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Climatic and biotic thresholds of coral-reef shutdown

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Climate change is now the leading cause of coral-reef degradation and is altering the adaptive landscape of coral populations[1,2]. Increasing sea temperatures and declining carbonate saturation states are inhibiting short-term rates of coral calcification, carbonate precipitation and submarine cementation[3–5]. A critical challenge to coral-reef conservation is understanding the mechanisms by which environmental perturbations scale up to influence long-term rates of reef-framework construction and ecosystem function[6,7]. Here we reconstruct climatic and oceanographic variability using corals sampled from a 6,750-year core from Pacific Panamá. Simultaneous reconstructions of coral palaeophysiology and reef accretion allowed us to identify the climatic and biotic thresholds associated with a 2,500-year hiatus in vertical accretion beginning ~4,100 years ago[8]. Stronger upwelling, cooler sea temperatures and greater precipitation—indicators of La Niña-like conditions—were closely associated with abrupt reef shutdown. The physiological condition of the corals deteriorated at the onset of the hiatus, corroborating theoretical predictions that the tipping points of radical ecosystem transitions should be manifested sublethally in the biotic constituents[9]. Future climate change could cause similar threshold behaviours, leading to another shutdown in reef development in the tropical eastern Pacific.

Climatic and oceanographic variability have played a dominant role in the development of reefs throughout the Phanerozoic eon[10], and the recent past is no exception. In Panamá and several other locations in the Pacific, coral reefs stopped accreting vertically for 2,500 years, beginning ~4,100 cal yr BP (ref. 8; calibrated ^{14}C calendar years before 1950; Fig. 1a). Correlations with regional palaeoclimate proxies suggest that enhanced variability of the El Niño/Southern Oscillation (ENSO) was the ultimate cause of reef shutdown in the tropical eastern Pacific[8] (TEP). Climatic shifts at that time led to environmental and cultural impacts on a global scale[11,12].

In this study we investigated the long-term impacts of environmental variability on coral physiology and reef development in the TEP to ascertain the climatic, oceanographic and biotic controls on ecosystem state in the past. We quantified the range of environmental conditions that corals experienced during the past ~6,750 years to determine whether significant changes in climate or oceanography were associated with changes in coral physiology or reef accretion. We then evaluated the environmental and physiological thresholds that characterized the catastrophic phase shift to the hiatus.

In Pacific Panamá, El Niño-like periods are characterized by a warm, dry climate and a reduction in seasonal upwelling. Those conditions are reversed during La Niña-like periods (Supplementary Discussion and Supplementary Fig. 1). Contemporary environmental variability is high at Contadora Island, a site in Pacific Panamá that is exposed to intense seasonal upwelling and the interannual impacts of ENSO. We extracted a 2.68-m, vertical push-core, designated EP09-28, from the uncemented reef framework at Contadora. The framework is built of branch fragments of *Pocillopora* spp. corals packed in fine sediment (Supplementary Fig. 3). Through geochemical analysis of the coral skeletons, we reconstructed reef palaeoenvironments and changes in coral physiology during the entire Holocene history of the Contadora reef, from its initiation ~6,750 cal yr BP to present (Supplementary Table 4 and Supplementary Fig. 7).

To constrain environmental conditions before and after the hiatus we measured the elemental ratios and isotopic compositions of 133 diagenetically unaltered *Pocillopora* skeletons distributed throughout the core (Supplementary Fig. 4). Our palaeoclimatic reconstructions are based on temperature calibrations for Sr/Ca and oxygen isotopes (δ^{18}O) using modern *Pocillopora damicornis* colonies from Contadora (Fig. 2 and Supplementary Figs 5 and 6). Whereas Sr/Ca in coral skeletons is primarily driven by temperature, δ^{18}O reflects a combination of temperature and seawater δ^{18}O ($\delta^{18}O_{sw}$), which generally tracks hydrologic variability[13] (Fig. 2). We identified a significant relationship between Sr/Ca and temperature (Fig. 2a), and between coral-reconstructed $\delta^{18}O_{sw}$ and local precipitation (Fig. 2c), in the modern corals. The modern-day calibration confirmed that Sr/Ca and δ^{18}O records from pocilloporid corals capture the seasonal range in climate characterized by intense winter-time upwelling of cooler water (high Sr/Ca and high δ^{18}O) accompanied by dry conditions (high $\delta^{18}O_{sw}$).

At each sampled horizon in the core, we used multiple coral fragments to reconstruct: palaeotemperature and palaeosalinity from Sr/Ca and δ^{18}O (ref. 13); oceanic palaeoproductivity (upwelling), primarily from the local reservoir correction ΔR (= Δ^{14}C; ref. 8; Supplementary Methods) and to a lesser extent from Ba/Ca (ref. 14); and coral physiology from δ^{13}C and B/Ca (refs 15–18). Although there has been much debate over the interpretation of δ^{13}C in coral skeletons, its variability is generally assumed to be driven by metabolic processes in the

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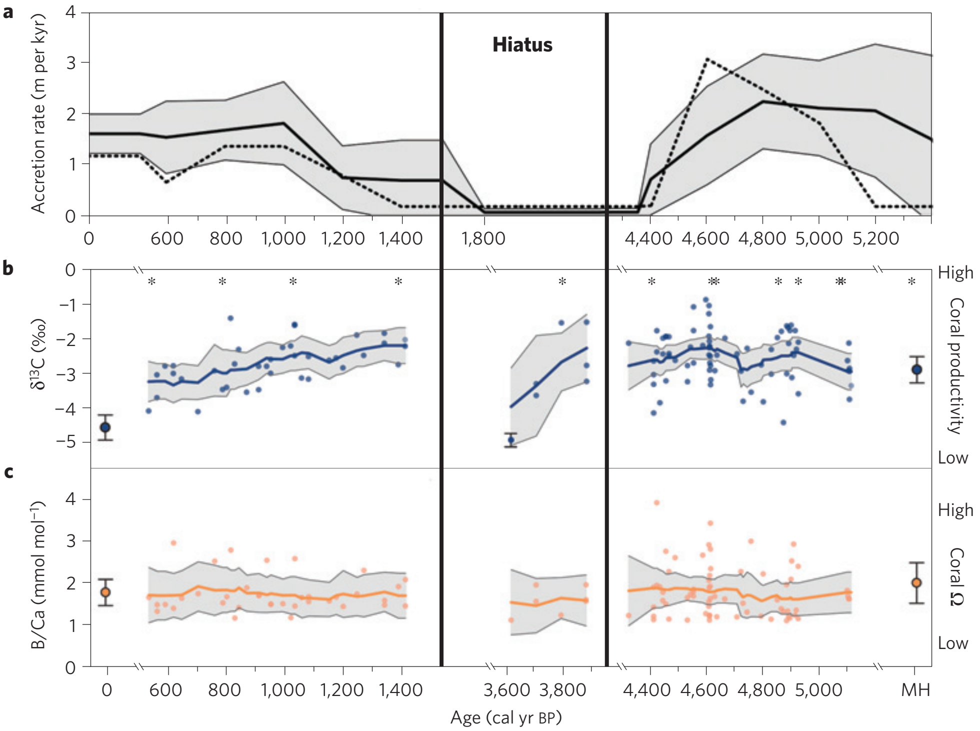

Figure 1 | Palaeoecological reconstructions of reef development in the Gulf of Panamá from the mid-Holocene (~6,750 cal yr BP) to present. Data are shown in relation to the hiatus in reef development (thick black outline). Bold lines represent 200-yr running means and grey shading represents the 95% CI. **a**, Reef accretion from the core used for geochemistry (dotted line) and variability from four additional cores from Contadora. **b**, Coral productivity (blue) from δ^{13}C. The data from ~3,600 cal yr BP are shown as the mean ±95% CI of replicate samples. **c**, Internal aragonite saturation state of the corals (Ω; orange) from B/Ca. In **b**,**c**, measurements from mid-Holocene (MH) coral samples are aggregated into means (±95% CI), as are modern samples. Asterisks indicate the location of U-series dates used to construct an age model for the core.

coral holobiont[15,16]. Photosynthetic activity by the zooxanthellae preferentially fixes the lighter ^{12}C isotope, which enriches ^{13}C in the coral skeleton during periods of high coral productivity[15]. We thus interpret changes in δ^{13}C as an indicator of the productivity of the coral–zooxanthellae symbiosis[15,16]. Changes in B/Ca in foraminifera have been linked to carbonate saturation state at the internal sites of calcification, a relationship that is apparently independent of external pH (ref. 17). Variability in B/Ca is also independent of pH in corals[18], indicating that the mechanism by which boron is incorporated into coral skeletons may be similar. We interpret B/Ca in the coral skeletons as an indicator of the internal saturation state of the coral. We evaluated average trends in the geochemical data from multiple individuals within 200-yr time windows against observed changes in vertical reef accretion[8] (Supplementary Methods). Analysis of an ensemble of late-twentieth-century coral fragments allowed us to quantify within-population geochemical and isotopic variability, for comparison with potential signals in the palaeo-reconstructions.

Accretion was relatively slow when reef development initiated at Contadora ~6,750 cal yr BP (Fig. 1a). The geochemistry indicates that this period was cool, wet and characterized by moderate upwelling (Fig. 3), corroborating existing records of high oceanic productivity in the TEP from ~7,000–5,000 cal yr BP (refs 19,20). Our findings are consistent with a persistent, La Niña-like state in the tropical Pacific during the mid-Holocene[19–21].

Sea temperatures reconstructed from Sr/Ca reflect warming from ~19 °C at ~5,100 cal yr BP to ~25.5 °C at ~4,600 cal yr BP (Fig. 3a), which may be related to the decline in upwelling during that time (Fig. 3d,e). In contrast, δ^{18}O remained fairly stable over this period (Fig. 3b), suggesting that Pacific Panamá was relatively dry during the warmest interval (Fig. 3c). These changes are consistent with stronger or more frequent El Niño events, or a dampened seasonal cycle around 4,600 cal yr BP; however, this trend is not apparent in other records from the region[19,21]. Accretion rates were highest when temperature peaked ~4,600 cal yr BP, but declined precipitously in the run-up to the hiatus (Fig. 1a). Reconstructions of ΔR suggest that upwelling became significantly more intense and water temperatures cooled beginning 400 years before the hiatus (Fig. 3). Despite high environmental variability ~5,100–4,400 cal yr BP, average coral productivity and internal aragonite saturation state remained stable (Fig. 1b,c).

The physiological condition of the corals declined markedly at the onset of the hiatus. Coral productivity, as reflected by δ^{13}C, was lower and more variable 3,900–3,600 cal yr BP than in any other part of our record (Fig. 1b). Indeed, six replicate analyses from the same coral confirm the anomalously low δ^{13}C-value at ~3,600 cal yr BP. The fact that the other elemental ratios from this specimen—B/Ca, Sr/Ca, and Ba/Ca—fell within the range of other corals from the same period (Figs 2a,d and 1c) argues against a diagenetic explanation for the low ^{13}C-value. Average B/Ca was also 12% lower 3,900–3,600 cal yr BP than during the preceding centuries, although the trend was not significant. The decline in coral condition just before reef shutdown corroborates theoretical predictions that ecosystems on the brink of collapse exhibit early warning signs of increasingly wide ecological excursions and progressively slower rates of recovery from disturbance[9].

The observed environmental changes during the 300 yr following reef shutdown—significantly stronger upwelling, significantly cooler temperatures and higher precipitation (Fig. 3)—are consistent with a La Niña-like climate from 3,800 to 3,200 cal yr BP (ref. 21). We posit that more frequent or stronger La Niña events during this interval provided the initial physiological trigger that shut down reef accretion in Pacific Panamá. Elevated precipitation would have increased terrigenous input, resulting in higher turbidity

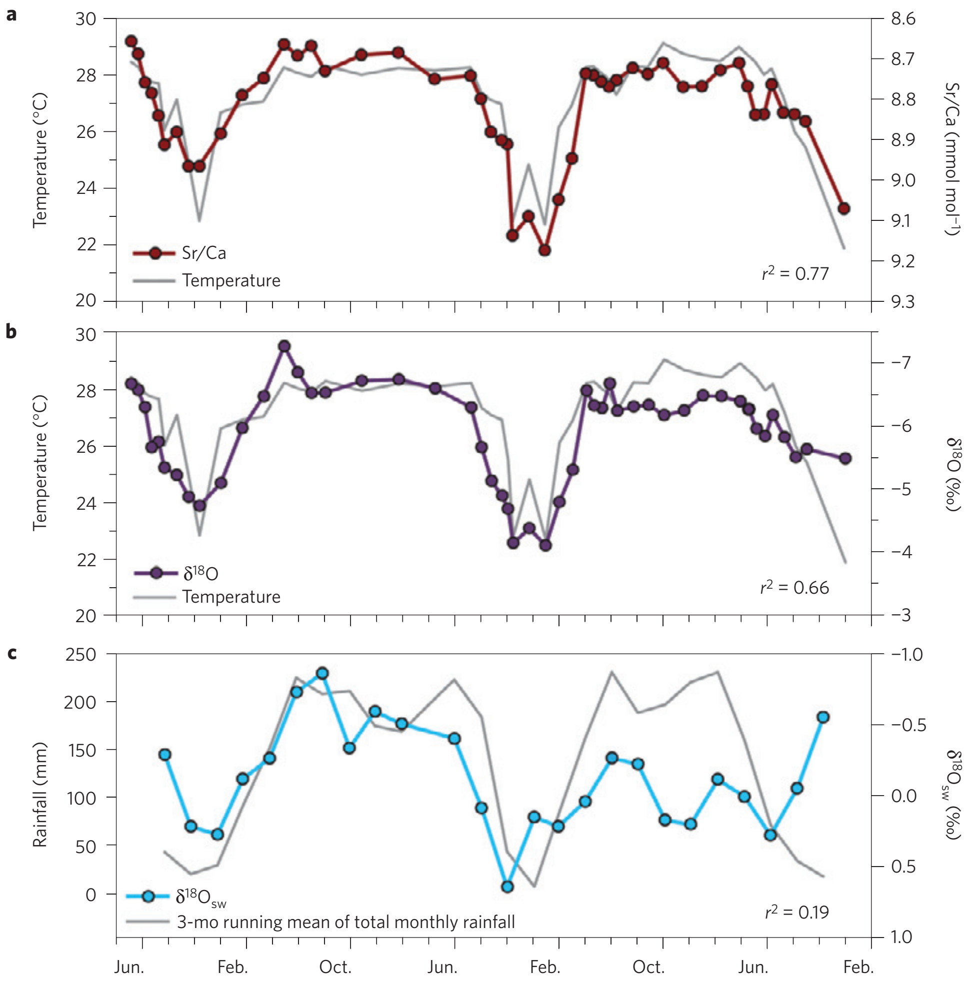

Figure 2 | Trends in Sr/Ca, δ^{18}O and $\delta^{18}O_{sw}$ in a representative modern colony of *Pocillopora damicornis* from Contadora Island, Gulf of Panamá, winter 2006–summer 2008. a, Relationship between Sr/Ca (red) and *in situ* temperature (grey). **b**, Relationship between δ^{18}O (purple) and *in situ* temperature (grey). **c**, Relationship between $\delta^{18}O_{sw}$ (cyan) and the three-month running mean of total monthly rainfall in Panamá City (grey).

and lower light penetration to the reef. Reduced water temperatures (Supplementary Fig. 1c) and decreased light penetration driven by more intense upwelling would have reduced coral productivity relative to heterotrophic feeding[15,16] and slowed *Pocillopora* growth rates[22]. Upwelling would have also decreased oceanic pH and aragonite saturation state[3], which could explain the 12% decline in B/Ca at the start of the hiatus. The onset of La Niña-like conditions triggered initial reef shutdown and enhanced ENSO variability continued to suppress reef development for the next two millennia[8].

As the hiatus also occurred in Panamá's Gulf of Chiriquí, where there is no upwelling[22], we infer that climatic cooling and a reduction in light initiated reef shutdown throughout the region. Increased upwelling would have further stressed the corals in the Gulf of Panamá, which explains the more protracted hiatus at Contadora relative to the Gulf of Chiriquí. Contemporaneous hiatuses in Costa Rica, Australia and Japan also occurred in low-light environments, consistent with our interpretation[8].

Reef accretion resumed at Contadora from 1,750 to 1,400 cal yr BP and remained high to present (Fig. 1a). Reduced ENSO variability and a more El Niño-like state[21,23] allowed Panamanian reefs to recover during the late Holocene. By 1,400 cal yr BP, the environment was characterized by relatively weak upwelling and a favourable regime of temperature and precipitation (Fig. 3). Upwelling intensity remained low in the Gulf of Panamá from 1,400 cal yr BP to present (Fig. 3d,e), but temperature and precipitation were more variable during the last millennium.

The Medieval Climate Anomaly (MCA; 1,150–700 cal yr BP) reflects relatively warm conditions that are similar, within error, to temperatures in the late twentieth century (Fig. 3a–c) and are consistent with an El Niño-dominated state in Pacific Panamá. In contrast, temperatures during the Little Ice Age (LIA; ~600–550 cal yr BP) were ~5 °C cooler (Fig. 3a–c), suggesting a return to La Niña-like conditions after the MCA. The LIA represents the coldest, wettest interval in our record. Reef accretion declined despite weak upwelling throughout the late Holocene, supporting our conclusion that changes in temperature and precipitation were the ultimate cause of the hiatus in Pacific Panamá. The suggestion that the MCA was characterized by a more El Niño-like state, whereas the LIA was more La Niña-like, is supported by reconstructions throughout the tropical Pacific[23,24]; however, there remains little consensus about the broad-scale impacts of the MCA and the LIA on the region[25,26].

A steady decrease in coral δ^{13}C from 1,400 cal yr BP to present suggests that coral productivity declined in the recent past. The anomalously low δ^{13}C of modern corals (Fig. 1b) is primarily a result of the so-called ^{13}C Suess effect: a decrease in atmospheric δ^{13}C caused by the burning of fossil fuels[27]. Cooler sea temperatures during the LIA may explain the low coral productivity after 600 cal yr BP, but temperatures were higher from 1,400 to 600 cal yr BP (Fig. 3). Another possible cause of declining coral productivity is the putative increase in the frequency of El Niño events in recent millennia[21,23]. El Niño events cause high-temperature

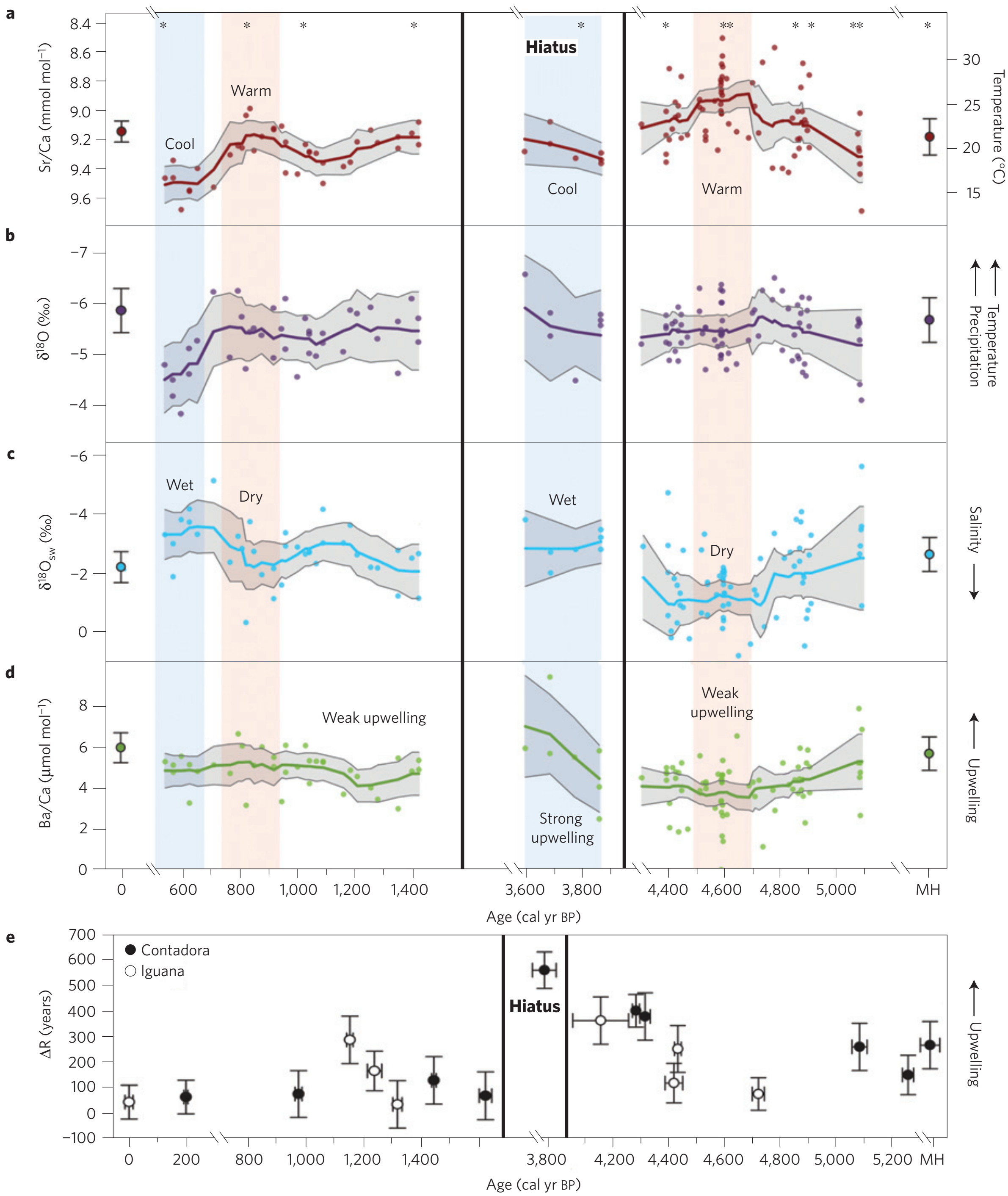

Figure 3 | Environmental variability in the Gulf of Panamá from the mid-Holocene (~6,500 cal yr BP) to present. Data are shown in relation to the hiatus in reef development (thick black outline). Bold lines represent 200-yr running means and grey shading represents 95% CIs. **a**–**c**, Palaeoclimatic reconstructions were derived from: Sr/Ca-based temperature reconstructions (red; **a**), combined temperature and precipitation from $\delta^{18}O$ (purple; **b**) and $\delta^{18}O_{sw}$ (salinity) calculated by subtracting the reconstructed Sr/Ca-based temperatures from the $\delta^{18}O$ signature of the corals (cyan; **c**). **d**,**e**, Reconstructions of upwelling from: Ba/Ca (green; **d**), and ΔR from Contadora (black) and Iguana Islands (white; **e**). In **b**,**c**, measurements from the mid-Holocene (MH) coral samples are aggregated into means (±95% CI), as are the modern samples. Asterisks indicate the location of U-series dates used to construct an age-model for the core.

stress and coral bleaching, reducing coral productivity and driving $\delta^{13}C$ to more negative values[16].

Despite high environmental variability and declining coral productivity during the late Holocene, B/Ca varied little from 1,400 to 550 cal yr BP (Fig. 1c). The precision of our B/Ca measurements was low relative to the range of measured B/Ca (Supplementary Table 3), which may partially explain this result. Upwelling reduces the pH of sea water, which leads to lower carbonate saturation states in upwelling regions[3]. Assuming that B/Ca reflects corals' internal saturation state[17,18], B/Ca should be strongly and negatively correlated with indicators of upwelling such as ΔR and Ba/Ca if internal saturation state is purely a function of the external environment. The only detectable, albeit nonsignificant decline in B/Ca—12%—occurred during the onset of the hiatus, when upwelling intensity was higher, and pH presumably lower, than at any other time in the record.

Secular trends in ocean acidification through the Holocene[28] suggest that changes in carbonate chemistry did not drive the observed hiatus. Our results are consistent with the suggestion that corals have the capacity to buffer their internal carbonate chemistry against changes in the external environment and, therefore, might not be noticeably affected by the changes in oceanic acidity expected in the near future[2,29]. The projected increase in extreme thermal stress over the coming decades will cause enormous damage to coral reefs before the impacts of ocean acidification on corals are realized[1,29].

Although these results are derived from a single core, the high degree of replication inherent in our sampling strategy allows us to calculate a robust estimate of the uncertainties in our coral reconstructions. Our geochemical and isotopic data from core EP09-28 suggest that the reef at Contadora was remarkably resistant to climatic and oceanographic variability over the past 6,750 years. Reef development persisted despite marked variations in upwelling intensity, precipitation and average sea temperatures that ranged from 16 to 26 °C (from Sr/Ca) outside the hiatus. At the onset of the hiatus, however, the reef reached a critical ecological and environmental threshold beyond which coral growth and vertical framework accretion could not be sustained. The reef was growing in at least 1.5 m of water (relative to mean sea level) since initiation (Supplementary Fig. 2), excluding sea level as the primary cause of significant palaeoecological change. Environmental shifts after ~4,100 cal yr BP were associated with marked changes in the palaeophysiology of the corals, most notably the decline in coral productivity ($\delta^{13}C$). The inferred environmental tipping point was followed by a decline in coral growth and then whole-reef degradation[8,9].

Climatic and oceanographic variability controlled the growth of coral populations and the development of coral reefs in the tropical eastern Pacific during the Holocene. If the sublethal trend of declining coral productivity at the onset of the hiatus was an early warning sign of deteriorating ecosystem state and impending collapse[9], then the decline of coral productivity during the late Holocene could likewise portend a reef shutdown. Whereas the 2,500-yr collapse of Panamanian reefs was provoked by a shift to a cooler climate, anthropogenic climate change is now increasing sea temperatures on a global scale. Average sea temperatures at Contadora are now within only a few degrees of the maximum temperatures that supported coral growth during the Holocene (Fig. 3a). In a global coral-reef landscape characterized by declining coral cover, reduced growth and calcification, and negative trajectories of reef accretion, mitigating and reversing anthropogenic climate change are critical steps to ensuring the continuity of coral populations, reef-framework accretion, and the ecosystem services that coral reefs provide[1–7].

Methods

We developed temperature calibrations for *Pocillopora damicornis* by relating the Sr/Ca and $\delta^{18}O$ profiles of three modern corals from Contadora to *in situ* temperatures measured for the period during which the corals grew. We drilled the skeletons of the corals at submonthly resolution along their longitudinal growth axes. The resulting 72 samples were analysed for Sr/Ca and $\delta^{18}O$ in K.M.C.'s laboratory. $\delta^{18}O$ was measured on ThermoFisher Delta Plus V with a Kiel device. Average reproducibility of standards (1σ) was less than ±0.06‰ on average. Sr/Ca was measured on a HORIBA Jobin-Yvon Ultima 2C inductively coupled plasma-optical emission spectrometer. Average reproducibility of standards (1σ) was less than ±0.07%.

For the palaeoenvironmental reconstructions, we extracted a 268-cm core of *Pocillopora*-dominated reef framework from Contadora Island (8° 37′ 60″ N, 79° 01′ 44″ W), in the Gulf of Panamá upwelling system. Coral skeletons were dated throughout the core ($n=17$; asterisks in Figs 1 and 3) using U/Th analysis by inductively coupled plasma mass spectrometry (Supplementary Table 4). The U-series dates were used to create an age model for the geochemical data (Supplementary Fig. 7).

A total of 133 subfossil *Pocillopora* branch fragments in good taphonomic condition were sampled in a roughly even distribution throughout the core for geochemical analysis. Scanning electron microscopy showed diagenetic alteration to be negligible (Supplementary Fig. 4). The branch fragments were split longitudinally and drilled along their growth axes using a micromill. Carbonate powders from each branch fragment were combined into a homogenized sample representing ~1–2 yr of coral growth[22].

Geochemical analyses of the subfossil branch fragments were conducted at the Stable Isotope Laboratory at the Rosenstiel School of Marine and Atmospheric Science. Stable-isotope ratios ($\delta^{18}O$ and $\delta^{13}C$) were measured using standard techniques on a Thermo-Finnigan Delta Plus mass spectrometer with a Kiel device. Reproducibilities (1σ) of the in-house standard—optically clear calcite—were less than ±0.10 ‰ for $\delta^{18}O$ and $\delta^{13}C$. Elemental concentrations of strontium (Sr), barium (Ba) and boron (B) were measured with a Varian Vista-PRO CCD (charge-coupled device) simultaneous inductively coupled plasma-optical emission spectrometer using standard techniques. Analytical precisions (1σ) of measurement on the in-house element-to-calcium standard were ±0.02% for Sr/Ca, ±0.19% for Ba/Ca, and ±0.55% for B/Ca.

We used our modern temperature calibration for Sr/Ca and $\delta^{18}O$ in *Pocillopora* to derive palaeotemperatures from the core record. Relative palaeosalinities ($\delta^{18}O_{sw}$) were then calculated by subtracting each Sr/Ca temperature signal from the corresponding $\delta^{18}O$ value. All other geochemical tracers were evaluated on a relative scale. Geochemical data are presented as 200-yr running means with 95% confidence intervals (CIs). Each 95% CI is a combined error that incorporates the uncertainty associated with analytical precision, geochemical variability within individual corals (Supplementary Table 1), variability among corals growing contemporaneously in the same environment (Supplementary Table 2), and variability among corals within the 200-yr window. The procedure for quantifying these uncertainties is described in the Supplementary Methods.

The local reservoir correction, ΔR, provides a measure of the offset between the conventional radiocarbon ages and the true ages of samples collected in the marine environment[8]. Upwelling reintroduces old carbon from deep waters to the surface, which increases the apparent age of shallow water-masses in upwelling regions. Thus, ΔR is a proxy for changes in upwelling intensity. We collected individual fragments of *Pocillopora* ($n=15$) and *Psammocora stellata* ($n=3$) from 5 cores from Contadora Island ($n=12$) and 4 cores from Iguana Island ($n=7$), both of which are located in the upwelling-influenced Gulf of Panamá[8]. Each coral fragment, weighing 0.5–3 mg, was broken into two samples for dating. One sample from each coral was ^{14}C-dated using accelerator mass spectrometry at the National Ocean Sciences AMS (NOSAMS) facility at Woods Hole and the other was dated by U/Th using inductively coupled plasma mass spectrometry by H.C. and R.L.E. Treating U/Th age as the true age, we obtained the expected radiocarbon age of that sample from the global marine calibration curve. The difference between the measured and expected radiocarbon ages of the coral yielded ΔR (Supplementary Methods).

The palaeoenvironmental data were evaluated against vertical reef accretion rates for Contadora and the proxies for palaeophysiology of the corals: $\delta^{13}C$ and B/Ca. We calculated millennial-scale rates of reef accretion (in m per kyr) from core EP09-28 and four additional cores from Contadora. The five cores were dated using a combination of bulk ^{14}C-dating with standard techniques (Beta Analytic), ^{14}C-dating by accelerator mass spectrometry (NOSAMS), and U-series dating (H.C. and R.L.E.). Vertical-accretion rates were calculated by dividing the length of an interval in the core, corrected for compaction, by the time over which that interval was deposited.

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Author contributions

L.T.T. conceived and designed the study, analysed the data, and wrote the paper. R.B.A. designed the study and wrote the paper. K.M.C. analysed the data and wrote the paper. H.C. and R.L.E. analysed the U-series data. P.R.G. and H.R.S. analysed the modern geochemical samples. All authors contributed to the discussion of results.

Additional information

The geochemical data set is available online in NOAA's Paleoclimatology database (http://www.ncdc.noaa.gov/paleo/study/17915). Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to L.T.T.

Competing financial interests

The authors declare no competing financial interests.