

LETTER

Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching

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Abstract

Caribbean reef corals have declined precipitously since the 1980s due to regional episodes of bleaching, disease and algal overgrowth, but the extent of earlier degradation due to localised historical disturbances such as land clearing and overfishing remains unresolved. We analysed coral and molluscan fossil assemblages from reefs near Bocas del Toro, Panama to construct a timeline of ecological change from the 19th century—present. We report large changes before 1960 in coastal lagoons coincident with extensive deforestation, and after 1960 on offshore reefs. Striking changes include the demise of previously dominant staghorn coral *Acropora cervicornis* and oyster *Dendroostrea frons* that lives attached to gorgonians and staghorn corals. Reductions in bivalve size and simplification of gastropod trophic structure further implicate increasing environmental stress on reefs. Our paleoecological data strongly support the hypothesis, from extensive qualitative data, that Caribbean reef degradation predates coral bleaching and disease outbreaks linked to anthropogenic climate change.

Keywords

Acropora cervicornis, Bocas del Toro, climate change, corals, *Dendroostrea frons*, historical ecology, land use, molluscs, shifting baselines.

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INTRODUCTION

Over exploitation of Caribbean reef megafauna and fishes began centuries before the arrival of Columbus in 1492 (Jackson 1997; Jackson *et al.* 2001; Pandolfi *et al.* 2003; McClenachan *et al.* 2010). In contrast, Caribbean reef corals did not appear to be affected by human activities until the 1980s (Hughes 1994). Since this period, coral cover in the Caribbean has declined by an average of 80% (Gardner *et al.* 2003) and branching species of *Acropora* and *Porites* corals have been replaced by non-branching species of *Agaricia* and *Porites* (Aronson *et al.* 2004, 2005; Green *et al.* 2008). This recent and widespread collapse of Caribbean coral communities has been convincingly attributed to various combinations of coral and urchin disease, coral bleaching and overgrowth by seaweeds (Gladfelter 1982; Hughes 1994; Brown 1997). Surveys of fossil reefs have revealed that such drastic changes in Caribbean coral communities are unprecedented over the last *c.* 200 000 years despite large fluctuations in sea level and climate (Pandolfi & Jackson 2006; Greer *et al.* 2009), implicating anthropogenic disturbance in the recent decline.

Although quantitative ecological surveys of Caribbean reefs did not begin until the late 1970s, earlier qualitative ecological surveys, century-scale coral growth rate records, and the severity and novelty of coral disease symptoms indicate that widespread coral disease and bleaching outbreaks are recent phenomena in this region (Glynn 1991; Goreau 1992; Harvell *et al.* 1999; Halley & Hudson 2007; Carilli *et al.*

2010). The appearance and intensification of mass coral disease and bleaching events in the Caribbean and elsewhere have been widely attributed to anthropogenic climate change (Harvell *et al.* 1999; Donner *et al.* 2007; Hughes *et al.* 2007).

In contrast, earlier qualitative surveys and naturalists' observations suggest that coral abundance and community composition had already begun to degrade significantly on some Caribbean reefs by the early 1900s, with particularly strong reductions in dominant *Acropora* species (Lewis 1984; Pandolfi *et al.* 2003). These results suggest that local anthropogenic stressors such as land clearing and overfishing may have precipitated a decline in Caribbean reef corals prior to the onset of widespread coral bleaching and disease. However, the paucity of quantitative data for Caribbean reef communities prior to the 1980s has prevented the development of an accurate ecological baseline, and has made it difficult to assess the importance of local anthropogenic stressors in recent reef decline. To help resolve this fundamental issue, we developed a novel paleontological sampling technique to construct a timeline of quantitative ecological change extending from the 19th century to the present on coral reefs near Bocas del Toro in western Caribbean Panama. To investigate the role of historical land clearing in reef decline, we sampled scleractinian coral and molluscan fossil assemblages across a gradient of exposure to land-based pollution in a region with a well-documented history of deforestation extending to the 19th century (Guzmán 2003).

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MATERIALS AND METHODS

Sampling

We collected coral, bivalve and gastropod death assemblages (fossil material) at 5 m water depth from three lagoonal and three offshore reef sites near the Bocas del Toro archipelago by excavating the reef framework and associated sediments from large circular pits. Material was excavated by inserting a 60 cm-diameter circular metal frame into the sediment/coral rubble matrix on areas of the modern reef with little or no living coral. The metal frame was hammered into the reef framework as excavation progressed. Coral rubble and sediments were excavated down to 80 cm below the reef surface by extracting four separate 20 cm-thick layers within each pit (Fig. 1). Material was excavated using small scoops and sieved underwater using a 7 mm mesh. Coral life assemblages (living coral) were surveyed at each site using 40 m point-intercept transects with 5 cm sampling increments (Fig. 1). Each transect line was placed 1–2 m away from its corresponding pit. Depending on the total extent of reef area available for survey, transect lines were generally 20–50 m apart, covering a large area of a reef site and spanning a gradient of water motion. We did not sample recent molluscs. Three replicates were sampled at each of the six reef sites. Offshore sites were less exposed to terrestrial runoff than lagoonal sites as evidenced by striking differences in water clarity. Layers (horizons) within pits were presumed to be in stratigraphic order because: (1) most coral skeletons were in life position and showed no evidence of biological or physical re-working,

(2) the study region is well outside the Atlantic hurricane zone (Neumann *et al.* 1978) precluding large-scale physical transport of rubble and (3) clear and progressive gradients in the relative abundance of species were observed among adjacent layers (Figs. 2 and 3).

Coral and molluscan assemblages

Coral species proportions were determined by per cent weight for death assemblages and by per cent cover for life assemblages, whereas bivalve and gastropod species proportions were determined by per cent total individuals in the death assemblage. Bivalve shells with hinges and gastropod shells with an apex or aperture were counted as individuals.

A total of 31 taxonomic groups (species or congeneric species) were identified for corals, 73 for bivalves and 85 for gastropods (Table S1). Small scleractinian cup corals from the families Rhizangiidae and Dendrophyllidae and the hydrozoan coral *Stylaster* were not included in the analyses of reef corals because they were very minor components of the coral community. The hydrozoan coral *Millepora* was included in the analyses because it is a major component of coral communities in shallow reef zones of Bocas del Toro.

Radiocarbon dating

Ages of the different layers in the pits (“death horizons”) were determined from radiocarbon dates from 1 to 2 coral fragments from each horizon and pit. The results of the radiocarbon analyses were reported as the “fraction modern” including background subtraction and $\delta^{13}\text{C}$ correction (Stuiver & Polach 1977) which is equivalent to $F^{14}\text{C}$ defined in Reimer *et al.* (2004), and as calendar years AD from the calibration of radiocarbon ages. Radiocarbon ages were converted to calendar years using one of two reference datasets. Fraction modern values < 0.927 (corresponding to ages older than *c.* 1750 AD) were converted to calendar years using the Calib 6.0 program (Stuiver & Reimer 1986) and the IntCal/MarineCal09 calibration dataset (Reimer *et al.* 2004). Fraction modern values > 0.927 were converted to calendar years using the Calibomb program (Reimer *et al.* 2004) and a surface water $F^{14}\text{C}$ reconstruction for the Caribbean from a *Montastraea faveolata* coral core from Puerto Rico (Kilbourne *et al.* 2007). The calibration procedure included conservative estimates of measurement uncertainty for all parameters, and provided calendar age probability distribution functions and ranges that included one standard deviation (Tables S2 and S3).

Due to the dramatic increase in bomb-produced ^{14}C concentrations in surface ocean waters that began in the late-1950s and peaked in the mid-1970s, we could unambiguously distinguish samples from before and after circa 1960 (Tables S2 and S3). Samples with calendar ages older than 1960 and 1960 or younger were labelled “pre-bomb” and “post-bomb” respectively. Coral fragments with very high fraction modern values could be readily assigned post-bomb calendar ages, often with very high precision (± 5 years or less). Due to a large number of fluctuations in ocean surface water $F^{14}\text{C}$ (or its corollary age-corrected $\Delta^{14}\text{C}$) values during the 19th and 20th centuries, fraction modern values often corresponded to more than one possible calendar age range. For a given sample, all possible calendar age ranges were either pre-bomb or post-bomb. When possible, some age ranges were eliminated by assuming stratigraphic order of ages among horizons within a pit. The calibrated age for each coral fragment was estimated by including all remaining possible age ranges and computing the midpoint of the range.

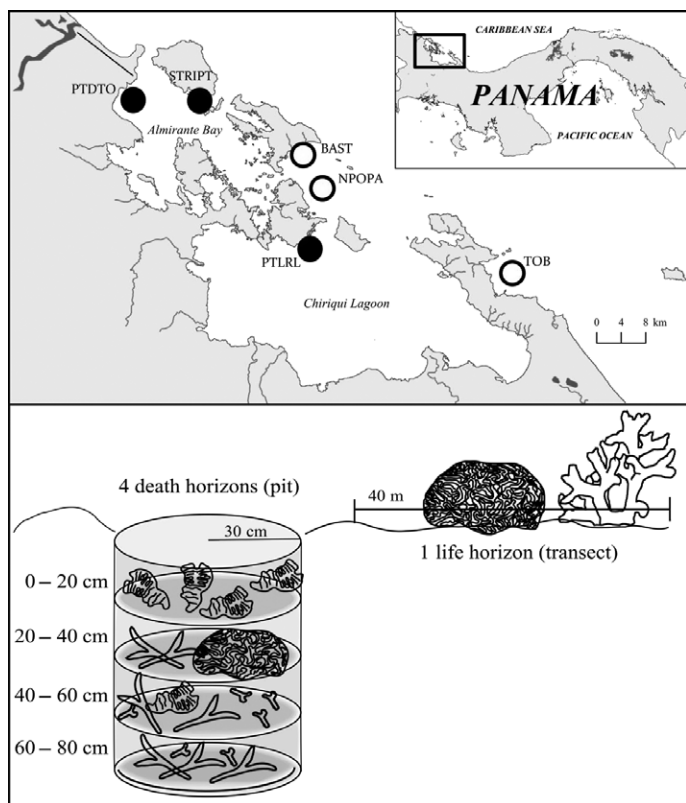


Figure 1 Study sites and sampling scheme for coral life and death assemblages and mollusc death assemblages from the Bocas del Toro region of western Caribbean Panama. Solid circles are lagoonal sites and open circles are offshore sites. Three replicates were sampled per site. PTDTO = Punta Donato, STRIPT = STRI Point, BAST = Bastimentos Island, NPOPA = North Popa Island, PTLRL = Punta Laurel, TOB = Tobobé.

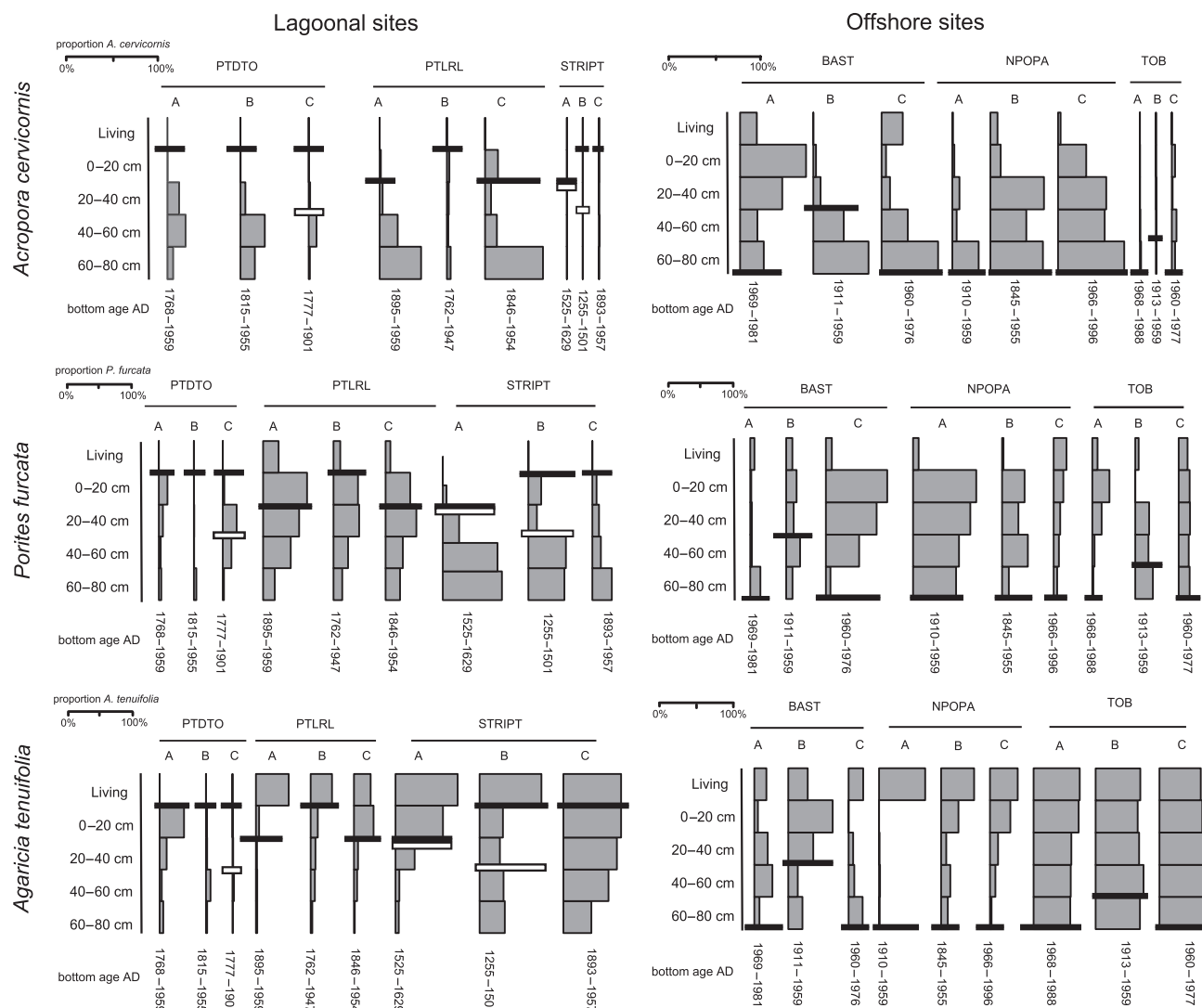


Figure 2 Proportion of the three most abundant coral species by individual pit and horizon. White horizontal line indicates boundary between pre- and post-1900 AD, solid horizontal line indicates boundary between pre- and post-1960 AD.

Radiocarbon dates were produced for 139 coral fragments. Fragments from the finger coral *Porites furcata* were selected for dating because it was the most widely distributed species among death horizons and pits. The lettuce coral *Agaricia tenuifolia* was used in three horizons that did not contain *P. furcata*. The tip of each fragment was selected so that the most recent growth was dated. Only samples that were free of visible calcareous overgrowth and internal boring were selected for analysis. AMS- ^{14}C analyses were performed at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory.

Data analysis

Changes in coral and mollusc communities before 1960 were assessed from 10 pits (nine lagoonal and one offshore) containing more than one pre-bomb horizon, and changes after 1960 were assessed from eight pits (all offshore) with one or no pre-bomb horizons. Within each of the two time periods, the oldest (deepest) and youngest (shallowest) layers were compared. Coral death assemblages from pits were also compared with coral life assemblages from line transect

surveys. All coral and mollusc taxonomic groups which comprised on average 5% or more of their respective ecological communities ("common" taxa) in the pre-1960, post-1960, or living reef were included in analyses of temporal change.

Statistical significance of temporal changes in coral and mollusc community composition was determined using the two-tailed version of the Wilcoxon signed-ranks nonparametric paired t -test, treating each pit as a sampling unit. Statistical significance of changes in total mass of coral skeletons and mollusc abundance was determined using the Friedman rank sum test, a nonparametric repeated-measures analysis of variance (ANOVA). For all analyses, statistical significance was determined at the $P = 0.05$ level.

RESULTS

Excavations yielded 1 088 kg of coral material, 23 658 bivalve individuals, and 13 666 gastropod individuals total. Coral communities were typically dominated by branching *Acropora cervicornis* and *Porites furcata* or foliaceous *Agaricia tenuifolia* (Fig. 2). *Acropora cervicornis* was dominant or subdominant in older horizons at offshore sites as well as

at lagoonal sites that today are characterised by turbid waters (D'Croz *et al.* 2005). Molluscan communities were dominated by the herbivorous gastropod *Cerithium* spp. and the epifaunal suspension-feeding bivalves *Dendrostea frons*, *Chama* spp., and *Barbatia cancellaria* (Fig. 3).

Significant temporal changes were detected in community composition despite high variability within and among sites. Ten pits with more than one pre-bomb horizon (primarily from lagoonal sites) displayed significant changes in coral community composition prior to

1960 and eight pits that contained one or no pre-bomb horizons (all from offshore sites) displayed significant changes after 1960. The calibrated radiocarbon ages of the deepest pre-bomb horizons varied greatly, from *c.* 50–750 years BP, although the majority of pits had maximum ages that extended back to the late 1700s or 1800s. (Figs. 2 and 3). The large age range is due to variation in sedimentation rates among pits and fundamental limits and uncertainties associated with the calibration of radiocarbon ages (Guilderson *et al.* 2005). By

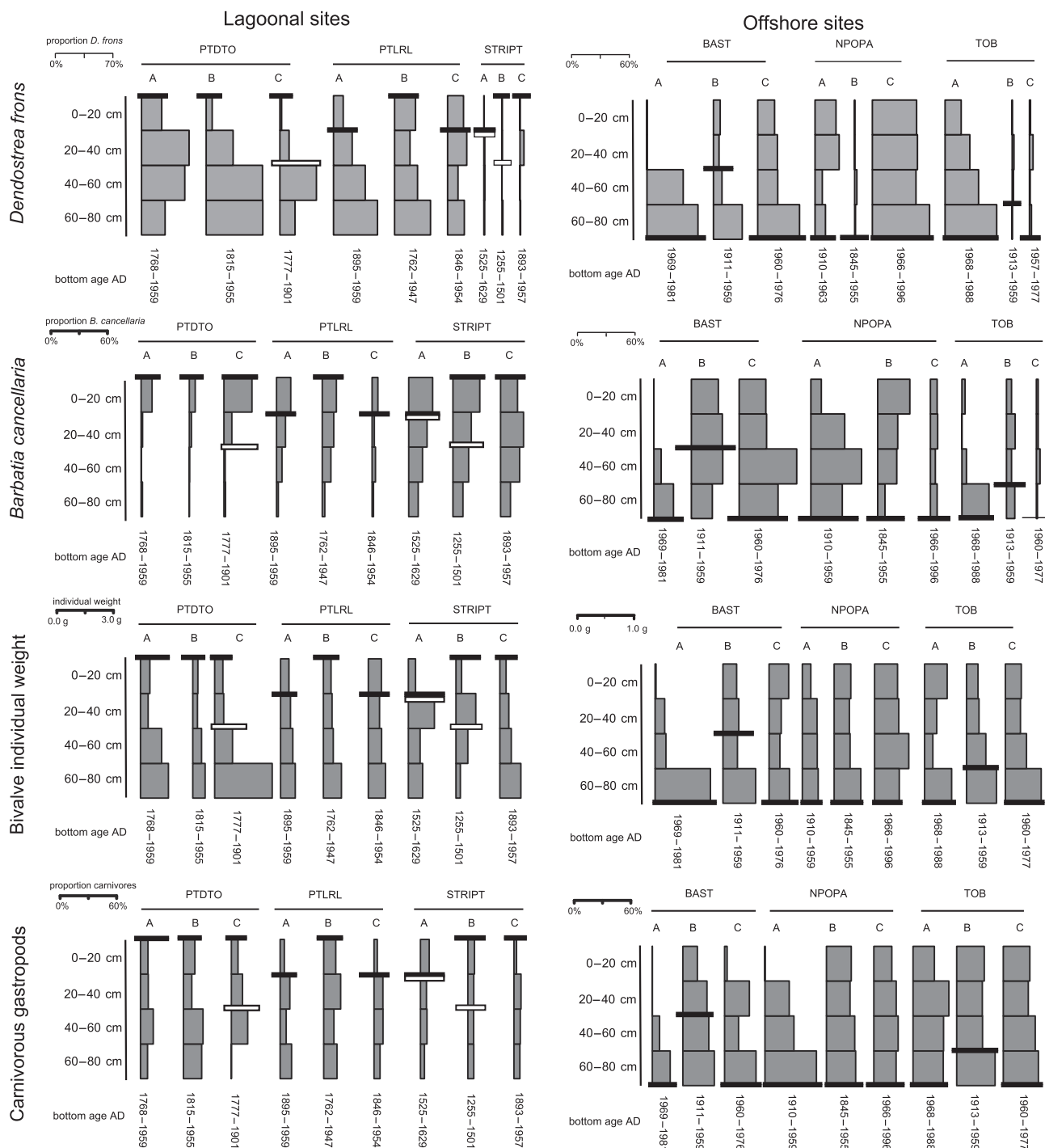


Figure 3 Molluscan community parameters by individual pit and horizon. White horizontal line indicates boundary between pre- and post-1900 AD, solid horizontal line indicates boundary between pre- and post-1960 AD.

comparison, coral rubble accumulation rates measured from lagoonal sites in Bocas del Toro and Belize predict a possible age range of 80–140 years respectively (Aronson *et al.* 2004; Hilbun 2009).

In the seven pits (six lagoonal and one offshore) that contained more than one pre-bomb horizons and where *A. cervicornis* was present, relative abundance of *A. cervicornis* declined from an average of 28% to 6% of the total coral community prior to 1960, after which it continued to decline to 0% of the living coral community (Fig. 2). Relative abundance of branching *P. furcata* increased prior to 1960 from 10% to 26% of the coral community in pits that lost *A. cervicornis*, but did not change in pits where *A. cervicornis* was originally absent (Fig. 2). As the total amount of coral material did not vary significantly among horizons within pits nor across pits, the increase in *P. furcata* relative abundance represents replacement of *A. cervicornis* by this species prior to 1960. Relative abundance of *A. tenuifolia* increased non-significantly from 12% to 23% prior to 1960 and to 42% of the living coral community, constituting a significant increase over the full time series.

At offshore pits with one or no pre-bomb horizons, relative abundance of *A. cervicornis* declined significantly after 1960 from 33% to 7% from the oldest death horizon to the living coral community (Fig. 2). Relative abundance of *P. furcata* first increased non-significantly from 18% to 37% from the oldest to youngest death horizons, and then decreased non-significantly to 9% in the living community. Relative abundance of *A. tenuifolia* remained stable at 31% throughout the post-1960 death horizons, then increased nearly significantly to 51% in the living community ($P = 0.1$). In summary, coral species proportions across death and life horizons revealed a gradual and progressive two-phase successional sequence of dominance by branching *A. cervicornis* → branching *P. furcata* → foliaceous *A. tenuifolia* that occurred before 1960 at lagoonal sites and continued during the post-1960 period to the present at offshore sites (Fig. 2). This differs from the single-phase replacement of *P. furcata* by *A. tenuifolia* reported in a coring study from this region (Aronson *et al.* 2004, 2005). Significant change was not observed for the other common taxonomic groups of corals *Colpophyllia natans*, *Madracis mirabilis*, *Millepora* spp., *Porites astreoides* and *Siderastrea* spp.

Significant changes in molluscan community composition and size structure also occurred before and after 1960 (Fig. 3). Prior to 1960, the previously dominant oyster *D. frons* declined from 40% to 18% at lagoonal sites whereas the mussel *B. cancellaria* increased from 6% to 18%. The oyster also declined from 27% to 12% at offshore sites after 1960. Because the number of bivalves did not vary significantly among

horizons, this represents a decline in the absolute abundance of *D. frons* throughout the time series. *Dendrostroma frons* most commonly lives attached to branching plexaurid and gorgoniid octocorals and secondarily on *A. cervicornis* (Forbes 1971; Fig. 4), whereas *B. cancellaria* typically attaches onto dead coral heads and rubble (Cerridwen & Jones 1991). Neither bivalve was harvested in the past nor is harvested today (Linares 1980; Carpenter 2002). Significant changes were not observed for the other common taxonomic groups of bivalves *Caribachlamys imbricata*, *Chama congregata/macerophyllia*, *Ctenoides* spp., *Lima lima*, *Lucina nassula/muricata*, *Musculus* spp. nor gastropods *Arene cruentata*, *Astraea tecta*, *Cerithium* spp., *Columbella mercatoria*, *Coralliophila* spp., *Hemitoma octoradiata*.

Most *Dendrostroma* from the pits exhibit the claw-like structures characteristic of attachment to gorgonians (Fig. 4). Therefore, decline in *D. frons* prior to 1960 strongly implies a comparable historical decline in abundance of its gorgonian and/or acroporid hosts. Disease decimated Caribbean gorgonians in the 1980s and 1990s (Smith *et al.* 1996), but primarily affected species not commonly associated with *D. frons*. Thus, the decline of *D. frons* before the first detailed ecological surveys of Caribbean reefs in the late 1970s signifies a mass mortality of gorgonians in Bocas del Toro predating by decades or more the first reported gorgonian disease outbreaks. Relative abundances of *A. cervicornis* and *D. frons* were highly positively correlated prior to 1960 primarily at lagoonal sites and after 1960 at offshore sites (Spearman $\rho = 0.66$ and $= 0.84$, respectively; $P < 0.001$ in both cases), suggesting that the loss of *A. cervicornis* habitat may have also contributed to the decline in the oyster. Average bivalve shell weight, which is a proxy for size, declined by more than half before 1960 primarily at lagoonal sites and after 1960 at offshore sites (Fig. 3). The decline was more apparent in epifaunal bivalves (pre-1960: $P = 0.06$; post-1960: $P = 0.10$). Shell weight of infaunal bivalves did not decrease. Changes in gastropod trophic structure occurred after 1960 at offshore sites. The proportion of carnivorous gastropods was halved from 32% to 16%, resulting in a similar level of herbivore dominance between offshore sites in the most recent death horizon and lagoonal sites (Fig. 3). None of the gastropods affected were harvested in the past nor are harvested today (Linares 1980; Carpenter 2002).

DISCUSSION

These changes in coral and molluscan communities (summarised in Table 1) demonstrate that reefs near Bocas del Toro experienced

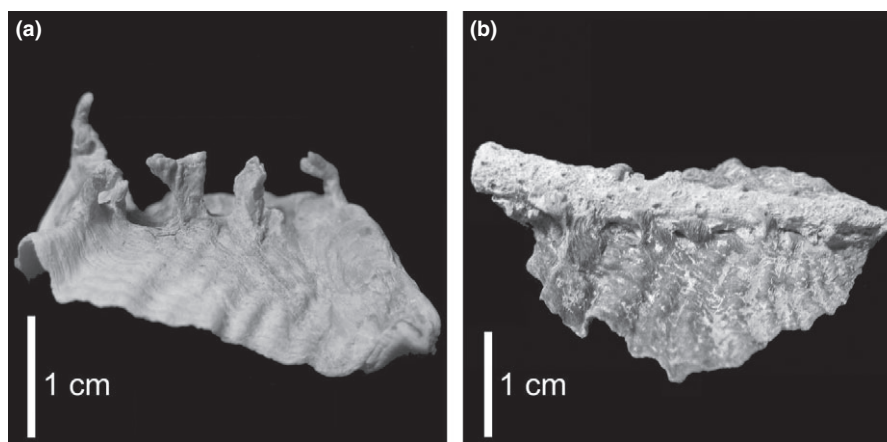


Figure 4 Attachment structures of *Dendrostroma frons*. (a) Hooks that attached to a branching gorgonian. (b) Specimen attached to branching staghorn coral *Acropora cervicornis*.

Table 1 Significant temporal changes in coral and molluscan communities from Wilcoxon signed-ranks test

Relative abundance/weight	Pre-1960				Post-1960				Pre-1960 – modern			
	Change	<i>n</i>	V	<i>P</i>	Change	<i>n</i>	V	<i>P</i>	Change	<i>n</i>	V	<i>P</i>
<i>Acropora cervicornis</i>	28–6%	7	21	< 0.05	33–7%	8	36	< 0.05	28–0%	7	21	< 0.05
<i>Porites furcata</i>	10–26%	7	1	= 0.05	–	–	–	–	–	–	–	–
<i>Agaricia tenuifolia</i>	–	–	–	–	31–51%	8	6	= 0.10	12–42%	10	6	< 0.05
<i>Dendrostroma frons</i>	40–18%	10	42	< 0.05	27–12%	8	32	= 0.05	–	–	–	–
<i>Barbatia cancellaria</i>	6–18%	10	0	< 0.05	–	–	–	–	–	–	–	–
Bivalve weight (all)	1.06–0.50 g	10	47	< 0.05	0.50–0.26 g	8	36	< 0.01	–	–	–	–
Bivalve weight (epifaunal)	0.90–0.43 g	10	46	= 0.06	0.43–0.34 g	8	30	= 0.10	–	–	–	–
Carnivorous gastropods	–	–	–	–	32–16%	8	1	< 0.05	–	–	–	–

n = number of pits, V = sum of ranks of paired differences resulting in a positive sign.

substantial ecological change before 1960 that was very likely underway by the 19th century. Acroporids are particularly sensitive to sedimentation as well as to bleaching and disease (Gladfelter 1982; Rogers 1990). Changes in molluscan size and trophic structure also signal deterioration of reef environmental conditions. Reef mollusc communities dominated by small individuals and low trophic levels indicate higher turbidity and nutrient loading from terrestrial runoff and restricted water flow (Jackson 1972) that disproportionately affect larger and higher trophic level species (Odum 1985; McClanahan 1992). The shift in trophic structure of gastropod communities at offshore sites towards that of higher turbidity and higher nutrient lagoonal sites suggests that degraded conditions are expanding offshore. Overall, changes were greater at lagoonal sites, but the pits from this environment also extended further back in time.

The timing of these changes implicates historical local anthropogenic disturbances such as land clearing and fishing as ultimate causes. Human population and deforestation have increased substantially over the past century in the Bocas del Toro region, increasing runoff of sediments, nutrients and pollutants to adjacent coral reef environments (Guzmán 2003) that negatively impact corals (Fabricius 2005) and mollusc (Sindermann 1996). Large-scale land clearing began at the turn of the 20th century for intensive banana production and has rapidly increased for tourism since the 1980s (Guzmán 2003). Our data suggest that the first episode of intensive land clearing transformed lagoonal reefs from communities dominated by *A. cervicornis* that requires clear waters (Rogers 1990) to turbid-water communities that are unsuitable for *A. cervicornis* and are now dominated by *A. tenuifolia*. Similar changes have occurred within the past 50 years offshore, severely threatening the last remaining large stands of *A. cervicornis* in the region (Guzmán 2003).

These results are in contrast to an earlier coring study in Almirante Bay in Bocas del Toro that reported a widespread replacement of *P. furcata* by *A. tenuifolia* in recent decades (Aronson *et al.* 2004, 2005). The discrepancy in study results is likely due to the greater variety of reef environments and substantially greater amount of material sampled in our large diameter pits relative to the narrow diameter cores. In addition, we quantified the relative abundance of all coral taxa in our pits whereas only the dominant coral species was assessed in the cores. As a result, our novel paleontological sampling technique enabled us to discern a more complex trajectory of change than that reported in the coring studies.

The dramatic historical transformations we quantified on reefs near Bocas del Toro are consistent with results of previous qualitative surveys from other regions of the Caribbean. A comparison of historical data and naturalist's observations with paleoecological data

revealed that reef corals including *Acropora* spp. were depleted at sites across the Caribbean as early as the 19th century (Pandolfi *et al.* 2003), and the proportion of sites dominated by *Acropora* corals in particular had declined before the 1980s (Jackson *et al.* 2001). Similarly, paleoecological data from the opposite end of the southern Caribbean in Barbados showed that *A. palmata* underwent a dramatic decline within the past centuries concurrent with large-scale land clearing during the onset of European colonisation (Lewis 1984). Together, these data contradict arguments that Caribbean reef coral decline began in the most recent decades (Aronson *et al.* 2004, 2005) or is restricted to specific portions of the Caribbean, such as Jamaica (Bruno *et al.* 2009), and demonstrate that major reef decline was occurring in the Caribbean at least decades before coral bleaching and disease outbreaks linked to anthropogenic climate change. Our results strengthen the argument that local, historical anthropogenic stressors, such as land clearing and overfishing, precipitated a decline in Caribbean reef corals that has intensified in recent decades from climate change impacts. These results, coupled with increasing evidence that protection from local disturbances may increase reef resilience to climate change (Hughes *et al.* 2007; Knowlton & Jackson 2008), highlight the importance of managing local impacts such as fishing and land clearing to stem the tide of reef decline.

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AUTHORSHIP

KLC and JBCJ designed research and wrote the article; KLC, CVA, JLP and TPG performed research; KLC, JBCJ and TPG analysed data.

REFERENCES

- Aronson, R.B., Macintyre, I.G., Wapnick, C.M. & O'Neill, M.W. (2004). Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology*, 85, 1876–1891.
- Aronson, R.B., Macintyre, I.G., Lewis, S.A. & Hilbun, N.L. (2005). Emergent zonation and geographic convergence of coral reefs. *Ecology*, 86, 2586–2600.
- Brown, B.E. (1997). Coral bleaching: causes and consequences. *Coral Reefs*, 16, S129–S138.
- Bruno, J.F., Sweatman, H., Precht, W.F., Selig, E.R. & Schutte, V.G.W. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*, 90, 1478–1484.
- Carilli, J.E., Norris, R.D., Black, B., Walsh, S.M. & McField, M. (2010). Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Glob. Change Biol.*, 16, 1247–1257.
- Carpenter, K.E. (2002). *The Living Marine Resources of the Western Central Atlantic. Vol. 1, Introduction, Mollusks, Crustaceans, Hagfishes, Sharks, Batoid Fishes and Chimaeras*. Food and Agriculture Organization of the United Nations, Rome.
- Cerridwen, S.A. & Jones, B. (1991). Distribution of bivalves and gastropods in the Pleistocene Ironshore Formation, Grand Cayman, British West Indies. *Carib. J. Sci.*, 27, 97–116.
- D'Croz, L., Del Rosario, J.B. & Gondola, P. (2005). The effect of fresh water runoff on the distribution of dissolved inorganic nutrients and plankton in the Bocas del Toro archipelago, Caribbean Panama. *Carib. J. Sci.*, 41, 414–429.
- Donner, S.D., Knutson, T.R. & Oppenheimer, M. (2007). Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. *Proc. Natl. Acad. Sci. USA*, 104, 5483–5488.
- Fabrizius, K.E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Poll. Bull.*, 50, 125–146.
- Forbes, M.L. (1971). Habitats and substrates of *Ostrea frons*, and distinguishing features of early spat. *Bull. Mar. Sci.*, 21, 613–625.
- Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, 301, 958–960.
- Gladfelter, W.B. (1982). White-Band Disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. *Bull. Mar. Sci.*, 32, 639–643.
- Glynn, P.W. (1991). Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol. Evol.*, 6, 175–179.
- Goreau, T.J. (1992). Bleaching and reef community change in Jamaica: 1951–1991. *Am. Zool.*, 32, 683–695.
- Green, D.H., Edmunds, P.J. & Carpenter, R.C. (2008). Increasing relative abundance of *Porites astreoides* on Caribbean reefs mediated by an overall decline in coral cover. *Mar. Ecol. Prog. Ser.*, 359, 1–10.
- Greer, L., Jackson, J.E., Curran, H.A., Guilderson, T.P. & Teneva, L. (2009). How vulnerable is *Acropora cervicornis* to environmental change? Lessons from the early to middle Holocene. *Geology*, 37, 262–266.
- Guilderson, T.P., Reimer, P.J. & Brown, T.A. (2005). The boon and bane of radiocarbon dating. *Science*, 307, 362–364.
- Guzmán, H.M. (2003). Caribbean coral reefs of Panama: present status and future perspectives. In: *Latin American Coral Reefs* (ed. Cortes, J.). Elsevier Science, Amsterdam, pp. 241–274.
- Halley, R.B. & Hudson, J.H. (2007). Fidelity of annual growth in *Montastrea faveolata* and the recentness of coral bleaching in Florida. In: *Geological Approaches to Coral Reef Ecology* (ed. Aronson, R.B.). Springer, New York, pp. 166–177.
- Harvell, C.D., Kim, K.K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., Grimes, D.J. *et al.* (1999). Emerging marine diseases—climate links and anthropogenic factors. *Science*, 285, 1505–1510.
- Hilbun, N. (2009). Land use and reef ecology in the Bocas del Toro Archipelago, Panama. PhD Dissertation (online only), UMI ProQuest, Ann Arbor. Publication no. 3388768.
- Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.
- Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O. & McCook, L. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr. Biol.*, 17, 360–365.
- Jackson, J.B.C. (1972). The ecology of the mollusks of *Thalassia* communities, Jamaica, West Indies. II. Molluscan population variability along an environmental stress gradient. *Mar. Biol.*, 14, 304–337.
- Jackson, J.B.C. (1997). Reefs since Columbus. *Coral Reefs*, 16, S23–S32.
- Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J. *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 292, 629–637.
- Kilbourne, K.H., Quinn, T.M., Guilderson, T.P., Webb, R.S. & Taylor, F.W. (2007). Decadal- to interannual-scale source water variations in the Caribbean Sea recorded by Puerto Rican coral radiocarbon. *Clim. Dyn.*, 29, 51–62.
- Knowlton, N. & Jackson, J.B.C. (2008). Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biol.*, 6, 215–220.
- Lewis, J.B. (1984). The *Acropora* inheritance: a reinterpretation of the development of fringing reefs in Barbados, West Indies. *Coral Reefs*, 3, 117–122.
- Linares, O.F. (1980). Ecology and prehistory of the Aguacate Peninsula in Bocas del Toro. In: *Adaptive Radiations in Prehistoric Panama* (eds Linares, O.F. & Ranere, A.J.). Harvard University Press, Cambridge, pp. 57–66.
- McClanahan, T.R. (1992). Epibenthic gastropods of the Middle Florida Keys: the role of habitat and environmental stress on assemblage composition. *J. Exp. Mar. Biol. Ecol.*, 160, 169–190.
- McClenahan, L., Hardt, M., Jackson, J. & Cooke, R. (2010). Mounting evidence for historical overfishing and long-term degradation of Caribbean marine ecosystems: comment on Julio Baisre's "Setting a baseline for Caribbean fisheries". *J. Isl. Coastal. Arch.*, 5, 165–169.
- Neumann, C.J., Cry, G.W., Caso, E.L. & Jarvian, B.R. (1978). *Tropical Cyclones of the North Atlantic Ocean. 1871–1977*. National Climatic Center, Asheville, NC.
- Odum, E.P. (1985). Trends expected in stressed ecosystems. *Bioscience*, 35, 419–422.
- Pandolfi, J.M. & Jackson, J.B.C. (2006). Ecological persistence interrupted in Caribbean coral reefs. *Ecol. Lett.*, 9, 818–826.
- Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G. *et al.* (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301, 955–958.
- Reimer, P.J., Baillie, M.G.L., Bard, E., Bayliss, A., Beck, J.W., Blackwell, P.G. *et al.* (2004). INTCAL09 and Marine09 Radiocarbon age calibration curves, 0–50 000 years CAL BP. *Radiocarbon*, 51, 1011–1150.
- Rogers, C.S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol. Prog. Ser.*, 62, 185–202.
- Sindermann, C.J. (1996). *Ocean Pollution: Effects on Living Resources and Humans*. CRC Press, Boca Raton.
- Smith, G.W., Ives, L.D., Nagelkerken, I.A. & Ritchie, K.B. (1996). Caribbean sea-fan mortalities. *Nature*, 383, 487.
- Stuiver, M. & Reimer, P.J. (1986). A computer program for radiocarbon age calibration. *Radiocarbon*, 28, 980–1021.
- Stuiver, M. & Polach, H.A. (1977). Reporting of ^{14}C data. *Radiocarbon*, 19, 355–363.

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