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17. Materials and methods are available as supporting material on *Science* Online.
18. The seven cultural periods with their ranges of ages for the 14 regions studied are as follows: prehuman [40,000 years before the present (yr B.P.) to 1609 A.D.], hunter-gatherer (20,000 yr B.P. to 1824 A.D.), agricultural (3500 yr B.P. to 1800 A.D.), colonial occupation (1500 to 1800 A.D.), colonial development (1800 to 1900 A.D.), early modern (1900 to 1950 A.D.), and late modern (1950 to present). Not all cultural periods existed for all sites. For example, Bermuda was unpopulated until 1609, when colonial occupation began, and there was no agricultural stage in Australia before Western colonization.
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Supporting Online Material
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Materials and Methods
Tables S1 to S3

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Long-Term Region-Wide Declines in Caribbean Corals

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We report a massive region-wide decline of corals across the entire Caribbean basin, with the average hard coral cover on reefs being reduced by 80%, from about 50% to 10% cover, in three decades. Our meta-analysis shows that patterns of change in coral cover are variable across time periods but largely consistent across subregions, suggesting that local causes have operated with some degree of synchrony on a region-wide scale. Although the rate of coral loss has slowed in the past decade compared to the 1980s, significant declines are persisting. The ability of Caribbean coral reefs to cope with future local and global environmental change may be irretrievably compromised.

It is becoming increasingly acknowledged that coral reefs are globally threatened (*1, 2*). Recent assessments suggest that 11% of the historical extent of coral reefs is already lost, while a further 16% is severely damaged (*3*). For the Caribbean basin, a wealth of quantitative, small-scale studies now exist that describe changes such as reduced coral cover, reduced physical and biological diversity, and increases in the spatial and temporal extent of macroalgae [e.g., (*4, 5*)] on individual reefs. These have contributed to qualitative summaries of regional and subregional scope (*3, 6*), which suggest a general pattern of decline and degradation. However, the extent and spatiotemporal variability of these changes have not been quantified on a Caribbean-wide scale. Here, we assess the extent of decline in coral cover across the Caribbean through the integration of existing data sets in a meta-analysis framework (*7*).

Data describing change in percent hard coral cover over time for monitored reef sites within the wider Caribbean basin were obtained from a range of sources (*8*). A total of 263 sites from 65 separate studies (table S1) across the Caribbean were included in the overall meta-analysis (Fig. 1).

Using the software Meta-Win (*9*), we carried out meta-analyses on the total data set to quantify two separate effect sizes: (i) overall absolute change in percent coral cover (C_A) as summarized across the duration of all studies, irrespective of year or length of study; and (ii) overall annual rate of change in percent coral cover (C_R) between surveys carried out at different points in time (calculated relative to the initial percent coral cover) (*8*). The latter has the advantage of partially accounting for differences in study duration and initial coral cover; however, it assumes a constant rate of decline between years. To allow for the possibility of nonlinear declines, we also calculated year-on-year rates of change in coral cover [$\Delta N = \log(N + 1)_{t+1} - \log(N + 1)_t$, where N is percent coral cover and t is year of study] for all studies with data from successive years (*8*). Finally, we calculated weighted (*8*) and unweighted mean absolute percent coral cover across all sites for each year between 1977 and 2001. We examined spatial and temporal variability in C_A and C_R by splitting the data set into subregions and time periods (*8*). Throughout, confidence intervals were generated by bootstrapping (*9*), corrected

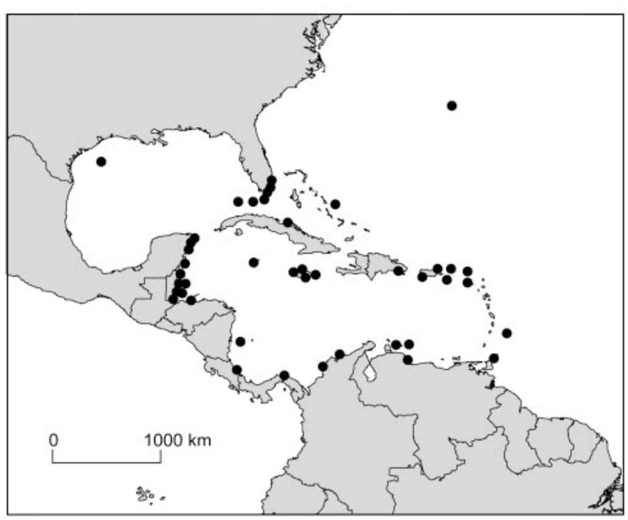

Fig. 1. Regional distribution of study sites in the wider Caribbean basin. The separate study sites from which monitoring data were sourced are shown as circles.

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for bias for unequal distribution around the original value. Mean effect sizes are considered significant when the confidence intervals do not include zero.

Our analysis shows a clear and striking decline in absolute coral cover, with the majority of study sites reporting a decrease over their respective periods of observation ($\bar{C}_A$ = –7.79, 95% CI = –11.6 to –4.34). When considering only the endpoints of the time series, the analysis describes a fall from ~50% in the 1970s to ~10% at present (Fig. 2A). The overall mean annual rate of change in percent coral cover was also negative and significantly different from zero ($\bar{C}_R$ = –5.46, 95% CI = –7.7 to –3.0). In addition, the majority of individual year-on-year changes were negative and significantly different from zero (Fig. 2B). Potential nonindependence of data generated by the inclusion of multiple sites from each study, as well as inclusion of studies of varying duration and survey method, contributed little overall bias (*8*).

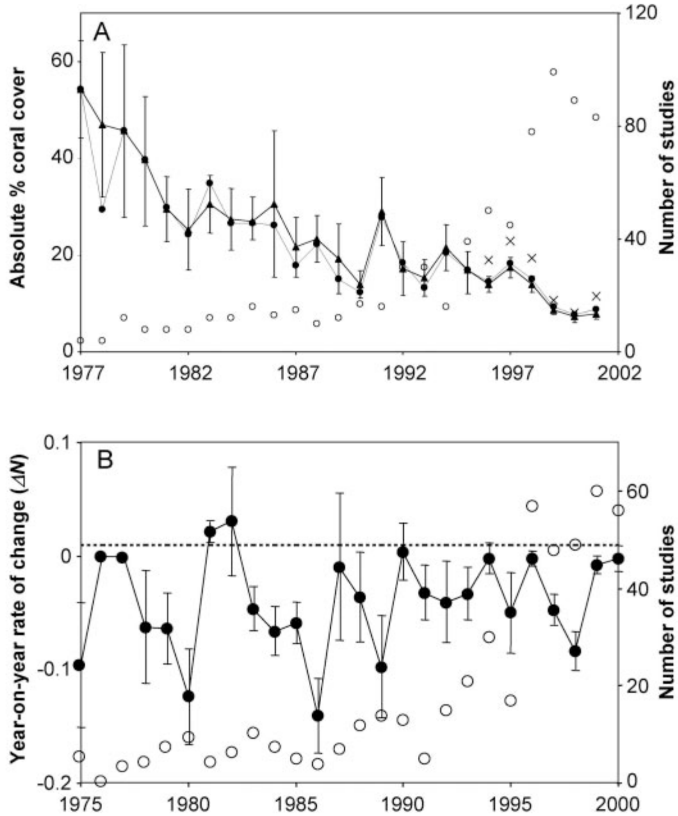

Fig. 2. Total observed change in percent coral cover across the Caribbean basin during the past three decades. (**A**) Absolute percent coral cover from 1977 to 2001. Annual coral cover estimates (▲) are weighted means with 95% bootstrap confidence intervals. Also shown are unweighted mean coral cover estimates for each year (●), the unweighted mean coral cover with the Florida Keys Coral Monitoring Project (1996–2001) omitted (×), and the sample size (number of studies) for each year (○). (**B**) Year-on-year rate of change [mean $\Delta N \pm$ SE (*8*)] in percent coral cover across all sites reporting data for at least two consecutive years between 1975 and 2000 (●), and the sample size (number of studies) for each period (t, t + 1) (○).

The use of weighted or unweighted yearly mean cover produced almost identical patterns of decline (Fig. 2A). In addition, the largest study (Florida Keys) was established in the mid-1990s, when most Florida Keys reefs were already highly degraded, and could therefore significantly influence the overall pattern of decline. However, exclusion of this study had little effect on the overall magnitude or pattern of change (*8*) (Fig. 2A).

There was no significant spatial variation in overall annual rate of change in percent coral cover (Q_B = 9.66, P > 0.08; Fig. 3A). In terms of absolute loss of percent coral cover, all regions showed significant declines, but there was a significant difference between regions (Fig. 3B, Q_B = 60.5, P < 0.001). The higher loss in coral cover in Jamaica can likely be attributed to the interaction of multiple stressors, notably Hurricane Allen in 1980, the onset of white band disease of *Acropora*, and the subsequent mass mortality of the urchin *Diadema antillarum*, all in the context of historical overfishing (*5, 10*).

The temporal variation in coral decline was highly significant both for rate of change (Q_B = 33.3, P < 0.01; Fig. 3C) and for absolute change in percent coral cover (Q_B = 63.3, P < 0.001; Fig. 3D). All time periods, except that beginning in 1990, exhibited mean rates of change that were significantly negative. Between 1990 and 1994, the mean effect size for rate of change was significantly positive (Fig. 3C). By contrast, only the 1980 and 1985 time intervals showed significant negative changes in absolute coral cover (Fig. 3D).

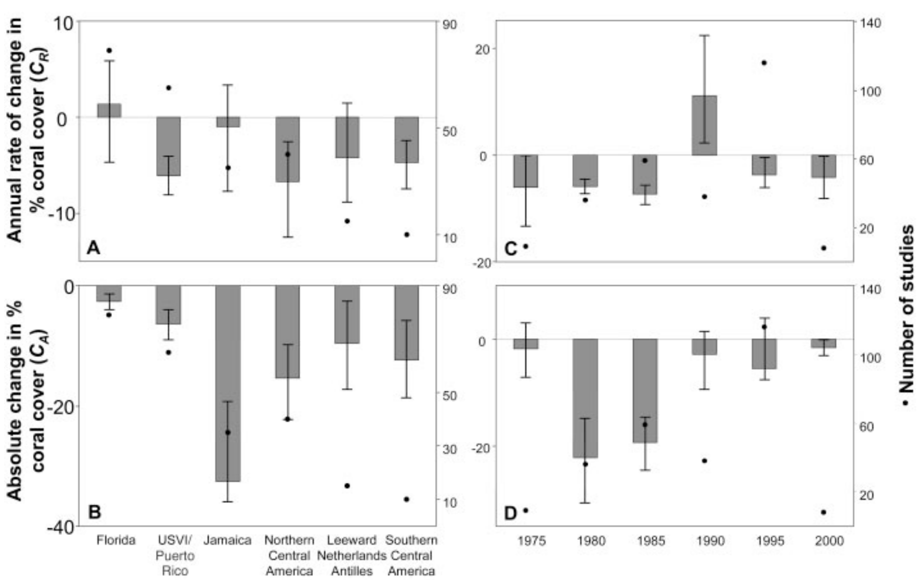

Fig. 3. Coral cover change for subregions of the Caribbean and for 5-year time periods from 1975 to 2000, expressed as annual rate of change in percent coral cover, C_R (**A** and **C**), and as change in absolute percent coral cover, C_A (**B** and **D**). The Leeward Netherlands Antilles includes Venezuela. Temporal averages were taken across all studies whose midpoint fell within each time interval; time periods are indicated by the first year of the interval. For the interval starting in 2000, only 2 years are included. Bootstrap-generated 95% confidence intervals and sample sizes are shown.

The spatiotemporal patterns of decline of Caribbean corals provide insights into the possible causes of this striking change. Part of the rapid decline in the early 1980s (Figs. 2B and 3D) coincided with the mass die-off of *D. antillarum* in 1983 (*11*). The collapse of *Diadema* populations triggered drastic increases in the abundance of the macroalgae on which they graze, resulting in significant declines in coral cover (*12, 13*). Before 1983, increases in macroalgae, and the subsequent

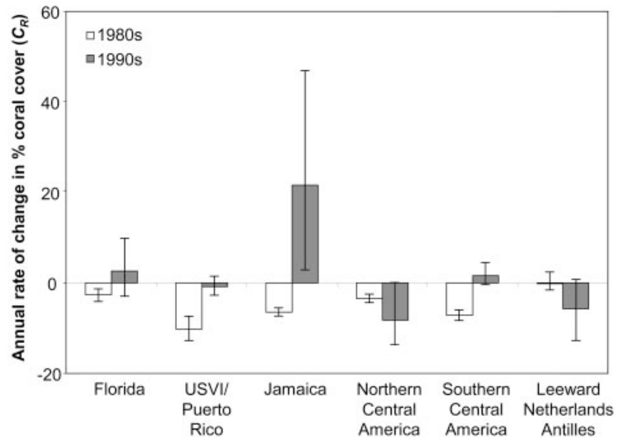

Fig. 4. Subregional variability in mean rate of change in coral cover observed during the decades starting in 1980 (open bars) and 1990 (shaded bars). Geographic regions are as in Fig. 3. Bootstrap-generated 95% confidence intervals are shown. Sample sizes for the 1980s and 1990s, respectively, are as follows: Florida, 4 and 64; U.S. Virgin Islands (USVI)/Puerto Rico, 33 and 26; Jamaica, 29 and 7; northern Central America, 12 and 29; southern Central America, 8 and 3; and Leeward Netherlands Antilles, 4 and 12.

phase shift from coral to algae-dominated states, were facilitated by coral mortality (*14*). Major agents of coral mortality include white band disease of *Acropora* (*15*) as well as hurricanes, whose spatial variability (in both occurrence and impact) may influence regional differences in coral decline (Fig. 3B). Although the majority of absolute loss occurred more than a decade ago (Fig. 3D), there is no clear evidence of abatement in the overall rate of loss during the 1990s (Fig. 3C). At a subregional level, a reduced rate of loss or even a suggestion of recovery is apparent for four of the six geographic regions studied during the 1990s when compared to the 1980s, but there is some evidence that the rate of decline has increased (although there is considerable variation) for both the Leeward Netherlands Antilles/Venezuela and northern Central America during this period (Fig. 4). In the latter case, the Mesoamerican Barrier Reef System was described as being in generally good condition before 1998 (*16*), but the severe degradation after bleaching caused by the 1998 El Niño–Southern Oscillation event and Hurricane Mitch are well documented (*17, 18*).

The recent decreases in rates of loss in coral cover in Florida, the U.S. Virgin Islands, and southern Central America, as well as the apparent recovery in Jamaica, may be cause for guarded optimism. However, our analyses considered only changes in overall coral cover, which may mask changes in coral community composition. Although a number of studies have shown recent increases in coral cover, many have also reported a shift from communities dominated by framework builders such as *Acropora* and *Montastrea* toward those dominated by non–framework builders, such as *Agaricia* and *Porites*, and sponges [e.g., (*19, 20*)]. The long-term consequences of such species shifts are unknown, although some current opinion suggests that they may have detrimental consequences for the ability of coral reefs to keep pace with rising sea levels and temperatures, because many such opportunistic species are highly susceptible to temperature shifts and storm damage (*21*).

Recent paleoecological work suggests that this pattern of decline in many areas of the Caribbean is unprecedented within the past few millennia (*22, 23*). There is no convincing evidence yet that global stressors [e.g., temperature-induced bleaching and reduced rates of carbonation via enhanced levels of atmospheric CO_2 (*24*)] are responsible for the overall pattern of these recent coral declines. More likely, local factors originating both naturally (e.g., disease, storms, temperature stress, predation) and anthropogenically [e.g., overfishing, sedimentation, eutrophication, habitat destruction (*14, 25, 26*)] are occurring at Caribbean-wide scales. Some of these processes have shown at least partial synchrony in the timing of their onset across different sites. Although further collaborative research will help to identify the relative importance of these factors, there is an urgent need to both identify and effectively conserve local areas of high coral cover, which could play an important role as refugia and as a source of larval supply for degraded sites (*27*). Given current predictions of increased human activity in the Caribbean, the growing threat of climate change on coral mortality and reef framework building, and the potential synergy between these threats (*28, 29*), the situation for Caribbean coral reefs does not look likely to improve in either the short or the long term.

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