different corals to erosion following mortality. In the Caribbean, the largest changes in coral cover occurred as a result of the disease-induced die-off of acroporids in the late 1970s and early 1980s (Aronson & Precht 2006; Schutte *et al.* 2010). The erect branching structures of *Acropora* corals contributed disproportionately to reef complexity before that time. Although the robust skeleton of *A. palmata* may have persisted longer than the fragile framework of *A. cervicornis* in some locations, the regional trends of declining coral cover and architectural complexity suggest that most dead *Acropora* were relatively rapidly broken down and eroded following mortality (Aronson & Precht

2006; Chapter 1). In our study, similarly rapid annual rates of change of both coral cover and architectural complexity were apparent during the *Acropora* die-off period (1978-1985; coral cover = -23.19, bias-corrected 95% CI = -2.73 to -1.49; rugosity = -27.03, bias-corrected 95% CI = -14.64 to -9.57), suggesting a rapid response of architectural complexity to coral cover loss during this period. However, very few studies are available for these years (n = 3), and therefore the lack of a delayed decline in reef complexity reported here refers primarily to the years since the demise of *Acropora*, in which Caribbean reefs have been dominated by a combination of massive and weedy corals.

The absence of a dose-response in the coral cover – architectural complexity relationship (figure 3) suggests temporal variation in the rates of change of each attribute. Coral communities have continuously changed since the mass mortality of acroporids. Important reef-building corals such as *Montastrea* have been declining throughout the region and stress-resistant coral species that contribute relatively little to the reef framework and architectural complexity have increasingly dominated Caribbean reefs (Hughes 1994; Edmunds & Carpenter 2001; Aronson *et al.* 2002; Green *et al.* 2008). Thus changes in coral composition leading to ‘flatter’ reef communities, together with possible changes in carbonate budgets as a consequence of higher amounts of bare substrata (Eakin 1996; Glynn 1997), can occur in the absence of declines in coral cover. Previous studies do indeed suggest that rates of loss of Caribbean reef architecture have remained high in recent years (Chapter 1), while coral loss has almost ceased (Schutte *et al.* 2010).

The rapid increase in architectural complexity with increasing coral cover (figure 4), despite the absence of a dose-response between these two variables (figure 3) suggests extensive fine-scale spatial variation in coral community structure. Some spatial variation may be attributable to the underlying reef framework and other organisms, such as sponges and soft corals (e.g. Diaz & Rutzler 2001; Halford *et al.* 2004). However, it is likely that much of the variation in reef structural complexity at any given time reflects variation in coral species assemblages (Chapter 3). For example, reefs dominated by tall, branched species such as *Acropora* spp would have higher levels of architectural complexity than reefs with similar coral cover but dominated by smaller, flatter corals such as *Agaricia* spp. Coral identity may therefore be an important mediator of reef complexity and, consequently, the impact of coral loss on reef architecture will differ among sites, with sites dominated by architecturally-complex reef-building corals bearing the greatest losses in rugosity following coral mortality. Unfortunately, coral species composition was seldom reported in the studies included here, hence we could not explore the effect of coral identity on patterns of architectural complexity change.

The near-immediate loss of architectural complexity following declines in coral cover in the Caribbean differs from the pattern reported in the Indo-Pacific region, where a lagged response in the aftermath of widespread coral mortality following mass bleaching events was apparent (Wilson *et al.* 2006; Graham *et al.* 2007; 2008; Pratchett *et al.* 2008). However, these studies encompassed different temporal scales; our Caribbean analyses explore year-by-year changes throughout a multidecadal period of continual coral and reef architecture loss, whereas the Indo-Pacific studies spanned either side of a discrete catastrophic coral mortality event. In addition, there are important historical and ecological differences between these two regions that are likely to influence these processes, with Caribbean reefs typically having fewer coral species, less ecological redundancy and frequent hurricane impacts (Bellwood *et al.* 2004; Briggs 2005). To determine whether our findings can be broadly generalised would require longitudinal studies of Indo-Pacific reefs.

Architectural complexity is clearly not a simple function of coral cover. Therefore, to restore the ecosystem services that Caribbean corals provide to other species, including humans, these two critical reef attributes may require different types of management and at different spatial scales. Much of coral reef conservation at present focuses on ecological management and control of the cover of coral and algae (Gardner *et al.* 2003; Côté *et al.* 2006; Bruno & Selig 2007; Mumby *et al.* 2007; Bruno *et al.* 2009). However, restoring coral cover on reefs may not necessarily provide the architectural complexity that underpins important coral reef ecosystem services relating to nutrient recycling, dissipation of wave energy and fish production (Szmant 1997; Lugo-Fernandez *et al.* 1998; Sheppard *et al.* 2005; Cinner *et al.* 2009). Consequently, we also need to understand the biotic and abiotic drivers of architectural complexity at a range of spatial scales.

Chapter 3

Drivers of region-wide declines in architectural complexity on Caribbean reefs

Abstract
Severe declines in the cover of live hard coral on reefs have been reported worldwide and, in the Caribbean region, the architectural complexity of coral reefs has also declined markedly. While the drivers of coral cover loss are relatively well understood, little is known about the drivers of regional-scale declines in architectural complexity. We use a dataset of 49 time series reporting reef architectural complexity to explore the effect of hurricanes, coral bleaching and fisheries on the Caribbean-wide annual rates of change in reef complexity. Hurricane impacts greatly influence reef complexity, with the most rapid rates of decline in complexity occurring at sites impacted during their survey period, and with lower rates of loss occurring at unimpacted sites. Reef architectural complexity did not change significantly following mass bleaching events or thermal anomalies. Interestingly, the rates of change in architectural complexity were similar in and out of marine protected areas (MPAs); however, significant declines in complexity were observed inside but not outside of MPAs, possibly because reductions in fishing can lead to increased bioerosion by herbivores within MPAs. Our findings suggest that the major drivers of coral mortality, such as coral bleaching, do not immediately influence reef complexity. Instead, direct physical impacts and reef bioerosion appear to be important drivers of the widespread loss of architecturally complex reefs in the Caribbean.

Submitted:

Alvarez-Filip L., Dulvy N.K., Gill J.A., Perry A.L., Watkinson A.R. & Côté I.M. Drivers of region-wide declines in architectural complexity on Caribbean reefs *Coral Reefs*.

Introduction

Natural systems are changing rapidly (Balmford *et al.* 2003), as a consequence of human perturbations of the natural environment and global biochemical cycles (Vitousek *et al.* 1997; Rockstrom *et al.* 2009). Coral reefs provide a clear example of how anthropogenic activities have, at different scales, led to the degradation of natural habitats. At local scales, a wide range of human stressors such as nutrient enrichment and overfishing (Hughes 1994; Roberts 1995; Bryant *et al.* 1998; Szmant 2002) can modify natural disturbance regimes of coral reefs by transforming pulse events into persistent disturbance or even chronic stress (Nyström *et al.* 2000). At the global scale, anthropogenic alteration of the climate causing rising sea temperatures has increased bleaching-induced mortality of reef-building corals (Hoegh-Guldberg 1999). Under these new, more stressful conditions, increases in the intensity of natural disturbances such as hurricanes or diseases (Rosenberg & Loya 2004; Webster *et al.* 2005; Bruno *et al.* 2007), previously natural but less-frequent parts of tropical reef dynamics (Connell 1978), may become an obstacle to reef recovery and development.

Caribbean reefs are among the most heavily impacted of marine ecosystems (Halpern *et al.* 2008). Over the last four decades, the region has seen declines in coral cover of ~80% (Gardner *et al.* 2003) and a severe reduction in the proportion of highly complex reefs (Chapter 1). Architectural complexity is strongly related to the abundance of reef-building corals (Chapter 3). However, the poor match between annual rates of change in coral cover and architectural complexity (Chapter 2) suggests that the drivers of loss of coral cover and architectural complexity may differ. A decoupling of rates of change of coral cover and reef complexity is likely to have an impact on the response of reef biodiversity and environmental services to habitat degradation. For instance, while coral cover loss has almost ceased in recent years (Schutte *et al.* 2010), declines in fish abundance began to be evident in the late 1990s (Paddack *et al.* 2009), likely following ongoing declines in reef complexity (Chapter 1).

Given the extreme importance of coral reefs for biodiversity, human livelihoods and key environmental services such as coastal protection, there is an urgent need to discriminate among the effects of different drivers of coral degradation in order to identify effective conservation strategies for restoring reef complexity (Pandolfi *et al.* 2005; Mora 2008; Chapter 2). The drivers of coral loss in the Caribbean are relatively well understood: in the late 1970s the widespread disease-induced die-off of complex acroporid corals triggered extensive coral loss (Aronson & Precht 2006; Schutte *et al.* 2010), and it is likely that a combination of loss of herbivory through overfishing and diseases (Carpenter 1988; Pandolfi *et al.* 2005), increased frequency and severity of mass bleaching events (McWilliams *et al.* 2005; Eakin *et al.* in press), and increasing coastal development (Mora 2008) exacerbated coral mortality in subsequent years. Hurricanes have played a relatively small role in the regional loss of coral cover, although, they can have considerable localized impacts (Gardner *et al.* 2005). In contrast to our sophisticated understanding of the drivers of changing coral cover, little is known about the drivers of the regional-scale changes in architectural complexity in Caribbean reefs or elsewhere.

Here we use a unique Caribbean-wide dataset of time series of reef architectural complexity to explore the influence of hurricanes, mass bleaching events and fishing (by comparing protected to unprotected reefs) on the rate of change in architectural complexity. We hope to improve understanding of whether the major drivers of coral cover loss have also impacted the structural integrity of Caribbean reefs, and thus to provide information of importance for developing strategies for reef recovery and conservation.

Material and methods

Data collation

We collated data from replicated studies (i.e. data collected over more than one year) that reported architectural complexity for reefs sites within the wider Caribbean. We used the rugosity index to describe reef architecture, as this is the most commonly used method for measuring reef complexity in the region (Chapter 1). We used online literature search tools to browse in the most relevant journals for Caribbean reef studies, and contacted scientists and reef managers directly to obtain the required information (details in Chapter 1). This resulted in a total of 27 studies with temporal replication between 1978 and 2008 (figure 1), reporting information for 49 reef sites and ranging in duration from two to 17 years (mean = 6.29 ± 4.23 SD years; table 1).

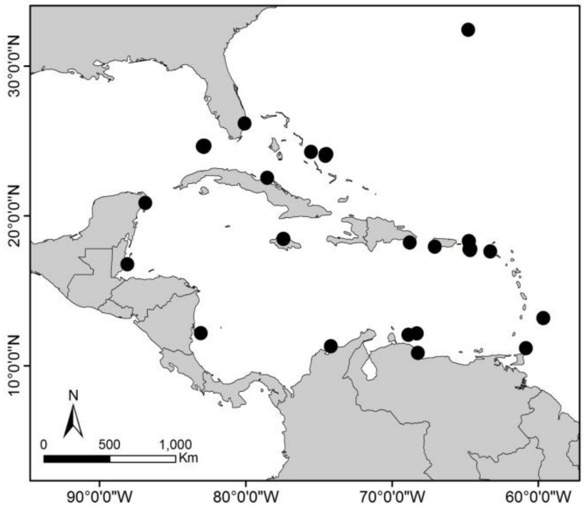

Figure 1. Regional distribution of reef sites from which surveys of architectural complexity, replicated over more than one year, were collated.

Table1. Details of the studies from which data were collated to assess the effects of bleaching, hurricanes and protection from fishing on annual rates of change in reef architectural complexity.

Data source	Country / Island	Years	Number of sites[a]	Mean # replicates	Transect length
Alvarez-Filip[1]	Mexico	2006 - 2008	1	41	3
Baron et al. 2004	Florida (US)	1983 - 1991	1	19	8
Bythell et al. 2000[2]	USVI	1990 - 2000	3	4	20
Caricomp[3]	16 reef sites	1993 – 1996	17	5	10
Clarke 1996	USVI	1979 - 1995	1	9	10
Edmunds 2002[4]	USVI	1994 - 2007	2	3	10
Jaap et al. 1991	Florida (US)	1989 - 1991	5	2	20
McGrath et al. 2007	Bahamas	1995 - 2004	3	10	5
NOAA[5]	Puerto Rico & USVI	2001 - 2007	9	47	6
Rogers et al. 1982	USVI	1978 - 1979	1	3	10
Rogers et al. 1991	USVI	1989 - 1990	1	5	20
Steneck 1993	Jamaica & USVI	1982 - 1988	5	76	10

[a] ‘Sites’ represent an average of many data points (e.g. transects and, in some studies, locations). For transects reported separately for the same location but at different depths, each depth stratum (e.g. 5-10 m and 15-20 m) was considered as a separate site.

[1] Unpublished data

[2] Data complemented with previous reports

[3] Caricomp data from 1993 to 1996, except when indicated, and include records for Bahamas, Barbados (1993-2006)[4], Belize, Bermuda, Bonaire, Colombia, Cuba, Curacao, Dominican Republic (1996-2001)[4], Jamaica, Mexico, Nicaragua, Puerto Rico, Saba, Trinidad & Tobago (1994-2000)[2] and Venezuela.

[4] Complemented with unpublished data provided by the corresponding authours.

[5] Data obtained from the Caribbean Coral Reef Ecosystem Monitoring Project of the National Oceanic & Atmospheric Administration, Biogeography Team. Data accessed in Octuber 2008 (http://ccma.nos.noaa.gov/ecosystems/coralreef/reef_fish.html)

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Drivers of change of reef architectural complexity

Coral bleaching

We tested for an effect of coral bleaching on regional reef architecture in two ways: temporally by focusing on years of mass bleaching and spatially by exploring the effect of local, small-scale temperature anomalies. We first assumed that in the seven years between 1978 and 2008 in which bleaching was widespread (sometimes referred to as ‘‘mass bleaching events”: 1987, 1990, 1995, 1998, 1999, 2003 and 2005; McWilliams *et al.* 2005; Perry 2008; Eakin *et al.* in press), bleaching affected all sites in this study. For each mass bleaching event, we calculated the annual rate of change in rugosity from the year prior to the mass bleaching event to the last year of the time series or the year immediately before the next mass bleaching event, in order to account for the possible erosion of architectural complexity after coral mortality. The mass bleaching events of 1998 and 1999 were classed together because they occurred in consecutive years and, for time series that spanned more than one bleaching event, each event was included separately in the analysis. In addition, to avoid confounding the effect of bleaching with the effect of physical damage on reef architecture, only data from reefs that were not impacted by a hurricane after a bleaching episode were included. Some of the time series did not contain data spanning any of the years of mass bleaching events, and were therefore not included in these analyses.

Secondly, although region-wide thermal anomalies have been linked to the geographic extent and intensity of bleaching across the Caribbean (McWilliams *et al.* 2005; Perry 2008; Donner 2009), thermal stress does not usually occur homogeneously through the entire seascape (e.g. Selig *et al.* 2010; Eakin *et al.* in press). Consequently, we also explored the effect of variation in summer sea surface temperature (SST) anomalies on the annual rates of change in architectural complexity within individual 1° latitude by 1° longitude cells. We used historical SST data from the HadISST 1.1 dataset (Hadley Centre, UK Meteorological Office) to calculate the average summer monthly (August, September and October) SST anomalies (relative to the means for these months for the baseline period of 1961-1990) for each year between 1989 and 2006, for all cells within our dataset. These monthly anomalies were then averaged within each year, giving annual summer mean SST anomalies for each cell that contained information on reef rugosity in each specific year. The rates of change in reef rugosity were then calculated for all consecutive years in each time series, then the average of all sites that contained information for specific pair of years was calculated and related to the average SST anomaly for all those sites in that pair of years.

Hurricanes

We classified whether sites were impacted by a hurricane using the method of Gardner *et al*. (2005). A hurricane was considered to have impacted a reef if its track passed within a given distance of the site, with its range of effect increasing with hurricane strength. Thus, tropical storms or hurricanes of category 1 or 2 passing within 35 km of a site, category 3 hurricanes passing within 60 km, or category 4 or 5 hurricanes passing within 100 km of a given site were recorded as impacts. The hurricane history of each site was obtained from the web-based tool of the NOAA Coastal Services Center (http://csc.noaa.gov).

We compared annual rates of change in architectural complexity at sites impacted and unimpacted by hurricanes. In addition, because the time elapsed between hurricanes influences the magnitude of the loss of coral cover seen in response to hurricane impacts (Connell 1997; Gardner *et al.* 2005), we also compared the rates of complexity change between sites that had been impacted in the 10 years prior to the focal hurricane impact and sites that were not impacted. We therefore measured the effect of hurricanes at four categories of sites: (i) reef sites impacted 10 years before the onset of their study and during their survey period (before-during); (ii) sites impacted only during their survey period (during); (iii) sites impacted only within the 10 years before their survey period (before); and (iv) sites not impacted by hurricanes from 10 years prior to the onset of their study to the end of their survey period (non-impacted).

Marine Protected Areas

We tested for effects of fishing on changes in reef architecture by determining whether sites were protected (i.e. within the boundaries of a Marine Protected Area [MPA], and hence not subject to fishing) or unprotected (i.e. subject to fishing) during their survey period. Protection status was determined using the global database of Marine Protected Areas (Wood 2007). Rates of change in rugosity were then compared between protected and unprotected sites.

Because the duration of protection has been shown to be important in determining MPA success in increasing fish diversity and density (Claudet *et al.* 2008; Molloy *et al.* 2009), both of which are important factors contributing to restoring habitat quality (Mumby & Steneck 2008; Mumby & Harborne 2010; Selig & Bruno 2010), we also calculated the number of years between the official designation of the MPA and the first survey for each site. We then correlated the age of reserves with their annual rates of change in architectural complexity.

Meta-analysis

To estimate annual rates of change in reef architecture we used a weighted meta-analytic approach (Rosenberg *et al.* 2000). The standardised effect size was the annual rate of change (ARC) for each study, calculated as:

$$ARC = (\log End - \log Start) / d$$

where *End* and *Start* represents the final and initial reef rugosity of the time series, respectively, and *d* is the number of years elapsed between the two estimates. This metric has been previously used in studies of ecological change on coral reefs (Côté *et al.* 2005; Côté *et al.* 2006; Paddack *et al.* 2009; Chapter 2), and its properties as an effect size have been thoroughly investigated (Côté *et al.* 2005). In meta-analyses, effect sizes are often weighted by the inverse of the sample variance to incorporate a measure of the robustness of each effect size estimate (Rosenberg *et al.* 2000). However, survey area has been found to yield more biologically realistic weightings for coral reef benthic data (Côté *et al.* 2005). For this reason, we used the natural logarithm of the area surveyed (i.e. transect length multiplied by the number of replicate transects) as a weighting factor in our analyses (see also Mosqueira *et al.* 2000; Côté *et al.* 2001). Statistically significant effect sizes were identified from 95% bias-corrected bootstrapped confidence intervals (generated from 9999 iterations) which did not encompass zero. The Q_M statistic was used to test for differences in rates of change in architectural complexity in the different treatments. A significant Q_M implies that there are differences in mean effect sizes among groups, thus a non-significant Q_M does not preclude individual groups showing significant effect sizes (i.e. individual confidence intervals do not overlap zero). All meta-analyses were conducted in MetaWin Version 2.0 (Rosenberg *et al.* 2000). Annual rates of change and confidence intervals are presented back-transformed to percentages to facilitate their interpretation.

Results

Coral bleaching

A total of 31 studies spanned one or more bleaching events; eleven encompassed one, 14 encompassed two and six encompassed three mass bleaching events. Eighteen of these 57 separate bleaching events occurred in locations that simultaneously experienced a hurricane impact and therefore were removed from the analysis. Thus, in total, 39 separate bleaching events, with a mean duration of 3.1 (± 1.4 SD) years, were used to explore the link between coral bleaching and subsequent changes in architectural complexity.

Overall, architectural complexity did not decline significantly after mass bleaching events, with an annual rate of change of -0.87 % (CI = -2.47 % to 0.46 %). There were no statistically significant differences in the rates of architectural complexity change among the seven mass bleaching events ($Q_M = 5.81$, $P = 0.22$; figure 2a). The only significant decline in architectural complexity occurred just after the mass bleaching event of 1995, although the very limited number of studies makes this conclusion tentative (figure 2a).

Rates of change in architectural complexity were also not related to SST anomalies ($R^2 = 0.002$, $P = 0.88$; figure 2b), and the seven years referred to as mass bleaching events in the literature all had positive SST anomalies but similar rates of change in architectural complexity as the other years (figure 2b).

Hurricanes

Annual rates of change in architectural complexity varied significantly between reefs that had been impacted either before, during, before and during or not impacted by a hurricane ($Q_M = 14.31$, $P = 0.04$). The most rapid rates of decline in rugosity occurred at sites impacted during their survey period only, while considerably lower rates of decline were recorded at sites that were impacted both before and during their survey period (figure 3). Architectural complexity on sites that were not impacted by a hurricane during their survey period (i.e. the ‘before’ and ‘non-impacted’ groups) did not decline significantly (figure 3).

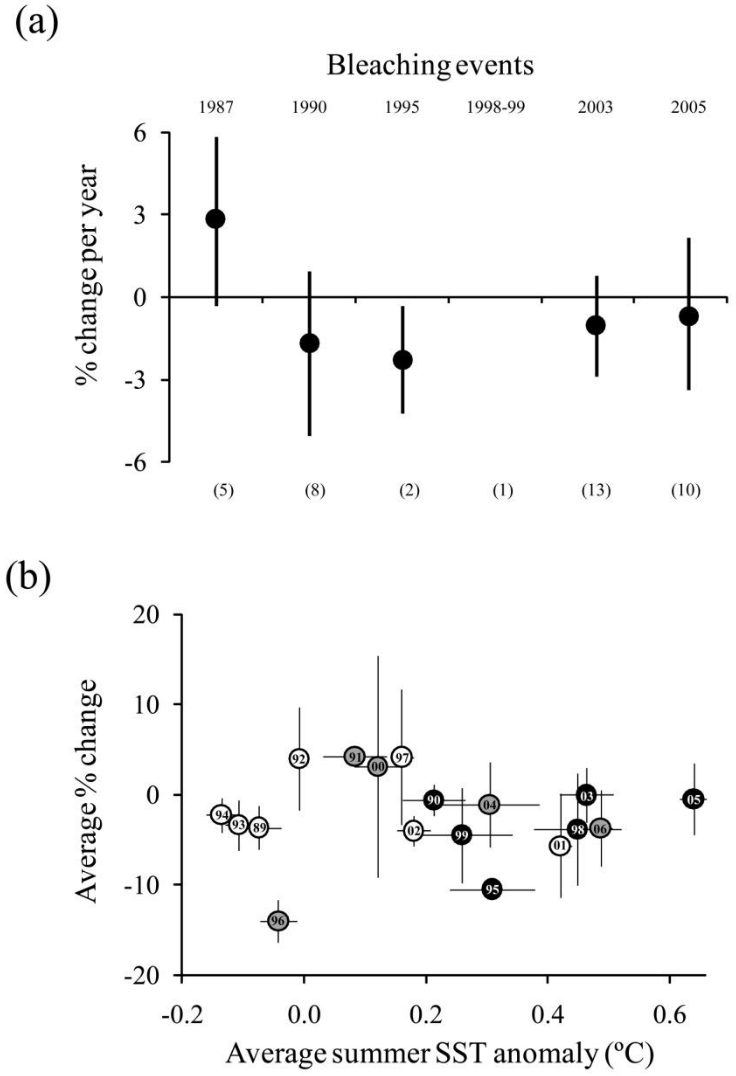

Figure 2. Effect of widespread bleaching events and SST anomalies on rates of architectural complexity change in the Caribbean. (a) Annual percentage change in reef rugosity on reef sites after widespread bleaching events. The total number of sites is given in parentheses (1998-1999 is excluded as only one bleaching event was available) and bars show 95% bias-corrected bootstrapped confidence intervals (b) Average (± SE) change in rugosity on reef sites between pairs of consecutive years and average (± SE) summer SST anomaly in the first year of each pair (black = years of mass bleaching events, grey = one year after mass bleaching events, white = all other years). Points are labelled by year, from 1989 to 2006.

Fishing (Marine Protected Areas)

Rates of change of architectural complexity did not differ significantly between sites that were fished and sites within MPAs ($Q_M = 0.04$, $P = 0.92$), although reef rugosity did decline significantly inside but not outwith MPAs (figure 4a). Annual rates of change in reef architectural complexity within MPAs did not vary with the duration of site protection ($R^2 = 0.002$, $P = 0.848$; figure 4b).

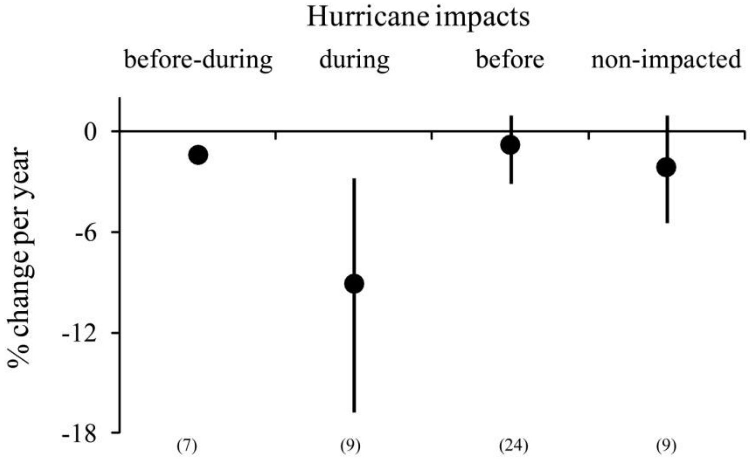

Figure 3. Effect of hurricane impacts on rates of architectural complexity change in the Caribbean. Annual percentage change in reef rugosity for reef sites impacted 10 years before the onset of their study and during their survey period (before-during); only during their survey period (during); only 10 years before their survey period (before); and not impacted by hurricanes from 10 years prior the onset of their study to the end of their survey period (non-impacted). Numbers in parentheses indicate the number of sites included in the analysis for each group. Bars show the 95% bias-corrected bootstrapped confidence intervals.

Discussion

This study describes the effect off three major disturbances of coral reefs degradation on the structural integrity of reefs throughout the Caribbean. While hurricanes and fishing appear to have significantly influenced the rate of change of region-wide reef complexity, coral bleaching appears to have had little influence on architectural complexity loss. Our results therefore suggest that at least one of the major drivers of coral mortality, i.e. bleaching (Aronson & Precht 2006; Schutte *et al.* 2010), may not have an immediate influence on reef complexity. Instead, direct physical impacts and reef bioerosion may be the most important drivers of the widespread loss of architecturally complex reefs in the Caribbean.

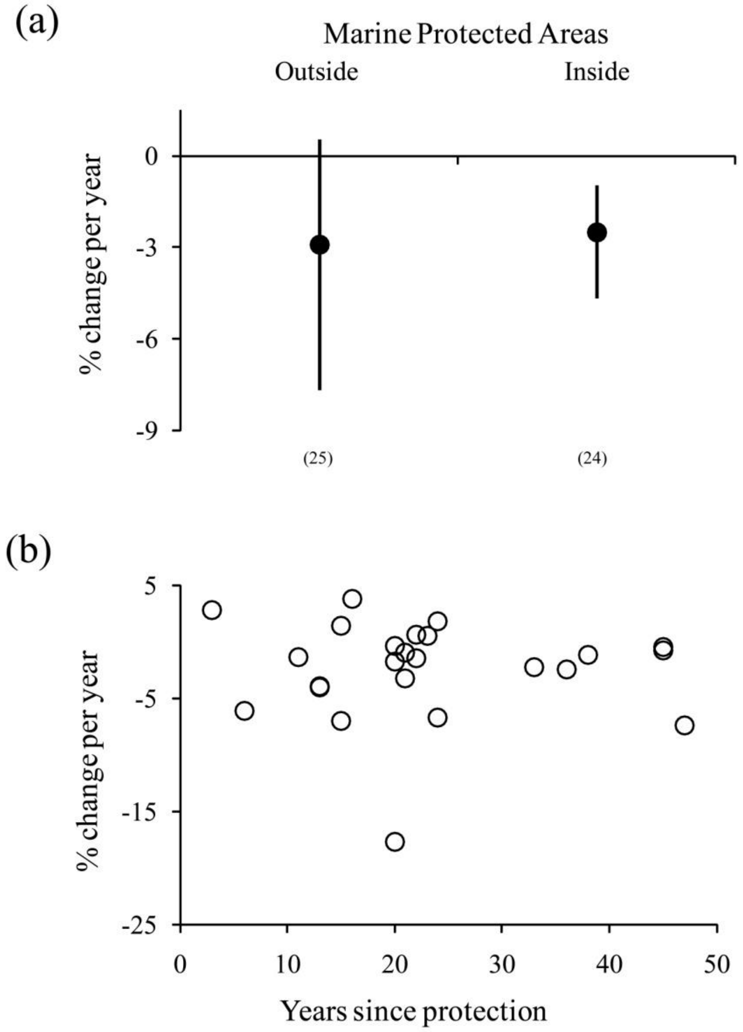

Figure 4. Effect of Marine Protected Areas (MPA) on rates of change in reef architectural complexity in the Caribbean. (a) Annual percentage change in reef rugosity for reefs inside and outwith MPAs. Numbers in parentheses indicate the number of sites included in the analysis for each group. Bars show the 95% bias-corrected bootstrapped confidence intervals. (b) Relationship between annual rate of change in complexity and years since protection for 24 sites inside MPAs.

Physical disturbances such as hurricanes and direct damage due to destructive human practices are likely to simultaneously affect the tissue and skeletons of reef corals, thus producing rapid declines in architectural complexity following coral mortality (e.g. Woodley *et al.* 1981; Alvarez-Filip & Gil 2006). The magnitude of damage may vary depending on the composition of coral assemblages (e.g. branching corals are more susceptible to breakage) and intensity of disturbances (Hughes & Connell 1999). The strong influence of hurricane impacts on region-wide reef architectural complexity reported here contrasts with previous studies which have shown that hurricanes are not a major driver of recent regional declines in coral cover in the Caribbean (Gardner *et al.* 2005),likely because biological drivers are thought to be more important than physical disturbances in impacting the live tissue of corals as they can generally occur at larger spatial scales and/or can spread rapidly (Aronson & Precht 2006; Hoegh-Guldberg *et al.* 2007; Schutte *et al.* 2010). Interestingly, declines in architectural complexity following hurricane impacts were less severe on reefs that had been impacted by another hurricane during the previous 10 years. This may indicate reductions in the abundance of coral colonies that are particularly susceptible to physical disturbances (e.g., branching species). Indeed, branching species can dominate reefs that have not experienced a hurricane for several years (Woodley *et al.* 1981; Rogers 1993). Hurricane-impacted reefs on which these species are less abundant may thus provide less scope for subsequent hurricanes to cause further damage to reef architecture (Woodley *et al.* 1981; Alvarez-Filip *et al.* 2009). However, consecutive hurricanes impacts are likely to maintain coral reefs in less structurally complex states, an effect that is likely to be compounded by the increase in activity of Atlantic Ocean hurricanes (Saunders & Lea 2008).

Biological disturbances such as diseases, predator outbreaks or climate-induced coral bleaching usually kill coral tissue without initially compromising the integrity of the coral skeleton. After tissue death, the exposed coral skeletons are subject to local rates of physical, chemical and biological erosion (Hutchings 1986; Glynn 1997). Coral skeletons of erect branching corals (e.g., *Acropora*) may then break down into coral rubble (Sheppard *et al.* 2002; Graham *et al.* 2006), whereas massive coral skeletons typically gradually erode *in situ* (Sheppard *et al.* 2002). One probable reason for the absence of significant declines in architectural complexity following coral bleaching or anomalously warm sea surface temperatures may be the lack of extensive coral mortality following bleaching at the reef-sites included in our meta-analysis. Although reef accretion can be halted after coral bleaching (Hoegh-Guldberg *et al.* 2007; Baker *et al.* 2008), recovery of live coral tissue after bleaching events would reduce any impact on reef complexity. In addition, most of the studies included in this analysis took place during a period in which Caribbean reefs have been dominated by massive and weedy corals (post-*Acropora* die-off; (Aronson & Precht 2006; Chapter 2). As the erosion of massive coral skeletons is likely to be a slow process, the period of time after bleaching events (average ≈ 3 years for data in figure 2a) may not have been sufficient to detect an impact on reef structure. However, previous studies have shown that regional declines in reef complexity in the Caribbean followed coral mortality with no evidence of a time-lag (Chapter 2), which also suggests that biological disturbances (which typically operate more slowly than physical disturbances) have not played a direct role in the recent region-wide declines in Caribbean reef complexity.

The removal of fishing pressure, through the establishment of marine protected areas, is widely recognized as an important tool for the protection of biological diversity and fisheries management (Sale *et al.* 2005; Gaston *et al.* 2008). On coral reefs, there is a broad range of positive effects within protected areas, such as increased biomass, abundance, average size and diversity of fish and invertebrates (Halpern 2003; Claudet *et al.* 2008; Molloy *et al.* 2009). However, regional- and local-scale studies have found that large declines in coral cover can occur in spite of protection (Coelho & Manfrino 2007; Graham *et al.* 2008; Mora 2008), although recent evidence suggests that coral cover is maintained to a greater extent inside marine reserves (Selig & Bruno 2010). The latter is probably because protection from fishing can restore key ecological processes such as herbivory, which can aid the recovery of coral colonies through the removal of space competitors or other sources of stress (e.g. macroalgae; Mumby & Harborne 2010). These positive effects of protection might only become apparent long after reserve establishment, for instance coral cover inside some Caribbean marine reserves experienced continuous declines for up to 14 years after implementation (Selig & Bruno 2010). The significant decline in architectural complexity inside MPAs, but not on unprotected reefs, could have resulted from MPA designation of reef sites that were initially in better condition, and thus had 'more to lose' than unprotected reefs. However, this seems unlikely in our case, as average rugosity at the start of the time series was similar for protected and unprotected reefs (protected = 1.66 ± 0.9 SE; unprotected = 1.73 ± 0.13 SE; $T_{(47)} = -0.61$, $P = 0.55$). Alternatively, protection from fishing may lead to enhanced rates of bioerosion by herbivorous fish inside MPAs (Hutchings 1986; McClanahan 1994), which could increase rates of loss of reef architecture on protected reefs. Because of over-exploitation and disease, Caribbean reefs have had relatively low densities of macro-bioeroders since the early 1980s (Carpenter 1988; Pandolfi *et al.* 2005), which likely slowed down rates of reef architecture loss (Mallela & Perry 2007; Chapter 1). The implementation of MPAs can greatly enhance the number and biomass of grazers such as parrotfishes (e.g. Mumby 2006; Mumby *et al.* 2006), which can in turn increase rates of erosion on reefs that are already failing to accrete as a consequence of the loss of reef-building corals (Bruggemann *et al.* 1996). This scenario does not imply that MPAs are not fulfilling their function; indeed, they may be critically important for the recovery of key components of coral reefs such as the associated fish communities. However, our results highlight the necessity of understanding the full range of interactions between the components of coral reefs to design management tools that will successfully secure the long-term persistence of these ecosystems.

Over the last four decades, Caribbean reefs have undergone rapid and severe rates of decline in coral cover and reef architecture (Gardner *et al.* 2003; Chapter 2), generating a debate in the scientific community about the major disturbances (local *vs* global) that have driven these declines (Aronson & Precht 2006; Knowlton & Jackson 2008). While a growing body of evidence indicates that the cover of reef-building corals is influenced by large-scale drivers such as changing climate and the spread of human development (Knowlton & Jackson 2008; Mora 2008; Schutte *et al.* 2010), here we show that changes in reef architecture may be more sensitive to local reef conditions (e.g. rates of erosion and hurricane impacts) and hence may be relatively independent of changing coral cover. Thus, while reversing coral decline is likely to require international regulations to reduce the impacts of human activities, our results suggest that the protection and recovery of reef architecture will depend largely on the protection and enhancement of conditions at the local reef scale.

Chapter 4

Coral identity underpins reef complexity on Caribbean reefs

Abstract
The architectural complexity of ecosystems can greatly influence their capacity to support biodiversity and deliver ecosystem services. Understanding the components underlying this complexity can aid the development of effective strategies for ecosystem conservation. Caribbean coral reefs support and protect millions of livelihoods, but recently the anthropogenic change is shifting communities towards reefs dominated by stress-resistant and less architecturally complex coral species. We quantify the influence of coral composition, diversity and morpho-functional traits on the architectural complexity of reefs across 91 sites at Cozumel, Mexico. Although reef architectural complexity increases with coral cover and species richness, it is highest on sites that are low in taxonomic evenness and dominated by morpho-functionally important reef-building coral genera, particularly *Montastrea*. Sites with similar coral community composition also tend to occur on reefs with very similar architectural complexity, suggesting that reef structure tends to be determined by the same key species across sites. Our findings suggest that a major emphasis on facilitating the endurance of healthy populations of key morpho-functional groups may be required to halt the rapid and severe declines in reef architectural complexity across the Caribbean. Specifically, these results provide support for prioritising and protecting particular reef types, particularly those dominated by *Montastrea* corals, in order to enhance reef complexity.

Submitted:

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Introduction

The architectural complexity of ecosystems often underpins the biodiversity and ecosystem services that they support. Architectural complexity is very often defined or provided by foundation taxa (e.g. trees, oysters, stony corals) that have a disproportionate influence on ecosystem structure, function and stability (MacArthur 1984; Bruno & Bertness 2001; Ellison *et al.* 2005). However, within these broad groups of foundation taxa, different species can contribute disproportionately to architectural complexity. Understanding the influence of different species and taxa on ecosystem structure and function can therefore be key to the development of effective conservation priorities and actions.

Coral reefs are among the most rapidly changing and valuable ecosystems in the world. It is estimated that nearly 70 per cent of the world's coral reefs are threatened by anthropogenic activities (Wilkinson 2008) and are experiencing unprecedented rates of degradation (Veron 2008). In the Caribbean, for instance, the architectural complexity of reefs has declined substantially over the past forty years with the loss of ~80% of the most complex reefs (Chapter 1). Because of the importance of reef-building corals as foundation species within the diverse reef ecosystem, patterns of degradation and ecological resilience on coral reefs are typically measured through changes in overall coral cover (e.g. Gardner *et al.* 2003; Bruno & Selig 2007; Mumby *et al.* 2007). However, changes in coral cover do not capture the changes in reef architectural complexity (Chapter 2) that can underpin a suite of important ecosystem services such as the dissipation of wave energy, nutrient recycling and the abundance, diversity and trophic structure of coral reef fishes (Szmant 1997; Lugo-Fernandez *et al.* 1998; Sheppard *et al.* 2005; Wilson *et al.* 2007; 2010).

There is considerable potential for taxon identity and the composition of reef-building corals to influence the architectural complexity of reefs, as hard scleractinian corals are a taxonomically and morphologically diverse group (Veron & Stafford-Smith 2002; Dullo 2005). While qualitative differences in the relative contribution of different coral species to reef complexity are apparent for most of the reef scientist, the contribution of coral identity and community composition to architectural complexity has yet to be quantified at the larger reef scales. Quantifying the relative contribution of different coral species to the architectural complexity of the reefscape is therefore particularly important in order to understand the trajectory of coral reefs under changing environmental conditions. A growing body of evidence suggests that loss of the main reef-building coral taxa is accompanied by an increase in the relative abundance (leading to eventual dominance) of stress-tolerant, early-colonizing corals that form smaller and less-architecturally complex colonies such as *Porites* and *Agaricia* (Aronson *et al.* 2002; Green *et al.* 2008; Lirman & Manzello 2009). This shift towards weedy coral species may constrain reefs into a state of lower potential architectural complexity (Steneck *et al.* 2009), even if overall coral cover remains stable.

Here we explore the contribution of coral community composition to reef architectural complexity across a broad range of sites in Cozumel, Mexico. First, we quantify whether sites with similar coral community composition also tend to be similar in terms of architectural complexity. Second, we test whether greater coral species diversity is related to greater architectural complexity. Finally, we explore how the taxonomic and functional attributes of coral dominance influence the relationship between coral cover and architectural complexity.

Materials and methods

Study area

This study was carried out with the permission and support of the Parque Nacional Arrecifes de Cozumel. Cozumel is a continental island in the North-Western Caribbean (figure 1). Cozumel is surrounded by coral reefs, the most developed of which are on the western side of the island and primarily comprise shelf-edge reefs, which typically have a complex reef framework formed by calcareous formations of several meters depth, and barrier reefs which are less well-developed (Jordán-Dahlgren 1988). The reefs along the south-west coast have been under official protection since 1980 (Alvarez-Filip *et al.* 2009; figure 1).

Field surveys

In total, 91 sites along the south-west coast of Cozumel, all separated by at least 200 m (figure 1), were surveyed between October 2007 and February 2008. At each site, one

30 m transect between 10 and 15 m depth was randomly located on the top of the frontal reefs and parallel to the coast. To evaluate coral abundance, we used the point intercept method to record the occurrence of coral species every 25 cm along each transect (120 counts per transect).

Reef architectural complexity was quantified using the rugosity index, which is the ratio of a length of chain moulded to the reef surface to the linear distance between its start and end point (Chapter 1). A perfectly flat surface has a rugosity index of one, with larger numbers indicating more complex surfaces. Scores rarely exceed three, which would be typical of historic reef complexity in the Caribbean prior to the 1980s (Chapter 1). A three metre chain (0.7 cm link-length) was used to estimate reef rugosity at five equally spaced points along the same 30 m transect, which were then averaged to give transect-level rugosity.

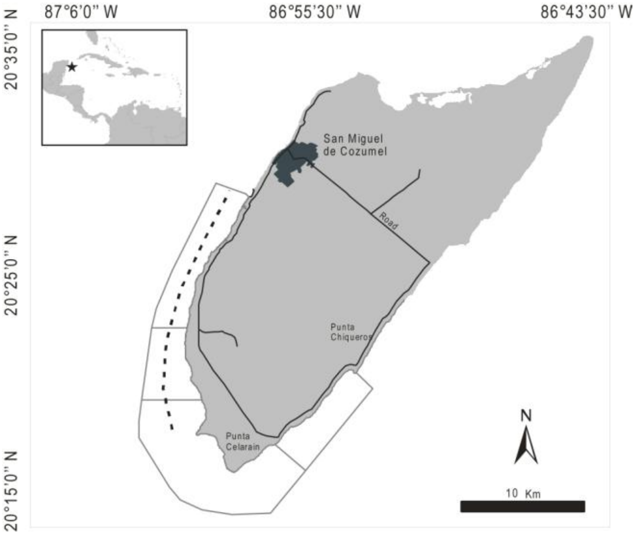

Figure 1. Map of Cozumel Island and (inset) the location within the Caribbean Sea. The continuous line delimits the polygon of the Marine Protected Area (Parque Nacional Arrecifes de Cozumel) and the bold dotted line represents the area surveyed in this study.

Data Analyses

To examine whether transects with similar coral community composition also tended to have similar architectural complexity, we constructed matrices of site community composition and site rugosity for all pairs of sites. The similarity matrix for coral community composition was constructed using all coral species and their relative cover in each site, and computed using the Bray-Curtis similarity coefficient. The architectural complexity matrix was constructed by calculating the relative percentage similarity in rugosity between each pair of sites using the following formula:

$$\%\ similarity = [(R_L - R_S) / MD)] \times 100$$

where R_L and R_S are the larger and smaller values of rugosity for each pair of comparisons independent of their position in the matrix, and *MD* is the maximum observed difference between all the pairwise comparisons of R_L and R_S. We evaluated whether architectural complexity among sites is a function of coral community composition by comparing both matrices using a Mantel test based on 10,000 permutations (Mantel 1967).

To test whether greater coral species diversity is related to greater architectural complexity, we quantified coral diversity using three univariate dimensions of diversity (Magurran 2004): coral species richness (number of species recorded at each site), evenness in species abundance (the Pielou index of percentage areal cover of each species) and taxonomic diversity. For the last dimension, we calculated the average taxonomic distinctness (Δ^+) and the variation in taxonomic distinctness (Λ^+) using a widely-used and accepted coral taxonomy (Veron & Stafford-Smith 2002). Average taxonomic distinctness measures average evolutionary relatedness as the mean path or branch length of the local community and the variation in taxonomic distinctness is the variance in path or branch lengths of the local community (Clarke & Warwick 1998; Clarke & Warwick 2001). We also calculated richness and evenness of the morpho-functional groups. We then used linear regressions to explore the strength and nature of the associations between each of these measures of coral diversity and reef architectural complexity.

To explore the influence of species identity and morpho-functional attributes on reef structure, we grouped coral species by genus and by morphology. Morpho-functional groups were constructed from the maximum size and colony shape of each coral species (table 1). Following Reyes-Bonilla (2004), three shape categories (massive or nodular; branching, ramose or phaceloid; platy, foliaceous or encrusting) and three size categories (small (<10 cm); medium (10 to 30 cm); large (>30 cm)) were used. Combining shape and size categories resulted in seven different morpho-functional groups (table 1).

Table 1. Mean cover (± standard error) and morphological information of the coral species recorded in the 91 sites surveyed.

Genus	Species	Average cover (± SE)	Colony shape[a]	Colony size[b]	Morphology group[c]
Acropora	*A. cervicornis*	*0.03 (0.03)*	B	L	BL
	A. palmata	*0.16 (0.1)*	B	L	BL
Madracis	*M. decactis*	*0.16 (0.04)*	M	M	MM
	M. formosa	*0.02 (0.01)*	B	M	BM
Stephanocoenia	*S. michelini*	*0.24 (0.05)*	M	M	MM
Eusmilia	*E. fastigiata*	*0.39 (0.07)*	B	M	BM
Colpophyllia	*C. natans*	*0.06 (0.04)*	M	L	ML
Diploria	*D. clivosa*	*0.03 (0.02)*	M	L	ML
	D. labyrinthiformis	*0.05 (0.02)*	M	M	MM
	D. strigosa	*0.07 (0.04)*	M	M	MM
Montastrea	*M. annularis*	*1.43 (0.39)*	M	L	ML
	M. cavernosa	*0.97 (0.12)*	M	L	ML
	M. faveolata	*1.68 (0.26)*	M	L	ML
	M. franksi	*0.09 (0.03)*	M	M	MM
Favia	*F. fragum*	*0.02 (0.01)*	M	S	MS
Dendrogyra	*D. cylindricus*	*0.01 (0.01)*	M	L	ML
Dichocoenia	*D. stokesi*	*0.04 (0.02)*	M	M	MM
Meandrina	*M. meandrites*	*0.13 (0.04)*	M	M	MM
Isophyllastrea	*I. rigida*	*0.02 (0.01)*	M	M	MM
Mycetophyllia	*M. lamarckiana*	*0.15 (0.04)*	P	M	PM
Agaricia	*A. agaricites*	*4.56 (0.41)*	P	L	PL
	A. humilis	*0.03 (0.02)*	M	L	ML
	A. lamarcki	*0.02 (0.01)*	P	L	PL
	A. tenuifolia	*0.43 (0.13)*	P	L	PL
Siderastrea	*S. radians*	*0.02 (0.01)*	M	S	MS
	S. siderea	*1.45 (0.16)*	M	L	ML
Porites	*P. astreoides*	*2.45 (0.3)*	M	M	MM
	P. colonensis	*0.03 (0.02)*	P	M	PM
	P. divaricata	*0.02 (0.01)*	B	L	BL
	P. furcata	*0.10 (0.04)*	B	L	BL
	P. porites	*0.82 (0.13)*	B	L	BL
Millepora	*M. alcicornis*	*0.27 (0.06)*	B	M	BM
	M. complanta	*0.06 (0.02)*	P	L	PL

[a] M = massive or nodular; B = branching, ramose or phaceloid; P = platy, foliaceous or encrusting.
[b] S = small (<10 cm); M = medium (10 to 30 cm); L = large (>30cm).
[c] Morphological group is the combination of shape and size.

The 91 transects then were categorised depending on the single most dominant (highest relative abundance on the site) genus and morpho-functional group. We used linear regression to compare the relationships between architectural complexity and cover of (a) the three most abundant genera (*Agaricia*, *Porites* and *Montastrea*) and (b) the three most abundant morpho-functional groups (figure 2b). Differences between each pair of linear models were explored by dividing the difference between both regression coefficients by the square root of the sum of the squared standard errors. Assuming normally distributed residuals, this estimate follows a t-distribution with *n*-2 degrees of freedom (Zar 1999).

Results

A total of 33 species of reef-building corals were recorded in Cozumel during this study (table 1). *Agaricia*, *Montastrea* and *Porites* were the dominant genera (figure 2a), and corals with massive and foliaceous colonies that form large colonies were the most abundant morpho-functional groups (figure 2b). Both coral cover and reef architectural complexity vary greatly across the study area, from flat sites with low coral cover to highly complex areas of reef. Average coral cover for the 91 sites was 16% (± 1.32 SE, range: 0 - 52%) while rugosity indices averaged 1.49 (± 0.04 SE, range: 1.02 - 2.77).

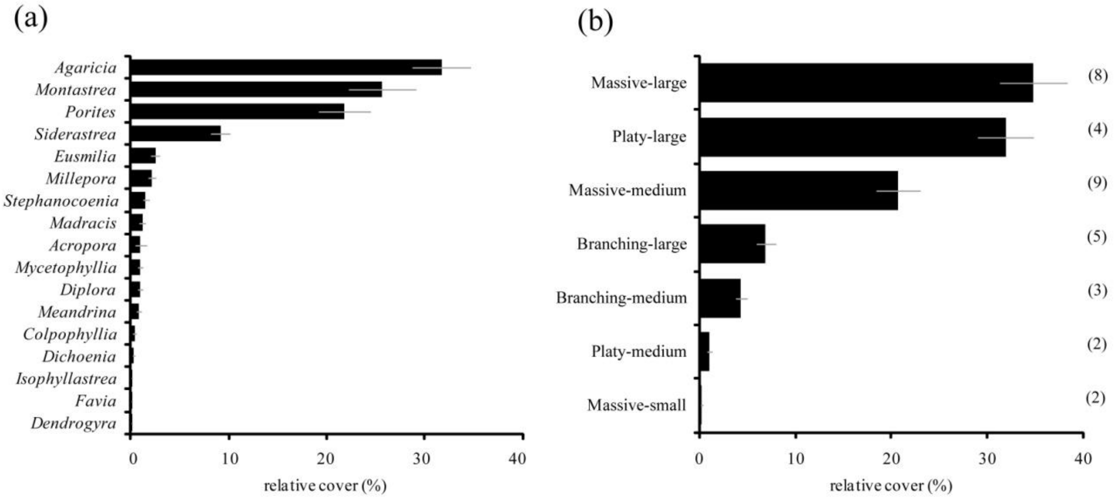

Figure 2. Mean percent cover (± standard error) of hard corals on Cozumel reefs, grouped by (a) genus and (b) morphology (see table 1 for definitions of morpho-functional groups). For (b) the total number of species included in each morpho-functional group is given in parentheses.

Pairs of sites with similar coral community composition tend to also have similar levels of architectural complexity (Mantel test, $r_m = 0.18$; $p < 0.001$).Very high similarity in coral community composition (> 70% similarity) only occurred in reefs with similar architectural complexity (> 50% similarity in rugosity), regardless of whether the sites were similarly complex or similarly flat (figure 3).

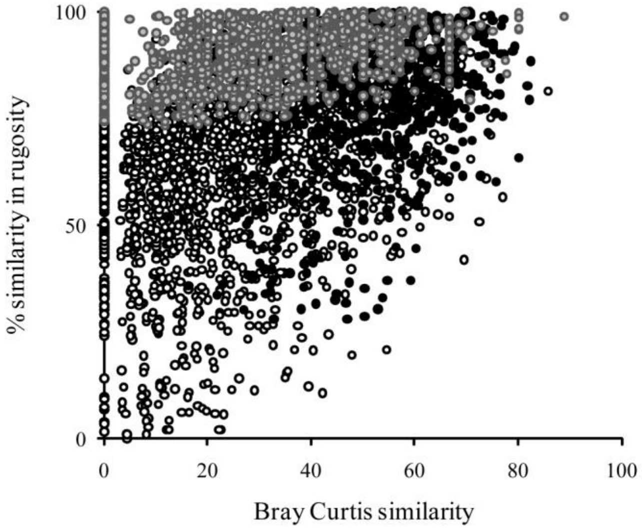

Figure 3. Similarities in coral community composition (Bray-Curtis similarity coefficient) and reef architecture (% similarity in rugosity indices) for 4095 different pairs of sites from 91 sites in Cozumel. Circle colour indicates pairs of sites which both have rugosity values > 1.5 (black), both < 1.5 (grey) or one from each category (white).

Architectural complexity is positively associated with the number of coral species: sites with fewer than five coral species tend to be relatively flat while more diverse sites, with between 8 and 13 species, had the greatest complexity (figure 4a). However, the evenness in coral cover among coral species declined with increasing coral species richness ($r = -0.40$; $P < 0.001$), and consequently sites with greater architectural complexity tended to be dominated by one or few coral species (figure 4b). The relationship between taxonomic distinctness among coral species and architectural complexity is dome-shaped, with a small number of flat reefs tending to be either particularly distinct or particularly related (figure 4c). The variation in taxonomic distinctness was not significantly related to architectural complexity (figure 4d). From the morphological and functional perspective, greatest complexity is found on reefs with higher morpho-functional diversity (figure 4e), but dominance by relatively few morpho-functional types (figure 4f).

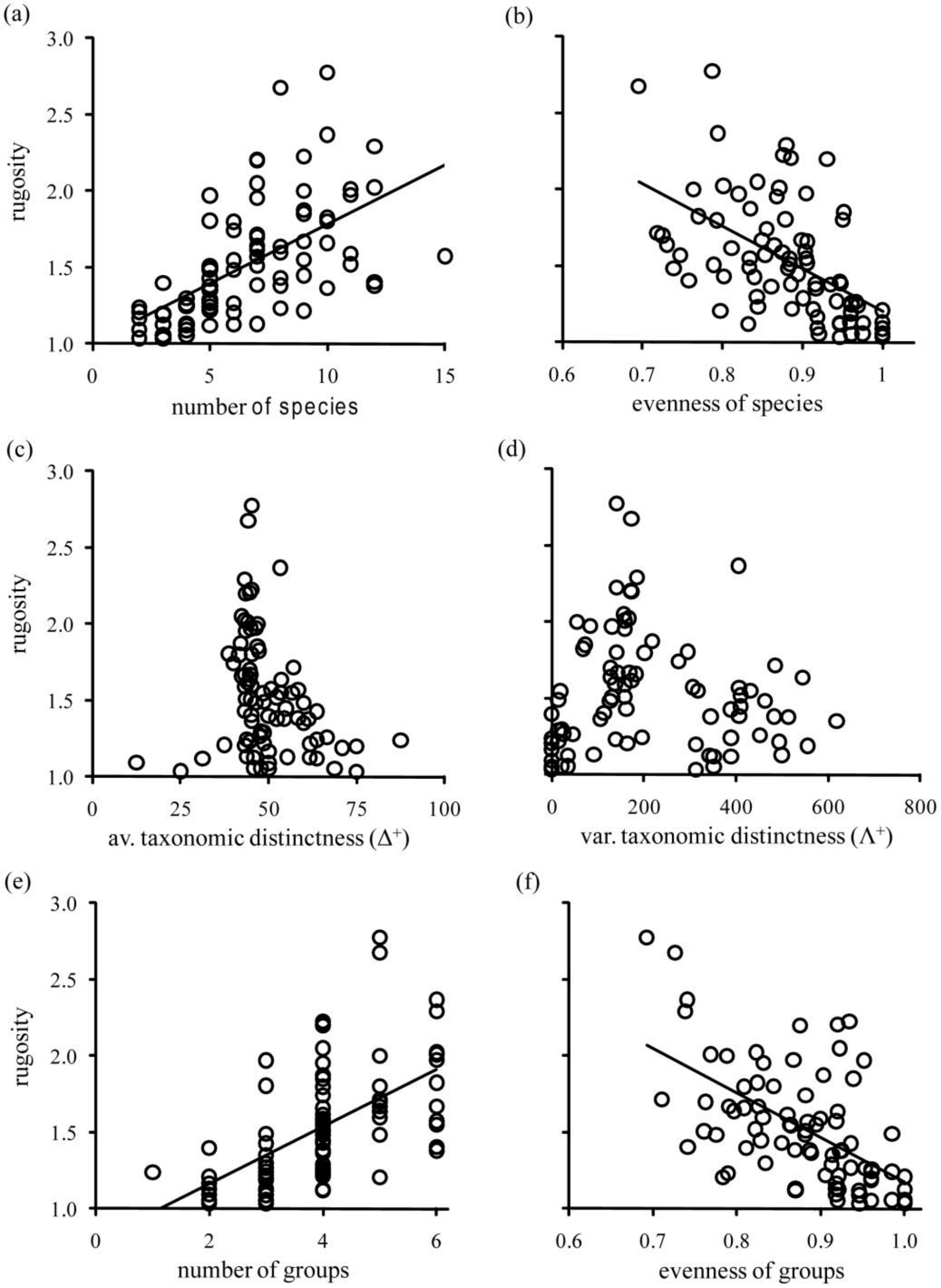

Figure 4. The relationships between reef architectural complexity on 91 sites in Cozumel and (A) total number of coral species ($y = 1.06 + 0.08x$; $R^2 = 0.34$; $P < 0.001$); (B) Pielou index of coral species evenness ($y = 3.99 - 2.79\ x$; $R^2 = 0.30$; $P < 0.001$); (C) average taxonomic distinctness of coral species; (D) variation in taxonomic distinctness of coral species; (E) total number of coral morpho-functional groups ($y = 0.79 + 0.19x$; $R^2 = 0.33$; $p < 0.001$); and (F) Pielou index of morpho-functional groups evenness ($y = 4.08 – 2.90x$; $R^2 = 0.32$; $p < 0.001$).

Reefs with greater coral cover tend to have greater architectural complexity but the variance in architectural complexity also increases with coral cover (figure 5a). Much of variance in architectural complexity at high levels of coral cover is the result of dominance by a particular coral genus. Sites dominated by species from the genus *Montastrea* have greater architectural complexity for a given coral cover, followed by *Agaricia* then *Porites* (figure 5b). On *Montastrea*-dominated sites, architectural complexity increased more rapidly with increasing coral cover than on *Porites*-dominated sites (T_{24} = -2.23; P = 0.03). However, the slopes of relationships between coral cover and architectural complexity for *Agaricia* and each of the other two genera did not differ significantly (*Agaricia vs Montastrea*: T_{49} = 1.65, P= 0.10; *Agaricia vs Porites*: T_{47} = -1.23, P = 0.22).

The differences in architectural complexity for given levels of coral cover are also strongly related to the morpho-functional attributes of the dominant species. Sites dominated by massive and large coral species have greater architectural complexity for a given coral cover, followed by sites dominated by large platy, foliaceous or encrusting (PL) and then medium size massive corals (figure 5c). Architectural complexity on sites dominated by massive and large coral species also increased significantly more rapidly with increasing coral cover than on reefs dominated by medium size massive corals (T_{34} = -2.72, P = 0.01). However, the slope of the architectural complexity -coral cover relationship on large platy, foliaceous or encrusting -dominated reefs did not differ significantly from the other two morphological groups (PL *vs* ML: T_{54} = 1.56, P = 0.13; PL *vs* MM: T_{30} = -0.81; P = 0.43).

Discussion

Reef architectural complexity increases with increasing coral cover, but the rate of increase in complexity depends on the coral community composition and, in particular, the identity of the dominant species and their associated morphological and functional traits. The most architecturally complex sites are dominated by few coral species (and morpho-functional groups) and the identity of these corals largely explains the differences in the architecture of these sites. These findings underscore the importance of considering coral species composition and shifts in coral dominance on Caribbean reefs in order to understand the implications of changes in these ecosystems on the associated biodiversity and ecosystem services.

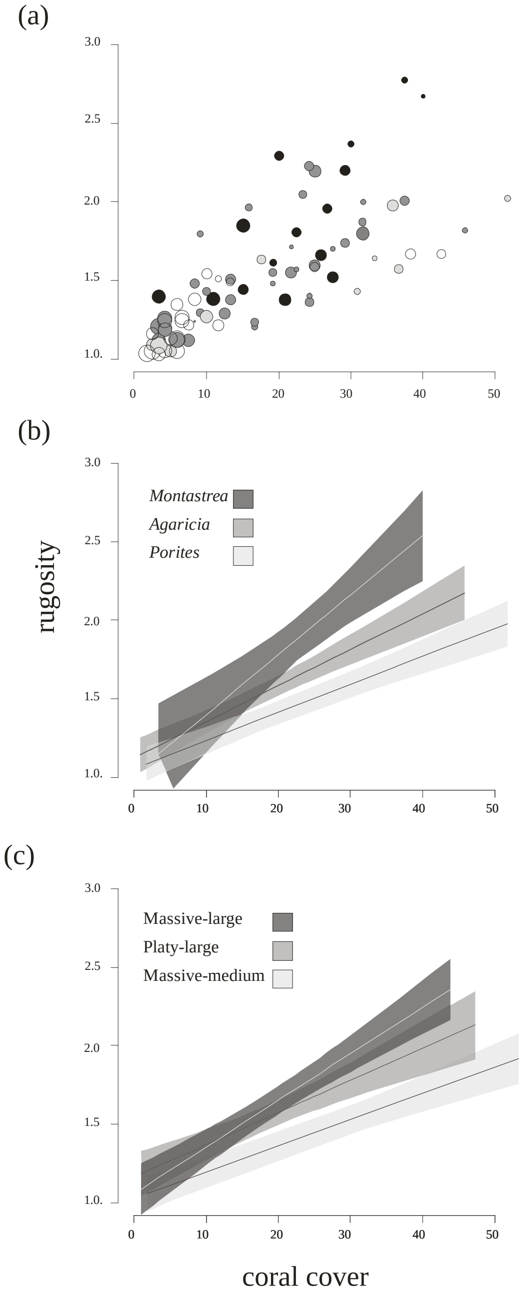

Figure 5. The relationship between coral cover and architectural complexity indices across 91 sites in Cozumel ($R^2 = 0.61$; slope = 0.024; $P < 0.001$) for (A) sites dominated by *Montastrea* (black), *Agaricia* (dark grey), *Porites* (pale grey) or no dominant species (white), and the linear regression and 95% confidence intervals for sites dominated by the three most common (B) coral genera: *Montastrea* ($y = 1.02 + 0.04x$; $R^2 = 0.61$; $P < 0.001$); *Agaricia* ($y = 1.12 + 0.02x$; $R^2 = 0.55$; $P < 0.001$) and *Porites* ($y = 1.05 + 0.02x$; $R^2 = 0.84$; $P < 0.001$) and (C) morphological groups: ML ($y = 1.05 + 0.03x$; $R^2 = 0.62$; $P < 0.001$); PL ($y = 1.16 + 0.02x$; $R^2 = 0.50$; $P < 0.001$) and MM ($y = 1.02 + 0.02x$; $R^2 = 0.93$; $P < 0.001$). See table 1 for details of morphological groups. In (A) increasing point size represents increasing evenness (Pielou index) of coral community composition.

Species diversity is considered a fundamental feature of ecosystem structure and function (Loreau *et al.* 2001; Hooper *et al.* 2005) and, in coral reefs, greater species diversity might be expected to increase reef complexity simply because of the large variety of coral forms and shapes (e.g. Chabanet *et al.* 1997; Bruno & Bertness 2001).

However, positive relationships between the number of coral species and architectural complexity may in fact be a consequence of the positive relationship between coral cover and architectural complexity, as species diversity is also positively associated with coral cover (this study: $r = 0.83$, $P < 0.001$; Bell & Galzin 1984). Moreover, taxonomic relatedness indices show that most sites shared a very similar species composition and that there is no clear effect of increasing taxonomic composition on reef architectural complexity. By contrast, the distribution of species abundances clearly shows that predominance by one or few species increases the complexity of the reef structure. Historically, Caribbean reefs have comprised small numbers of abundant species rather than a high diversity of coral species (Johnson *et al.* 2008), supporting the importance of coral dominance in structuring Caribbean reefs. In addition, Caribbean corals have relatively low diversity and redundancy in comparison with other regions of the world. For example, there are 120 massive coral species in the Great Barrier Reef, Australia while the Caribbean harbours fewer than 25 (Bellwood *et al.* 2004). This lack of functional diversity might explain why Caribbean reef architectural complexity relies more on the presence and identity of dominant species than on the combined structural attributes of a wider range of species.

We found that the strength of the positive effect of foundation species in providing structure to the habitat largely depends on the identity of the dominant taxa. At the reefscape scale, architectural complexity increased faster in sites dominated by large-massive species, such as *Montastrea*, than in sites dominated by short-lived and stress-resistant species. Among Caribbean reef-building corals, *Montastraea* species play critical roles in reef construction and community ecology (Harborne *et al.* 2008; Harborne 2009). The relative abundance of such massive species is declining in the Caribbean (Edmunds & Elahi 2007). For example, Cozumel reefs were largely dominated by *Montastrea* species in the 1980s (Muckelbauer 1990) but more recently they have been increasingly dominated by *Agaricia* and *Porites* (Alvarez-Filip *et al.* 2009; figure 2). Cozumel reefs may therefore no longer be providing the structural benefits that they were in recent decades. Similar shifts from assemblages dominated by physically large and long-lived coral species toward assemblages dominated by weedy corals are being recorded throughout the Caribbean (Steneck *et al.* 2009), highlighting the large-scale consequences that these changes in coral community composition may have for the architectural complexity of Caribbean reefs.

On sites with relatively low coral cover (≤ 20 %), architectural complexity varies little, even across sites dominated by different coral species and types (figures 5 b,c), probably because dominant species are not abundant enough (high evenness; figure 5a) to contribute significantly to the reef framework. Assuming that this also applies elsewhere in the Caribbean, our findings may help to explain the rapid structural homogenization towards relatively flat reefs reported in recent decades (Chapter 1). Most Caribbean reefs have been near or below 20% coral cover since the early 2000s (Gardner *et al.* 2003; Bruno *et al.* 2009; Schutte *et al.* 2010), which may suggest that the abundance of previously dominant corals in most reefs is now too low to contribute significantly to reef architectural complexity. It is likely that the high frequency of disturbances or chronic mortality that Caribbean reefs are facing may prevent some structurally-important species from dominating (Hughes & Connell 1999), and these reefs are therefore likely to remain in the current low-complexity and high evenness state.

More complex reefs tend to have greater numbers of individuals, biomass or richness of reef-associated fishes and invertebrates (Luckhurst & Luckhurst 1978; Dulvy *et al.* 2002; Idjadi & Edmunds 2006; Wilson *et al.* 2007). Consequently, our findings suggest that assemblages with dominant reef-building species such as *Montastrea* spp (or *Acropora* spp.) would be expected to facilitate more biodiverse and functionally-important coral reefs in the Caribbean. However, important regional differences in the species richness and functional composition of reef systems (Bellwood *et al.* 2004) also highlight the need to explore the generality of these findings. Assessing whether similar patterns occur in regions with considerably higher diversity of coral forms and functional redundancy, such as in the Indo-West Pacific, would enrich our understanding of the role of coral species composition in the provision of ecological and ecosystem services. In the Caribbean, however, it is likely that halting rates of architectural complexity loss will require a major emphasis on facilitating the maintenance and endurance of healthy populations of these key coral species, rather than focussing efforts on restoring the overall abundance of scleractinian corals. This seems to be particularly important for those reefs that have relatively high coral cover (> 20%), where the presence of healthy populations of these key coral species may considerably increase the reef architectural complexity.

Chapter 5

Coral reef architectural complexity influences fish community and food web structure

Abstract

Coral community shifts towards reefs dominated by stress-resistant corals have contributed to the severe declines in the architectural complexity of reefs throughout the Caribbean. Complex reef architecture provides important refuges and resources for many reef fishes and thus widespread declines in reef complexity could have severe consequences for the structure and function of fish assemblages. Here, we explore the influence of reef architecture on fish assemblages by comparing the size and trophic structure of reef fishes along a 15-reef gradient of coral cover, coral species dominance and architectural complexity in Cozumel, Mexico. Our results show that reefs with high architectural complexity, in particular those dominated by robust *Montastrea* corals, supported fish assemblages with greater recruitment and longer food chains (higher mean trophic levels). The association between coral complexity and fish communities is highly size-structured and is greatest for smallest size classes and is less so for larger size classes. The greater abundance of both small fish and the key early life stages of larger fishes on more complex reefs suggests that architectural complexity may influence entire reef fish assemblages, even though larger fish are less dependent on reef complexity. Key reef-building corals such as *Montastrea* are thus likely to be disproportionately important for maintaining reef fish communities, and shifts in Caribbean coral communities may compromise fish recruitment and recovery and truncate food chains.

Submitted:

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Introduction

Habitat architecture is known to profoundly influence the abundance and diversity of species through the provision of niches and diverse ways of exploiting environmental resources (e.g. MacArthur & MacArthur 1961; Bazzaz 1975; Bell *et al.* 1991; Tews *et al.* 2004). In many ecosystems, the architecture of the habitat is defined by the abundance and morphological attributes of certain foundation species. Many of these species, such as numerous overstorey trees, reef-building corals and kelp, have experienced or are experiencing widespread declines (Steneck *et al.* 2002; Gardner *et al.* 2003; Ellison *et al.* 2005). These declines commonly result in dominance shifts towards more stress-resistant species that often have rapid growth rates and are likely to provide fewer structural benefits (Ellison *et al.* 2005; Steneck *et al.* 2009). Understanding the influence of changes in the relative abundance of different foundation species on associated biodiversity can therefore provide valuable insights into the potential consequences of changing habitat structure resulting from environmental disturbances.

In tropical reefs systems, the architectural complexity of coral species is important for providing a wide variety of refuge spaces, such as crevices, holes and branches, which can influence the diversity and structure of reef-associated communities (Bell & Galzin 1984; Jones & Syms 1998). For instance, at small spatial scales (< 1 km) the recruitment of fish larvae depends in part on the availability of suitable refuges, and the post-settlement movements of fish recruits are largely influenced by the availability of microhabitat structures (Jones 1991; Tolimieri 1995; Caley & John 1996; Caselle & Warner 1996; Schmitt & Holbrook 1999; Johnson 2007). In juvenile and adult fishes, levels of competition and predation can also be influenced by the complexity of reef habitats, as more complex habitats may reduce competition by providing a greater spectrum of resources, and reduce predation by providing more prey refuges and/or reducing encounter rates between predators and prey (Holbrook & Schmitt 1988; Hixon & Beets 1993; Almany 2003; 2004).

Coral reefs are currently changing very rapidly, particularly in the Caribbean where structurally complex reefs are becoming increasingly scarce, at least partly as a consequence of the loss of key reef-building corals (Gardner *et al.* 2003; Chapters 1 & 2). Such rapid declines in reef complexity are likely to have severe consequences for biodiversity and associated environmental services. The consequences for coral reef fishes are of particular concern because reef fisheries are extremely valuable and are an important source of protein and livelihood for many vulnerable coastal human communities (Newton *et al.* 2007; Allison *et al.* 2009). Declines in reef architectural complexity may therefore result in reductions in overall species richness, particularly of reef specialists (Beukers & Jones 1997; Graham *et al.* 2006; 2007), with potential long-term consequences for large-bodied species of importance for local fisheries (Graham *et al.* 2007).

As different species of coral vary in their vulnerability to environmental perturbations, the variety of natural and human disturbances can greatly impact the relative abundance of key coral species, potentially resulting in a differential loss of specific microhabitats. For example, in the Caribbean, rapid declines in live coral cover have been accompanied by a shift in communities towards reefs dominated by stress-resistant and less architecturally complex corals (Hughes 1994; Aronson *et al.* 2002; Green *et al.* 2008; Lirman & Manzello 2009). In this region, mid-water reefs now dominated by stress-resistant corals such as *Porites* and *Agaricia* provide consistently less architectural-complex reefs in comparison to *Montastrea*-dominated sites (Chapter 4). As these shifts in coral community composition can potentially have severe consequences for associated reef-fishes, there is thus a pressing need to understand the response of fish communities to the changes in coral community composition and associated loss of reef complexity.

Here we test whether more structurally-complex areas of coral reef support greater abundances or diversity of fish along a 15-reef gradient of architectural complexity in Cozumel, Mexico. As the architectural complexity of reef-building corals may be especially important for small-bodied fishes, including recruits and juveniles from larger species that rely directly on reef microhabitat features to settle and feed, we explore these relationships using both size-based and trophic-guild perspectives.

Methods

Field surveys

Cozumel is a continental island located 22 km off the east coast of the Yucatán Peninsula in the North-Western Caribbean. The island is approximately 46 km long on the north-south axis and 16 km wide (figure 1). Cozumel is surrounded by coral reefs, the most developed of which are on the western side of the island and primarily comprise shelf-edge reefs (mostly in the southwestern area), which typically have a complex framework formed by calcareous formations of several meters height, and barrier reefs, mostly in the central part of the island, which are less well-developed (Jordán-Dahlgren 1988). The reefs located in the southwest coast have been under official protection from fishing since 1980 (Alvarez-Filip *et al.* 2009; figure 1).

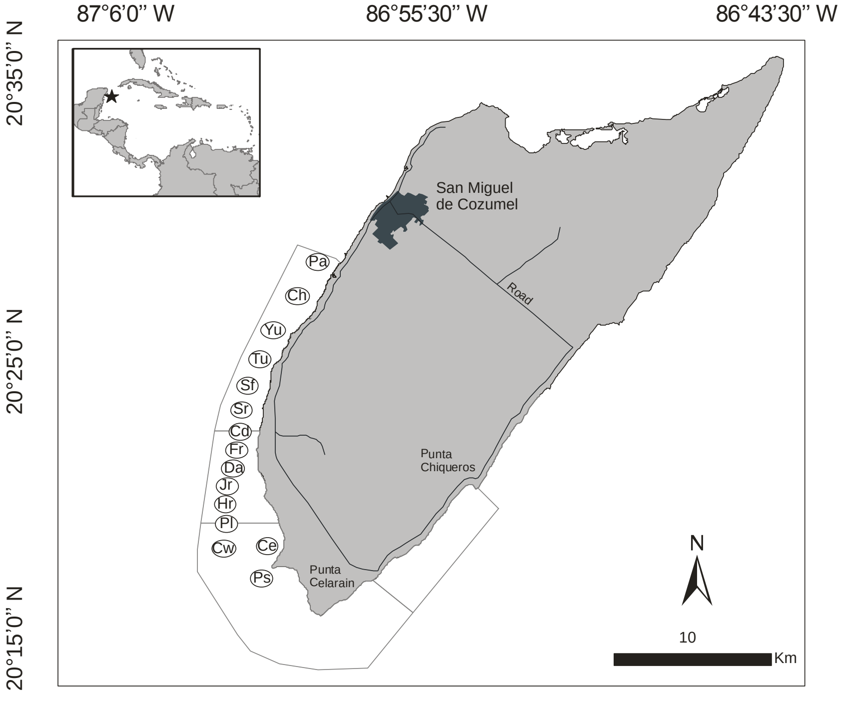

Figure 1. The location of reef sites on Cozumel Island, Mexico. The continuous line delimits the polygon of the Marine Protected Area (Parque Nacional Arrecifes de Cozumel) and the circles indicate surveyed reefs (Pa= Paraiso, Ch= Chankanaab, Yu= Yucab, Tu= Tunich, Sf= San Francisco, Sr= Santa Rosa, Cd= Cedral, Fr= Francesa, Da= Dalila, Jr= Jardines, Hr= Herradura, Pl= Palancar, Cw= Colombia West, Ce= Colombia East, Ps= Punta Sur).

Description of reef structure and fish assemblages

Benthic composition, architectural complexity and reef fish assemblages were surveyed in 15 mid-water depth (10-15 m) reefs within Cozumel's protected area between October 2007 and February 2008 (figure 1). The surveyed area in each reef (i.e. transects and the area between them) covered ca. 2000 m^2, and the 15 reefs sites were all at least 500 m apart. Between three and eight 30 x 5 m transects (150 m^2; number of transects per reef is given in figure 2) were surveyed on each reef. In each transect, a plastic tape measure was unrolled as the diver was moving forward identifying all the conspicuous fishes that crossed the transect line. Individuals were counted in an instantaneous manner to avoid the possibility of double counting and inflated density estimates (Ward-Paige *et al.* 2010). The fork length of each fish was estimated within 10 cm categories (≤ 10, 10 – 20, 20 – 30, 30 – 40, 40 – 50 cm), which is well within the precision possible with minimal training (Dulvy *et al.* 2004). The surveyor was previously trained in fish identification and size estimation, and has carried out similar surveys in the study area for several years. Count time was not standardised because this was dependent on fish abundance, diversity and subsequent habitat measures. All transects were haphazardly located within the reefs and surveyed between 09:00 and 16:00 h by the same observer.

Benthic community structure was characterised using the point intercept method (Loya 1972) in each 30 m transect once the fish census was complete. The percentage cover of each benthic component (live coral species, soft coral, turf algae, macroalgae, sponges, bare rock and sand) was identified every 25 cm, resulting in 120 estimates per 30 m transect.

Architectural complexity was measured with two complementary methodologies: a chain measure of local reef-relief and a larger-scale visual categorical estimate. For the small scale we used the rugosity index, which is the ratio of a length of chain moulded to the reef surface to the linear distance between its start and end point (Chapter 1). A perfectly flat surface would have a rugosity index of one, with larger numbers indicating more complex surfaces. A three metre chain (0.7 cm link-length) was used to estimate reef rugosity five times evenly distributed along each 30 m transect, and the average was calculated as a measure of transect-level rugosity. The reefscape-scale visual assessment of architectural complexity consists of assigning each transect a score from 0 (flat surface) to 5 (exceptionally complex reef with numerous caves and overhangs; Wilson *et al.* 2007).

Description of fish assemblages

Fish assemblages were characterized using three univariate metrics that describe the overall fish community (total number of species, total number of individuals and total biomass) and four metrics that describe food-web structure (mean trophic level, trophic guilds and the slope and intercept of the size spectra). The three community metrics were calculated at the transect level and then averaged across transects to produce reef-level fish community metrics. Total fish biomass was calculated by converting the estimates of fish length to weight using species-specific length-weight conversions (Froese & Pauly 2009). Food chain length was estimated using mean trophic level which was calculated for each reef by averaging the trophic level (obtained from Fishbase; Froese & Pauly 2009) of each individual recorded on all transects within each reef. In addition to the mean trophic level, fishes were also grouped into six major trophic guilds (planktivores, herbivores, omnivores, invertivores, carnivores and piscivores) following Paddack *et al.* (2009). In aquatic environments, organismal function varies with the size of individuals, particularly for those that grow by several orders of magnitude during their life (Jennings 2005). The size-frequency distribution (size spectrum) of fish can therefore have profound ecological implications, because most life history and ecological characteristics, such as growth schedules, age at maturity, lifespan, reproductive output, density dependence in juvenile survival and relative prey sizes are related to body size in marine fishes (Jennings *et al.* 1999; Froese & Binohlan 2000; Denney *et al.* 2002; Goodwin *et al.* 2006; Barnes *et al.* 2010). The size spectrum of the fish community on each reef was calculated by plotting the total number of individuals in each of the five 10 cm length categories, up to 50 cm. Individuals larger than 50 cm were very rare (n = 3) and therefore were excluded from the analyses. The fish size spectrum was then described by the slope and intercept of a linear regression of this size frequency distribution (Dulvy *et al.* 2004). Body length data were $\log_{10}(x + 1)$ transformed before analysis, and the midpoint of size classes was rescaled to zero to remove the correlation between slope and intercept (Daan *et al.* 2005). The intercept of size spectra provides a description of overall productivity or energy entering the community (Trenkel & Rochet 2003; Jennings 2005; Jennings *et al.* 2008; Wilson *et al.* 2010) and the slope describes the flow and depreciation of energy across fish size classes (Kerr & Dickie 2001; Jennings 2005; Wilson *et al.* 2010), with steeper slopes indicating an increase in the relative abundance of small fish, a decrease in large fish abundance, or both, and this in turn can be dissected by examining the relative contribution of each size class along the environmental or impact gradient (Dulvy *et al.* 2004).

Data analyses

Benthic data were averaged within transects and then within individual reefs, and the average percentages of cover of the benthic components were normalized using arcsine square root transformation. Exploratory analyses revealed strong positive covariation between the percentage cover of coral and both measures of architectural complexity (chain and visual estimation methods; table 1) across the 15 reefs. Hence, we calculated a combined index of coral “cover-complexity” from the first axis of a principal component analysis of these three variables. This first PCA axis explained 99.6% of the variance, and comprised coral cover (coefficient = 0.11), chain rugosity (coefficient = 0.23) and the visual estimation of habitat complexity (coefficient = 0.97).

Table 1. Associations between the percentage cover of different benthic components of the reefs and reef architecture. Values on the lower left of the table are Spearman-correlation coefficients and values in the upper right of the table (in italics) are P values.

	Rugosity	Visual	Rock	Sand	Coral	Macroalgae	Turf	Sponges
Rugosity	-	*<0.001*	*0.523*	*0.002*	*<0.001*	*0.269*	*0.486*	*0.209*
Visual	0.909	-	*0.378*	*0.001*	*<0.001*	*0.199*	*0.694*	*0.178*
Rock	-0.167	-0.228	-	*0.073*	*0.363*	*<0.001*	*0.181*	*0.174*
Sand	-0.703	-0.750	0.446	-	*<0.001*	*0.021*	*0.830*	*0.001*
Coral	0.907	0.915	-0.235	-0.801	-	*0.252*	*0.619*	*0.149*
Macroalgae	0.284	0.328	-0.892	-0.554	0.294	-	*0.125*	*0.051*
Turf	-0.181	-0.103	0.341	0.056	-0.130	-0.387	-	*0.277*
Sponges	-0.321	-0.343	0.346	0.738	-0.365	-0.480	-0.279	-

The influence of different components of reef structure and benthic community on all fish assemblage metrics were first explored with hierarchical partitioning analysis (Mac Nally 2000, 2002). The metrics that were identified from these analyses as responding to variation in reef structure were then included in analyses (also using hierarchical partitioning) of the influence of different dominant coral types on the structure of fish assemblages. We restricted this second analysis to four categories: the three most dominant coral genera in Cozumel, *Montastrea*, *Agaricia* and *Porites*, which have been shown to have different colony and size structure and hence different contributions to reef complexity (Chapter 4), and one category including all the other remaining coral genera.

Hierarchical partitioning is a multiple-regression technique which calculates goodness of fit measures for all possible combinations of independent variables in linear models, in order to calculate the average contribution of each predictor (Chevan & Sutherland 1991; Mac Nally 2000). Hierarchical partitioning provides both the independent and the joint effects of each predictor, with independent values representing the explanatory power associated with a single predictor and joint values representing the explanatory power of the parameter of interest in combination with other variables (Mac Nally 2002). In some situations, significant independent effects can be suppressed by antagonistic joint effects, in which case hierarchical partitioning technique converts antagonistic effects into negative joint contributions, effectively unmasking the independent contributions (Chevan & Sutherland 1991). Independent effects of the explanatory benthic variables on the fish assemblages were tested with 1000 permutations of the data matrix and significance was evaluated at the 5% level (Mac Nally 2002). We used hierarchical partitioning rather than traditional multiple regressions or other multivariate analysis, because this method deals well with multicollinearity of predictor variables (Mac Nally 2000, 2002). We conducted hierarchical partitioning within R using the *hier.part* package (R 2009). Hierarchical partitioning does not calculate the direction of the effects of the explanatory variables, so these were derived from Pearson correlations.

Results

Fish and habitat description

In Cozumel there is a pattern of increasing coral cover from the north to the south of the island (figure 2), and the reefs are largely dominated by *Agaricia*, *Montastrea* and *Porites*, although the surface cover of these species varies considerably between reef sites with the northernmost and southernmost reefs having a particularly high relative cover of *Montastrea* species (figure 2).

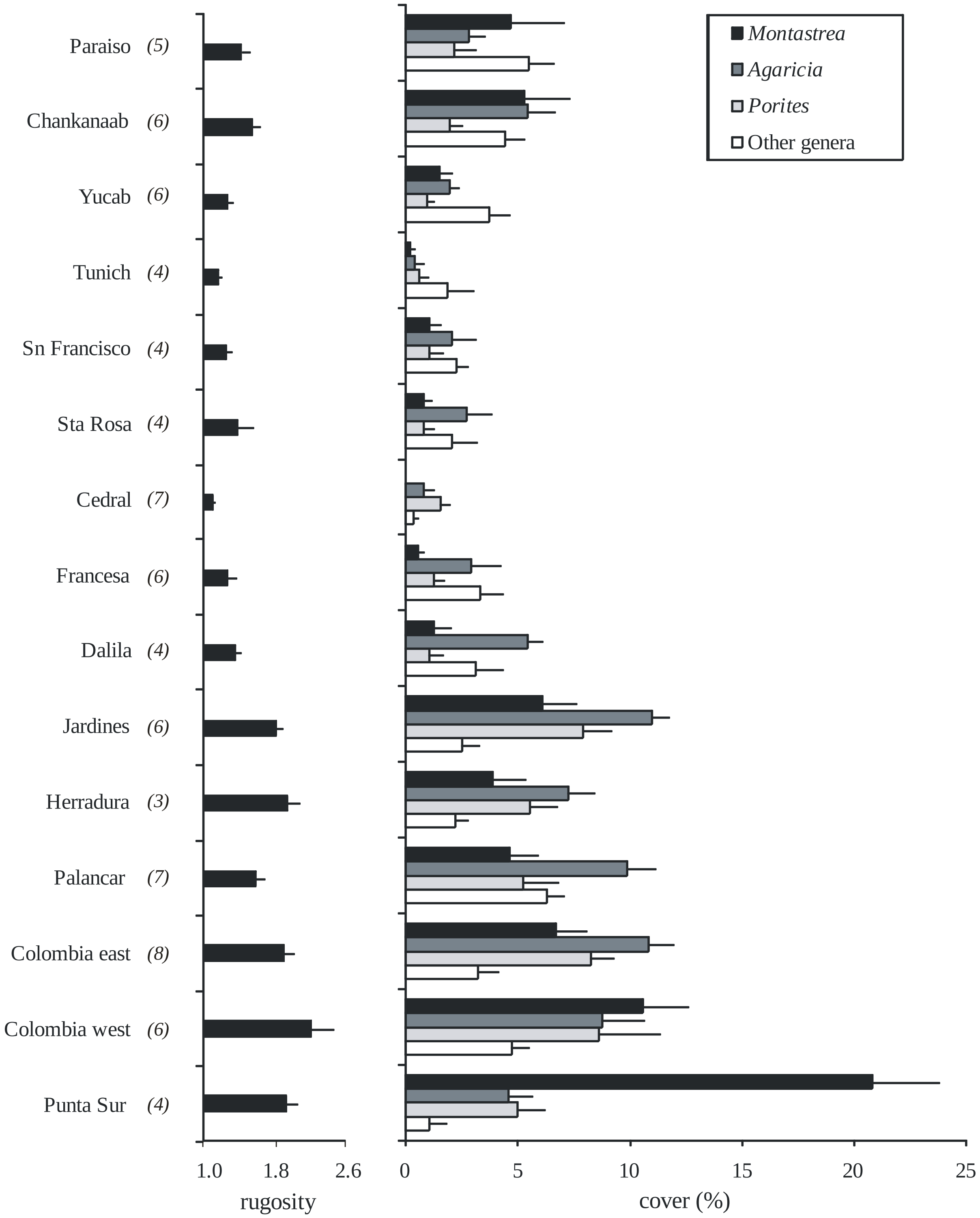

Figure 2. Mean (± SE) reef rugosity and cover of *Agaricia*, *Montastrea*, *Porites* and all other coral genera on the 15 surveyed reefs. Reefs are ordered from north to south (see Figure 1). The total number of transects is provided in brackets.

A total of 10,965 individuals from 93 species of fish were recorded across the 15 reefs (appendix 3). The most common fishes were those that mainly feed on plankton and algae (appendix 3), and there is a clear trend of decreasing abundance with body size; the smallest individuals (< 10 cm) represented 48.1 % of the total abundance while larger individuals (> 40 cm) accounted for only 0.7 % of total abundance.

Influence of benthic components on fish assemblages

Fish species richness and total fish abundance are both positively associated with cover-complexity and negatively associated with the percentage cover of bare rock and sand (figure 3), but total fish biomass is unrelated to any of the benthic community components or structure (figure 3). However, much stronger links are apparent between reef structure and the trophic and size structure of fish assemblages. The food chain length (as indexed by mean trophic level) and the size spectra slope and intercept of fish communities all increase significantly with increasing cover complexity but not with any of the other benthic components (figure 3). The intercept of the fish size spectra increases and the slope of the size spectra decreases with cover-complexity (Figure 3). The higher intercept and steeper slope of fish size spectra on reefs with greater coral-complexity results from greater densities of the smallest size class (<10 cm) on complex reefs. While mean trophic level and size spectra slope are related only to cover-complexity, the size spectra intercept is also influenced by a joint contribution from different benthic components (figure 3), suggesting that while the overall productivity of fish communities is influenced by several different benthic components, the food chain length is mainly driven by cover-complexity.

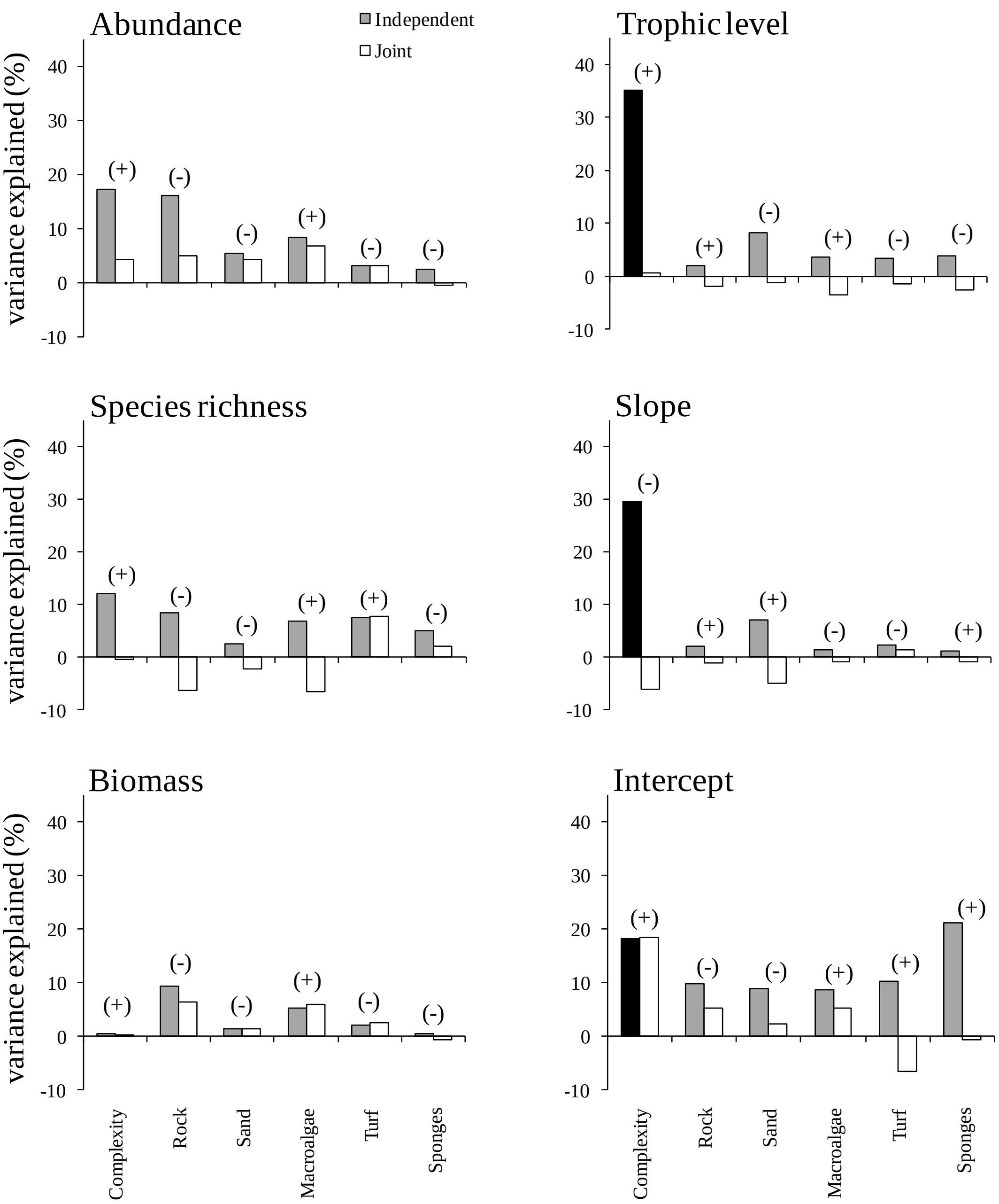

Figure 3. Results of hierarchical partitioning analyses of the contribution of reef complexity and the cover of reef benthic components to the community and food-web structure of reef fishes. Bars show the independent (black = statistically significant, grey = not significant) and joint (white) effects, and +/- indicates the direction of each relationship. Joint effects are either additive (above the line) or antagonistic (below the line) to the independent effects.

Influence of coral genera on size and trophic structure of fish assemblages

The abundance of the two smallest fish size classes (< 20 cm) is significantly greater on reefs with greater cover of *Montastrea*, whereas other coral genera have no significant effect on the abundance of fishes from any size categories (figure 4). The positive relationship between the abundance of small fishes and cover-complexity corresponds to the pattern indicated by the size spectra analyses (figure 3), suggesting that the abundance of complex scleractinian corals strongly influences the abundance of small fish. Initially the smallest fishes (< 10 cm) are most dependent on the presence of the most architecturally-complex corals (i.e. *Montastrea*), and this relationship decays for increasingly larger size classes, suggesting a strong ontogenetic detachment from scleractinian corals. Fishes in the second size-category (10 - 20 cm) are also more abundant in the presence of *Montastrea*, but the presence of other types of corals also appear to influence their abundance, given the considerable positive contribution of the joint effects to the variation in abundance of this size-class. Although abundance of fish in size classes greater than 20 cm are not significantly related to the cover of any coral genera, those in size classes 20 – 30 and 30 – 40 cm tend to be positively associated with the cover of all coral genera while the largest fish (40 – 50 cm) tend to be negatively associated with coral cover (Figure 4).

The abundance of carnivores, omnivores and herbivores all increased significantly with increasing cover of *Montastrea* corals (figure 5) but the cover of *Porites*, *Agaricia* or other coral species did not significantly influence the abundance of fish species of any trophic group. The strong and positive influence of *Montastrea* on carnivorous fish abundance, in addition to the increase in mean trophic level with coral complexity (figure 3), suggests that reefs with greater architectural complexity support longer food chains with more predator-dominated fish communities compared to flatter reefs with lower coral cover.

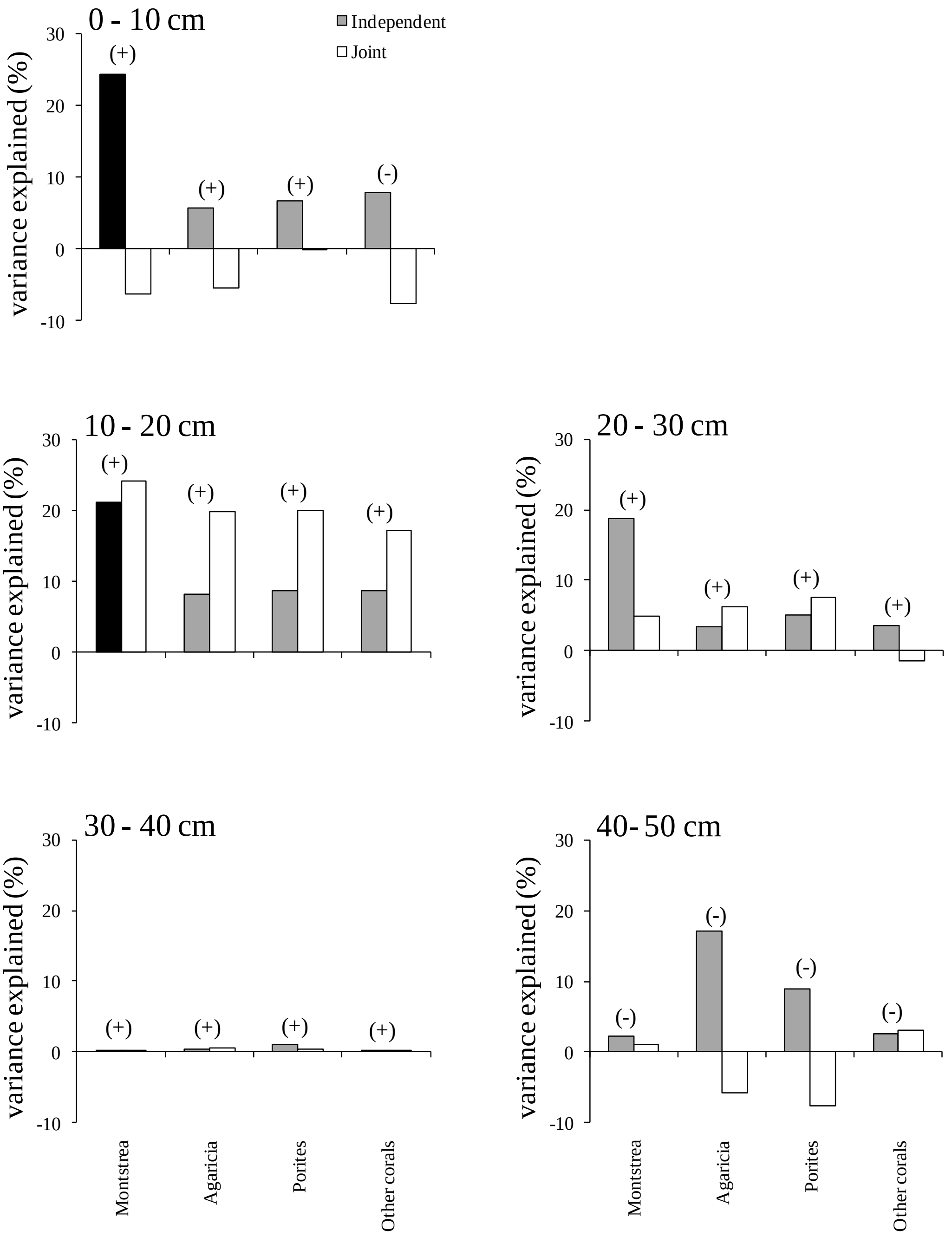

Figure 4. Results of hierarchical partitioning analyses of the contribution of different coral genera to the abundance of reef fishes of five different size classes. Bars show the independent (black = statistically significant, grey = not significant) and joint (white) effects, and +/- indicates the direction of each relationship. Joint effects are either additive (above the line) or antagonistic (below the line) to the independent effects.

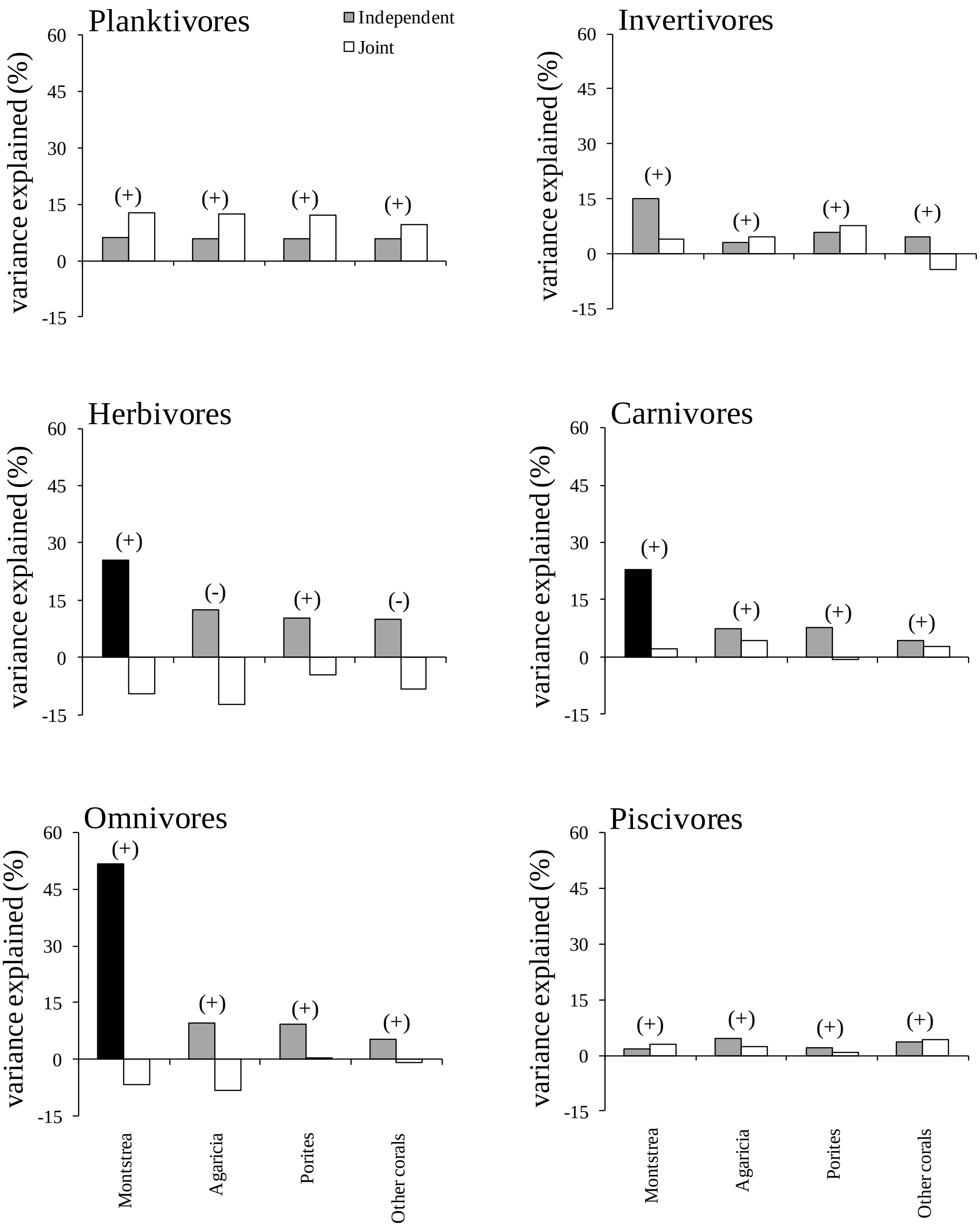

Figure 5. Results of hierarchical partitioning analyses of the contribution of the cover of different coral genera to the abundance of six major trophic guilds of reef fishes. Bars show the independent (black = statistically significant, grey = not significant) and joint (white) effects, and +/- indicates the direction of each relationship. Joint effects are either additive (above the line) or antagonistic (below the line) to the independent effects.

Discussion

The cover and complexity of coral reef has profound implications for fundamental processes structuring coral reef fish communities. Here, we show that coral cover and complexity have positive influences on the abundance and recruitment of small fishes and the food chain length and presumably energy flow through the Caribbean fish assemblages of Cozumel, Mexico. Across reefs varying greatly in coral cover, complexity and composition, greater abundances of small-bodied reef-associated fishes are supported on 'healthier' more architecturally-complex reefs, in particular those dominated by robust *Montastrea* corals. However, the dependence of fishes upon complex reef structures declines for larger-bodied fish size classes. This suggests that complex reef structures are most important for maintaining reef fish communities by facilitating the presence of key early-life stage individuals and small-bodied fishes that are preyed upon by larger fishes (Caley & John 1996; Beukers & Jones 1997). The relatively weak contribution of cover-complexity and other benthic components to the variation in species richness, abundance and biomass suggests that a size-based food web view of coral reef ecology may provide more insights into coral reef community structure, function and energy flow than the classical terrestrial species-based functional perspective.

The positive influence of corals, particularly of the genus *Montastrea* on reef fishes is most evident in small-bodied individuals and probably at small spatial scales. This suggests that the complexity provided by reef-building corals is an important mediator of the energy entering the reef system and the productivity of the reef-fish community (see also Jennings & Dulvy 2005; Shin *et al.* 2005). These results are consistent with experimental and observational analyses showing that, at small spatial scales (< 1 km), the recruitment of fish larvae depends in part on the availability of suitable refuges, and the post-settlement movements of fish recruits are largely related to the availability of microhabitat structures (Jones 1991; Tolimieri 1995; Caselle & Warner 1996; Schmitt & Holbrook 1999; Johnson 2007). The steepness of the size spectra on more complex reefs has been attributed to the depleted abundances of apex predators, for example fishing can change the size distribution of fish communities by directly reducing the number of large-bodied fishes that in consequence will result in prey release (Dulvy *et al.* 2004; Graham *et al.* 2005; Wilson *et al.* 2010). However, Cozumel reefs have been under protection for 30 years, and have relatively high abundances of apex predators (relative to other Caribbean reefs; Knowlton & Jackson 2008; Alvarez-Filip *et al.* 2009). Therefore the steepening of the slope in the size-spectrum, in combination with the elevated intercept, is likely to result from a stronger association of small-bodied fishes to the coral complexity rather than an effect of fisheries exploitation of larger fish.

The dependence of reef fishes on complex reef structures declines gradually with increasing body-length, which hints at an ontogenetic habitat shift. Small-bodied fishes are strongly related to coral complexity, and particularly to cover of *Montastrea*, probably because coral colonies from this genus develop many holes and crevices that may function as shelter for small fish (Goreau 1959). For example, these corals are known to attract high numbers of damselfishes of the genus *Stegastes* that commonly recruit and ‘garden’ in these corals (Precht *et al.* 2010). Indeed, the small-scale pre-and-post settlement processes of reef-fishes are more likely to be explained by the presence of *Montastrea* than by other corals such as those from the genus *Porites*, likely due to the more suitable microhabitat characteristics provided by *Montastrea* (Tolimieri 1995). Our results are also consistent with previous studies that have shown that, at patch scales, *Montastrea*-dominated reefs are the most species-rich habitats on Caribbean reefs and have the greatest intra-habitat variability (Harborne *et al.* 2008; Harborne 2009).

The abundance of fish of body lengths 10 - 30 cm seem to be influenced by the overall cover of reef-building corals, not just *Montastrea* corals. This may be a consequence of increases in the home range size with increasing body size, as larger Caribbean reef fishes tend to also increase in mobility (Kramer & Chapman 1999), and are therefore less likely to be associated with specific attributes of individual coral colonies. More generally, home range size scales positively with body size and the degree of exclusivity of habitat use declines with increasing size due to the metabolic scaling of energy acquisition (Jetz *et al.* 2004). The reduction in dependence on reef complexity of large-bodied fishes suggests that factors such as the availability of prey (Hixon & Beets 1993) and/or reef conditions at larger scales (e.g. the effect of protection at Marine Reserve scales; Kramer & Chapman 1999) may be stronger influences on the abundance of these adult fishes.

The complexity or reef structures, and in particular the cover of *Montastrea* corals, also appears to favour the presence of higher-trophic level (especially carnivorous) fish. However, although increased abundance of fishes from higher trophic levels might be expected to increase the overall biomass of the fish assemblage, we found no significant increase in total fish biomass with increasing cover-complexity. This might be explained by three, non-mutually exclusive reasons. First, the abundance of higher trophic level fishes could be primarily represented by juvenile individuals that may be using the corals for refuge or searching for small prey items (e.g. Rooker 1995; McCormick 1998; Gratwicke *et al.* 2006). Although the dietary mode of carnivorous fishes persists throughout their lives, prey size and composition often change as body size increases (Wainwright & Bellwood 2002; Cole 2010), thus small-bodied carnivorous fish may in fact represent lower trophic levels than the maximum category used in these analyses. Second, overall fish biomass on these reefs may be dominated by widely-distributed fishes pertaining to other trophic categories such as herbivores or omnivores (e.g. scarids, surgeonfish or grunts; appendix 3) which may reduce the effect of carnivorous fishes of relatively low abundance on total biomass. Finally, there are some small-bodied fishes of high trophic level (e.g Hamlet fish; Froese & Pauly 2009), which also may help to explain the lack of a clear relationship between mean trophic level and overall biomass.

The cover of *Monstastrea* corals also appears to positively influence the abundance of fishes of lower trophic guilds such as omnivores and herbivores. The omnivorous fishes recorded in this study are commonly recognized as reef-dependent species that feed on reef benthic flora and fauna (appendix 3; Froese & Pauly 2009), hence the greater number of refuges for small invertebrates and benthic algae provided by the massive structures of *Montastrea* may support a greater number of food items for these fishes (e.g. Idjadi & Edmunds 2006). The relationship between herbivorous fishes and *Montastrea* cover is more complex; the complex structures and ramets of *Montastrea* may support greater algal diversity and biomass (Mumby *et al.* 2005; Piñón-Gimate & Collado-Vides 2008), and thus be attractive to herbivorous fishes. In addition, some herbivorous fish such as *Scarus viridie* and *Stegastes planiforms* are common grazers of *Montastrea* colonies (Rotjan & Lewis 2008; Mumby 2009; Precht *et al.* 2010; Rotjan & Dimond 2010) and may therefore be attracted by the live tissue of these corals.

The ongoing decline in reef architectural complexity throughout the Caribbean may therefore have profound effects on fish communities (Paddack *et al.* 2009; Chapters 1 & 2). In particular, our findings suggest that recent declines in the overall density of fish communities (Paddack *et al.* 2009) may be in part a consequence of ongoing declines in the cover of *Montastrea* in reefs through the entire region (Hughes & Tanner 2000; Bruckner & Bruckner 2006; Steneck *et al.* 2009). Our study suggests that changes in the abundance of *Montastrea* populations could have significant and direct detrimental effects on the abundance of small-bodied fish, with subsequent impacts on the abundance of adult fishes through failures in recruitment and reductions on the transfer of energy through the food web (Graham *et al.* 2005; Graham *et al.* 2007; Wilson *et al.* 2010). This may result in bottlenecks limiting the flow of energy and production of fish assemblages and fisheries yields.

Montastrea historically ranked in importance with *Acropora palmata* and *A. cervicornis* in overall contribution to Western Atlantic reef structure (Jackson 1992). Acroporids have now almost vanished from Caribbean reefs and important functional attributes have been lost with the demise of these highly complex coral structures. Both acroporid species are now listed as Critically Endangered by the International Union for the Conservation of Nature (Bruckner 2003; Aronson & Precht 2006). More recent declines in the abundance of *Montastrea* populations and increases in the relative abundance of stress-resistant coral species are compromising the capacity of reefs to provide habitat for reef-associated biodiversity even further (Green *et al.* 2008; Steneck *et al.* 2009; Chapters 2 & 4). Our findings indicate that these recent changes in coral composition on Caribbean reefs may result in a very little ecological space for fish species to inhabit. The extreme importance of these fish populations in sustaining millions of livelihoods highlights the urgent need to identifying and implement means of preserving and improving reef habitat quality throughout the Caribbean.

Concluding remarks

Caribbean reef ecosystems have undergone severe changes in the last few decades, owing to a variety of anthropogenic and natural causes. Previous studies have described in detail the rapid declines in the cover of reef-building corals, shifts in coral community composition and increases of macroalgae on Caribbean reefs (Aronson *et al.* 2002; Gardner *et al.* 2003; Bruno *et al.* 2009; Schutte *et al.* 2010). This thesis has shown that these ecological changes have resulted in rapid but non-linear declines in reef architectural complexity during the last four decades (Chapter 1). The massive die-off of *Acropora palmata* and *A. cervicornis* (Elkhorn and Staghorn corals) during the 1970s and 1980s triggered the decline in reef architectural complexity throughout the region (Aronson & Precht 2006; Schutte *et al.* 2010; Chapters 1 & 2). Subsequently, three major issues are likely to have fostered the ongoing degradation of reef architecture. First, increasing levels of coral stress resulting from climate-induced bleaching events, coastal development and the loss of ecological resilience (e.g. herbivory) may have reduced rates of reef accretion (Williams *et al.* 2001; Pandolfi *et al.* 2005; Aronson & Precht 2006; Mora 2008). Second, reductions in live coral cover may prevent the recovery of reef structure following direct physical impacts and erosion. In particular, this thesis provides evidence that hurricane impacts and enhanced bioerosion in perturbed reefs may have played a significant role in the region-wide declines in architectural complexity in recent decades (Chapter 3). Finally, changes in the ecological composition of benthic communities towards reefs dominated by stress-resistant corals that contribute little to reef complexity may have gradually decreased architectural complexity on many reefs within the Caribbean (Green *et al.* 2008; Wilkinson 2008; Steneck *et al.* 2009; Chapter 2 &4). In Chapters 2 and 4, for example, I demonstrate that live coral cover does not necessarily reflect reef complexity at local and regional scales, and that coral species composition and the morph-functional attributes of dominant corals are important for defining the contribution of coral cover to reef complexity. The capacity of reef systems to support biodiversity and provide environmental services to humans is therefore likely to rely more on the presence of key structure-forming corals than on overall coral cover (Chapter 5).

It is important to highlight some inherent problems and necessary caveats of this thesis. (1) The regional-scale analyses reported in Chapters 1, 2 & 3 use data I collated from a considerable number of published and unpublished studies reporting reef architectural complexity and coral cover. Literature searching and data collation for these analyses was as extensive as possible, but accessing grey literature is problematic, even though much is available on the internet. A great deal of key information is unpublished and, in some cases, valuable data are owned by specialists who were not keen to collaborate in these studies (e.g. CARICOMP), thus not all relevant data could be included in the analyses. Nonetheless, the relatively high sample size and good spatial representation of sites suggests that the results are robust and likely to be representative of the Caribbean region. (2) There is also important variation in the methods used in the studies included in the analyses. For example, key aspects of methodologies such as levels of replication and lengths of transects often differ considerably among studies and among scientists within a study. However, this type of variation can be considered with the statistical tools that I employed in the thesis (e.g. meta-analysis; Arnqvist & Wooster 1995), and I therefore controlled for such variation as much as possible throughout the thesis. (3) Many of the analyses in the thesis use the rugosity index, which is a descriptor of small-scale reef relief. This is clearly an important scale for many organisms such as fishes and invertebrates (Luckhurst & Luckhurst 1978; Idjadi & Edmunds 2006; Chapter 5), but reefs also exhibit larger scales of architectural complexity that were not considered in these analyses. For example, geomorphologic differences (e.g. spur and grooves, forereefs) can be very important in defining larger-scale patterns of diversity and abundance of reef-associated species (Karlson *et al.* 2004; Connolly *et al.* 2005). Therefore the results presented in this thesis should be considered with reference to the fine scale and could not necessarily be extrapolated to larger structural scales. However, it is likely that larger scales of ‘complexity’ follow at some degree the patterns depicted at finer scales, as suggested by the high correlation between fine (reef rugosity) and reefscape (visual estimations, remote sensing) scales that local studies have reported (Kuffner *et al.* 2007; Wilson *et al.* 2007; Chapter 5).

Implications for conservation

Reversing reef degradation is a major challenge for scientists and reef managers concerned with maintaining reef ecosystems and the security and well-being of Caribbean coastal communities. Among scientists and managers, it is commonly accepted that the overall cover or abundance of reef-building corals directly relates to the ‘state’ or ‘health’ of tropical reefs, and therefore that restoring coral cover is key to restoring ecosystem functioning and services (Mumby *et al.* 2007; Selig & Bruno 2010). The presence of healthy coral populations is indeed likely to indicate reefs that are more resilient to environmental change. For example, healthy coral populations can indicate reefs that have not shifted to macroalgae-dominated alternate states (Hughes 1994; Nyström *et al.* 2000; Williams *et al.* 2001; Bruno *et al.* 2009). However, this thesis has shown that changes in coral cover do not always capture changes in reef architectural complexity (Chapter 2), which is a reef attribute more likely to have direct ecological, economical and social relevance (Sheppard *et al.* 2005; Pratchett *et al.* 2008; Cinner *et al.* 2009). To restore the ecosystem services that Caribbean corals provide to other species, including humans, coral cover and reef architecture may therefore require different types of management and at different spatial scales. The major threats to reef-building corals are occurring at regional and global scales; hence international regulations to reduce the impacts of human activities are probably the most appropriate scales at which to protect reef corals. By contrast, reef architecture may be more sensitive to local-scale reef conditions (e.g. rates of erosion and hurricane impacts) and hence, for the purposes of management, may be relatively independent of changing coral cover at this scale (Chapters 2 & 3). Halting and reversing rates of reef complexity loss may therefore depend largely on the protection and enhancement of conditions at the local reef scale.

Halting rates of architectural complexity loss in the Caribbean will also require a major emphasis on facilitating the maintenance and endurance of healthy populations of key structure-forming coral species (Chapters 2 & 4). At local scales, conservation goals that consider the status of key reef-building coral such as *Acropora* and *Montastrea* in addition to overall changes in benthic cover may therefore be necessary. At larger temporal and spatial scales, more information on the changes in coral community composition and the status of key coral species is needed. While the rapid loss of acroporid corals in the 1980s is well described and has resulted in considerable amounts of effort in designing conservation and restoration plans for populations of these species (Bruckner 2003), the state of populations of *Montastrea* corals and other important reef-building corals in the Caribbean is much less well known. For instance, the temporal changes in areal cover and population demographics of *Montastrea* corals has only been described for a few sites (Edmunds 2002; Bruckner & Bruckner 2006; Edmunds & Elahi 2007). Future research in the Caribbean should therefore aim to understand the region-wide trends of change and current status of *Montastrea* corals, and to identify changes at the community level across different reefs.

Implications of reef complexity decline

The ecosystem services provided by coral reefs are critical to the biodiversity and social and economic welfare of millions of people (Moberg & Folke 1999; Cinner *et al.* 2009), and there is therefore an urgent need to understand the long-term effects of reef degradation in the Caribbean and elsewhere. Although collapsing reef structures may lead to subsequent declines in a wide range of reef-associated species and the loss of important ecosystem services such as coastal protection (Sheppard *et al.* 2005; Wilson *et al.* 2006), I have focussed mainly on the possible impacts of reef degradation on associated fish communities. This focus is because (i) fishes contribute to critical ecosystem functions and support local fisheries and tourism across the developing world (Bellwood *et al.* 2003; Newton *et al.* 2007; Allison *et al.* 2009; Uyarra *et al.* 2009); and (ii) large amounts of existing relevant information, including regional estimates of fish abundance since the 1950s and international programs that report information for at least two decades (Paddack *et al.* 2009; AGRRA and CARICOMP), allow a detailed description of the consequences of reef flattening for those fish communities.

The only existing region-wide and long-term study of changes in fish assemblages in the Caribbean indicates that overall fish abundance may have begun to respond negatively to habitat degradation (Paddack *et al.* 2009). However, significant declines in overall fish density are only apparent during the last few years, during a time characterised by a reduction in rates of coral cover loss and a resumption of architectural complexity decline in the Caribbean (Paddack *et al.* 2009; Schutte *et al.*

2010; Chapter 1). Interestingly, significant declines in fish abundance were not apparent during the rapid declines in architectural complexity and coral cover in the 1970s and 1980s. This raises the question of whether the declines in fish abundance in the late 1990s is the result of a lagged response to the loss of acroporid corals in the late 1970s and early 1980s (Paddack *et al.* 2009), or is a threshold effect in response to expanding and high levels of habitat degradation that Caribbean reefs have experienced in recent years. In the Caribbean, most fish species do not require specific reef features (as suggested by their wide distribution throughout the region and across reef types; Carpenter 2002; Sandin *et al.* 2008), and it is therefore possible that their populations could have persisted due to the habitat provided by the remaining coral species, despite the loss of acroporid corals. By the late1990s, it is possible that, some reefs were too degraded to provide the minimum structural attributes required by many fish species and thus only during this time period the effects of habitat degradation on fish populations become evident. Chapter 5 of this thesis indeed suggests that the decrease in relative cover of the primary remaining important reef-building corals, *Montastrea*, might be one of the drivers of region-wide declines in fish density, as many small-bodied fish (size classes and species) are strongly associated with the structural complexity provided by *Montastrea* corals. In addition, reductions in energy transfer to higher trophic levels on less structurally-complex reefs may in turn result in reduced density (or biomass) of predators (Dulvy *et al.* 2004; Whiteman & Côté 2004; Graham *et al.* 2007; Pratchett *et al.* 2008; Wilson *et al.* 2010).

There is, however, also the possibility that other ecological dimensions (not captured by total fish density) of reef fish assemblages may have been affected by the earlier rapid declines in Caribbean reef complexity. It is possible, for example, that fish community composition may have changed as consequence of declines in the abundance of particular fish species that depend on habitat features (e.g. coral branches) that were lost with the decline in acroporids and increases in abundance of more generalist species (Chesson 2000). Attaining a better understanding of the large-scale impacts and consequences of reef degradation for reef-associated fishes would be helped by integrating information on coral cover, rugosity, algae and fish abundance. This would allow more direct exploration of the consequences and timing (e.g. lag effects) of habitat degradation for a range of diversity and trophic dimensions of fish assemblages, and would allow tests of well-established paradigms such as the role of the loss of herbivory in increasing the dominance of macroalgae and subsequent phase shifts (Hughes 1994; Nyström *et al.* 2000; Mumby *et al.* 2007; Bruno *et al.* 2009). Integration of such information may even allow a test of the hypothesis proposed in Chapter 3 of the role of herbivorous grazers in increasing rates of bioerosion in fisheries closure areas.

The influence of reef structure and composition (reef architecture, coral cover and coral identity) on reef-associated species is rarely explored across different spatial scales and geographical locations (exceptions include Nunez-Lara *et al.* 2005; Newman *et al.* 2006; Semmens *et al.* 2010). Consequently, the relationship between reef biodiversity and the structure of coral reefs is poorly understood and the importance of putative drivers of coral cover and architectural complexity loss in a hierarchy of different spatial scales needs to be explored, from coral colony scales to whole reef systems. Identifying the spatial scales at which different drivers of reef degradation affect different species would improve understanding of the effect of losing different levels of organization in reef systems, which may be important considerations in reef management or restoration planning (Acosta & Robertson 2002; Connolly *et al.* 2005; MacNeil *et al.* 2009). Large-scale spatial analyses of this sort would also allow exploration of the role of the remaining 'healthy' reefs as a source of recruits in a matrix of degraded reefs, and thus in supporting wider biodiversity and ecosystem functioning. In addition, large-scale spatial analyses of reef structure would also allow exploration of the possible effects of habitat degradation on taxa that have not been systematically recorded, such as most reef-associated invertebrates, which are usually diverse groups with strong relationships to the complexity of reef structure (Idjadi & Edmunds 2006; Miloslavich *et al.* 2010)

Future change and the carbonate budget on reefs

The balance between the production (calcification) and loss (biological, physical, and chemical erosion) of calcium carbonate on a coral reef determines whether or not reef structures are maintained. Predictions based on experimental and field observations indicate that the combined effects of rising temperatures and ocean acidification could increase the frequency of bleaching events and reduce coral calcification drastically (Hoegh-Guldberg *et al.* 2007; Kleypas & Yates 2009). If rates of $CaCO_3$ production by corals and other reef calcifiers cannot keep up with rates of erosion, the majority of coral reefs could switch from net accreting to net eroding structures (Veron *et al.* 2009). Increasing our knowledge of how processes such as bioerosion or dissolution of corals operate in Caribbean reefs is therefore of the utmost importance. An important future research area would be to model the effects of ocean acidification and increasing sea temperatures on the carbon budget of Caribbean reefs, as both variables have been reported to influence coral growth and calcification considerably in other regions of the world (De'ath *et al.* 2009; Cantin *et al.* 2010). The role of bioerosion should also be explored more thoroughly in future studies. For instance, this thesis suggests that biological erosion (as result of enhanced abundance of herbivores fish inside MPAs) might be an important process contributing to the loss of architectural complexity on Caribbean reefs (Chapter 3). Models designed to explore methods of restoring architectural complexity on coral reefs may therefore need to include both ‘positive’ (e.g. control of macroalgae abundance) and ‘negative’ (e.g. bioerosion) effects of herbivores fishes and invertebrates, as well as information on coral cover and composition on reefs, in order to identify appropriate strategies of intervention and management.

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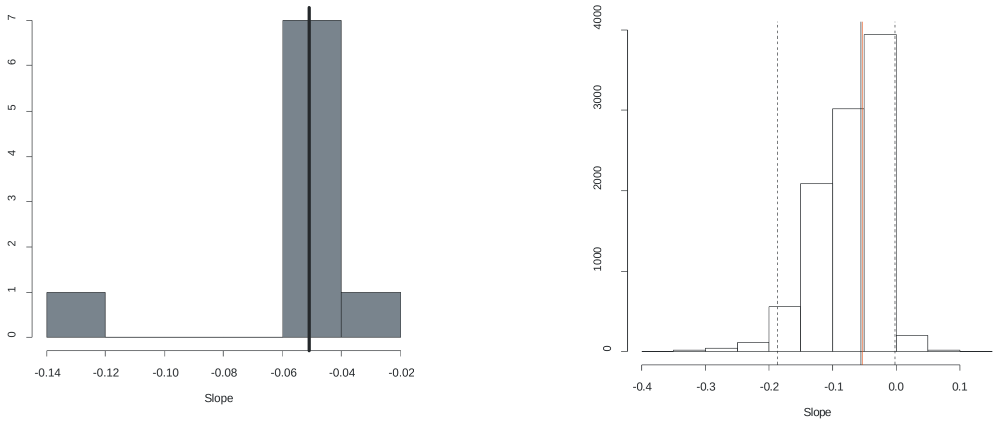
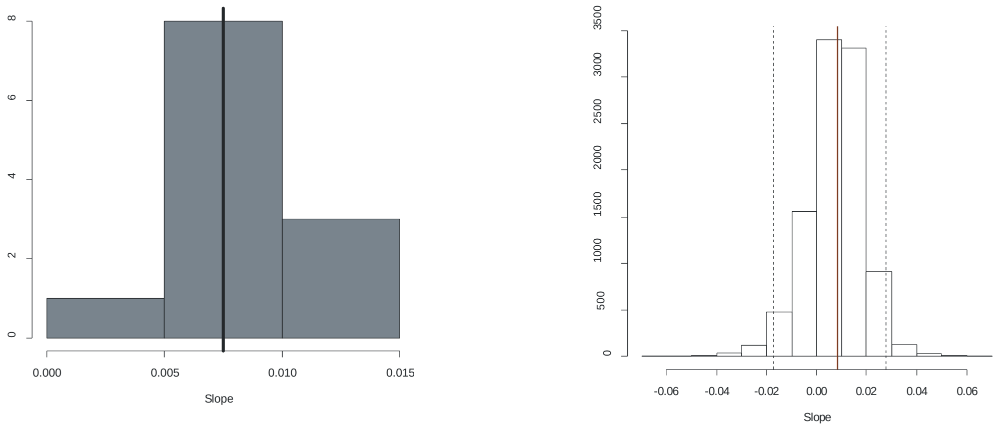
Appendix I

1969 to 1984



1985 to 1997



1998 to 2008

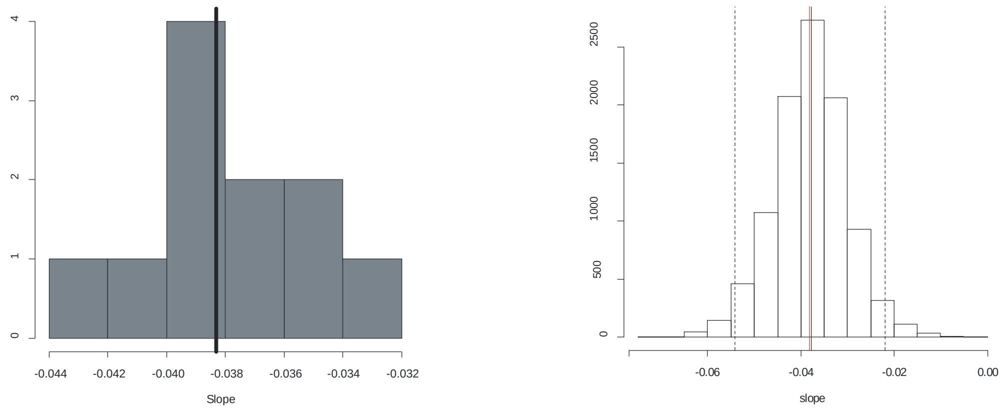


Figure A1.1. Frequency distributions of the estimates of the slope for each section of the segmented regression weighted by sample size (break-points: 1985 and 1998) in the Jackknife (grey bars) and Bootstrap (white bars) analyses. Black lines indicate the median slope obtained in each analysis. Red line is the slope of the linear model weighted by sample size in each time period. Dotted lines are the bootstrap quantiles (0.025 and 0.975).

Table A1.1. Summary of Akaike Information Criterion analysis of linear and non-linear models of change in yearly mean rugosity over time for the 250 studies for which rugosity data were available for more than one year. Abbreviations as in Table 1 in chapter 1.

Model	**R^2**	**Slope**	**df**	**AIC_c**	**Δ AIC_c**	**AIC_c W**
Segmented model (wt)	**0.62**	**-0.169***	**22**	**-22.1**	**0**	**0.9972**
Linear model (wt)	0.39	-0.019	26	-8.8	13.3	0.0013
Robust linear model (wt)	*	-0.017	26	-8.5	13.7	0.0011
Segmented model	0.65	-0.231*	22	-4	18.1	0.0001
Generalized additive model (wt)	0.99	-0.036*	5.5	7.9	30	0.0000
Linear model	0.24	-0.021	26	17.5	39.7	0.0000
Robust linear model	*	-0.014	26	18.9	41	0.0000
Generalized additive model	0.99	-0.046*	5.8	27.9	50	0.0000

*average slope of the different model segments

Appendix II

Table A2.1. Supplementary site information of the time series reporting coral cover and reef rugosity for Caribbean reefs.

Data source	**Region**	**Country / Island**	**Site Name**	**Years**	**No. Years**	**Depth (m)**	**Mean # replicates**	**Transect length**
Bythell et al, 2000[1,2,3]	Lesser Antilles	St. Croix, USVI	Buck Island BI-2	1989-2000	12	9	4	20
Bythell et al, 2000[1,2,3]	Lesser Antilles	St. Croix, USVI	Buck Island BI-4	1989-2000	12	3	4	20
Bythell et al, 2000[1,2,3]	Lesser Antilles	St. Croix, USVI	Buck Island BI-5	1990-2000	11	5	4	20
Caricomp-Dominican Republic[4,*]	Greater Antilles	Dominican Republic	El Peñón	1996-2001	6	10	6	10
Caricomp-Trinidad&Tobago[4,5]	Lesser Antilles	Trinidad & Tobago	Buccoo Reef	1994-2000	7	10	5	10
Caricomp-Bahamas[4]	SW North Atlantic	San Salvador, Bahamas	Fernandez Bay	1994-1995	2	10	5	10
Caricomp-Barbados[4,*]	Lesser Antilles	Barbados	Bellairs North Reef	1993-1994	2	10	5	10
Caricomp-Barbados[4]	Lesser Antilles	Barbados	Bellairs South Reef	1993-1994	2	10	5	10
Caricomp-Belize[4]	Central America	Belize	Carrie Bow	1993-1995	3	10	5	10
Caricomp-Bermuda[4]	SW North Atlantic	Bermuda	Hog and Twin Breaker	1993-1995	3	10	5	10
Caricomp-Bonaire[4]	South America	Bonaire	Barcadera Reef	1994-1995	2	10	5	10
Caricomp-Colombia[4]	South America	Colombia	Chengue Bay	1993-1995	3	10	5	10
Caricomp-Cuba[4]	Greater Antilles	Cuba	Cayo Coco	1994-1995	2	10	5	10
Caricomp-Curacao[4]	South America	Netherland Antilles	Santa Barbara Reef	1994-1995	2	10	5	10
Caricomp-Jamaica[4]	Greater Antilles	Jamaica	"Site A"	1993-1995	3	10	5	10

continue TableA2.1.

Data source	**Region**	**Country / Island**	**Site Name**	**Years**	**No. Years**	**Depth (m)**	**Mean # replicates**	**Transect length**
Caricomp-Mexico[4]	Central America	Mexico	Puerto Morelos	1993-1995	3	10	5	10
Caricomp-Nicaragua[4]	Central America	Nicaragua	Great Corn Island	1993-1995	3	10	5	10
Caricomp-Puerto Rico[4]	Greater Antilles	Puerto Rico	Media Luna & Turrumote	1994-1995	2	10	5	10
Caricomp-Saba[4]	Lesser Antilles	Saba	Ladder Labyrinth	1993-1995	3	10	5	10
Caricomp-Venezuela[4]	South America	Venezuela	Playa Caiman	1994-1995	2	10	5	10
Edmunds et al, 2002[6,*]	Lesser Antilles	St. John, USVI	Yawsi	1992-1998	7	9	3	10
Edmunds et al, 2002[6,*]	Lesser Antilles	St. John, USVI	Tektite	1994-1999	6	14	3	10
Jaap et al, 1991[7]	SW North Atlantic	Florida (US)	Bird Key Reef	1989-1991	3	10.5	2	20
Jaap et al, 1991[7]	SW North Atlantic	Florida (US)	Loggerhead Key	1989-1991	3	7	2	20
Jaap et al, 1991[7]	SW North Atlantic	Florida (US)	Pulaski Shoal	1989-1991	3	9	2	20
Jaap et al, 1991[7]	SW North Atlantic	Florida (US)	Texas Rock	1989-1991	3	20	2	20
Jaap et al, 1991[7]	SW North Atlantic	Florida (US)	White Shoal	1989-1991	3	5	2	20
McGrath et al, 2007[8]	SW North Atlantic	San Salvador, Bahamas	Lindsay reef	1995-2004	10	5	10	5
McGrath et al, 2007[8]	SW North Atlantic	San Salvador, Bahamas	Rice bay	1995-2004	10	5	10	5
McGrath et al, 2007[8]	SW North Atlantic	San Salvador, Bahamas	Rocky point	1995-2004	10	5	10	5
Rogers et al, 1982[9]	Lesser Antilles	St. Croix, USVI	Robin bay	1978-1979	2	5	3	10

continue TableA2.1.

Data source	Region	Country / Island	Site Name	Years	No. Years	Depth (m)	Mean # replicates	Transect length
Rogers et al, 1991[10]	Lesser Antilles	St. John, USVI	Yawsi	1989-1990	2	11.7	5	20
Steneck, 1993[11]	Greater Antilles	Jamaica	Discovery Bay	1978-1987	10	3	18	10
Steneck, 1993[11]	Greater Antilles	Jamaica	Discovery Bay	1978-1987	10	10	20	10
Steneck, 1993[11]	Lesser Antilles	St. Croix, USVI	Teague and Salt River	1982-1988	7	3	38	10
Steneck, 1993[11]	Lesser Antilles	St. Croix, USVI	Teague and Salt River	1982-1988	7	10	51	10
Steneck, 1993[11]	Lesser Antilles	St. Croix, USVI	Teague and Salt River	1982-1988	7	30	76	10

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[*] complemented with information provided by the principal researcher

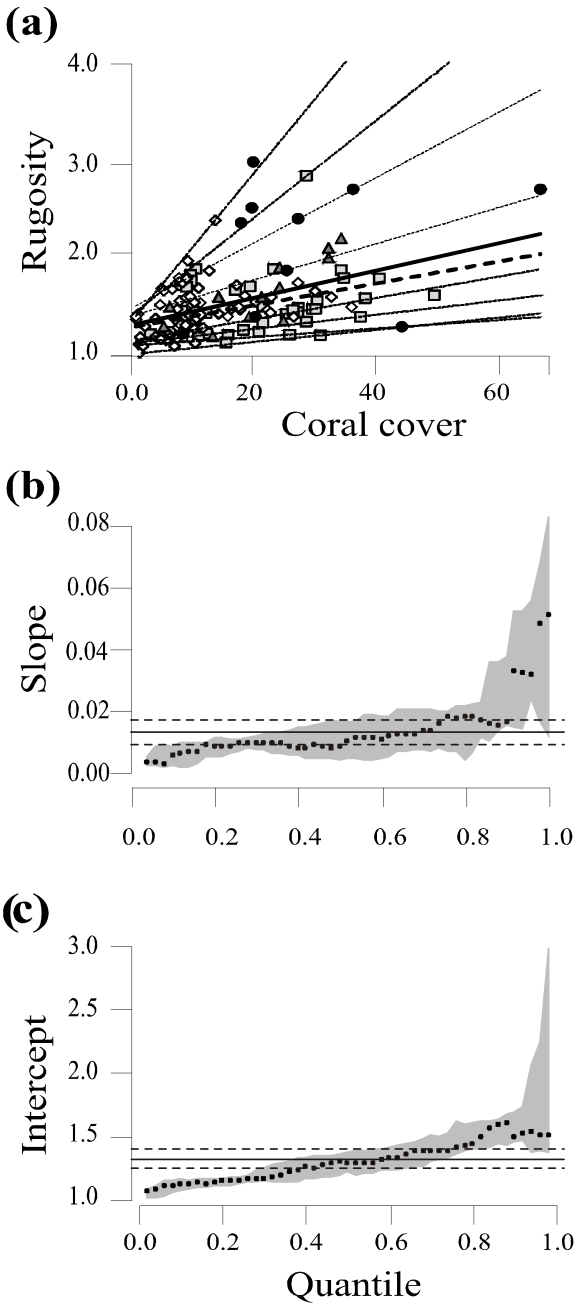

Figure A2.1. *(a)* Relationship between coral cover and reef rugosity on 140 unreplicated reef surveys through the Caribbean from 1977 to 2008. The decade in which each study was conducted is indicated (circles= 1970s, triangles= 1980s, squares= 1990s, diamonds=2000s). Nine estimated quantile regression lines (0.01, 0.05, 0.1, 0.25, 0.5, 0.75, 0.9, 0.95, 0.99 quantile) are superimposed on the scatterplot; the median (0.5 quantile) is indicated with a black dashed line and the others are indicated with grey dotted lines. The least square estimate of the mean function is indicated by the black solid line (R^2 = 0.19, Slope = 0.013, P<0.001). The (b) slopes and (c) intercepts of the quantile regressions are shown from the 0.01 quantile to the 0.99 quantile, with90% confidence bands (grey shading), and the mean (solid line) ± 90% confidence intervals (dashed lines) from the ordinary least squares regression.

Appendix III

Table A3.1. Fish species recorded in this study.

Species	Relative abundance (n = 10,965)	% occurrence per transect (n = 85)	Trophic group	Mean size (± SD) in cm
Chromis cyanea	17.67	91.25	Planktivore	9.27 (4.95)
Thalassoma bifasciatum	14.27	96.25	Planktivore	7.42 (4.29)
Stegastes partitus	8.50	95.00	Herbivore	5.00 (0.00)
Stegastes adustus	6.34	88.75	Herbivore	11.69 (4.71)
Halichoeres garnorti	5.85	72.50	Invertivore	7.35 (4.24)
Acanthurus coerulus	4.82	93.75	Herbivore	23.96 (9.27)
Clepticus parrae	2.95	28.75	Planktivore	11.64 (6.05)
Sparisoma viride	2.93	88.75	Herbivore	20.95 (14.59)
Haemulon sciurus	2.80	25.00	Invertivore	23.73 (7.80)
Haemulon flavolineatum	2.75	53.75	Invertivore	23.94 (5.49)
Lutjanus apodus	2.46	23.75	Carnivore	30.15 (6.71)
Lutjanus mahogoni	2.22	17.50	Carnivore	26.77 (7.14)
Chromis multilineata	1.80	28.75	Planktivore	10.18 (5.01)
Stegastes planifrons	1.78	62.50	Herbivore	10.33 (5.00)
Scarus iserti	1.68	55.00	Herbivore	13.97 (11.33)
Sparisoma aurofrenatum	1.61	66.25	Herbivore	17.78 (12.03)
Abudefduf saxatilis	1.60	33.75	Omnivore	13.00 (5.36)
Caranx ruber	1.38	27.50	Carnivore	23.41 (5.30)
Haemulon plumierii	1.23	27.50	Invertivore	25.74 (4.34)
Acanthurus chirurgus	0.96	33.75	Herbivore	25.19 (9.09)
Acanthurus bahianus	0.92	33.75	Herbivore	27.08 (6.97)
Microspathodon chrysurus	0.78	43.75	Herbivore	13.00 (7.20)
Scarus taeniopterus	0.69	40.00	Herbivore	21.18 (10.95)
Melichthys niger	0.67	36.25	Omnivore	24.46 (5.94)
Stegastes variabilis	0.67	20.00	Herbivore	10.34 (5.02)
Kyphosus spp	0.62	20.00	Herbivore	32.72 (7.84)
Stegastes diencaeus	0.60	33.75	Herbivore	8.94 (4.92)
Haemulon aurolineatum	0.59	7.50	Invertivore	15.62 (2.42)
Ocyurus chrysurus	0.58	23.75	Carnivore	32.89 (7.86)
Canthigaster rostrata	0.57	32.50	Omnivore	5.48 (2.15)
Cephalopholis cruentatus	0.52	28.75	Carnivore	17.81 (6.75)
Halichoeres maculipinna	0.51	13.75	Invertivore	6.96 (4.01)
Chaetodon capistratus	0.47	27.50	Invertivore	5.00 (0.00)
Haemulon carbonarium	0.42	10.00	Invertivore	25.65 (4.42)
Paranthias furcifer	0.39	5.00	Planktivore	21.98 (5.58)
Holacanthus ciliaris	0.32	23.75	Invertivore	34.57 (10.24)
Haemulon melanurum	0.32	12.50	Invertivore	22.43 (4.43)
Haemulon striatum	0.29	12.50	Planktivore	19.69 (10.47)
Pomacanthus paru	0.26	20.00	Omnivore	25.17 (11.61)
Cephalopholis fulvus	0.24	21.25	Carnivore	16.15 (5.16)
Halchoeres bivittatus	0.22	7.50	Invertivore	9.58 (5.09)

continue TableA3.1

Species	**Relative abundance (n = 10,965)**	**% occurrence per transect (n = 85)**	**Trophic group**	**Mean size (± SD) in cm**
Pomacanthus arcuatus	0.21	16.25	Omnivore	34.13 (10.19)
Cantherhines macrocerus	0.20	12.50	Omnivore	36.59 (5.85)
Lutjanus analis	0.19	2.50	Carnivore	26.19 (5.46)
Holacanthus tricolor	0.19	16.25	Invertivore	26.43 (7.27)
Haemulon album	0.18	2.50	Invertivore	17.5 (4.44)
Anisostremus virginicus	0.16	15.00	Invertivore	32.06 (4.7)
Mulloidichthys martinicus	0.16	6.25	Invertivore	26.76 (3.93)
Scarus vetula	0.15	12.50	Herbivore	37.19 (6.82)
Chaetodon striatus	0.15	10.00	Invertivore	15.00 (0.00)
Lutjanus griseus	0.14	6.25	Carnivore	17.67 (7.99)
Holocentrus rufus	0.14	8.75	Invertivore	21.67 (4.88)
Bodianus rufus	0.13	7.50	Invertivore	22.14 (9.94)
Lutjanus campechanus	0.12	2.50	Carnivore	28.08 (11.09)
Sparisoma chrysopterum	0.12	11.25	Herbivore	26.92 (16.65)
Haemulon macrostomum	0.12	2.50	Invertivore	16.54 (3.76)
Serranus tigrinus	0.11	11.25	Carnivore	9.17 (5.15)
Haemulon parra	0.11	3.75	Invertivore	26.67 (3.89)
Chaetodon aculeatus	0.11	3.75	Omnivore	5.00 (0.00)
Mycteroperca venenosa	0.09	2.50	Carnivore	29.00 (9.66)
Canthidermis sufflamen	0.09	6.25	Invertivore	16.5 (14.15)
Aluterus scriptus	0.09	6.25	Omnivore	9.50 (14.23)
Scarus guacamaia	0.06	3.75	Herbivore	44.29 (10.18)
Holacanthus bermudensis	0.06	5.00	Invertivore	25.00 (5.77)
Stegastes leucostictus	0.05	5.00	Herbivore	5.00 (0.00)
Chaetodon ocellatus	0.05	1.25	Invertivore	11.67 (5.16)
Gramma loreto	0.05	3.75	Invertivore	5.00 (0.00)
Holocentrus adscensionis	0.05	3.75	Invertivore	17.00 (4.47)
Hypoplectrus puella	0.04	3.75	Carnivore	15.00 (0.00)
Sparisoma rubripinne	0.04	5.00	Herbivore	32.50 (5.00)
Sparisoma atomarium	0.04	3.75	Herbivore	20.00 (10.00)
Lactophrys triqueter	0.04	3.75	Invertivore	27.5 (5.00)
Trachinotus falcatus	0.03	3.75	Carnivore	41.67 (14.43)
Scarus coeletinus	0.03	1.25	Herbivore	50.00 (0.00)
Balistes vetula	0.03	3.75	Invertivore	40.00 (8.66)
Xanthichthys ringens	0.03	2.50	Invertivore	15.00 (0.00)
Mycteroperca bonaci	0.03	3.75	Piscivore	35.00 (25.98)
Hypoplectrus nigricans	0.02	1.25	Carnivore	15.00 (0.00)
Acanthostracion polygonia	0.02	2.50	Invertivore	30.00 (7.07)
Diodon holocanthus	0.02	2.50	Invertivore	5.00 (0.00)
Diodon hystrix	0.02	2.50	Invertivore	5.00 (0.00)
Calamus calamus	0.02	1.25	Invertivore	25.00 (0.00)
Chaetodon sedentarius	0.02	2.50	Omnivore	15.00 (0.00)
Sphyraena barracuda	0.02	2.50	Piscivore	50.00 (0.00)

continue TableA3.1

Species	**Relative abundance (n = 10,965)**	**% occurrence per transect (n = 85)**	**Trophic group**	**Mean size (± SD) in cm**
Epinephelus guttatus	0.01	1.25	Carnivore	25.00 (0.00)
Gymnothorax milaris	0.01	1.25	Carnivore	25.00 (0.00)
Lutjanus cyanopterus	0.01	1.25	Carnivore	35.00 (0.00)
Lutjanus jocu	0.01	1.25	Carnivore	35.00 (0.00)
Scorpaena plumieri	0.01	1.25	Carnivore	25.00 (0.00)
Pseudupeneus maculatus	0.01	1.25	Invertivore	15.00 (0.00)
Cantherhines pullus	0.01	1.25	Omnivore	25.00 (0.00)
Gymnothorax moringa	0.01	1.25	Piscivore	35.00 (0.00)
Mycteroperca tigris	0.01	1.25	Piscivore	15.00 (0.00)