Coral calcification is dependent on the mutualistic partnership between endosymbiotic zooxanthellae and the coral host. Here, using newly developed geochemical proxies ($\delta^{11}$B and B/Ca), we show that Porites corals from natural reef environments exhibit a close ($r^2 \sim 0.9$) antithetic relationship between dissolved inorganic carbon (DIC) and pH of the corals’ calcifying fluid (cf). The highest DIC$_{cf}$ ($\sim \times 3.2$ seawater) is found during summer, consistent with thermal/light enhancement of metabolically (zooxanthellae) derived carbon, while the highest pH$_{cf}$ ($\sim 8.5$) occurs in winter during periods of low DIC$_{cf}$ ($\sim \times 2$ seawater). These opposing changes in DIC$_{cf}$ and pH$_{cf}$ are shown to maintain oversaturated but stable levels of carbonate saturation ($\Omega_{cf} \sim \times 5$ seawater), the key parameter controlling coral calcification. These findings are in marked contrast to artificial experiments and show that pH$_{cf}$ upregulation occurs largely independent of changes in seawater carbonate chemistry, and hence ocean acidification, but is highly vulnerable to thermally induced stress from global warming.

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Scleractinian corals together with their endosymbiotic dinoflagellates, *Symbiodinium* (zooxanthellae), have been spectacularly successful in building the tropical coral reef edifices that dominate many shallow-water environments and harbour more than one-third of the oceans’ biodiversity. The ongoing viability of these iconic tropical reef systems is however in question\(^1\,2,3\), with symbiont-bearing shallow-water corals now facing the combined challenge of both global warming and ocean acidification from rapidly rising levels of CO\(_2\) (ref. 4). Critical to the success of reef-building corals is their ability to convert seawater DIC into calcium carbonate, the major constituent of their skeletons. While much progress has been made in identifying many of the key elements of the biologic machinery that are integral to the biocalcification process\(^5\,7\) (Fig. 1), there are still significant gaps in our understanding. Foremost is the relationship between declining seawater pH and its impact on pH upregulation of the coral’s extracellular calcifying fluid\(^8\,10\), a process that occurs at least in part via Ca-ATPase pumping of Ca\(_{2+}\) ions into the calcifying region to exchange for the removal of protons\(^11\). Of equal but largely overlooked importance, are the mechanisms via which the various pH-dependent species of DIC (that is, CO\(_2\), HCO\(_3^-\), or CO\(_3^{2-}\)) are produced, transported, and then inter-converted at the site of calcification. It has also long been recognized\(^12\,13\) that light plays a key role in driving rates of calcification, and that light-enhanced calcification occurs as a result of the photosynthetic activity of endosymbiotic dinoflagellates (zooxanthellae), providing both energy and additional carbon needed to drive calcification. The exact mechanism(s) by which coral calcification is linked to endosymbiont photosynthesis has, however, remained largely enigmatic at the polyp scale (Fig. 1) the zooxanthellae are physically separated from the site of calcification\(^13\,15\) and, apart from pH, few direct measurements exist\(^16\) of the chemical conditions necessary to constrain the biocalcification process.

Here we provide new evidence for an intimate link between the biologically mediated process of pH\(_E\) upregulation of the calcifying fluid and biological control over the concentration of DIC in the calcifying fluid (DIC\(_{cf}\)). We find that over annual timescales there is an inverse correlation between pH\(_{cf}\) and DIC\(_{cf}\). This acts to maintain relatively stable levels of aragonite saturation in the calcifying fluid, and hence near-optimal rates of coral calcification, despite large seasonally driven variations in metabolically supplied DIC.

**Results**

Reef-water and coral calcifying fluid carbonate chemistry. To reconstruct the carbonate chemistry of the calcifying fluid from which corals precipitate their aragonite skeleton, we use the boron isotopic composition (δ\(^{11}\)B) as a proxy for the calcifying fluid pH\(_E\) (refs 10,17,18). For determining the carbonate ion concentrations [CO\(_3^{2-}\)] in the calcifying fluid, we use the combined δ\(^{11}\)B-B/Ca proxy\(^19\). The application of the δ\(^{11}\)B-B/Ca carbonate ion proxy has now been made possible by recent experimental measurements of the B/Ca carbonate ion distribution coefficient\(^19\), a major limitation of previous studies\(^20\) (see ‘Methods’ section). To examine how the chemistry of the calcifying fluid varies seasonally under real-world reef conditions, we have analysed the skeletons of massive *Porites* colonies from both Davies Reef and Coral Bay Ningaloo Reef for which reef-water pH and sea-surface temperatures (SST) records are available\(^21,22\) (see ‘Methods’ section). Species of massive *Porites* coral are ideal for reconstructing seasonal changes in the composition of their calcifying fluid since they are long-lived and, more importantly, the architecture of their skeleton has a relatively straightforward chronology that facilitates well-constrained timing of their skeletal growth at seasonal resolution\(^23\). Given that only limited records of seasonal changes in local seawater carbonate chemistry are available\(^22,24\), these data are supplemented by model estimates\(^24\) of the reef-induced pH variability. The Great Barrier Reef and Ningaloo Reef sites (see ‘Methods’ section) have a typical seasonal range in temperature from ~23 to 28 °C, as well as relatively narrow seasonal ranges in seawater pH\(_{sw}\) (total scale) from ~8.02 in summer to ~8.08 in winter (Fig. 2). This limited seasonal range in average reef-water pH\(_{sw}\) of ~0.06 pH units is comparable to that observed in the open oceans\(^25\), a reflection of the tight balance between production and respiration\(^24\) combined with the limited residence time of waters in most wave and tidally driven reef systems\(^21\).

Covariation of calcifying fluid pH\(_E\) and DIC\(_{cf}\). In contrast to the limited variation in reef-water pH\(_{sw}\), we find that *Porites* colonies from both Davies Reef and Coral Bay exhibit strong seasonal changes in pH\(_E\) from ~8.3 during summer to ~8.5 during winter (Fig. 2). This represents an elevation in pH\(_E\) relative to ambient seawater of ~0.4 pH units together with a relatively large seasonal range in pH\(_E\) of ~0.2 units. These observations are in stark contrast to the far more muted changes based on laboratory-controlled experiments\(^8,17\). These inferred laboratory responses\(^10\) in calcifying fluid pH (pH\(_{cf}\)) are shown in Figs 2 and 4, where the expected seasonal range is ~0.02 pH units, an order of magnitude smaller than those actually observed in reef environments. The explanation for this unexpectedly large range in seasonal pH\(_E\) present under natural reef conditions becomes apparent from the exceptionally strong and inverse
The underlying reason for the dynamic, antiphase relationship between pH\textsubscript{cf} and DIC\textsubscript{cf} is explained by the ability of the coral to ‘control’ what is arguably one of its most fundamental...
physiological processes, the growth of its skeleton within which it lives. For example, during winter (Fig. 2), there is a large systematic decrease in the abundance of metabolic DIC (~25%), presumably as a consequence of reductions in both light and temperature. Since higher pH shifts the carbonate equilibria to favour $\text{CO}_3^{2-}$ relative to $\text{HCO}_3^-$, the greater increase in $\text{pH}_{\text{cf}}$ in winter (~8.5) compared to summer (~8.3) increases the concentration of carbonate ions within the calcifying fluid (and therefore $\Omega_{\text{cf}}$) for the same DIC$_{\text{cf}}$. This increase in winter pH$_{\text{cf}}$ therefore partially counters the seasonal slowdown in host-symbiont carbon metabolism. Hence during the cooler periods, higher pH$_{\text{cf}}$ enhances $\Omega_{\text{cf}}$ and hence partially mitigates the reduced temperature-dependent kinetics of calcification because rates of mineral precipitation are proportional to $(\Omega - 1)^n$, where $n$ is the temperature-dependent order of the reaction$^{28}$ ($n = 1.3$–2.0 for most reef habitats). During summer, the opposite behaviour is observed, with higher rates of metabolic DIC$_{\text{cf}}$ partially offset by decreases in pH$_{\text{cf}}$, resulting in a concomitant decrease in the carbonate saturation state of the calcifying fluid ($\Omega_{\text{cf}}$) and hence moderated (albeit still high) rates of calcification (Fig. 4c,d).

This implies that during summer, zooxanthellae-derived DIC$_{\text{cf}}$ is being supplied in excess of the ‘optimal’ requirements for the biologically mediated process of skeleton building. Thus, while existing mineral rate kinetics indicate that rates of calcification are still a factor of two- to fourfold higher in summer than in winter, this range is significantly less than the estimated eightfold higher summer rates (Fig. 4c,d) if constant levels of elevated pH$_{\text{cf}}$ upregulation were operative, as implied from the artificial constant seawater pH$_{\text{sw}}$ and temperature experiments$^{30}$.

Although our findings are based only on species of Porites from the Pacific and Indian Oceans, they nevertheless have important implications for our understanding of how reef-building corals in general will respond to climate change. The occurrence, for example, of the highest pH$_{\text{cf}}$ values during winter, when metabolically derived sources of energy are at a minimum, provides further evidence against the proposition that pH$_{\text{cf}}$ upregulation is an energetically costly process$^{29}$, and will therefore decline as seawater pH$_{\text{sw}}$ decreases due to ocean acidification. This is supported by results of the free ocean carbon enrichment experiment$^{30}$ conducted within the GBR Heron Island lagoon, where corals subjected to both natural and superimposed fluctuations in seawater pH$_{\text{sw}}$ exhibited essentially constant pH$_{\text{cf}}$ upregulation, a condition referred to by those authors$^{30}$ as ‘pH homoeostasis’. These findings, combined with measurements of even higher pH$_{\text{cf}}$ in zooxanthellate deep-sea corals$^{31}$ (pH$_{\text{cf}} > 8.6$), are thus consistent with inferences that Ca-ATPase-driven pH$_{\text{cf}}$ upregulation is a relatively energetically inexpensive process$^{32}$. These observations, in conjunction with the highly correlated and anti-cyclical seasonal changes in both pH$_{\text{cf}}$ and DIC$_{\text{cf}}$, therefore argue against the reduction of pH$_{\text{cf}}$ in summer being a result of the passive feedback from higher rates of calcification producing more protons thereby lowering pH$_{\text{cf}}$. Thus, while this possibility cannot yet be entirely excluded, the higher production rates of zooxanthellae-derived metabolites that are presumably available in the summer to facilitate enhanced Ca-ATPase activity, also suggest that the lower summer levels of pH$_{\text{cf}}$ is not due to intrinsic limitations in the Ca-ATPase $H^+$ pumping, but rather physiological controls on growth rate. Furthermore, similar anti-correlated changes in pH$_{\text{cf}}$ and DIC$_{\text{cf}}$ are present in Porites from both Davies and Ningaloo Reefs, despite large differences in growth rates.

Our findings also have major ramifications for the interpretation of the large number of experiments that have reported a strong sensitivity of coral calcification to increasing ocean acidification$^{32}$. An inherent limitation of many of these experiments$^{33}$ is that they were generally conducted under conditions of fixed seawater pH$_{\text{sw}}$ and/or temperature, light, nutrients, and little water motion, hence conditions that are not conducive to reproducing the natural interactive effects between pH$_{\text{cf}}$ and DIC$_{\text{cf}}$ that we have documented here. A characteristic common to a variety of coral species grown under these artificial conditions is the apparently constant but limited sensitivity (one-third to one-half) of pH$_{\text{cf}}$ relative to external changes in seawater pH$_{\text{sw}}$ (refs 10,17). While the reason for this apparently systematic but muted experimental response of pH$_{\text{cf}}$ is still uncertain, it likely involves reduced and/or constant levels of metabolically produced DIC$_{\text{cf}}$. Under such fixed conditions, we surmise that the supply of seawater DIC into the subcalcification space (Fig. 1) becomes the dominant source and hence major influence on levels of DIC$_{\text{cf}}$ with upregulation of pH$_{\text{cf}}$ therefore acting as the major controller of $\Omega_{\text{cf}}$ and thereby affecting the perceived sensitivity of pH$_{\text{cf}}$ to ocean acidification. This inference is supported by the fact that the observed pH$_{\text{cf}}$ of Porites from both Davies and Ningaloo Reefs were closest to the pH$_{\text{cf}}$ predicted from the constant condition experiments in winter when DIC$_{\text{cf}}$ levels are naturally lowest due to reduced light and/or temperature, hence most similar to experimental predicted
Porites coral (D-2) from Davies Reef (GBR), where opposing changes in pH\textsubscript{cf} relative to DIC\textsubscript{cf} (Fig. 1), endosymbionts disrupts the metabolic supply of DIC\textsubscript{cf} as well as to thermal stress. In extreme cases of coral bleaching, the loss of influenced by ocean acidification, it is however highly susceptible compared to those estimated from fixed condition experiments (\textsuperscript{10,17}).

We therefore conclude that the increasing frequency and intensity of coral bleaching events due to CO\textsubscript{2}-driven global warming constitutes the greatest immediate threat to the growth of shallow-water reef-building corals, rather than the closely associated process of ocean acidification.

**Methods**

**Reef sites.** *Porites* colonies were sampled from two reef systems: (1) Davies Reef (18.8\textdegree S, 147.63\textdegree E), a mid-shelf reef ~100 km east-northeast of Townsville, Queensland, Australia in the central Great Barrier Reef, and (2) Coral Bay (23.19\textdegree S, 113.77\textdegree E), part of the Ningaloo Reef coastal fringing system of Western Australia. At Davies Reef, the annual range of daily average SST is 23–28.5\textdegree C with a diurnal range of ~0.5\textdegree C or less\textsuperscript{41}. In situ seawater temperature data extending back to 1987 for the core site at Davies Reef (18.83\textdegree S, 147.63\textdegree E) was compiled from a number of different temperature sensors deployed between a depth of ~2 m to ~10 m maintained by the Australian Institute of Marine Science from October 1991 to December 2013 (http://data.aims.gov.au/aimsrtds/datatool.xhtml). To estimate seasonal changes in carbonate chemistry, we used the 24-h seawater carbonate chemistry data collected by Albright \textit{et al.}\textsuperscript{22} on the lagoon side of the Davies Reef flat around the summer and winter extremes in both light and temperature. Their data showed that the daily average pH at that reef site was 8.02 in summer and 8.08 in winter; a seasonal range that was similar to seasonal minima and maxima observed and hind-cast at Coral Bay and hence similar to what would be expected from seasonal variations in temperature-driven pCO\textsubscript{2} solubility. We therefore assumed that daily average pH at Davies Reef also followed seasonal variation. Their data showed that the daily average pH at that reef site was 8.02 in summer and 8.08 in winter; a seasonal range that was similar to seasonal minima and maxima observed and hind-cast at Coral Bay and hence similar to what would be expected from seasonal variations in temperature-driven pCO\textsubscript{2} solubility. We therefore assumed that daily average pH at Davies Reef also followed seasonal variation.

**Seasonal time series of calcifying fluid pH\textsubscript{cf} and \Omega_{cf} together with calculated calcification rates G.** (a) Calcifying fluid pH\textsubscript{cf} and \Omega_{cf} values for *Porites* coral (D-2) from Davies Reef (GBR), where \Omega_{cf} = [Ca\textsuperscript{2+}]\textsubscript{cf} [CO\textsubscript{3}\textsuperscript{2-}]\textsubscript{cf}/K\textsubscript{spar}. Dashed line shows the \Omega_{cf} calculated using fixed experimental\textsuperscript{10,17} pH\textsubscript{cf} values (see Fig. 2a,b). (b) Same as previous for Coral Bay (Ningaloo Reef, Western Australia) *Porites* (CB-2). (c) Calcification rates calculated using the inorganic rate equation\textsuperscript{28} G = k(\Omega - 1)^n, where k and n are the temperature-dependent constant and order of the reaction, respectively\textsuperscript{28}. Because of opposing changes in pH\textsubscript{cf} relative to DIC\textsubscript{cf} (Fig. 1), \Omega_{cf} and hence coral growth rates are strongly modulated reducing seasonal variations by twofold compared to those estimated from fixed condition experiments (\textsuperscript{G}\textsuperscript{*}). (d) Same as previous for *Porites* from Coral Bay (Ningaloo Reef, Western Australia).
resolution produced by Reynolds et al. \(^{42}\) before June 2010 and then at \(\sim 1\) km resolution produced by Chao et al.\(^{43}\) Both SST data products were then calibrated against in situ observations of temperature collected from a moored depth of \(\sim 17\) m as described by Falter et al.\(^{21}\) and previous model studies of wave-driven circulation. The carbonate chemistry of Coral Bay and offshore waters (\(\sim 2\) km) were monitored between May 2011 and June 2012 and intermittently since then, with seasonal changes in offshore seawater pH \((\text{pH}_{\text{sw}})\) (total scale) being found to be strongly correlated with seasonal changes in offshore temperature (\(\text{pH}_{\text{sw}} = -0.012 \times T + 8.37, \quad r^2 = 0.86, \quad n = 13\)). To determine seasonal changes in pH at the back-reef site where the coral cores were recovered, the offshore pH was adjusted to account for the deviation in temperature due to local heating and cooling (see above), as well as the daily average decrease in total alkalinity of \(\sim 10\) mmol kg\(^{-1}\) at back-reef sites observed from measurements.\(^{44}\)

**Boron isotopic ratio (\(\delta^{11}B\)).** Changes in the isotopic ratio of \(^{11}B\) (\(\sim 80\%\)) and \(^{10}B\) (\(\sim 20\%\)) are expressed in delta notation (in per mil, \(\%\)) as:

\[
\delta^{11}B_{\text{carb}} = \left(\frac{^{11}B_{\text{sw}} / ^{10}B_{\text{sw}}}{^{11}B_{\text{NIST951}} / ^{10}B_{\text{NIST951}}} - 1\right) \times 1,000.
\]

where \(^{11}B_{\text{NIST951}}\) is the isotopic ratio measured in the NIST SRM 951 boric acid standard. In seawater, boron exists as two different species, boric acid (\(\text{B(OH)}_3\)) and the borate ion (\(\text{B(OH)}_4^-\)), with their relative abundance being pH dependent. The sensitivity of the \(\delta^{11}B\) proxy to the calcifying fluid \(\text{pH}_{\text{cf}}\) arises from the incorporation of only the boron ion species into the aragonite structure\(^{45-47}\), with the \(\delta^{11}B\) isotopic composition reflecting the pH sensitivity of the borate versus boric acid speciation. The pH of the calcifying fluid (\(\text{pH}_{\text{cf}}\)) can thus be calculated from the \(\delta^{11}B\) measured in the coral carbonate (\(\delta^{11}B_{\text{carb}}\)). The equation used to convert the \(\delta^{11}B_{\text{carb}}\) isotopic composition measured in the coral skeleton to a pH of the calcifying fluid (\(\text{pH}_{\text{cf}}\)) is given by:\(^{48}\)

\[
\text{pH}_{\text{cf}} = \text{pK}_a - \log \left(\frac{\delta^{11}B_{\text{carb}}}{\delta^{11}B_{\text{sw}}} \times 1,000\text{[H}^+\text{]}\right) - 1
\]

where \(\delta^{11}B_{\text{sw}}\) represents the \(\delta^{11}B\) in seawater \(\delta^{11}B_{\text{sw}} = 39.61\%\) and \(\text{pK}_a\) has a well-established value of 8.597 at 25 °C and a salinity of 35. Here we also assume that the calcifying fluid has the same \(\delta^{11}B\) composition as seawater since that is the ultimate source of boron and, due to the low K of B/Ca (ref. 19), the boron composition and concentration of the calcifying fluid remains essentially constant during calcification. Recent studies utilizing the \(\delta^{11}B\) in coral precipitation as well as direct measurements of calcifying fluid pH using pH-sensitive dyes\(^{49,50}\), have also confirmed that under highly controlled artificial conditions of constant pH and temperature, corals upregulate the \(\text{pH}_{\text{cf}}\) of their calcifying fluid by \(\sim 1/3\) to \(1/2\) relative to ambient seawater pH.

**B/Ca constraints on calcifying fluid DIC concentrations.** Prior studies indicate that borate rather than boric acid is the predominant species occupying the lattice position normally taken up by the carbonate ion\(^ {51}\). In corals that precipitate aragonite skeletons. Although there are a number of reaction pathways through which this substitution could occur\(^ {19,20}\), it is likely to involve de-protonation of the borate species to create a divalent base ion with the same charge as that of the carbonate ion species (\(\sim 2\)), to preserve the charge neutrality of the growing crystal:

\[
\text{Ca}^{2+} + \text{B(OH)}_4^- = \text{CaH}_2\text{BO}_4^- + \text{H}^+.
\]

The partitioning of borate versus carbonate into aragonite is thus likely to be sensitive to solution \(\text{pH}\)\(^ {19,20}\). Here the relevant partition coefficient \(K_{\text{B/Ca}}\) is related to the molar ratio \(\text{B/Ca}_{\text{sw}}\) to the concentrations of the carbonate \(\text{CO}_3^{2-}\) and boron \([\text{B(OH)}_4^-]_{\text{sw}}\) species in the precipitating solution is determined using:

\[
K_{\text{B/Ca}} = \frac{\text{CO}_3^{2-} / [\text{B(OH)}_4^-]_{\text{sw}}}{\text{B/Ca}_{\text{sw}}}.
\]

Holcomb et al.\(^ {19}\) conducted experiments quantifying the ratio of boron to calcium in aragonite precipitated inorganically under a wide range of carbonate chemistries (including \(\text{pH}\)) and total DIC and boron concentrations, as well as conditions of \(\text{pH}\) and DIC appropriate to those in the calcifying fluid of corals. Furthermore, Holcomb et al.\(^ {19}\) also showed the close relationships between \(\text{B/Ca}\), \(\text{CO}_3^{2-}\) and \(K_{\text{B/Ca}}\) based on substitution reactions between \(\text{B(OH)}_4^-\) and \(\text{CO}_3^{2-}\). Re-analysing the Holcomb et al.\(^ {19}\) data, we find (Fig. 5) that the observed \(K_{\text{B/Ca}}\) as defined in equation (4) shows the expected decrease as a function of the concentration of the total active protons within the precipitating solution. Thus, using the definition of \(K_{\text{B/Ca}}\) from equation (4) and its dependency on \(\text{pH}_{\text{cf}}\) as given by the inorganic data of Holcomb et al.\(^ {19}\), we can now calculate the concentration of carbonate ions within the calcifying fluid (that is, \(\text{CO}_3^{2-}\)) from measurements of \(\text{B/Ca}_{\text{sw}}\) and \(\text{pH}_{\text{cf}}\) the latter derived from the skeletal boron isotopic ratio (\(\delta^{11}B_{\text{carb}}\)). We further assume that \([\text{B(OH)}_4^-]_{\text{sw}}\) is equal to the total concentration of boron of ambient seawater and only a function of seawater salinity

**Data availability.** The coral geochemical and seawater carbonate chemistry and temperature data are available in Supplementary Data.

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