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HURRICANES AND CARIBBEAN CORAL REEFS: IMPACTS, RECOVERY PATTERNS, AND ROLE IN LONG-TERM DECLINE

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Abstract. The decline of corals on tropical reefs is usually ascribed to a combination of natural and anthropogenic factors, but the relative importance of these causes remains unclear. In this paper, we attempt to quantify the contribution of hurricanes to Caribbean coral cover decline over the past two decades using meta-analyses. Our study included published and unpublished data from 286 coral reef sites monitored for variable lengths of time between 1980 and 2001. Of these, 177 sites had experienced hurricane impacts during their period of survey. Across the Caribbean, coral cover is reduced by ~17%, on average, in the year following a hurricane impact. The magnitude of this immediate loss increases with hurricane intensity and with the time elapsed since the last impact. In the following year, no further loss is discernible, but the decline in cover then resumes on impacted sites at a rate similar to the regional background rate of decline for nonimpacted sites. There is no evidence of recovery to a pre-storm state for at least eight years after impact. Overall, coral cover at sites impacted by a hurricane has declined at a significantly faster rate (6% per annum) than nonimpacted sites (2% per annum), due almost exclusively to higher rates of loss in the year after impact in the 1980s. While hurricanes, through their immediate impacts, appear to have contributed to changing coral cover on many Caribbean reefs in the 1980s, the similar decline in coral cover at impacted and nonimpacted sites in the 1990s suggests that other stressors are now relatively more important in driving the overall pattern of change in coral cover in this region. The overall lack of post-hurricane recovery points to a general impairment of the regeneration potential of Caribbean coral reefs.

Key words: Caribbean coral reefs; conservation; coral decline; disturbance; hurricanes; large-scale patterns; temporal trends.

Introduction

Coral reefs are under threat worldwide. An estimated 58% of reefs are classified as threatened (Bryant et al. 1998), and 11% of the original extent of coral reefs has already been lost (Wilkinson 2000). The composition of remaining coral reefs is also changing rapidly. For example, coral cover on reefs across the Caribbean has decreased by ~80% in the past three decades (Gardner et al. 2003), and some formerly abundant coral species have almost disappeared from the region (e.g., Precht et al. 2002). On many reefs, the decline in coral has coincided with increased cover of macroalgae, causing apparently stable community shifts to algal-dominated states (Done 1992, Hughes 1994). The causes of coral decline are thought to include a combination of direct anthropogenic factors, such as overfishing, pollution, and sedimentation (Grigg and Dollar 1990, Rogers and Beets 2001), as well as climate change (Hughes et al. 2003) and natural disturbances (Aronson and Precht 2001).

Hurricanes and tropical storms are perhaps the most obvious and frequent natural disturbances affecting reef communities. They have long been recognized as being important determinants of both the structure (e.g., Geister 1977, Blanchon 1997) and function (Connell 1978, Rogers 1993, Harmelin-Vivien 1994) of reef ecosystems. A number of studies have documented the severe immediate consequences of hurricane impacts at single sites in terms of reduced coral cover (e.g., Woodley et al. 1981, Harmelin-Vivien and Laboute 1986), highlighting the effects as being impressive in magnitude, speed, and patchiness. However, hurricanes can also sometimes have minimal or indiscernible impacts (e.g., Shinn 1976, Bythell et al. 1993). Variability in immediate effects of hurricanes has been ascribed either to natural variability in reef structure, the presence of other overriding stresses (Bythell et al. 1993), and/or the scale of observation (Rogers 1992, Bythell et al. 2000).

By contrast, the longer-term trajectories and recovery patterns of coral populations following disturbances are poorly understood (Hughes and Connell 1999). Against a background of generally declining coral cov-

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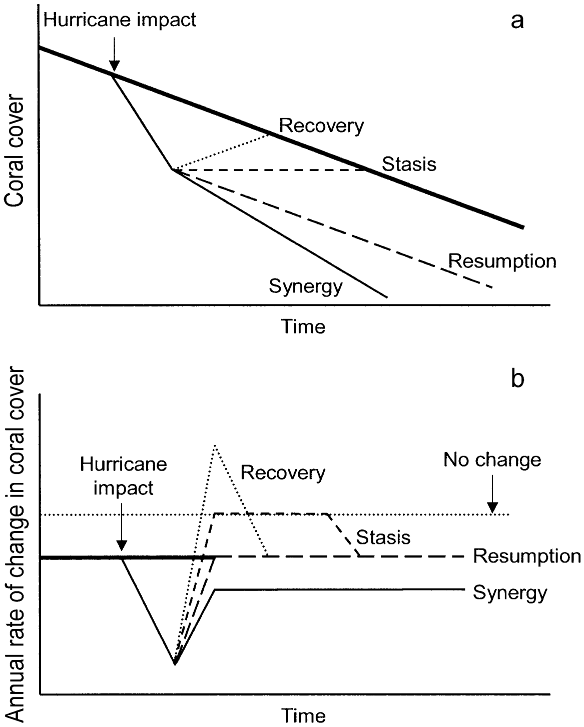

FIG. 1. Four possible trajectories of change in coral cover following a hurricane impact, expressed as (a) absolute coral cover and (b) annual rate of change in coral cover. The bold lines represent change in coral cover at nonimpacted sites.

er (e.g., Gardner et al. 2003), four long-term trajectories for post-hurricane coral cover are possible (Fig. 1). After the immediate loss in coral resulting from a hurricane impact, coral cover could increase temporarily due to the successful attachment and growth of coral fragments broken during the storm (Fong and Lirman 1995, Lirman 2000*a*, *b*; recovery trajectory) before declining again at a pre-storm rate. Second, coral cover could remain temporarily stable before starting to decline (stasis trajectory). This effect could occur through asexual reproduction, as above, and/or because species susceptible to other causes of decline are removed by the hurricane (e.g., Woodley et al. 1981). Third, coral cover could immediately resume its decline at a pre-storm rate (resumption trajectory), making any effect of hurricanes on coral loss simply additive to that of other causes of decline. Finally, coral cover could immediately resume its decline, but at an increased rate owing to synergistic effects between hurricanes and other causes of decline (synergy trajectory; Hughes and Connell 1999, Nyström et al. 2000).

This final trajectory is perhaps the most difficult to identify and explain. One potential scenario for synergy is that hurricane-induced coral mortality, coupled with the depletion of grazing organisms through overfishing or disease, could lead to larger increases in macroalgae than either factor could have caused individually. This could happen, for example, if the combination of stressors pushed macroalgal cover beyond the suggested threshold at which herbivores can control macroalgae (Williams and Polunin 2001). Similarly, the more limited impact of hurricanes on coral predators than on corals could shift coral–predator ratios below the breakpoint where coral recovery is possible (Knowlton et al. 1990). However, although hurricanes and low grazing/high predation pressure may potentially have multiplicative effects on coral mortality, such true synergistic effects have rarely been unambiguously demonstrated and their mechanisms of action are unclear.

The four trajectories outlined above can be visualized in terms of absolute coral cover (Fig. 1a), or in terms of rates of change in coral cover (Fig. 1b). The latter may be more readily detectable in real data, because rates of change can be expressed relative to cover at the time of impact or relative to coral cover in the previous year, thus standardizing intersite variation in initial coral cover and making patterns easier to detect. It is of course possible that individual reefs may sequentially adopt two or more of these possible trajectories.

Most previous studies of the impacts of hurricanes on coral reefs have focused on a single site, where stressors in addition to hurricanes were acting. Jamaica is a prime example. In 1980, Hurricane Allen hit Jamaican reefs after nearly four hurricane-free decades and sharply reduced coral abundance (Woodley et al. 1981). The subsequent region-wide mortality of the grazing sea urchin *Diadema antillarum* in 1983 (Lessios et al. 1984), which occurred in the context of chronic overfishing in Jamaica (Jackson et al. 2001), coincided with a protracted algal bloom along much of the Jamaican coastline (Hughes 1994). A second hurricane in 1988 further depressed the reefs into a fully degraded state (Woodley 1989). This situation may also have been exacerbated by localized inputs of anthropogenic nutrients (Lapointe et al. 1997). It is clear that consideration of these changes in coral cover while focusing on a single stressor would have resulted in a biased understanding of the effects of hurricanes. In addition, extrapolation of this understanding to other sites where different stressors operate would be unwise.

The example of Jamaica provides strong justification for trying to integrate the results of multiple studies carried out in many locations at various times to understand better the effects of hurricanes on coral reefs. In this paper we use meta-analyses to examine the impacts of hurricanes on reefs across the Caribbean basin over the past two decades. Although numerous qualitative summaries exist for this region (e.g., Wilkinson 2000, Aronson and Precht 2001), there is currently no quantitative evaluation of the immediate and longer-term responses of coral reefs to hurricane activity across the Caribbean. A large-scale meta-analytical approach has recently proven successful in documenting the long-term decline of Caribbean corals (Gardner et al. 2003). Meta-analysis also reduces the inherent risks of extrapolating from a small number of studies (e.g., Hughes 1994, Adams 2001), particularly when inferring contemporary status and trends (Aronson and Precht 2001) or common histories of cause and effect (Hughes and Connell 1999). Our aims were therefore to (1) evaluate the overall magnitude of immediate hurricane impacts on coral cover, (2) assess intersite variability in the immediate aftermath of hurricanes and possible correlates of this variability, and (3) quantify the contribution of hurricanes to the long-term pattern of change in coral cover on Caribbean reefs. Such an approach may allow an evaluation of the potential implications of recent decadal-scale increases in hurricane activity in the western Atlantic (Goldenberg et al. 2001) for coral reefs in the Caribbean.

METHODS AND MATERIALS

Data acquisition

Data on hard coral cover for reefs within the wider Caribbean basin were obtained through electronic and manual literature searches, as well as personal communication with reef scientists, site managers, and institutional librarians. Electronic literature searches were conducted using the Scientific Citation Index (SCI) and Aquatic Sciences and Fisheries Abstracts (ASFA) from 1981 and 1988, respectively, to 2001. All relevant references cited in these publications were also checked. The only selection criteria employed were that the study reported percent hard coral cover, with replicated measurements, from a site within the region. Sites were deemed separate as defined by each study, except when a single site crossed a steep depth contour (e.g., cross-reef transects; Dustan and Halas 1987). In these few cases, transects were re-pooled into groups of similar depth.

To provide a hurricane history for each monitored site, we obtained GIS-based hurricane and tropical storm information for the entire Caribbean basin from the National Climatic Data Center of the North American Oceanographic and Atmospheric Administration (available online; see also Neumann et al. 1999)[5]. These data include six-hourly track information on location, wind speed, and hurricane intensity category from 1851 to 2001.

Due to the spatial clumping of study sites, we pooled groups of closely neighboring sites into a smaller set of ‘‘hurricane zones’’ (30 km diameter). Using ArcView GIS 3.2 (ESRI, Redlands, California, USA) we created buffers around each hurricane zone in order to query the data set with respect to historical hurricane impacts. As suggested in previous studies (Stoddart 1985, Done 1992, Treml et al. 1997), we used a 35 km diameter buffer to capture the zone of influence of tropical storms and hurricanes of Categories 1 and 2, a 60-km buffer to capture Category 3 hurricanes, and a 100-km buffer to capture hurricanes of Categories 4 and 5. For each hurricane-impacted site, the number and intensity of each storm on record intersecting each buffer zone were recorded, as well as the minimum distance (kilometer) from the storm. A further 33 sites that were not identified in the GIS analysis were included in the impacted category owing to field observations of hurricane effects from distant but intense storms.

Meta-analyses

Meta-analysis is a set of quantitative methods designed to synthesize the results of disparate studies (Hedges and Olkins 1985). It provides greater statistical power than traditional vote-counting summaries (Gurevitch and Hedges 1999), and allows the calculation of an overall, quantitative estimate (i.e., the effect size) of the magnitude of the effect under study. In addition, it allows consideration of the consistency of effect sizes across studies, as well as an evaluation of the importance of potential explanatory variables (Cooper and Hedges 1994). The limited spatial and temporal extent of many coral monitoring programs, which has drawn much recent criticism (e.g., Connell 1997, Murdoch and Aronson 1999), can therefore be partly overcome using meta-analysis.

We quantified two separate effect sizes to investigate the temporal pattern of change in coral cover at sites impacted by hurricanes during their period of study: (1) relative change in coral cover, i.e., the change in coral percent cover between any given year and the year of impact, relative to cover at the time of impact, and (2) year-on-year rate of change in coral cover, i.e., the change in coral percent cover between any two consecutive years, relative to the first year’s cover. Each effect size was calculated for each site and then averaged for each of 6–8 years prior to and after a hurricane impact. We estimated coral cover at the time of impact (i.e., Year 0) from measurements taken within one year before the hurricane, and coral cover one year post-impact (i.e., Year 1) from measurements taken up to 12 months after a hurricane.

We compared the overall rates of coral cover change between impacted and nonimpacted sites, and between decades, for the year immediately post-impact and for all subsequent years. For the former, we used year-on-year rate of change in coral cover, as defined previously, with the rate of change in coral cover at nonimpacted sites being derived from all pairs of consecutive years without impact (first averaged within site). For the latter, we used a third effect size, namely, the relative annual rate of change in coral percent cover C_R, which was calculated as:

$$C_R = 100[(PC_A - PC_B)/PC_B]/d$$

where PC_A and PC_B are the coral percent cover at the end and start of a time series, respectively, and d is the duration of the time series in years (see Gardner et al. 2003). For impacted sites, the time series was divided into pre- and post-impact years, and separate C_R were calculated for each time period as above. Thus, for

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[5] ⟨http://hurricane.csc.noaa.gov/hurricanes⟩

these sites, the years prior to impact contributed to the nonimpacted sites category, while post-impact years, omitting the year immediately following impact, contributed to the impacted sites category. The overall annual rate of change in coral percent cover obtained for nonimpacted sites was used to generate a ''null model'' against which we gauged temporal changes in coral cover at impacted sites.

In these comparisons, sites were allocated to a particular decade on the basis of either the year of the hurricane (impacted sites) or the year in which the study began (nonimpacted sites). Differences in coral cover change between groups (e.g., impacted vs. nonimpacted, 1980s vs. 1990s) were assessed using the statistic Q_B (Hedges and Olkins 1985), the significance of which was tested against a distribution generated from 5000 iterations of a randomization test (Adams et al. 1997, Rosenberg et al. 2000).

Although conventional meta-analyses usually account for within-study sampling error through weighting means by the inverse of the sample variance (Hedges and Olkins 1985), we avoided this procedure because monitoring data, by definition, provide repeated measurements of the same replicates. There is currently no method within meta-analysis to account for such dependence over time (Gurevitch and Hedges 1999), and hence no reliable measure of pooled variance for the effect size can be generated in such situations (see Gurevitch and Hedges 1999, Hedges et al. 1999).

Confidence intervals around mean effect sizes were generated by bootstrapping (Rosenberg et al. 2000), corrected for bias in unequal distribution around the original value. Mean effect sizes are considered significant when the confidence intervals do not include zero. All meta-analyses were conducted using the software MetaWin (V.2; Rosenberg et al. 2000).

Testing for nonindependence among studies

The problem of nonindependence of data both within and between studies in meta-analysis is well recognized (Gurevitch and Hedges 1999). As mentioned, within-study dependence cannot be accounted for statistically when analyzing repeated-measures data. However, we quantified the potential bias derived from using multiple sites from the same study by calculating the overall relative annual rate of change in coral cover using only one site drawn at random from each study (averaged over five repeats). In addition, we repeated the analysis omitting the largest study, the Florida Keys Coral Reef Monitoring Program (Porter et al. 2002), which contributed 43 separate sites. We also tested for bias introduced by differences in the coral cover survey method employed (video transects, photoquadrats, line-intercept transects, and chain transects) using the Q_B test.

When considering only one randomly chosen site from each study, the relative annual rate of change in coral cover was −4.2 (95% CI = −7.0 to −1.3), which is not significantly different from that obtained across all sites (−5.46, 95% CI = −7.7 to −3.0; Gardner et al. 2003). The removal of the Florida Keys Coral Reef Monitoring Project also had little effect on the overall result (overall mean = −6.3, 95% CI = −8.8 to −3.6). Finally, sites surveyed using different methods did not differ in their respective annual rate of change in percent cover ($Q_B = 5.84$, df = 3, $P = 0.17$). The problem of nonindependence of data and biases owing to different survey methods therefore appear to be negligible.

Correlates of variability in rate of immediate post-impact coral loss

To examine more closely intersite variation in immediate response to hurricanes, we investigated potential correlates of the year-on-year rate of change in coral cover measured within one year of a hurricane impact. The potential correlates included the following continuous variables: (1) reef depth (meter), (2) initial coral percent cover measured within one year prior to the hurricane impact, (3) year of the study's midpoint, (4) minimum distance between the hurricane and the study site (kilometer), (5) maximum intensity of the hurricane (knots [knots × 0.514 = m/s]), (6) average intensity of hurricanes impacting each site since 1851, (7) time since last hurricane impact (years), and (8) average return time between hurricanes for each site since 1851.

In addition, we compared year-on-year rate of change in coral cover measured within one year of a hurricane impact among four subregions: Florida, U.S. Virgin Islands and Puerto Rico, Jamaica, and northern Central America. We also compared immediate rates of change in coral cover between sites that had been impacted in the 10 years prior to the impact under consideration (as defined by GIS analysis) and sites that had not.

The relationships between immediate rate of change in coral cover and continuous variables were analyzed using simple regressions in which the significance of the slope was tested with a randomization test, making it analogous to the significance level for Q_B (Rosenberg et al. 2000). Differences in immediate rate of change among sub-regions and categories of hurricane history were estimated using the Q_B statistic as described previously.

Temporal trends in absolute coral cover

Finally, we calculated the average absolute percent cover separately for impacted and nonimpacted sites, for each year between 1980 and 2001 (analogous to Fig. 2 in Gardner et al. 2003). As described previously, for sites that were hit by hurricanes during their period of study, the years prior to impact contributed to the nonimpacted trend, while post-impact years contributed to the impacted trend. We acknowledge that our definition of ''impacted'' and ''nonimpacted'' sites is a simplification because many nonimpacted sites may

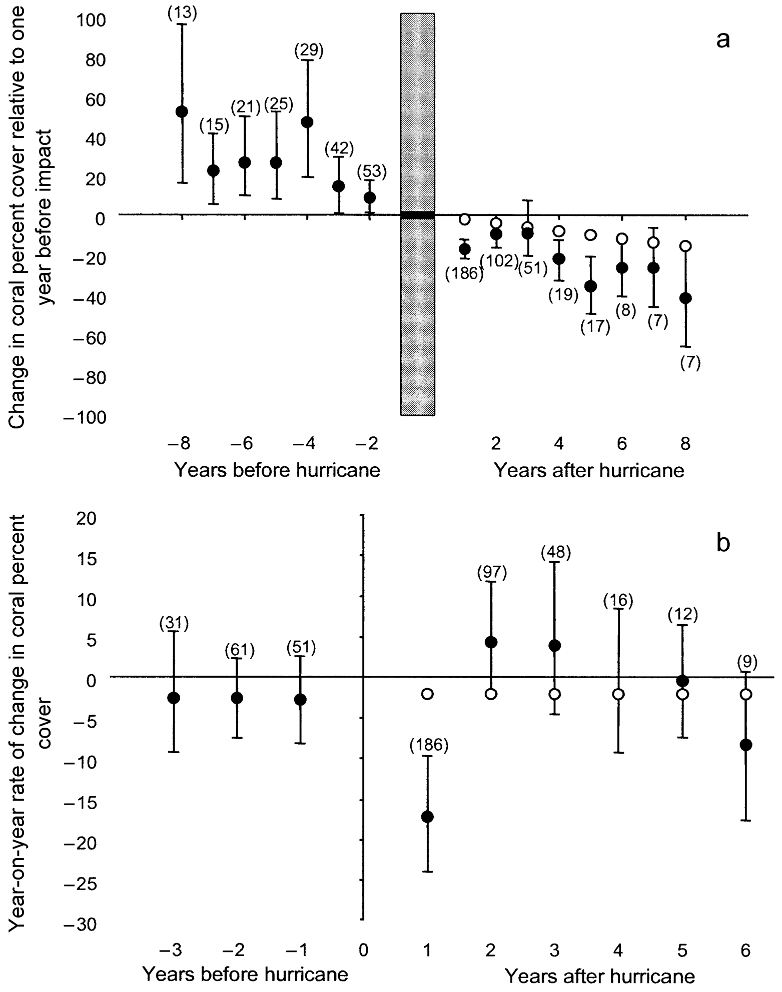

FIG. 2. (a) The change in coral percent cover relative to cover one year before hurricane impacts, and (b) year-on-year rate of change in coral percent cover, for years before and after a hurricane impact. Means (solid circles) are presented with bootstrapped 95% confidence intervals. Open circles represent the expected change in coral cover given the rate of change observed at nonimpacted sites (−2.1% per annum). The gray bar in panel (a) represents the time period over which coral cover at the time of hurricane impact was estimated. Sample sizes are given in parentheses.

have been hit by hurricanes at some point prior to the first survey. To minimize the effect of very recent hurricane impacts, no site hit within two years of the initial survey was categorized as nonimpacted.

RESULTS

Our search yielded 67 separate studies representing a total of 286 monitoring sites from across the wider Caribbean basin (see Gardner et al. 2003, Supplementary Online Material for full details of each individual site). Of this total, 177 sites from 49 studies had experienced hurricane impacts during their period of survey. These sites suffered a total of 255 separate impacts derived from 20 different hurricanes. The remaining 109 sites (18 studies) were not affected by a hurricane during their survey period.

Hurricane impacts were nonrandomly distributed in space and time. The frequency of hurricanes was higher in the north and east of the region than in the south and west, with average return times of hurricanes being approximately twice as long in northern Central America (17.5 years) as in Florida (9.4 years). Two of the 20 hurricanes included in the data set occurred in the 1970s, six in the 1980s, and 12 in the 1990s.

Immediate and subsequent effects of hurricanes on coral cover

Coral percent cover, expressed relative to the year before impact, is shown in Fig. 2a for eight years pre- and post-hurricane impact. There was no significant difference in relative coral cover between any consecutive pairs of years for the years before ($Q_B < 1.9$, $P > 0.19$ in all cases) or after impact ($Q_B < 13.6$, $P > 0.11$ in all cases), except in the year immediately after impact ($Q_B = 42.6$, df = 371, $P < 0.001$). On average, relative coral cover measured within one year of impact

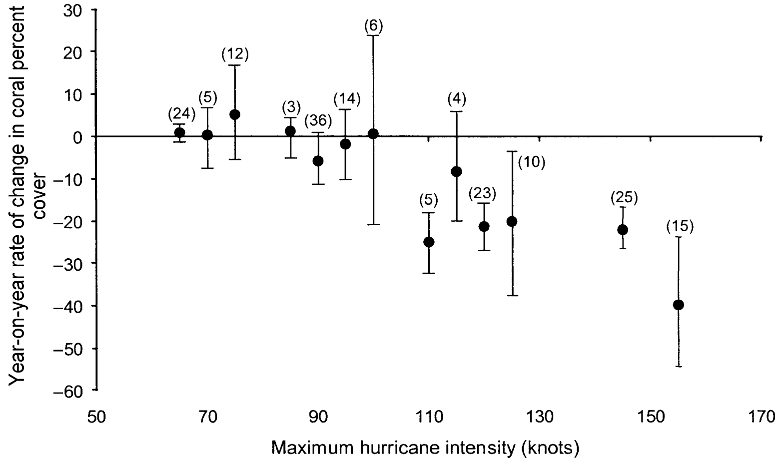

FIG. 3. Relationship between the year-on-year rate of change in coral percent cover, measured one year post-impact relative to just before impact, and maximum hurricane intensity (knots × 0.514 = m/s). Means are presented with bootstrapped 95% confidence intervals. Sample sizes are shown in parentheses.

was 17% lower than one year before impact (95% CI = −27.8 to −13.5; Fig. 2a). This decrease in coral cover was significantly higher than expected given the regional background rate of coral decline of Caribbean reefs (i.e., 2.1% per annum for nonimpacted sites, see below; Fig. 2a). In the second and third years following hurricane impact, coral loss abated before the decline resumed. From year 4 onward, there was some indication that the rate of decline increased beyond the null model of 2.1% per annum at some sites (Fig. 2a).

A similar pattern of immediate coral loss with little evidence of subsequent recovery emerged from the analysis of annual rate of change in coral cover, calculated between consecutive years rather than relative to one year pre-impact (Fig. 2b). The year-on-year changes in coral cover during years 3–6 post-hurricane were not significantly different from those expected given the background rate of decline for nonimpacted sites (i.e., all confidence intervals overlap −2.1%). However, this was not the case for year 2 post-impact. In the second year following a hurricane, the near-zero rate of change in coral cover tended to be lower than the loss due to background decline ($Q_B = 2.95$, df = 193, $P = 0.075$; Fig. 2b). Thus, in the year immediately following the large initial loss of coral cover, coral decline appears to be temporarily halted at many sites, but there is evidence for resumption, or perhaps an accelerating decline in subsequent years.

Correlates of inter-reef variation in immediate coral loss

There was considerable variation among sites in change in coral cover one year after impact (Fig. 2b). Hurricane intensity and frequency accounted for some of this variation. Immediate loss in coral cover increased significantly with maximum hurricane intensity (Fig. 3, Table 1). Immediate coral cover loss was also greater for reefs in areas with longer historical return times of hurricanes and when longer periods had elapsed since the last hurricane (Table 1). The immediate rate of coral cover loss, for example, was more than three times greater for sites unaffected by a hurricane in the decade preceding the start of the study than for sites impacted during that period (with impact,

TABLE 1. Potential correlates of immediate change in coral cover following a hurricane impact, measured one year post-impact relative to just before impact.

	Relationship with immediate change in coral cover	
Explanatory variable	*P*	Direction of slope
Reef depth (m)	0.86	
Percent cover of coral before hurricane	0.99	
Year of study midpoint	<0.001	positive
Minimum distance from hurricane (km)	0.54	
Maximum intensity of hurricane (knots)	<0.001	negative
Average intensity of hurricanes since 1851 (knots)	0.63	
Time since last hurricane (years)	0.004	negative
Average return time between hurricanes (years)	<0.001	negative

Notes: Because changes in coral cover are mostly negative, positive relationships represent a decreasing rate of loss in coral cover. $N = 186$, except for depth ($N = 168$), time since last hurricane ($N = 180$), and average return time ($N = 180$). P values were generated from randomization tests.

$\bar{C}_{\rm R} = -9.7$, 95% CI = −16.4 to −2.5, $n = 108$; without impact, $\bar{C}_{\rm R} = -27.8$, 95% CI = −34.7 to −20.4, $n = 78$; $Q_{\rm B} = 12.5$, $P < 0.001$).

Sites studied more recently showed lower rates of immediate loss than those monitored longer ago (Table 1). In addition, there were geographic differences in immediate post-hurricane coral cover loss ($Q_{\rm B} = 14.8$, df = 185, $P < 0.01$), with the highest rate of loss recorded in Jamaica ($\bar{C}_{\rm R} = -32.5$, CI = −47.7 to −21.4, $n = 8$) and northern Central America ($\bar{C}_{\rm R} = -32.2$, CI = −44.4 to −16.8, $n = 38$), and the lowest in Florida ($\bar{C}_{\rm R} = -8.6$, CI = −16.2 to −1.3, $n = 64$) and the U.S. Virgin Islands and Puerto Rico ($\bar{C}_{\rm R} = -17.0$, CI = −25.2 to −8.4, $n = 70$). These subregional rates of immediate loss were also significantly related to the sub-regional variation in return times of hurricanes ($r = -0.99$ $n = 4$, $P < 0.01$). Reef depth, minimum distance to hurricane, local average intensity of hurricanes since 1851, and pre-hurricane coral cover were not related to immediate change in coral cover (Table 1).

Contribution of hurricanes to long-term regional change in coral cover

Overall, coral cover at sites that were hit by a hurricane during their period of study declined at a significantly faster annual rate than sites that were not hit (impacted, −6.7%, 95% CI = −12.2 to −1.2, $n = 64$; nonimpacted: −2.1%, CI = −3.7 to −0.02, $n = 152$; $Q_{\rm B} = 3.94$, df = 215, $P = 0.04$). This difference is mainly due to the significant effect of hurricanes on rate of coral cover loss immediately after impact. When the first year post-impact is omitted, the rate of coral cover loss is significantly higher at nonimpacted sites (impacted, 4.2%, 95% CI = −0.7 to 10.5, $n = 44$; nonimpacted, −2.1%, CI = −3.7 to −0.2, $n = 152$; $Q_{\rm B} = 7.23$, df = 195, $P = 0.009$). Although the rate of change at impacted sites is positive, it is not significantly different from zero, which is consistent with the overall lack of recovery documented earlier (Fig. 2a, b).

Interestingly, the rate of immediate coral decline (i.e., year 1 post-hurricane) was significantly faster than the yearly rate of decline at nonimpacted sites in the 1980s ($Q_{\rm B} = 25.70$, df = 96, $P < 0.001$; Fig. 4a) but not in the 1990s ($Q_{\rm B} = 1.06$, df = 227, $P = 0.30$; Fig. 4a). By contrast, the longer-term rates of decline (i.e., rate excluding year 1 post-hurricane) of impacted and nonimpacted sites were not significantly different in the 1980s ($Q_{\rm B} = 0.37$, df = 66, $P = 0.61$; Fig. 4b), but did differ in the 1990s ($Q_{\rm B} = 10.26$, df = 138, $P = 0.003$; Fig. 4b). In the 1990s, coral cover at nonimpacted sites declined faster than at impacted sites (Fig. 4b). Although the mean change in coral cover at impacted sites in the 1990s was, as in the 1980s, not significantly different from zero, the data do suggest that there may be some recovery at some sites. Note that the intensity of hurricanes did not differ between the 1980s and the 1990s ($t_{18} = 0.95$, $P = 0.36$).

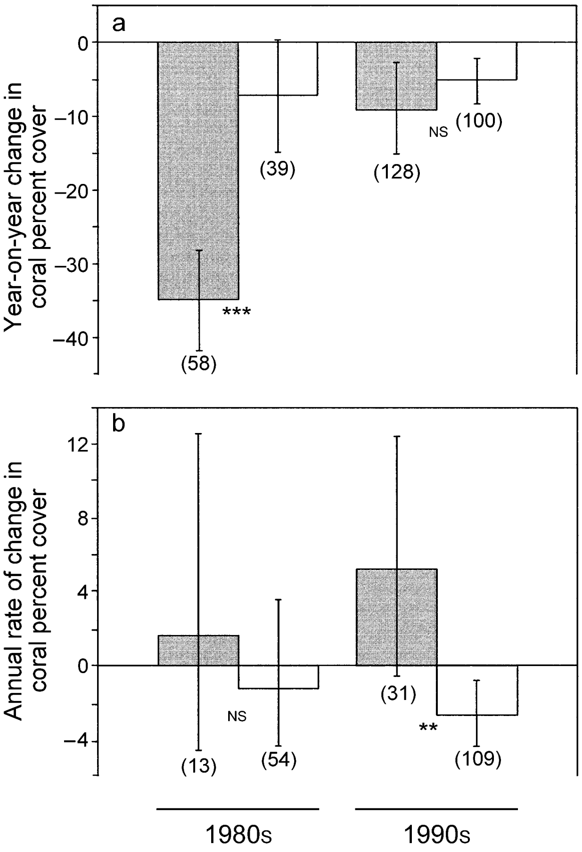

FIG. 4. (a) The year-on-year rate of change in coral percent cover at impacted sites (gray bars, measured one year post-impact relative to just before impact) and nonimpacted sites (open bars, measured between pairs of consecutive years at nonimpacted sites). (b) The annual rate of change in coral percent cover $C_{\rm R}$ at sites impacted (gray bars) and not impacted (open bars) by hurricanes, in the 1980s and 1990s. $C_{\rm R}$ for impacted sites excludes the year immediately post-impact. Means are presented with bootstrapped 95% confidence intervals. Sample sizes are given in parentheses.

** $P < 0.01$; *** $P < 0.001$; NS, not significant.

Absolute coral cover declined at both impacted and nonimpacted sites between 1980 and 2001 (Fig. 5). Coral cover was similar at impacted and nonimpacted sites in 16 of the 20 years of the time series ($Q_{\rm B} < 1.70$, $P > 0.19$ in all cases). Only in 1990 and 1993 was absolute coral cover significantly higher on nonimpacted sites (1990, $Q_{\rm B} = 6.26$, $P = 0.01$; 1993, $Q_{\rm B} = 6.25$, $P = 0.02$), while the reverse was observed in 1999 ($Q_{\rm B} = 4.30$, $P = 0.04$) and 2000 ($Q_{\rm B} = 5.80$, $P = 0.02$). These differences were not significant when Bonferroni corrected for multiple comparisons.

DISCUSSION

Hurricanes have significant immediate impacts on coral reefs. Our meta-analysis shows that across the Caribbean, coral cover is reduced by ∼17% up to one

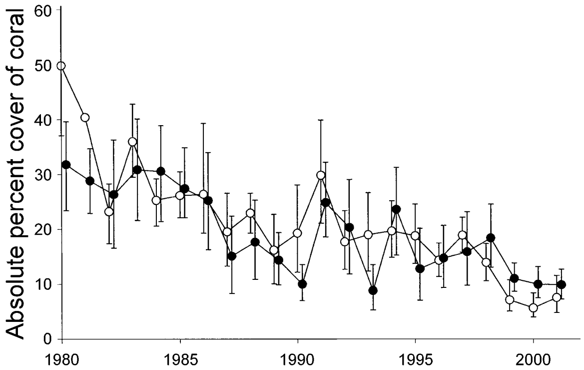

FIG. 5. Coral percent cover at impacted (solid circles) and nonimpacted (open circles) sites across the Caribbean Basin from 1980 to 2001. Means (with 95% bootstrapped confidence intervals) for each year are shown slightly staggered for clarity. $N = 1$ for 1980 and 1981.

year after a hurricane impact. In the year following this immediate loss, no further loss is discernible on many sites, but the decline in coral cover then resumes on impacted sites at a rate similar to, or perhaps slightly higher than, the regional background rate of decline (Gardner et al. 2003). There is no evidence of recovery to a pre-storm state eight years after a hurricane.

Overall, coral cover at sites impacted by a hurricane has declined at a significantly faster rate than at nonimpacted sites, due mainly to the high rates of loss experienced in the year immediately following impact in the 1980s. Notwithstanding immediate coral losses, the longer-term rates of decline of impacted and nonimpacted sites were similar in the 1980s, but impacted sites declined more slowly than nonimpacted sites in the 1990s. The significant decline in coral cover at sites unaffected by hurricanes over the past decade suggests that other stressors are now driving the overall pattern of change in coral cover in this region.

Correlates of inter-reef variability in immediate impacts of hurricanes

There was great variability among reefs in the immediate rate of loss of coral cover. Such variability has previously been ascribed to differences in physical characteristics of both the reefs and hurricanes, the biotic composition of the reef prior to the storm, as well as the current and historical environmental contexts (Stoddart 1985, Rogers 1992, Harmelin-Vivien 1994). In this study, we found that hurricane intensity and frequency, year of study, and geographical location influenced the magnitude of coral cover loss.

As expected, more intense hurricanes caused greater coral cover losses (see also Connell et al. 1997 for the Great Barrier Reef). However, neither reef depth nor minimum distance from the hurricane were associated with immediate change in coral cover, despite the intuitive expectation that shallow reefs and those closer to the center of hurricanes should suffer greater damage. In fact, significant effects on deeper reefs are not uncommon (Hughes 1989, Aronson et al. 1993), and the importance of distance from hurricane may be masked by the effect of intensity.

Sites studied more recently showed lower rates of immediate loss than those monitored longer ago. This result is consistent with the long-term pattern of decline of Caribbean corals, which shows a decreased rate of loss in the 1990s compared with the 1980s in hurricane-prone areas (Gardner et al. 2003).

Finally, our study highlights the importance of past hurricane regime in determining the immediate response of reefs to hurricane impacts (Woodley 1989, Hughes and Connell 1999). Immediate loss in coral cover increased with both the long-term average return time of hurricanes at a site and the time elapsed since the last hurricane. These results were further supported by the finding that coral cover at sites impacted within a decade of the onset of study declined less than sites not impacted in that time (see also Connell et al. 1997). Moreover, geographical variation in immediate coral cover loss, with Jamaica and northern Central America showing rates 2–4 times higher than Florida and the U.S. Virgin Islands/Puerto Rico, appears to be directly related to hurricane return times in these areas. However, this relationship between hurricane return times and coral decline may in part result from the reduced rates of coral loss in the 1990s (which may be due to the low absolute amounts of coral at this time), as hurricanes were twice as frequent during this period than they were during the 1980s.

Hurricanes may reduce the impact of subsequent storms through three possible mechanisms. First, damage to human infrastructure may reduce the number of fishermen or the number of tourists in years following a hurricane, with concomitant reductions in reef stress (Bacon 1989). Second, hurricanes may decrease the susceptibility of corals to other stressors, for example by reducing the effects of coral bleaching through short-term reductions in local sea temperatures (Kramer and Kramer 2000), thus making corals more resistant to further storm impacts. However, these mechanisms will generally act over shorter timescales than the fastest hurricane return times. It is more likely that hurricanes reduce the abundance of susceptible coral colonies, e.g., branching and tabular colonies, which can dominate reefs that rarely experience storms (e.g., Woodley et al. 1981), thus providing less scope for subsequent hurricanes to cause further damage (Woodley 1989, Liddell and Oldhorst 1992).

Longer-term post-impact changes in coral cover

We found no evidence of coral cover recovery for up to eight years post-hurricane (Fig. 2). This finding supports a global review that highlighted the Caribbean as lacking examples of reef recovery following disturbance (Connell 1997). Although eight years is a relatively short time period, it is roughly equivalent to the average return time of hurricanes in the most hurricane-prone parts of the Caribbean (e.g., 9.4 years in Florida and 12 years in the U.S. Virgin Islands and Puerto Rico between 1851 and 2001). Coral reefs in the northeastern Caribbean have probably developed under a regime of frequent hurricane impacts, and paleoecological records suggest that Caribbean reefs in general have exhibited stable persistence over thousands of years (e.g., Aronson and Precht 2001). It is therefore reasonable to expect that in the absence of other stressors, recovery should be measurable for many sites within a decade.

Instead, the pattern of change in coral cover after a hurricane is most consistent with a combination of the stasis and either the resumption or synergy trajectories presented earlier (Fig. 1). A comparison of Figs. 1b and 2b suggests that in the year following the large initial loss of coral cover, impacted reefs are temporarily buffered against further losses in coral cover. This period of stasis may be realized through the attachment and growth of broken coral fragments (e.g., Fong and Lirman 1995) and/or because very susceptible species were removed by the hurricane (e.g., Woodley et al. 1981). However, the effect is short-lived. From year 3 post-hurricane onward, coral cover on impacted reefs resumes its decline.

It is unclear whether this subsequent decline is at a rate that is similar to (i.e., resumption trajectory) or faster than (i.e., synergy trajectory) the rate of decline for nonimpacted reefs. The year-by-year analyses of change in coral cover following hurricane impact (Fig. 2a, b) suggest that the post-impact rate of decline in any given year was comparable to that of nonimpacted sites, although trends for increasing rates of decline from year 3 onward are suggested in both cases. The higher overall rate of coral cover loss on sites impacted by hurricanes during their period of study (6.7% vs. 2.1% per annum for nonimpacted sites) might be suggestive of a synergistic interaction, but this higher rate of decline is due to the highly significant immediate impact of hurricanes on coral cover change in the 1980s. There is therefore no evidence for longer-term synergistic effects or for such effects occurring at all in the 1990s. The recent post-hurricane trajectory of Caribbean coral reefs has therefore been characterized mainly by resumption to the background rate of coral decline, rather than recovery or synergy.

Contribution of hurricanes to regional coral decline

Have hurricanes caused the large-scale decline in coral cover evident throughout the wider Caribbean since the mid-1970s? The short answer is no. Our results suggest that hurricanes did contribute significantly to reducing coral cover on many Caribbean reefs in the 1980s. During this decade, coral cover at nonimpacted sites declined, owing mainly to the mass mortality of *Diadema antillarum* (Lessios et al. 1984) and the onset of white band disease in coral (Gladfelter 1982), but impacted sites lost coral cover significantly more quickly. The fact that reefs impacted in the 1980s exhibited such a strong and significant loss in coral cover in the year following impact suggests that interactions with other disturbances may have occurred to magnify the effects of hurricanes (e.g., Knowlton et al. 1981, 1990). Whether these interactions are simply additive or truly synergistic (i.e., multiplicative) cannot be determined with our analyses. However, it is clear that hurricanes in the 1980s set many Caribbean reefs on a lower, though parallel trajectory of decline than that of nonimpacted reefs. This effect is not clearly seen in Fig. 5 because of intersite variability in initial coral cover, timing of impact, and extent of immediate decline following impact.

By contrast, in the 1990s, hurricanes have played only a minor role in coral decline. Coral loss immediately post-impact was still significant in the 1990s, although less marked than in the 1980s, and no greater than the decline observed at nonimpacted sites. These results are consistent with three explanations which are not mutually exclusive. First, many of the coral species susceptible to hurricanes (e.g., *Acropora* spp.) virtually disappeared from the Caribbean through the 1980s, as a result of disease (Gladfelter 1982, Precht et al. 2002), thus reducing the potential for hurricanes to cause comparable damage in the 1990s. Second, the frequency of hurricanes increased in the 1990s, and the severity of immediate impacts decreases with shorter hurricane return times (Woodley 1992, Connell et al. 1997; see *Results*). Finally, non-hurricane-related causes of coral decline on Caribbean reefs may have changed, either in nature or impact, between decades. While some disturbances such as fishing have taken place for centuries on Caribbean reefs (Jackson et al. 2001), others such as loss of mangroves, which increases sedimentation, have intensified recently (FAO 2003). The importance of hurricanes as a source of disturbance affecting Caribbean corals has therefore diminished in recent years relative to other stressors.

CONCLUSIONS

In conclusion, hurricanes have severe immediate impacts on reefs, and they may have contributed, at least in the 1980s, to some of the decline in coral cover observed throughout the Caribbean (Gardner et al. 2003). The high rate of coral decline on hurricane-affected sites immediately following the initial impact in the 1980s is perhaps suggestive of synergy between hurricanes and other stressors during that decade. However, there is little evidence of synergy acting in the longer term between hurricanes and other disturbances.

Despite the fact that hurricanes now play a relatively smaller role in determining coral cover than they did in the 1980s, they can still have significant localized, immediate impacts (Fig. 4a). These impacts will be less marked during natural cycles of increased hurricane activity, such as those which have been noted recently in the western Atlantic (Goldenberg et al. 2001). However, predicted increases in hurricane intensity, driven by climate change (IPCC 2001), could negate the dampening effect of closely spaced impacts because coral loss is positively related to hurricane intensity (Fig. 3).

Finally, we found no evidence of coral recovery following hurricane impact within a period roughly equivalent to the natural return time of hurricanes in the hurricane-prone part of the region. Although local variability in the speed and extent of recovery should be expected, owing to site differences in initial coral mortality and subsequent rates of larval recruitment (Hughes and Connell 1999), our results point to a general impairment of the regeneration potential of Caribbean coral reefs. Lack of recovery is commonly associated with chronic, usually anthropogenic, impacts (Connell 1997), and in the Caribbean, fishing, sedimentation, and eutrophication are likely causes.

Such persistent multiple disturbances have been implicated in the profound ecological transition, from coral- to algal-dominated states, observed on many Caribbean reefs (McClanahan et al. 2002). If this condition represents an alternative stable state for coral reef communities (Knowlton 1992), the removal of stressors could fail to return Caribbean coral reefs to a coral-dominated state. While nothing can be done to control hurricane disturbance, there is fortunately some evidence that increases in grazing pressure, through the recovery of *Diadema antillarum* populations (Edmunds and Carpenter 2001, Miller et al. 2003), are leading to reductions in macroalgal cover and increases in coral abundance. Removing the key recent stressors may therefore yet allow Caribbean coral reefs to recover.

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