Catastrophe and the life span of coral reefs

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Abstract. A strong earthquake in the western Caribbean in 2009 had a catastrophic impact on uncemented, unconsolidated coral reefs in the central sector of the shelf lagoon of the Belizean barrier reef. In a set of 21 reef sites that had been observed prior to the earthquake, the benthic assemblages of 10 were eradicated, and one was partially damaged, by avalanching of their slopes. Ecological dynamics that had played out over the previous 23 years, including the mass mortalities of two sequentially dominant coral species and a large increase in the cover of an encrusting sponge, were instantaneously rendered moot in the areas of catastrophic reef-slope failure. Because these prior dynamics also determined the benthic composition and resilience of adjacent sections of reef that remained intact, the history of disturbance prior to the earthquake will strongly influence decadal-scale recovery in the failed areas. Geological analysis of the reef framework yielded a minimum return time of 2000–4000 years for this type of high-amplitude event. Anthropogenic degradation of ecosystems must be viewed against the backdrop of long-period, natural catastrophes, such as the impact of strong earthquakes on uncemented, lagoonal reefs.

Key words: Belize; coral bleaching; coral disease; coral reef; earthquake; paleoecology; resilience; sponges; submarine avalanche; T_{50}.

INTRODUCTION

A variety of physical, biological, and social phenomena exhibit threshold behaviors over a range of scales. Examples include earthquakes, avalanches, forest fires, extinction and cladogenesis, population fluctuations, and stock market crashes (Bak et al. 1989, Bak and Chen 1991, Bak and Sneppen 1993, Malamud et al. 1998, Miller 1998, Scheffer et al. 2009, Haldane and May 2011). Ecologists have begun to appreciate the role of threshold behaviors in general, and extreme, high-amplitude events in particular, in driving the structure and function of communities (O'Neill et al. 1986, Gaines and Denny 1993, Scheffer et al. 2001, Scheffer and Carpenter 2003).

Threshold behaviors at multiple scales, whether extrinsically or intrinsically driven, are a universal component of the dynamics of coral reefs (Done 1999, Aronson et al. 2002*a, b*, Hubbard et al. 2005). The current trend of rapid, anthropogenic degradation of reef ecosystems, therefore, raises questions about the scales at which their persistence, resistance, and resilience should be construed (Hughes et al. 2005, Dudgeon et al. 2010). Irrespective of human interference, however, extreme physical events, such as strong cyclones, lava flows, tsunamis, volcanic ash falls, and cold-water

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events, can remove benthic assemblages on coral reefs, resetting succession and the assembly of reef communities (Woodley et al. 1981, Tomascik et al. 1996, Baird et al. 2005, Pandolfi et al. 2006, Lirman et al. 2011). The impacts of such extreme events are generally saturating at small spatial scales and variable at larger scales. Understanding the interplay of natural catastrophes and anthropogenic perturbations, such as climate change, overfishing, and nutrient loading, is critical to describing the trajectories of coral reefs in a rapidly changing world. Scaling up threshold dynamics from small-scale phase shifts to regional patterns forms the rational basis for designing programs to protect and restore coral reefs (Nyström and Folke 2001, Precht and Aronson 2006).

Studies of the impacts of earthquakes on coral reefs have focused primarily on uplift and subsidence (Colgan 1989, Cortés et al. 1992, Aronson et al. 2004, Albert et al. 2007). Catastrophic slumping of reefs from tectonic activity has received less attention (Shaked et al. 2004, Tibor et al. 2010), and only a few qualitative reports have described in situ damage to corals from earthquakes (Stoddart 1972, van Woesik 1996). In this paper we quantify the catastrophic damage caused by a strong earthquake in 2009 to the uncemented, unconsolidated reefs in the central sector of the shelf lagoon of the Belizean barrier reef. We integrate ecological and geological data to estimate the return time (the expected time between occurrences) of an ecological catastrophe of that magnitude. From the return time, we estimate the natural "T_{50}" of reefs in the central lagoon. By

analogy to the LD_{50} notation of toxicology, we define T_{50} as the expected time to a 50% probability that a given reef assemblage will be eradicated under natural conditions. Finally, we evaluate the role of ecological history in setting the trajectory of recovery.

SCALING CATASTROPHE

In mathematics, catastrophic behavior is synonymous with threshold dynamics and can occur at all scales. For modern coral reefs, which developed during the Holocene over at most the last 10 000–12 000 years, an extreme event is here rated as catastrophic, in the popular sense of being disastrous, if its effects extend at minimum over a reef system and if it has not occurred previously on a semicentennial to millennial time scale (Woodley 1992, Aronson et al. 2002a, 2004, 2005a, Hubbard et al. 2005, Pandolfi et al. 2006). A set of rapidly repeating, high-amplitude events, all of which belong to a particular class of phenomena and occur in a reef system on a scale of years to decades, should be treated as a single, catastrophic perturbation. The reef assemblage is shifted to an earlier successional state by the initial event(s), and subsequent disturbances maintain that state (Colgan 1987, Hubbard 1997, Done 1999, Berumen and Pratchett 2006, van Woesik et al. 2011). In the case of the increasingly frequent recurrence of coral bleaching (Hoegh-Guldberg 1999, Hughes et al. 2003), for example, anthropogenic climate change should be construed as a single, catastrophic perturbation. That perturbation is producing multiple bleaching events, causing repeated bouts of coral mortality, and driving acclimation and adaptation in surviving coral populations (Thompson and van Woesik 2009).

STUDY AREA

The study area (Fig. 1), which encompasses 375 km^2 of the central shelf lagoon in Belize, has been described in detail elsewhere (Aronson and Precht 1997, Aronson et al. 2002a, 2005b). Pleistocene reefs grew on topographic highs in the lagoon, and Holocene reef growth over the last 8000–9000 years has exaggerated that antecedent topography, producing narrow "ribbon-reefs" in a rhombohedral configuration. The reefs grew to sea level and formed atoll-like features known as faroes or rhomboid shoals. They surround basins up to 30 m deep, and the steep outer flanks extend from 1–2 m depth to the lagoon floor at ~30 m. The frameworks of the rhomboid shoals are uncemented and consist primarily of coral skeletons packed in a sandy-mud to muddy-sand matrix (Macintyre and Aronson 2006). Components of the living benthos, including corals, sponges, and algae, rest atop or are loosely buried in the unconsolidated substratum.

From at least as early as the 1970s until ca. 1986, the flanks of Channel Cay (16.667° N, 88.167° W) and the other rhomboid shoals were dominated by vast, living thickets of the branching staghorn coral *Acropora cervicornis*. The lettuce coral *Agaricia tenuifolia* was the second-most dominant benthic component. Beginning in 1986, white-band disease (WBD) killed virtually all the *Ac. cervicornis* at Channel Cay and elsewhere in the study area at the same time it was killing acroporid corals throughout the Caribbean (Aronson and Precht 1997, 2001). WBD is a poorly characterized, infectious bacterial syndrome that only affects acroporid corals. Herbivory by the abundant echinoid *Echinometra viridis* suppressed algal growth and promoted the recruitment of agariciid corals onto the dead skeletons of *Ac. cervicornis*, so that by 1995 *Ag. tenuifolia* was the dominant space occupant at Channel Cay and the other shoals (Aronson and Precht 1997). *Ag. tenuifolia* was virtually extirpated in 1998, when high temperatures resulting from the 1997–1998 El Niño Southern Oscillation caused mass coral bleaching and subsequent mass mortality in the Belizean lagoon (Aronson et al. 2000). The dead skeletons of *Ag. tenuifolia* were then colonized by the encrusting sponge *Chondrilla caribensis* and to a lesser extent by macroalgae, algal turfs, and other sessile biota (Aronson et al. 2002b).

Paleoecological analysis placed these perturbations in the context of the late-Holocene history of the rhomboid shoals. Push-cores extracted from Channel Cay from the 1970s through 1995 showed that the internal architecture of the reef was composed almost entirely of an open framework of *Ac. cervicornis*, which dominated the reef geologically and ecologically for millennia (Shinn et al. 1979, Westphall 1986, Aronson and Precht 1997). Expanding the area of investigation to encompass a large proportion of the central lagoon, Aronson et al. (2002a) extracted 38 push-cores from 20 stations at water depths of 4.2–11.5 m on the outer flanks of the rhomboid shoals during the period 1995–2000 (Fig. 1). Radiocarbon dating showed the material in the cores to have been deposited sequentially, with older corals appearing below younger material and no significant age reversals. The cores revealed that *Ac. cervicornis* dominated for millennia, and that the areawide transition to another coral species, visible as a layer of imbricated skeletal plates of *Ag. tenuifolia* at the top of each core, was unprecedented since at least 3860 cal yr BP (Aronson et al. 2002a; cal yr BP stands for calibrated calendar years before present, where "present" is 1950). The two mass coral mortalities, from WBD and, a decade later, temperature-induced bleaching, were novel events on a millennial time scale.

Aronson et al. (2005b) re-cored 12 of the original 20 stations in 2004 (stations 1, 4, 5, 6, 7, 8, 11, 12, 15, 17, 19, and 20 in Fig. 1) after Hurricane Iris, a Category 4 storm on the Saffir-Simpson scale, passed over the study area in 2001. Hurricane Iris and two other storms in 2001 had negligible to minor impacts on all sites except site 1. In 2004, site 1 was covered with sediment. A core extracted from that site in 2004 lacked the uppermost *Ag. tenuifolia* layer, which was still present in cores from all the other sites.
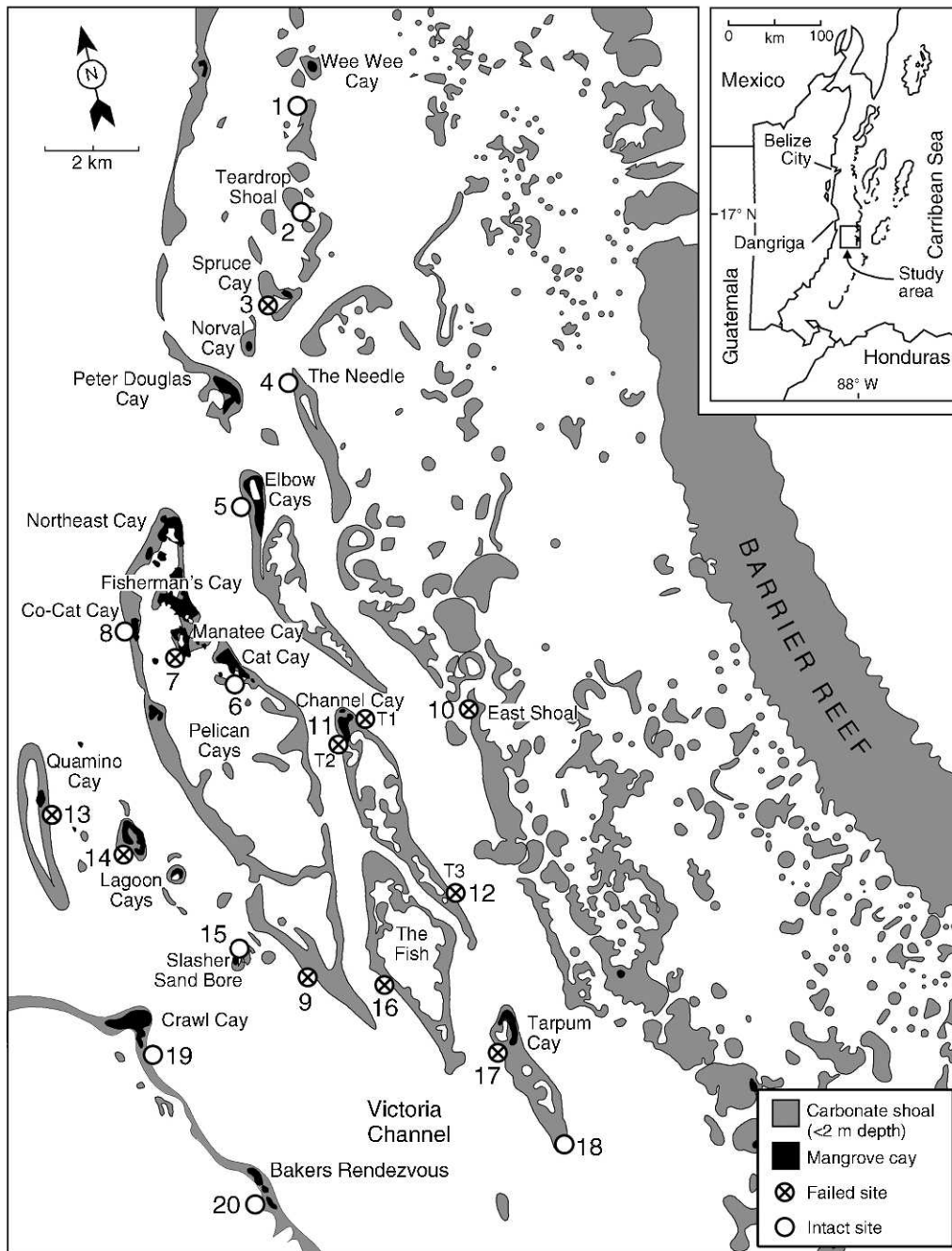
Fig. 1. Map of the central sector of the shelf lagoon of the Belizean barrier reef, showing locations of the coring stations and the three transects at Channel Cay. Sites that failed catastrophically in the 2009 earthquake are distinguished from those that remained intact. Site 11 and transect T2 are identical, as are site 12 and transect T3. Transect T1 does not have an associated site number. Carbonate shoals are shallow, submarine platforms composed of calcium carbonate sediments; mangrove cays are islands dominated by mangroves. Note the rhombohedral configuration and northwest–southeast orientation of the carbonate shoals in the study area. The figure is modified from Aronson et al. (2002a).

THE 2009 HONDURAN EARTHQUAKE

On 28 May 2009 at 08:24:45 UTC (02:24:45 local time), a powerful earthquake (M_W = 7.3) shook the Gulf of Honduras and surrounding areas (USGS 2009). The epicenter (16.783° N, 86.166° W) was located in the Caribbean Sea, 64 km northeast of the island of Roatán and 213 km from the study area, at a depth of 10 km. The earthquake occurred along the Swan Islands transform fault, at the tectonic boundary between the North American and Caribbean plates. Lasting ~30 s, this

major seismic event was felt in Honduras, Guatemala, El Salvador, Belize, and as far north as Cancún, Mexico. Residents of Dangriga, Belize, 35 km northwest of the study area, reported two aftershocks within 5 min of the initial shock and a third aftershock several days later (R. B. Aronson and W. F. Precht, *unpublished data*).

Methods

The benthic community of Channel Cay was monitored quantitatively at irregular intervals from April 1986 through November 2009. Channel Cay, like the other rhomboid shoals in the study area, is oriented northwest to southeast, reflecting the regional geology (Precht 1997, Purdy and Gischler 2003). The reef is 4 km long, with a maximum width of 0.5 km.

Two permanent transects, T1 and T2 (Fig. 1), were established on the northeastern and northwestern flanks of Channel Cay in 1986. A third transect, T3, was established on the southeastern flank in 1996. On each monitoring date, a fiber glass surveyor's tape was laid along the reef flank from 3 to 15 m depth. A diver swam along the tape, recording the benthic component under each 10-cm mark. The stations were monitored in April 1986; August 1990; June 1993; June 1994; July 1995; December 1996; August 1997; October 1998; January, March, June, and October 1999; February 2000; March and November 2001; July 2002; January 2006; December 2008; and November 2009. The data spanning April 1986 through March 2001 have been reported previously (Aronson and Precht 1997, Aronson et al. 2002b); the present paper extends our long-term data set through November 2009, or 23 yr after the initial data collection.

Juvenile hard corals (Scleractinia and Milleporina) and echinoids (which were exclusively *Echinometra viridis*) were surveyed in 0.25-m² quadrats placed haphazardly along lines extending 15–20 m on either side of each of the transect stations in June 1994, March 1999, February 2000, March 2001, July 2002, January 2006, December 2008, and November 2009. On each survey date, a quadrat was haphazardly placed on the substratum 25 times at each station at each of three depths: 5–6 m, 9 m, and 15 m. An underwater light aided in detecting juvenile corals, which were defined as colonies ≤5 cm in their longest dimensions (Edmunds et al. 1998). Juvenile corals were distinguished from fragments of larger colonies. Fragments were identified by their rough margins and/or their spatial proximity to similarly colored conspecifics that were clearly part of the same colony. Juvenile agariciids were of particular interest because of the ascendance of *Agaricia tenuifolia* to dominance in the 1990s. Although some agariciids could be identified to species, such identifications were not always reliable; therefore, juvenile agariciids were pooled for analysis.

The quadrats within a station and depth on a particular survey date could be construed as being nonindependent. To avoid this potential complication, as well as the problem of zero data for many of the individual quadrats, the data were pooled, yielding single estimates of the abundance of juvenile hard corals and *E. viridis* for each depth at each station on each survey date. The surveys in 1994 were conducted only at T1 and T2, only at 9 m and 15 m at those stations, and with 17 quadrats at each depth and station rather than 25. Estimates of abundance from the 1994 survey were normalized to 25 quadrats.

In June 2010 we revisited the 20 sites from the initial coring study plus the location of T1, which was not included in the coring study of Aronson et al. (2002a), to observe the impacts of the earthquake and determine the proportion of reef sites that had sustained damage (Fig. 1). To estimate the return time of an ecological impact of that magnitude, coral samples were collected at some damaged sites from the base of the intact reef framework that remained after the living community and part of the framework had fallen away. The coral samples were radiocarbon dated by Beta Analytic (Miami, Florida, USA) using standard techniques. Dates were calibrated to calendar years before 1950 (cal yr BP) after correcting for isotopic fractionation and the marine reservoir effect. The standard reservoir correction of 300 to 500 years was applied because no data on reservoir age are available for the Belizean barrier reef, and local corrections for elsewhere in the Caribbean are negligible.

Results

Physical impacts

The intensity of damage to coral reefs near the epicenter of the earthquake varied considerably, both within and between sites (Foster et al. 2010). Further west, in the central sector of the Belizean shelf lagoon, approximately half the reef slopes suffered catastrophic failure (Fig. 1). Rapid, late-Holocene accretion of the uncemented, open reef framework, which was dominated by branches of *Acropora cervicornis*, resulted in gravitational instability of the slopes. The primary mode of failure was avalanching, with large, initially cohesive slabs of semiconsolidated reef debris breaking free and sliding into deeper water. Collapse of the reefs was triggered by fractures developed during the earthquake.

The slides at Channel Cay exposed near-vertical walls, or crowns, of in-place reef framework, composed primarily of subfossil branch fragments of *Ac. cervicornis* (Fig. 2A). Fracture lines (crown cracks) oriented perpendicular to the reef slopes intersected the tops of the crowns at a water depth of 3 m. The vertical exposures were ≥5 m high, generally extending from 3 to ~9 m.

Slope angles were measured with an inclinometer in 6–9 m water depth at the three stations at Channel Cay from 1995 to 2000. The mean slope angle before the earthquake was 30.3° ± 0.096° (mean ± SE; range 11–47°, $n = 6$). By contrast, the mean slope angle of the crown faces was 80.0° ± 2.04° (range 75–85°, $n = 4$) in November 2009 (independent t test with variances separate: $t = 7.756$, df = 6.143, $P < 0.001$).
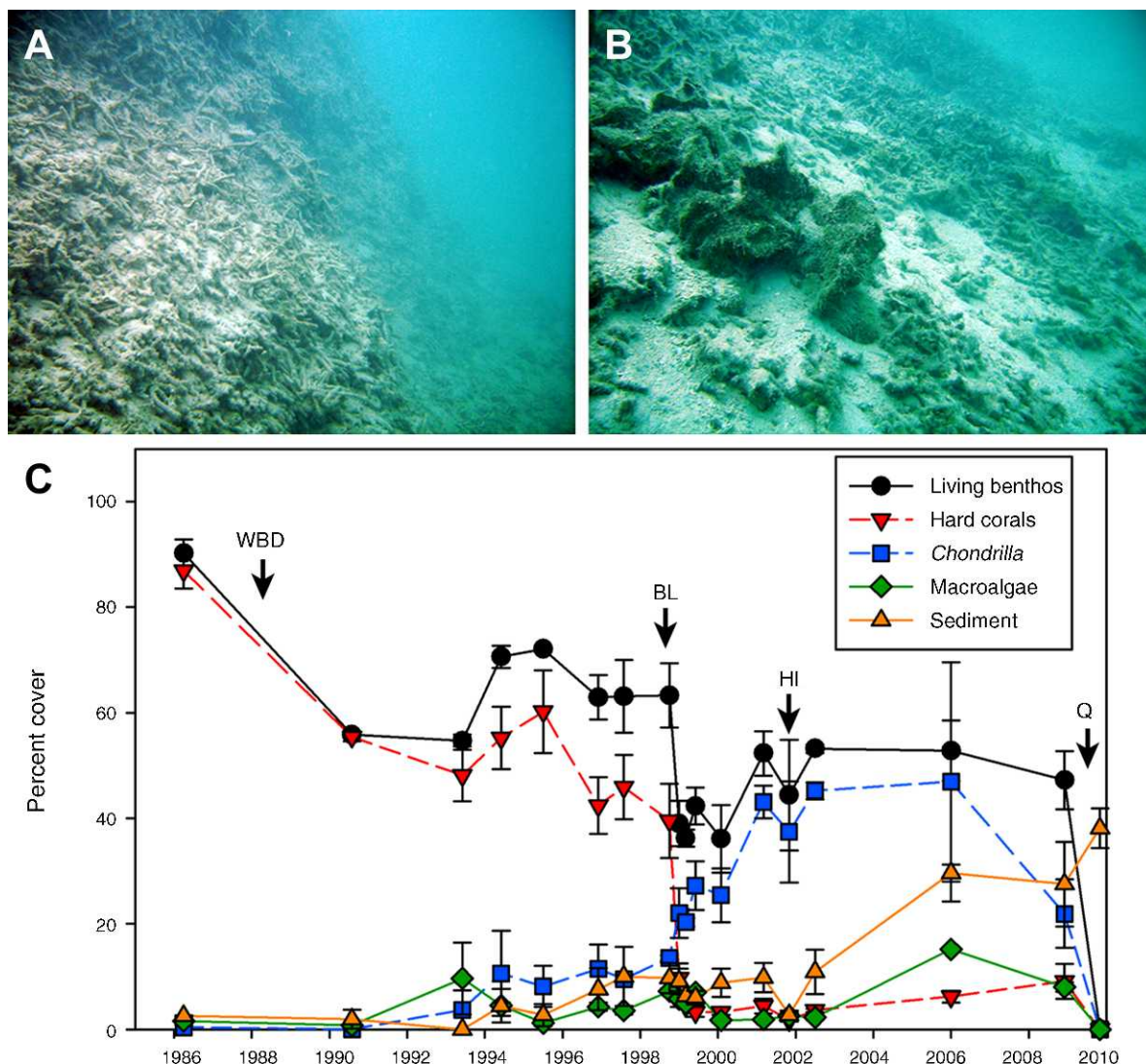
FIG. 2.   Effects of the May 2009 earthquake on the coral reef at Channel Cay, Belize. Photographs were taken in November 2009 from (A) a crown face at 6–9 m depth and (B) a debris field at 15–18 m depth. (C) Trajectory of the benthic community from 1986 to 2009. The plot shows estimates (mean ± SE) of the cover of components of the reef substratum: total living benthos, total hard corals, the encrusting sponge *Chondrilla caribensis*, macroalgae, and soft sediment. Arrows denote major disturbances during the last quarter century: the outbreak of white-band disease (WBD) after 1986, thermally induced coral bleaching (BL) in the summer of 1998, Hurricane Iris (HI) in 2001, and the earthquake (Q) in May 2009. Total hard substratum, which is the complement of "sediment," is not included in the plot.

Below the bases of the crowns at ~9 m water depth, the bed surfaces (i.e., the original reef-slope surfaces) on which the reef slabs failed extended downslope (Fig. 2B). Where the slides came to rest on the lagoon floor, large debris fields composed of modern and subfossil, allochthonous coral skeletons and associated sediments were deposited in water depths of 22–30 m. These debris fields extended up to 30 m from the toe-of-slope onto the floor of the lagoon. Slope angles were 30–55° at 9–18 m depth at the three stations.

Ecological impacts

The transect data from Channel Cay record biotic responses to a series of catastrophes over the decades leading up to the earthquake (Fig. 2C). The total cover of living hard corals declined after 1986 because the outbreak of white-band disease extirpated *Ac. cervicornis*. The opportunistic increase of *Agaricia tenuifolia* in the early 1990s caused an upswing in total coral cover and therefore, a partial recovery of the total cover of living benthos. Following the bleaching event in the fall of 1998, the cover of *Ag. tenuifolia* and hence, the total
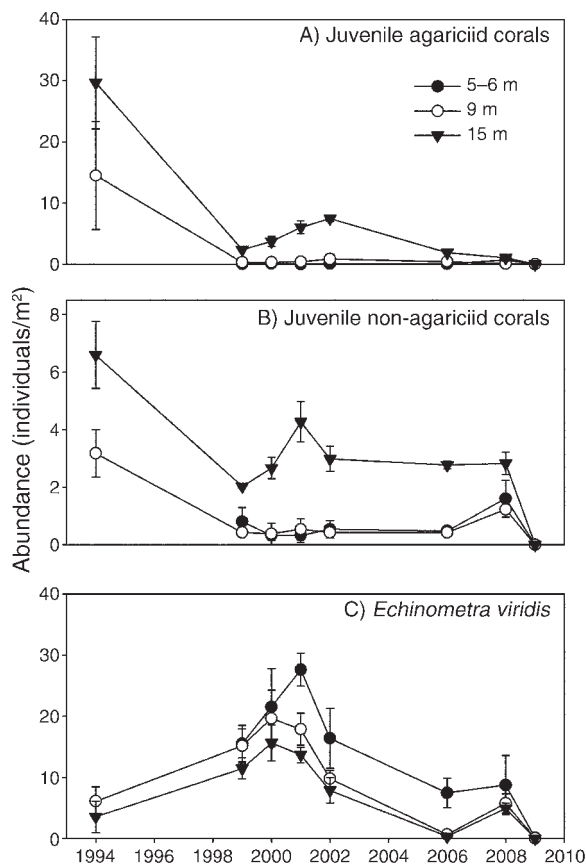
FIG. 3. Abundances (means ± SE) through time of juvenile corals and echinoids at Channel Cay. (A) Density of juvenile agariciids. (B) Density of juvenile non-agariciid corals; note the difference in vertical scale from the other two panels. (C) Density of *Echinometra viridis*.

cover of living benthos, declined markedly. The cover of sponges, which was almost exclusively the encrusting species *Chondrilla caribensis*, increased after the demise of the *Ag. tenuifolia* populations, so the total cover of living benthos recovered. Hurricane Iris depressed the cover of sponges and total living benthos slightly and temporarily, and the storm increased the cover of sediment (see also Aronson et al. 2005b).

The earthquake in 2009 brought these complex ecological dynamics to a halt. All benthic organisms along the transects were removed (in 3–9 m depth) or buried (in deeper water), leaving nothing exposed but sediment and the skeletal debris of corals. Living cover dropped from 47.2% ± 5.53% (mean ± SE) in December 2008 to zero in November 2009. The mean cover of dead coral skeletons, both branching and massive, on the debris fields at 9–15 m depth along the transects was 48.1% ± 3.43% in November 2009, and the remainder of the substratum was covered by fine sediment. On the crown faces, the mean cover of exposed, subfossil branches of *Ac. cervicornis* was

98.6% ± 1.36%, and again the remainder was fine sediment.

Randomized-block (repeated-measures) analysis of variance (ANOVA) showed significant temporal changes in the cover of hard corals, *Ac. cervicornis*, *Ag. tenuifolia*, and sponges from 1986 through 2001 (Aronson and Precht 1997, Aronson et al. 2002b). Eradication of the benthic communities along the transects in 2009 brought the mean cover of all categories of living benthos to zero with zero variance, obviating the need for further statistical analysis. The cover of macroalgae, a category that included fleshy and filamentous macroalgae as well as branching, calcified algae, remained low through 2001 (Aronson et al. 2002b). Subsequent variability of macroalgal cover, which was related to changes in the abundance of *Echinometra viridis*, is discussed below in this section.

The densities of juvenile corals of the family Agariciidae, non-agariciid juveniles, and *Echinometra* from 1994 through 2008 were analyzed using a randomized, incomplete-block ANOVA design, with survey date and depth as fixed factors and the transects as the blocks. The 2009 data were not included in the analysis because all means and variances had dropped to zero. Editing the data sets to remove transect T3, which was added after 1994, did not alter the results, and analyses of the entire data set are presented here. We used SPSS 18 for all statistical analysis (Norusis and SPSS 2010). Complete ANOVA tables are presented in the Appendix.

For juvenile agariciids, a Kolmogorov-Smirnov (K-S) test showed that the natural log-transformed (ln-transformed) data met the normality assumption for a parametric test ($D = 0.069$, df = 58, $P > 0.200$), and homogeneity of variances is not an assumption of unreplicated designs. The abundance of juvenile agariciids varied significantly among survey dates, depths, and blocks ($F_{6,36} = 19.883$, $P < 0.001$; $F_{2,36} = 130.156$, $P < 0.001$; and $F_{2,36} = 17.165$, $P < 0.001$, respectively). A posteriori comparisons using Tukey's HSD procedure revealed that the among-year variation was due primarily to significantly depressed abundances on all survey dates following 1994 ($P < 0.001$; Fig. 3A), as Aronson et al. (2002b) found for the period 1994–2002. The abundance of juvenile agariciids was significantly higher at 15 m than at shallower depths ($P < 0.001$) and significantly higher at 9 m than at 5–6 m ($P < 0.001$). There was also a significant survey date–depth interaction ($F_{11,36} = 4.055$, $P = 0.001$), driven primarily by an interaction with time of the data from 9 m and 5–6 m; removal of the shallowest depth level greatly reduced the probability of a significant interaction when the ANOVA was rerun ($F_{6,24} = 2.661$, $P = 0.040$). Although the initial ANOVA detected a significant difference between 9 m and 5–6 m, that result was confounded by anomalously high recruitment at 5–6 m in 2008. Overall, the data suggest a substantial decline in the abundance

of juvenile agariciids associated with and following the bleaching event of 1998.

Juvenile corals other than agariciids showed a similar qualitative pattern (Fig. 3B), albeit with some differences in the statistical details. A K-S test again confirmed normality of the ln-transformed data ($D = 0.105$, df $= 58$, $P = 0.175$). Randomized-block ANOVA showed significant effects of both survey date and depth ($F_{6,36} = 5.113$, $P = 0.001$; and $F_{2,36} = 42.482$, $P < 0.001$, respectively) but not block ($F_{2,36} = 0.652$, $P = 0.527$). There was no significant survey date × depth interaction ($F_{11,36} = 1.169$, $P = 0.342$). Tukey's HSD procedure suggested that the abundance of non-agariciid juveniles was significantly greater in 1994 than on all other survey dates ($P < 0.001$) and that abundance was significantly higher in 2008 than in 2000 ($P = 0.023$). Abundance was significantly higher at 15 m than at the two shallower depths ($P < 0.001$), but there was no significant difference between 9 m and 5–6 m ($P = 0.890$). As was observed for juvenile agariciids, there was a precipitous decline associated with the bleaching event of 1998.

Data on the abundance of *Echinometra viridis*, the most important herbivore in the system (Aronson and Precht 1997), were normally distributed following ln-transformation ($D = 0.090$, df $= 58$, $P > 0.200$). The abundance of *E. viridis* varied significantly among years, depths, and blocks ($F_{6,36} = 31.872$, $P < 0.001$; $F_{2,36} = 13.079$, $P < 0.001$; and $F_{2,36} = 5.106$, $P = 0.012$, respectively). *E. viridis* peaked in 2000–2001 (Fig. 3C). The abundance of these echinoids dropped from March 2001 to July 2002 in association with Hurricane Iris, although the cover of sediment had not yet increased appreciably, and there were no other obvious connections between the abundance of *E. viridis* and the storm (Fig. 2C). Tukey's HSD procedure highlighted significant differences among various pairs of years ($P < 0.05$), but the ANOVA also revealed a significant interaction between survey date and depth ($F_{11,36} = 3.249$, $P = 0.004$). Although overall trends in the abundance of *E. viridis* through time were similar among depths, there was a large and significant drop at 9 m and 15 m in 2006, which was not observed at 5–6 m. The drop in 2006 at only two depths was largely responsible for significant differences between 5–6 m and both 9 m and 15 m (Tukey's HSD procedure, $P = 0.003$ and $P < 0.001$, respectively); therefore, the significant effect of depth should be interpreted with caution.

The decline in abundance of sea urchins at 9 m and 15 m in 2006 was associated with an increase in macroalgal cover (Fig. 2C). From 1986 to 2002, mean macroalgal cover ranged from 0.7% to 9.7%, but in 2006 it rose to 15.2%. Macroalgal cover then declined to 8.4% in 2008 with the recovery of *E. viridis*, before dropping to zero in 2009 following the earthquake. Data on macroalgal cover for the period 1986–2008 were expressed as proportions and analyzed using a randomized, incomplete-block design, with time as a fixed factor and the transects as the blocks. The proportional data were normal (K-S test: $D = 0.114$, df $= 46$, $P = 0.171$), so they were not transformed. Macroalgal cover varied significantly among survey dates ($F_{16,27} = 3.622$, $P = 0.002$) but not among transects ($F_{2,27} = 2.310$, $P = 0.119$). Tukey's HSD procedure showed that macroalgal cover was significantly higher in the 2006 survey than in most other surveys, including the immediately preceding survey (2002; $P = 0.004$) but not the immediately following one (2008; $P = 0.406$). There were no significant differences between any other pairs of years.

At the other shoals, the trajectories of the benthic communities were qualitatively similar to the patterns observed at Channel Cay through December 2008, the time of our last visit to the rhomboid shoals prior to the earthquake. Visits to 21 sites (the 20 coring sites of Aronson et al. [2002a] plus T1) in 2009–2010 revealed that the slopes at 10 sites (48%) had completely failed and the slope at one site (site 3) showed minor slumping (Fig. 1). Of our subsample of 12 sites re-cored after Hurricane Iris, five (42%) had completely failed.

Aerial photographs of Channel Cay and other shoals showed that the avalanched slopes were discontinuous and formed scalloped, cusplike patterns. The avalanched slopes alternated laterally with areas of reef flank that remained intact. Observations throughout the study area by ourselves and other researchers confirmed the generality of this pattern (B. V. Shank, *personal communication*).

There was no association within the study area between the extent of damage to a site and the degree of wave exposure. Four sites on the windward sides of shoals and seven sites on the leeward sides were affected, whereas three windward sites and six leeward sites were not affected (G test with Williams's continuity correction; $G_{adj} = 0.233$, df $= 1$, $P > 0.50$). There was no apparent north–south bias in damage, either.

Return time

Cores extracted from 20 stations throughout the study area prior to the earthquake yielded well-ordered sedimentary packages, with younger sediments overlying older sediments (Aronson and Precht 1997, Aronson et al. 2002a). The sequential dates implied sequential reef deposition. In contrast, age reversals characterized reef deposits in which framework had slumped and flowed downslope (Wapnick et al. 2004). Because the crowns of the failed reef sections in Belize represent intact and sequentially deposited reef framework, coral samples from the bases of the crown faces provided minimum estimates of the time interval of continuous reef growth prior to the earthquake. The estimates were minima because the lowest portions of the vertical walls were buried under the slide debris, and only the exposed portions (the crown faces themselves) were accessible to sampling.

Coral samples from the bases of the exposed crown faces at four sites dated from 250 to 2280 cal yr BP

TABLE 1. Radiocarbon dates of coral samples from within reef frameworks at the bases of the crowns at Channel Cay, Belize.

Sample	Site	Water depth (m)	Depth-in-fwk (m)	Species	Date (cal yr BP) Mean	Date (cal yr BP) 2σ range
Q7	T1	9.0	6.0	S.s.	1410	1540–1320
Q8	T1	9.0	6.0	S.s.	1510	1590–1400
Q9	T1	9.0	6.0	A.c.	1650	1800–1510
Q10	T1	9.0	6.0	A.c.	1300	1380–1260
Q15	10	10.8	7.2	M.f.	2120	2280–1990
Q16	10	10.8	7.2	S.s.	2280	2330–2110
Q19	17	7.5	4.5	Mycet.	640	680–550
Q20	16	6.9	3.3	S.s.	250	300–70

Notes: All coral samples were in good-to-excellent taphonomic condition, and none showed signs of diagenetic alteration from aragonite to calcite. Depth-in-framework ("Depth-in-fwk") refers to the vertical distance between shelf-break of the reef and the depth at which the sample was taken. The 2σ range, which is the 95% confidence interval, is asymmetrical about the mean date because of the nonlinear shape of the calibration curve. Coral species are *Siderastrea siderea* (S.s.), *Acropora cervicornis* (A.c.), *Montastraea faveolata* (M.f.), and *Mycetophyllia* sp. (Mycet.).

(Table 1), with six of eight dates exceeding 1300 cal yr BP. Samples that were collected vertically deeper in the reef frameworks consistently yielded older dates, corroborating the inference that the exposed, vertical crown faces represent intact framework deposited in an ordered, sequential fashion. The maximum age among the eight samples, 2280 cal yr BP, is the minimum estimate of return time for an ecological catastrophe of this magnitude in this area.

Another minimum estimate of return time comes from the cores collected by Aronson et al. (2002a). Dates of coral samples from the bottoms of the cores, which penetrated ~4 m vertically into the intact reef frameworks, ranged from centuries to millennia before present, with a maximum date of 3860 cal yr BP (2σ range: 4068–3672 cal yr BP). Younger bottom dates for the same penetration depth indicate faster reef growth at other sites. Combining the two methods of estimation, the return time of an event causing this extent of damage (destruction of the benthic communities at half the reef sites) is at least 2000 to 4000 years under current tectonic conditions. The estimated time interval over which a given reef assemblage in the central lagoon has a 50% probability of being obliterated, T_{50}, is also 2000–4000 years.

DISCUSSION

Multiple catastrophes and reef dynamics

Multiple recent catastrophes describe the trajectory of reef assemblages in the central shelf lagoon of the Belizean barrier reef. The assemblages shifted in composition from the late 1980s to 2009, after three millennia of stasis. The outbreak of white-band disease (WBD) in the late 1980s and the bleaching event of 1998 were the primary drivers of recent phase shifts, with Hurricane Iris playing a minor role. In 2009, a submarine earthquake off Honduras changed the face of the system to a far greater extent than the outbreak of

WBD and the bleaching event, which themselves were catastrophic perturbations by any definition.

Benthic communities at approximately half the reef sites in the study area were demolished by the earthquake. Damage from the tectonic event, which extended over an area of at least hundreds of square kilometers, was unprecedented on a scale of millennia. Community-level attributes, including the intensity of herbivory, which were initially important in driving the composition of the benthos, had no impact on the final outcome for the failed reefs. Any differences among failed sites in the timing and details of their dynamics before 2009 were rendered moot.

Scope for recovery

Reef systems can take centuries to millennia to recover from large-scale, high-intensity, catastrophic physical disturbances such as volcanic eruptions and the ensuing ash falls. Working on uplifted Holocene reefs in Papua New Guinea, Pandolfi et al. (2006) observed that the disturbed surfaces were colonized and vertical accretion was restarted on a decadal to centennial scale, but recovery of the benthic assemblages to the predisturbance baseline was a millennial-scale process. Smaller-scale removals of reef assemblages exhibit more rapid recovery if upstream sources of larvae persist (Done 1992, Golbuu et al. 2007). Projections of the tempo and mode of recovery in the central shelf lagoon of Belize are strongly influenced by the history of disturbance prior to the earthquake (cf. Hughes 1989).

Nearly half the area of the debris fields at 9 m depth and deeper at the Channel Cay stations consisted of hard substratum, and qualitative observations suggested commensurate availability of hard surfaces at the other sites that had experienced catastrophic failure. Because approximately half the linear extent of ribbon reef in the rhomboid shoals remained intact, and because all the failed areas were adjacent to or near living communities

not destroyed by the earthquake, the state to which the avalanched habitats (at least the debris fields below the crown faces) are most likely to recover is dominance by *Chondrilla caribensis*, macroalgae, and other noncoral epibenthos that will colonize the exposed coral skeletons. Recruitment of coral larvae from more distant upstream sources remains a possibility.

Had the bleaching event of 1998 not occurred, areas that remained intact following the 2009 earthquake probably would have been dominated by *Agaricia tenuifolia*. The debris fields in the avalanched areas, therefore, would likely have recovered to dominance by *Ag. tenuifolia* on a decadal scale, judging from the rapidity with which that species rose to dominance on the rhomboid shoals after the loss of *Acropora cervicornis*. *Ag. tenuifolia* has a brooding reproductive strategy and is presumed to be hermaphroditic and capable of self-fertilization (Aronson et al. 2002*a*, Gleason et al. 2009). These known and postulated life history attributes account for its ability to colonize disturbed surfaces rapidly, but the failure of agariciid recruitment following the bleaching event of 1998 suggests that rapid colonization of the debris fields by *Ag. tenuifolia* is unlikely. *Ag. tenuifolia* cannot persist on uncemented slopes of >45° (Aronson et al. 2002*a*), so even if it had still dominated the intact areas, it would not have been able to recolonize either the crown faces in their current vertical configuration or the steeper debris slopes.

Had neither the outbreak of WBD nor the bleaching event occurred, *Ac. cervicornis* might have continued its millennial-scale dominance of the areas not destroyed by the earthquake. This species grows rapidly in a tangled, open framework. It reproduces primarily by fragmentation and implantation of its pointed branch tips in the substratum (Tunnicliffe 1981, Highsmith 1982). *Ac. cervicornis* is able to persist on steep slopes. It would have had the capacity to recolonize the hard and soft substrata of the debris slopes, and perhaps the crown faces as well; however, like *Ag. tenuifolia* it is now extremely rare. There are virtually no colonies of *Ac. cervicornis* available to fragment in the central shelf lagoon.

The prior losses of both *Ac. cervicornis* and *Ag. tenuifolia* drastically reduced the resilience of the assemblages on the reef slopes, both failed and intact, making recovery to a coral-dominated state unlikely in the near future. Continued shedding of skeletal debris and sedimentary matrix from the crown faces, which we observed during our postearthquake visits in 2009 and 2010, will slow colonization of the crown faces themselves and also create conditions inimical to corals on the debris slopes (e.g., Rogers 1990, Fabricius 2005). Rates of herbivory on the failed slopes should recover more rapidly, as juvenile and adult *Echinometra viridis* migrate from adjacent areas and as recruits settle from the water column.

The life span of coral reefs

Uncemented reef frameworks, such as those in the central lagoon of Belize, are far more vulnerable to earthquakes than the cemented and consolidated frameworks characteristic of fore-reef environments. We observed no impacts of the 2009 earthquake on the fore reef of the Belizean barrier reef. The same is true of tsunamis in tropical environments: reef assemblages anchored in soft sediments are more severely affected than assemblages cemented to the substratum (Baird et al. 2005). The extent of reef-slope failure from an earthquake will depend on the earthquake's magnitude and depth, the distance from the epicenter to the reef system, the lengths and angles of the slopes themselves, the subsurface layers of weakness, and any magnifying effects of the underlying structural features.

The 1991 earthquake at Limón, Costa Rica ($M_W =$ 7.7, 17.4 km depth) caused <1 m of subsidence in Bahía Almirante in northwestern Panamá, 90 km to the east of the epicenter (Phillips and Bustin 1996). Pflaker and Ward (1992) estimated a return time of 200–1100 years for an earthquake of that magnitude in that area. The Limón earthquake did not damage the uncemented reefs in Bahía Almirante, which were ecologically similar to the reefs of the central shelf lagoon in Belize (Aronson et al. 2004), for two principal reasons. First, reef slopes are shorter and less steep in Bahía Almirante than in the Belizean shelf lagoon (Aronson et al. 2004, 2005*a*), making them less likely to fail (Hampton et al. 1996). Second, the Panamanian reefs are not associated with local zones of tectonic weakness, whereas the Belizean reefs are founded on structural lineaments (Precht 1997, Purdy et al. 2003).

Coseismic fractures in the central lagoon, created during the 2009 event, mimic the antecedent structural template on which the rhomboid shoals are based (Precht 1997, Purdy and Gischler 2003), providing the first direct evidence of the role of neotectonics in sculpting and accentuating reef morphology. Vertical crown faces that we observed on some reef slopes before 2009 are evidence of prior slope-failure events in the Holocene. These failure surfaces could reflect the localized impacts of strong hurricanes in the study area (Aronson et al. 2005*b*). The absence of extensive debris fields at the bases of the rhomboid shoals prior to the 2009 earthquake (Shinn et al. 1979) suggests that such events in the past were confined to small areas. Cores extracted in 2008 from Station 11 at Channel Cay at 15–16 m depth, for example, displayed a spatially limited slump near the base of the reef that dated to ~1500 cal yr BP (Aronson et al. 2009).

Rare, large-scale, catastrophic events overwhelm the capacity of ecosystems to provide services to human populations. The Indonesian tsunami of 2006, for example, exceeded the ability of coral reefs and mangrove stands to protect shorelines (Baird et al. 2005, Kerr et al. 2006), despite initial claims to the contrary. The T_{50} of reefs in the central shelf lagoon of

Belize, the time scale on which they can be expected to provide ecosystem services, and the time scale on which they should be managed are millennial, as opposed to the decadal-to-centennial life spans of their constituent coral colonies and their human stewards. Ignoring the millennial-scale return time of major physical events can have dire consequences for society (Normile 2011), and the same is true for conservation. If half the reef resources in the central lagoon are likely to be destroyed by a high-amplitude, natural event every few millennia, irrespective of the degrading effects of climate change and any other present or future perturbations (Aronson et al. 2011), then the calculus of truly long-term planning should dictate expanding and intensifying protections in this environment to account for such catastrophes.

Literature Cited

Albert, S., J. Udy, G. Baines, and D. McDougall. 2007. Dramatic tectonic uplift of a fringing reef on Ranongga Is., Solomon Islands. Coral Reefs 26:983.

Aronson, R. B., I. G. Macintyre, S. A. Lewis, and N. L. Hilbun. 2005a. Emergent zonation and geographic convergence of coral reefs. Ecology 86:2586–2600.

Aronson, R. B., I. G. Macintyre, A. M. Moesinger, W. F. Precht, and M. R. Dardeau. 2009. History of reef coral assemblages on the rhomboid shoals of Belize. Smithsonian Contributions to the Marine Sciences 38:313–321.

Aronson, R. B., I. G. Macintyre, and W. F. Precht. 2005b. Event preservation in lagoonal reef systems. Geology 33:717–720.

Aronson, R. B., I. G. Macintyre, and W. F. Precht. 2011. Natural and anthropogenic catastrophe on the Belizean Barrier Reef. Pages 125–128 in M. L. D. Palomares and D. Pauly, editors. Too precious to drill: the marine biodiversity of Belize. Fisheries Centre Research Reports 19(6), University of British Columbia, Vancouver, British Columbia, Canada.

Aronson, R. B., I. G. Macintyre, W. F. Precht, T. J. T. Murdoch, and C. M. Wapnick. 2002a. The expanding scale of species turnover events on lagoonal reefs in Belize. Ecological Monographs 72:233–249.

Aronson, R. B., I. G. Macintyre, C. M. Wapnick, and M. W. O'Neill. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. Ecology 85:1876–1891.

Aronson, R. B., and W. F. Precht. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. Paleobiology 23:326–346.

Aronson, R. B., and W. F. Precht. 2001. White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25–38.

Aronson, R. B., W. F. Precht, I. G. Macintyre, and T. J. T. Murdoch. 2000. Coral bleach-out in Belize. Nature 405:36.

Aronson, R. B., W. F. Precht, M. A. Toscano, and K. H. Koltes. 2002b. The 1998 bleaching event and its aftermath on a coral reef in Belize. Marine Biology 141:435–447.

Baird, A. H., et al. 2005. Acehnese reefs in the wake of the Asian tsunami. Current Biology 15:1926–1930.

Bak, P., and K. Chen. 1991. Self-organized criticality. Scientific American 264(1):46–53.

Bak, P., K. Chen, and M. Cruetz. 1989. Self-organized criticality in the 'Game of Life.' Nature 342:780–782.

Bak, P., and K. Sneppen. 1993. Punctuated equilibrium and criticality in a simple model of evolution. Physical Review Letters 71:4083–4086.

Berumen, M. L., and M. S. Pratchett. 2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. Coral Reefs 25:647–653.

Colgan, M. W. 1987. Coral reef recovery on Guam (Micronesia) after catastrophic predation by Acanthaster planci. Ecology 68:1592–1605.

Colgan, M. W. 1989. El Niño and the history of eastern Pacific reef building. Pages 183–232 in P. W. Glynn, editor. Global ecological consequences of the 1982–83 El Niño–Southern Oscillation. Elsevier, Amsterdam, The Netherlands.

Cortés, J., R. Soto, and C. Jiménez. 1992. Earthquake associated mortality of intertidal and coral reef organisms (Caribbean of Costa Rica). Pages 235–240 in R. Richmond, editor. Proceedings of the seventh international coral reef symposium, Guam. Volume 1. University of Guam Press, Guam, USA.

Done, T. J. 1992. Constancy and change in some Great Barrier Reef coral communities: 1980–1990. American Zoologist 32:655–662.

Done, T. J. 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. American Zoologist 39:66–79.

Dudgeon, S. R., R. B. Aronson, J. F. Bruno, and W. F. Precht. 2010. Phase shifts and stable states on coral reefs. Marine Ecology Progress Series 413:201–216.

Edmunds, P. J., R. B. Aronson, D. W. Swanson, D. R. Levitan, and W. F. Precht. 1998. Photographic versus visual census techniques for the quantification of juvenile corals. Bulletin of Marine Science 62:937–946.

Fabricius, K. E. 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. Marine Pollution Bulletin 50:125–146.

Foster, N. L., M. Williams, S. Chan, C. Ramirez, and V. Vasquez. 2010. Damage to the reefs of Port Honduras Marine Reserve, Belize, during the 28 May 2009 earthquake. Coral Reefs 29:19.

Gaines, S. D., and M. W. Denny. 1993. The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. Ecology 74:1677–1692.

Gleason, D. F., B. S. Danilowicz, and C. J. Nolan. 2009. Reef waters stimulate substratum exploration in planulae from brooding Caribbean corals. Coral Reefs 28:549–554.

Golbuu, Y., S. Victor, L. Penland, D. Idip, Jr., C. Emaurois, K. Okaji, H. Yukihira, A. Iwase, and R. van Woesik. 2007. Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. Coral Reefs 26:319–332.

Haldane, A. G., and R. M. May. 2011. Systemic risk in banking ecosystems. Nature 469:351–355.

Hampton, M. A., H. J. Lee, and J. Locat. 1996. Submarine landslides. Review of Geophysics 34:33–59.

Highsmith, R. C. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series 7:207–226.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50:839–866.

Hubbard, D. K. 1997. Reefs as dynamic systems. Pages 43–67 in C. Birkeland, editor. Life and death of coral reefs. Chapman and Hall, New York, New York, USA.

Hubbard, D. K., H. Zankl, I. van Heerden, and I. P. Gill. 2005. Holocene reef development along the northeastern St. Croix shelf, Buck Island, U.S. Virgin Islands. Journal of Sedimentary Research 75:97–113.

Hughes, T. P. 1989. Community structure and diversity of coral reefs: the role of history. Ecology 70:275–279.

Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology and Evolution 20:380–386.

Hughes, T. P., et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

Kerr, A. M., A. H. Baird, and S. J. Campbell. 2006. Comments on "Coastal mangrove forests mitigated tsunami" by K. Kathiresan and N. Rajendran. Estuarine, Coastal and Shelf Science 67:539–541.

Lirman, D., et al. 2011. Severe 2010 cold-water event caused unprecedented mortality to corals of the Florida reef tract and reversed previous survivorship patterns. PLoS ONE 6:e23047. [doi:10.1371/journal.pone.0023047]

Macintyre, I. G., and R. B. Aronson. 2006. Lithified and unlithified Mg-calcite precipitates in tropical reef environments. Journal of Sedimentary Research 76:81–90.

Malamud, B. D., G. Morien, and D. L. Turcotte. 1998. Forest fires: an example of self-organized critical behavior. Science 281:1840–1842.

Miller, A. I. 1998. Biotic transitions in global marine diversity. Science 281:1157–1160.

Normile, D. 2011. Scientific consensus on great quake came too late. Science 332:22–23.

Norusis, M. J., and SPSS. 2010. PASW statistics 18: guide to data analysis. Addison–Wesley, Boston, Massachusetts, USA.

Nyström, M., and C. Folke. 2001. Spatial resilience of coral reefs. Ecosystems 4:406–417.

O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, New Jersey, USA.

Pandolfi, J. M., A. W. Tudhope, G. Burr, J. Chappell, E. Edinger, M. Frey, R. Steneck, C. Sharma, A. Yeates, M. Jennions, H. Laecinsky, and A. Newton. 2006. Mass mortality following disturbance in Holocene coral reefs from Papua New Guinea. Geology 34:949–952.

Pflaker, G., and S. N. Ward. 1992. Backarc thrust faulting and tectonic uplift along the Caribbean Sea coast during the April 22, 1991 Costa Rica earthquake. Tectonics 11:709–718.

Phillips, S., and R. M. Bustin. 1996. Sedimentology of the Changuinola peat deposit: organic and clastic sedimentary response to punctuated coastal subsidence. Geological Society of America Bulletin 108:794–814.

Precht, W. F. 1997. Divergent wrench faulting in the Belize southern lagoon; implications for Tertiary Caribbean Plate movements and Quaternary reef distribution: discussion. American Association of Petroleum Geologists Bulletin 81:329–333.

Precht, W. F., and R. B. Aronson. 2006. Death and resurrection of Caribbean coral reefs: a palaeoecological perspective. Pages 40–77 in I. Côté and J. Reynolds, editors. Coral reef conservation. Cambridge University Press, Cambridge, UK.

Purdy, E. G., and E. Gischler. 2003. The Belize margin revisited: 1. Holocene marine facies. International Journal of Earth Sciences (Geologische Rundschau) 92:532–551.

Purdy, E. G., E. Gishcler, and A. J. Lomando. 2003. The Belize margin revisited. 2. Origin of Holocene antecedent topography. International Journal of Earth Sciences (Geologische Rundschau) 92:552–572.

Rogers, C. S. 1990. Responses of coral reefs and reef organisms to sedimentation. Marine Ecology Progress Series 62:185–202.

Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Ness, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18:648–656.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Shaked, Y., A. Agnon, B. Lazar, S. Marco, U. Avner, and M. Stein. 2004. Large earthquakes kill coral reefs at the northwest Gulf of Aqaba. Terra Nova 16:133–138.

Shinn, E. A., R. B. Haley, J. H. Hudson, B. Lidz, and D. M. Robbin. 1979. Three-dimensional aspects of Belize patch reefs. American Association of Petroleum Geologists Bulletin 63:528.

Stoddart, D. R. 1972. Catastrophic damage to coral reef communities by earthquake. Nature 239:51–52.

Thompson, D. M., and R. van Woesik. 2009. Corals escape bleaching in regions that recently and historically experienced thermal stress. Proceedings of the Royal Society B 276:2893–2901.

Tibor, G., T. M. Neimi, Z. Ben-Avraham, A. Al-Zoubi, R. A. Sade, J. K. Hall, G. Hartman, E. Akawi, A. Abueladas, and R. Al-Ruzouq. 2010. Active tectonic morphology and submarine deformation of the northern Gulf of Eilat/Aqaba from analysis of multibeam data. Geo-Marine Letters 30:561–573.

Tomascik, T., R. van Woesik, and A. J. Mah. 1996. Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia. Coral Reefs 15:169–175.

Tunnicliffe, V. 1981. Breakage and propagation of the stony coral Acropora cervicornis. Proceedings of the National Academy of Sciences USA 78:2427–2431.

USGS. 2009. Magnitude 7.3–offshore Honduras. USGS, Department of the Interior, Washington, D.C., USA. http://earthquake.usgs.gov/eqcenter/eqinthenews/2009/us2009heak/

van Woesik, R. 1996. Earthquake effects on a coral reef in Japan. Coral Reefs 15:224.

van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and losers a decade after coral bleaching. Marine Ecology Progress Series 434:67–76.

Wapnick, C. M., W. F. Precht, and R. B. Aronson. 2004. Millennial-scale dynamics of staghorn coral in Discovery Bay, Jamaica. Ecology Letters 7:354–361.

Westphall, M. J. 1986. Anatomy and history of a ringed-reef complex, Belize, Central America. Thesis. University of Miami, Coral Gables, Florida, USA.

Woodley, J. D. 1992. The incidence of hurricanes on the north coast of Jamaica since 1870: are the classic reef descriptions atypical? Hydrobiologia 247:133–138.

Woodley, J. D., et al. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science 214:749–755.

SUPPLEMENTAL MATERIAL

Appendix

ANOVA tables, discussed in *Results*, for counts of juvenile corals, counts of *Echinometra viridis*, and the proportional cover of macroalgae at Channel Cay, Belize (*Ecological Archives* E093-029-A1).