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REPORT

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

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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 have used a dataset of 49 time series reporting reef architectural complexity to explore the effect of hurricanes, coral bleaching and fishing on 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 (in a time frame of <5 years) or positive thermal anomalies. Although the rates of change in architectural complexity were similar in and out of marine protected areas (MPAs), 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 major drivers of coral mortality, such as coral bleaching, do not influence reef architectural complexity in the short term (<5 years). Instead, direct physical impacts and reef bioerosion appear to be important drivers of the widespread loss of architecturally complex reefs in the Caribbean.

Keywords Coral bleaching · Drivers of change · Environmental change · Ecosystem services · Habitat complexity · Hurricanes · Marine reserves · Reef degradation

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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 extensive 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 has produced elevated sea temperatures, which in turn have 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 and 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 reef architectural complexity (i.e. reef relief complexity), with little evidence of a time-lag over the last 30 years (Alvarez-Filip et al. 2009a, 2011). Although architectural complexity is strongly related to the abundance of reef-building corals (Alvarez-Filip et al. in press), annual rates of change in coral cover and architectural complexity in the Caribbean are only weakly correlated (Alvarez-Filip et al. 2011), suggesting 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 (Wilson et al. 2006; Pratchett et al. 2008; Paddack et al. 2009).

Given the extreme importance of coral reefs for biodiversity, human livelihoods and key ecosystem 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 strategies for restoring reef complexity (Pandolfi et al. 2005; Mora 2008). 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 and Precht 2006; Schutte et al. 2010), and coral mortality in subsequent years is likely to have been exacerbated through 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. 2010) and increasing coastal development (Mora 2008). Hurricanes have played a relatively small role in the regional loss of coral cover, although they can have considerable localised impacts (Gardner et al. 2005). In contrast to our detailed 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.

Disturbances on coral reefs are commonly separated into biological disturbances (e.g. coral bleaching and diseases) and physical disturbances (e.g. tropical storms). Previous studies have suggested that physical disturbances are more likely to result in an immediate loss of habitat complexity (and therefore, greater impact on reef fishes; Wilson et al. 2006; Pratchett et al. 2008). However, in the long-term, the effects of biological disturbances may be analogous to physical disturbances, influencing both live coral cover and the architectural complexity of reef habitats (Wilson et al. 2006; Pratchett et al. 2008). Here, we use a unique Caribbean-wide dataset of time series of reef architectural complexity to quantify the influence of hurricanes, mass bleaching events and fishing (by comparing protected to unprotected reefs) on rates of change in architectural complexity over the last three decades.

Materials and methods

Data collation

We used the rugosity index to describe reef architecture, as this is the most commonly used method for measuring reef complexity in the region (Alvarez-Filip et al. 2009a). Reef rugosity is obtained by fitting a fine chain to the reef and dividing the contoured length by the linear distance (Rogers et al. 1982). A perfectly flat surface has a rugosity index of one, with larger numbers indicating more complex surfaces.

We collated data from replicated studies (i.e. data collected over more than 1 year) that reported architectural complexity for reefs sites within the wider Caribbean. We used online literature search tools to search through the most relevant journals for Caribbean reef studies, and contacted scientists and reef managers directly to obtain the required information (details in Alvarez-Filip et al. 2009a). This resulted in a total of 27 studies with temporal replication between 1978 and 2008 (Fig. 1), reporting

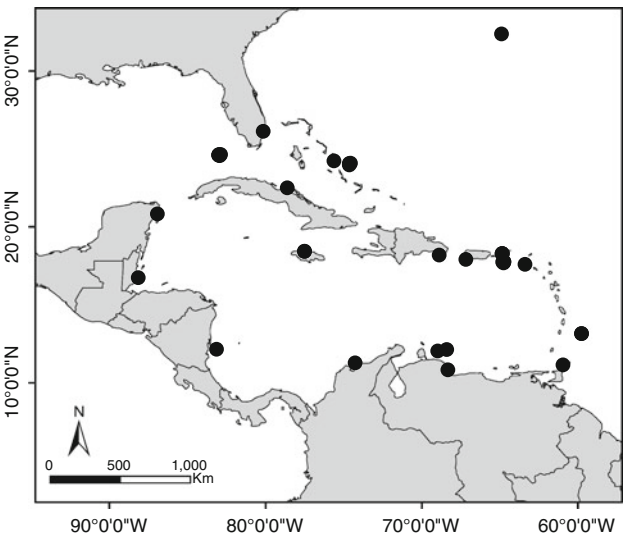

Fig. 1 Regional distribution of reef sites from which surveys of architectural complexity, replicated over more than 1 year, were collated

Table 1 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	Depth range (m)	Transect length (m)
Alvarez-Filip (2010)[b]	México	2006–2008	1	41	12	3
Baron et al. (2004)	Florida (US)	1983–1991	1	19	4	8
Bythell et al. (2000)[c]	USVI	1990–2000	3	4	3–9	20
Kjerfve et al. (1998)[d]	16 reef sites	1993–1996	17	5	10	10
Clarke (1996)	USVI	1979–1995	1	9	4–10	10
Edmunds 2002[e]	USVI	1994–2007	2	3	9–14	10
Jaap et al. (1991)	Florida (US)	1989–1991	5	2	5–20	20
McGrath et al. (2007)	Bahamas	1995–2004	3	10	5	5
NOAA[f]	Puerto Rico and USVI	2001–2007	9	47	5–25	6
Rogers et al. (1982)	USVI	1978–1979	1	3	5	10
Rogers et al. (1991)	USVI	1989–1990	1	5	12	20
Steneck (1993)	Jamaica and USVI	1982–1988	5	76	3–30	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

[b] Author's data

[c] Data complemented with previous reports

[d] Caricomp data from 1993 to 1996, except when indicated, and include records for Bahamas, Barbados (1993–2006)[e], Belize, Bermuda, Bonaire, Colombia, Cuba, Curaçao, Dominican Republic (1996–2001)[e], Jamaica, Mexico, Nicaragua, Puerto Rico, Saba, Trinidad and Tobago (1994–2000)[c] and Venezuela

[e] Complemented with data provided by the corresponding authors

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

information for 49 reef sites and ranging in duration from 2 to 17 years (mean = 6.29 ± 4.23 SD years; Table 1). Although different studies surveyed reefs at different depths and used different chain lengths to measure rugosity (Table 1), these methodological differences did not show significant relationships with rates of rugosity change (depth: $R^2 = 0.03$, slope <0.01, $P = 0.20$; chain length: $R^2 = 0.01$, slope <0.01, $P = 0.93$), and therefore were not considered in our analyses.

Drivers of change of reef architectural complexity

Hurricanes

We classified whether sites were impacted by hurricanes 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, impacts were recorded where tropical storms or hurricanes of category 1 or 2 passed within 35 km, category 3 hurricanes passed within 60 km, or category 4 or 5 hurricanes passed within 100 km of a given site. The hurricane history of each site was obtained from the web-based tool of the NOAA Coastal Services Center (http://www.csc.noaa.gov).

We compared annual rates of change in architectural complexity at sites impacted and not impacted by hurricanes. In addition, because the time elapsed between hurricanes influences the magnitude of coral cover loss that is observed in response to their impacts (Connell et al. 1997; Gardner et al. 2005), we also compared rates of complexity change between sites that had been impacted in the 10 years prior to the focal hurricane impact and sites that had not been impacted during this period. We therefore measured the effect of hurricanes at four categories of sites: (1) reef sites impacted within 10 years before the onset of their study and during their survey period ('before-during'); (2) sites impacted only during their survey period ('during'); (3) sites impacted only within the 10 years before their survey period ('before'); and (4) sites not impacted by hurricanes, from 10 years prior to the onset of their study to the end of their survey period ('non-impacted').

Coral bleaching

We tested for an effect of coral bleaching on regional reef architecture in two ways. First, we carried out temporal analyses, in which we focused on the 7 years between 1978 and 2008 during 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. 2010). The mass bleaching events of 1998 and 1999 were classed together because they occurred in consecutive years, which therefore gave a total of six mass bleaching events. We assumed that in each of these events, bleaching was likely to have affected all of the sites in this study (but see later for an exploration of spatial variation in bleaching). 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 final year of the time series, or to the year immediately before the next mass bleaching event, in order to account for the possible erosion of architectural complexity after coral mortality. For time series that spanned more than one bleaching event, each event was included separately in the analysis. Time series that did not span any mass bleaching events were excluded. In addition, to avoid confounding the effect of bleaching with the effect of hurricane damage to reef architecture, data were only included from reefs that were not impacted by a hurricane after a bleaching episode. However, we also explored the potential interaction between these two disturbances, by quantifying rates of change in architectural complexity on the 18 sites for which the time series spanned both a mass bleaching event and a hurricane impact, and on the nine sites that experienced a hurricane during their monitoring period but no mass bleaching event.

Second, we took a spatial approach to examining the potential impacts of bleaching on reef architecture. 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. 2010). Consequently, we 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. 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.

Marine protected areas

We tested for effects of fishing on changes in reef architecture by comparing rates of change in rugosity on sites that were protected (i.e. within the boundaries of a marine protected areas, MPAs) or unprotected (i.e. outside MPAs)) during their survey period. It is possible that some degree of fishing (either regulated or illegal) takes place inside MPAs, but we assumed that fishing impacts are considerably less in protected sites. In addition, two-thirds of the MPAs included in this study are classified in IUCN protection category II and thus receive a relatively high degree of protection (Wood 2007). We also tested for the effects of any interaction between protection from fishing and hurricane impact on changes in reef architecture. Lack of information on bleaching episodes for specific reef sites prevented exploration of any interaction between protection from fishing and effects of bleaching.

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 key factors in restoring reef habitat quality (Mumby and Steneck 2008; Mumby and Harborne 2010; Selig and 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:

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

where *End* and *Start* represent 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. 2006; Paddack et al. 2009), and its properties as a measure of 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 the 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

Hurricanes

Annual rates of change in architectural complexity varied significantly between reefs that had been either impacted before, before and during, 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 that were impacted only during their survey period, while considerably lower rates of decline were recorded at sites that were impacted both before and during their survey period (Fig. 2). Architectural complexity did not decline significantly on sites that were not impacted by a hurricane during their survey period (i.e. the 'before' and 'non-impacted' groups; Fig. 2).

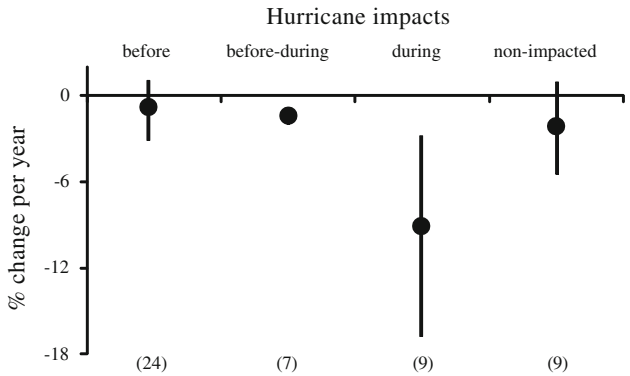

Fig. 2 Effect of hurricane impacts on rates of architectural complexity change in the Caribbean. Annual percentage change in reef rugosity for reef sites impacted only in the 10 years before their survey period (*before*), in the 10 years before the onset of their study and during their survey period (*before-during*), only during their survey period (*during*) and not impacted by hurricanes from 10 years prior to 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

Coral bleaching

A total of 31 studies spanned one or more of the seven 'mass' bleaching events; 11 encompassed one, 14 encompassed two and six encompassed three mass bleaching events, giving 57 bleaching incidents in total. Eighteen of these 57 occurred in locations that simultaneously experienced a hurricane impact and therefore were removed from the analyses. Thus, in total, 39 separate bleaching incidents, 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 change in architectural complexity among the seven mass bleaching events ($Q_M = 5.81$, $P = 0.22$; Fig. 3a). The only significant decline in architectural complexity occurred just after the mass bleaching event of 1995, although the very limited number of studies ($n = 2$) makes this conclusion tentative (Fig. 3a). A significant rate of decline in architectural complexity was apparent in the 18 time series that spanned both a mass bleaching event and a hurricane impact (annual rate of change = −3.53%, CI = −6.51 to −0.96%). This rate of decline was significantly greater than that for the 39 time series spanning a mass bleaching event but no hurricane impact ($Q_M = 3.91$, $P = 0.04$), but did not differ from the rate observed at the nine sites that experienced a hurricane impact without bleaching ($Q_M = 1.48$; $P = 0.17$). These results suggest little effect of bleaching and no interaction between bleaching and hurricanes in their impacts on architectural complexity.

Taking into account the spatial heterogeneity of bleaching across the study area, rates of change in architectural complexity were also not related to SST anomalies ($R^2 = 0.002$, $P = 0.88$; Fig. 3b). The 7 years referred to as mass bleaching events in the literature all had positive SST anomalies but similar rates of change in architectural complexity to the other years (Fig. 3b).

Fishing (marine protected areas)

Rates of change of architectural complexity did not differ significantly between unprotected sites and sites within MPAs ($Q_M = 0.04$, $P = 0.92$), although reef rugosity did decline significantly inside but not outside of MPAs (Fig. 4a). The high degree of variability in rugosity change on reefs outside MPAs (Fig. 4a) is in part a consequence of hurricane impacts, as rugosity declined significantly in unprotected reefs that were impacted by a hurricane ($n = 9$, annual rate of change = −5.95%, CI = −10.06 to −2.07%) but not in those not impacted ($n = 16$, annual rate of

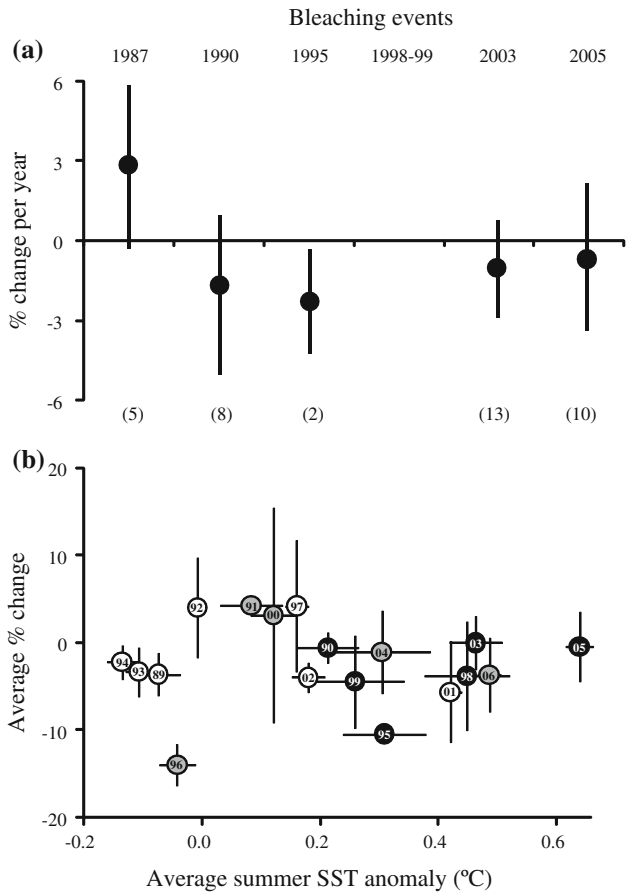

Fig. 3 Effect of widespread bleaching events and SST anomalies on rates of architectural complexity change in the Caribbean. **a** Annual percentage change in reef rugosity on reef sites after widespread ('mass') bleaching events. The total number of sites is given in parentheses (1998–1999 is excluded as data from only one site were available) and bars show 95% bias-corrected bootstrapped confidence intervals. **b** Average (±SE) change in rugosity on reef sites between pairs of consecutive years in relation to average (±SE) summer SST anomaly in the first year of each pair (*black* years of mass bleaching events, *grey* 1 year after mass bleaching events, *white* all other years). Points are labelled by year, from 1989 to 2006

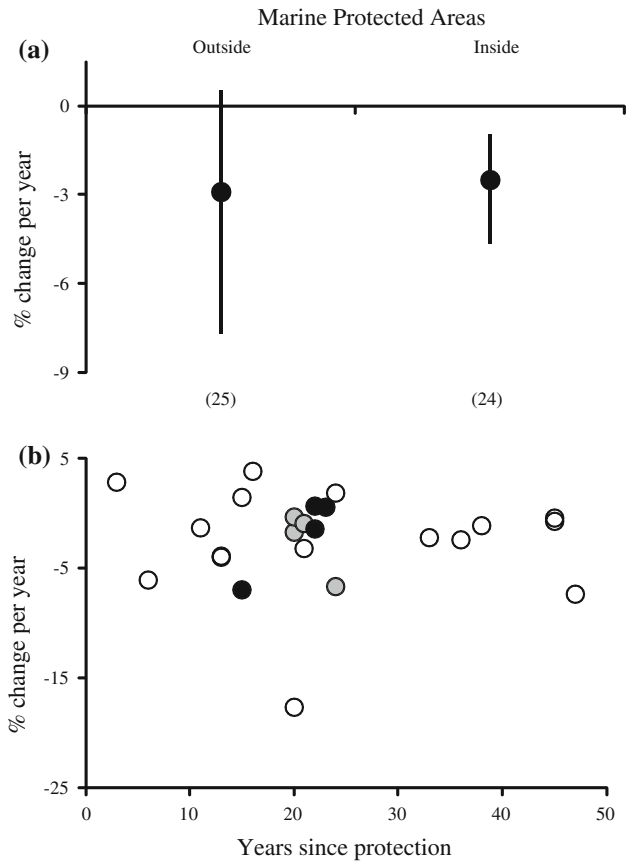

Fig. 4 Effect of marine protected areas (MPA) on rates of change in reef architectural complexity in the Caribbean. **a** Annual percentage change in reef rugosity for reefs inside and outwith MPAs. *Numbers* in parentheses indicate the number of sites included in the analysis for each group. *Bars* show the 95% bias-corrected bootstrapped confidence intervals. **b** Relationship between annual rate of change in reef complexity and years since protection for 24 MPA sites. The International Union for Conservation of Nature management category of each MPA is indicated (from highest to lowest degree of protection: *white* II; *grey* IV; *black* VI)

change = 2.87%, CI = −0.51 to 5.73%). However, the significant declines in rugosity on protected reefs were similar for those impacted and not impacted by hurricanes (impacted by hurricanes: $n = 7$, annual rate of change = −1.77%, CI = −2.49 to −1.04%; not impacted by hurricanes: $n = 17$, annual rate of change = −2.61%, CI = −5.43 to −0.56%). Annual rates of change in reef architectural complexity within MPAs did not vary with duration of site protection ($R^2 = 0.002$, $P = 0.85$; Fig. 4b).

Discussion

This study describes the effect of three major drivers of coral reef degradation on the structural integrity of reefs throughout the Caribbean. While hurricanes and, to a lesser extent but paradoxically, the effect of protection appear to have significantly enhanced the region-wide rates of decline of reef complexity, coral bleaching appears to have had little influence on architectural complexity loss. Thus, although bleaching can be a major driver of coral mortality (Aronson and Precht 2006; Schutte et al. 2010), direct physical impacts and reef bioerosion may be the most important drivers of the widespread loss of architecturally complex reefs in the Caribbean.

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 and Gil 2006; Wilson et al. 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 and Connell 1999). The strong influence of hurricane impacts on Caribbean-wide reef architectural complexity reported here contrasts with previous studies, which have shown that hurricanes are not a major driver of recent declines in coral cover across the region (Gardner et al. 2005). Unlike architectural complexity, physical disturbances such as hurricanes may be relatively less important in affecting live coral tissue, and therefore coral cover than biological drivers which generally occur at larger spatial scales and/or can spread rapidly (Aronson and 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; Alvarez-Filip et al. 2009b). 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. 2009b). However, consecutive hurricane impacts are likely to maintain coral reefs in less structurally complex states, an effect that is likely to be compounded by the projected increase in activity of Atlantic Ocean hurricanes (Saunders and 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; Wilson et al. 2006). Coral skeletons of erect branching corals (e.g. *Acropora* spp.) may then break down into coral rubble, whereas massive coral skeletons typically gradually erode in situ (Sheppard et al. 2002). Following particularly severe mass bleaching events, areas that were previously characterised by architecturally complex reef systems may be essentially flattened, or reduced to rubble (Pratchett et al. 2008). In our meta-analysis, however, the noted absence of significant declines in architectural complexity following coral bleaching or anomalously warm sea surface temperatures may be due to the lack of extensive coral mortality following bleaching at the reef sites included in our study. 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 after the *Acropora* die-off, during a period in which Caribbean reefs have been dominated by massive (e.g. *Montastraea* spp.) and weedy (e.g. *Porites*, *Agaricia*) corals. As the erosion of massive coral skeletons is likely to be a slow process, the period of time after bleaching events (average $\approx$ 3 years for data in Fig. 3a) may not have been sufficient to detect an impact on reef structure. However, regional declines in reef complexity in the Caribbean have been found to follow coral mortality with no evidence of a time-lag (Alvarez-Filip et al. 2011), which also suggests that biological disturbances (which typically operate more slowly than physical disturbances) have not played a direct role in the recent declines in Caribbean-wide reef complexity.

Marine protected areas are widely recognised as an important tool for the protection of biological diversity, largely through the removal or reduction of fishing pressure (Sale et al. 2005; Gaston et al. 2008). On coral reefs, a broad range of positive effects has been noted 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). Nevertheless, regional- and local-scale studies have found that large declines in coral cover can occur in spite of protection (Coelho and Manfrino 2007; Graham et al. 2007; Mora 2008), although recent evidence suggests that coral cover is maintained to a greater extent inside marine reserves (Selig and 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 and Harborne 2010). These positive effects of protection might only become apparent long after reserve establishment; for instance, coral cover inside some Caribbean marine reserves declined continuously for up to 14 years after implementation (Selig and Bruno 2010). In the case of architectural complexity, however, our findings suggest no apparent association between reef complexity and duration of protection, over periods of up to nearly 50 years. Overall, the significant decrease in architectural complexity inside MPAs, but not on unprotected reefs, could have resulted from the designation of MPAs at 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 $\pm$ 0.9 SE; unprotected = 1.73 $\pm$ 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; Aronson and Precht 2006), which likely slowed rates of reef architecture loss (Mallela and Perry 2007; Alvarez-Filip et al. 2009a). 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. 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 reef components to design management tools that will successfully secure the long-term persistence of these ecosystems.

Over the last four decades, Caribbean reefs have experienced rapid and severe declines in coral cover and reef architecture (Gardner et al. 2003; Alvarez-Filip et al. 2009a), generating a debate in the scientific community about the relative importance of major factors (local vs. global) that have driven these declines (Aronson and Precht 2006; Knowlton and Jackson 2008). While a growing body of evidence indicates that live cover of reef-building corals is influenced by large-scale drivers such as changing climate and the spread of human development (Knowlton and Jackson 2008; Mora 2008; Schutte et al. 2010), our results suggest that subsequent changes in reef architecture may be more sensitive to local reef conditions (e.g. rates of erosion and hurricane impacts). Thus, while reversing declines in coral cover is likely to require international regulations to reduce the impacts of human-mediated climate change, protecting and enhancing reef architecture may be aided by locally focused efforts to limit human activities (e.g. destructive fishing practices, anchoring, etc.) that have direct physical impacts on reefs.

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