the early endomesoderm cWnt signaling state could also be conserved, because Brachyury maintains transcription of cWnt ligands in both zebrafish and sea urchin embryos (*30*). Restricting Brachyury expression to either endoderm or mesoderm would also confine cWnt signaling. This could, in turn, reinforce lineage segregation, as seen with the Brachyury→Wnt1→endoderm and the Brachyury→cWnt→posterior mesoderm pathways in sea urchins and zebrafish, respectively (*30*). More generally, similar Notch-dependent mechanisms could modulate additional pathways such as Nodal/transforming growth factor–β that induce endomesoderm in vertebrate embryos (*31*). Finally, it is unknown whether Notch also insulates mesoderm or endoderm from incident cWnt signals through NLK activity in vertebrate embryos. We thus have uncovered a remarkable timing buffer that uses a cell contact–dependent signal to separate regulatory states within a broadly induced endomesoderm field without immediately altering its signaling milieu. This preserves the competence of each lineage and correctly institutes its specification. Individual lineage choices are then reinforced and cemented through successive signaling state changes.

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Growth of Western Australian Corals in the Anthropocene

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Anthropogenic increases of atmospheric carbon dioxide lead to warmer sea surface temperatures and altered ocean chemistry. Experimental evidence suggests that coral calcification decreases as aragonite saturation drops but increases as temperatures rise toward thresholds optimal for coral growth. In situ studies have documented alarming recent declines in calcification rates on several tropical coral reef ecosystems. We show there is no widespread pattern of consistent decline in calcification rates of massive *Porites* during the 20th century on reefs spanning an 11° latitudinal range in the southeast Indian Ocean off Western Australia. Increasing calcification rates on the high-latitude reefs contrast with the downward trajectory reported for corals on Australia's Great Barrier Reef and provide additional evidence that recent changes in coral calcification are responses to temperature rather than ocean acidification.

Coral growth is measurably influenced by the physical and chemical properties of the marine environment (*1*), which are changing rapidly owing to human interference in the global climate system (*2–4*). Emissions of CO_2 into the atmosphere from the combustion of fossil fuels, deforestation, and altered land use have resulted in current-day atmospheric CO_2 levels of around 390 parts per million (ppm), an increase of about 40% since preindustrial times. Increased concentrations of atmospheric CO_2 (along with other greenhouse gases) are associated with positive radiative forcing, which leads to a warming of the global climate system (*5*); about one-third of this extra CO_2 is taken up by the world's oceans (*6*). Oceanic uptake of anthropogenic CO_2 alters the seawater carbonate equilibrium by reducing both the pH and carbonate saturation states in the upper ocean layers (*2*, *7*) in a process known as ocean acidification (*8*). Reduced carbonate saturation state is expected to have profound effects on the calcification rates of a diverse range of marine calcifers, including reef-building corals (*4*, *9–11*). Warming of the tropical oceans is predicted to increase the frequency and severity of mass coral-bleaching events (*3*). Such changes in the marine environment are, therefore, likely to compromise coral calcification (facilitated by the coral-algal symbiosis), which forms the backbone of tropical coral reef ecosystems (*4*).

Annual density banding in certain massive corals allows retrospective analysis of historical calcification rates and inferences to be made about past environmental conditions and growth responses, including those before instrumental observations (*12*). Our study focused on coral reefs spanning an 11° latitudinal range in the southeast Indian Ocean to learn whether there have been any significant changes during the past 110 years in calcification rates on Australia's western coral reefs and how any observed changes relate to known changes in sea surface temperature (SST).

Twenty-seven long cores were collected, between October 2008 and September 2010, from massive *Porites* sp. colonies at six locations covering about 1000 km off the coast of Western Australia. Although some cores extend back to the 18th century, we focused on the period from 1900 to 2010, which was common to the majority (70%) of cores, to provide sufficient replication at each location and overlap with instrumental SST observations. The sampling locations included two reefs in the Rowley Shoals, Clerke Reef (17°16'S, 119°22'E) and Imperieuse Reef (17°31'S, 118°58'E); three locations within the Ningaloo Reef Tract, Bundegi (21°50'S, 114°11'E), Tantabiddi (21°54'S, 113°58'E), and Coral Bay (23°2'S, 113°49'E); and the Houtman Abrolhos Islands (28°28'S, 113°46'E) (Fig. 1). All sampled colonies were ≥2 m in height and selected from the leeward side of the reef or island at depths < 6 m below the lowest astronomical tide. Spatial and temporal variations in three annual coral growth parameters—annual extension (linear distance between adjacent density minima, cm year^{-1}), skeletal density (g cm^{-3}), and calcification

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Fig. 1. Map showing locations of six coral reef locations sampled for long coral cores along the West Australian coast.

Table 1. Results of generalized linear models testing the relationship between decadal SST and calcification anomalies in massive *Porites* for six coral reefs in Western Australia. Significant *P* values denoted with asterisks.

Location	Slope	SE	*t*	*P*
Clerke Reef	16.704	8.164	2.046	0.0711
Imperieuse Reef	5.039	4.744	1.062	0.3160
Bundegi	–14.442	6.515	–2.217	0.0539
Tantabiddi	8.113	3.043	2.666	0.0258*
Coral Bay	10.572	4.316	2.449	0.0368*
Houtman Abrolhos Islands	28.734	6.780	4.238	0.0022*

Table 2. Results of generalized linear models testing the relationship between calcification anomalies in massive *Porites* at each location and year over the period 1900–2010. Significant *P* values denoted with asterisks.

Location	Slope	SE	*P*	% Change over study period
Clerke Reef	0.022	0.034	0.5110	2.5
Imperieuse Reef	–0.038	0.028	0.1869	–4.1
Bundegi	–0.106	0.036	0.0038*	–11.6
Tantabiddi	–0.030	0.028	0.2811	–3.3
Coral Bay	0.056	0.025	0.0290*	6.2
Houtman Abrolhos Islands	0.216	0.046	<0.0001*	23.7

rate (the product of skeletal density and annual extension, g cm^{-2} year^{-1})—were examined, as measured by gamma densitometry using standard procedures (*13*).

Annual calcification rates for each core were converted to calcification anomalies calculated as the percent difference between the annual calcification rate and the long-term average for the period 1900–2010. Average calcification anomalies were then calculated for each of the six locations and for all 27 coral cores. Average monthly SST were obtained from the HadISST 1.1 database (*14*). Given the close proximity of some of the sampling locations, the same SST series was applied to Imperieuse and Clerke Reefs (Rowley Shoals) and Tantabiddi and Bundegi (Ningaloo Reef). SSTs were expressed as annual anomalies relative to the 1900–2010 average.

Linear regression (generalized linear model) and nonlinear regression (generalized additive models) models were used to examine the influence of time, SST, and location on the calcification average and anomaly data (*15*). First, both models were used to explore the relationship between average annual SST and calcification of massive *Porites* sampled across the six locations. Second, the models were used to test the relationship between decadal anomalies in SST and calcification to allow for high interannual variability in coral growth rates (*12*). Finally, both models were used to examine the relationship between calcification and year over the period 1900–2010 at each location. All models were analyzed by using the statistical package R (*16*, *17*).

Significant warming of the tropical southeast Indian Ocean during the 20th century (Fig. 2A) is comparable to that recorded on the Great Barrier Reef (GBR) (*18*) and for tropical oceans globally (*19*). Average annual SSTs (1900–2010) at the sampling locations ranged from 27.6°C (Rowley Shoals; Clerke/Imperieuse), 25.2°C (northern Ningaloo; Tantabiddi/Bundegi), and 24.0°C (southern Ningaloo; Coral Bay) to 21.5°C (Houtman Abrolhos Islands). This corresponds to an environmental gradient for reef growth comprising "typical" SST conditions at the Rowley Shoals moving closer to "marginal" SST conditions (*20*) at the high-latitude Houtman Abrolhos Islands [although high summer calcium carbonate production rates have been reported at this location (*21*)]. In recent decades, positive SST anomalies have become a dominant feature for the southeast Indian Ocean. Since 1980, there have only been 3 years (1986, 1987, and 1993) with SSTs cooler than the long-term average (Fig. 2A). Warming of SSTs averaged across all locations was significant from 1900–2010 (linear regression, $P < 0.001$, $R^2 = 0.40$). There was, however, no significant change (linear regression, $P = 0.158$, $R^2 = 0.02$) in calcification rates averaged across the 27 coral cores over the same period (Fig. 2B). There are, however, spatial differences along Australia's tropical coasts in the magnitude of recent observed SST warming (*18*). SST warming rates were 0.02°C/decade (Rowley Shoals), 0.06°C/decade (northern Ningaloo; Tantabiddi/Bundegi), and 0.08°C/decade (southern Ningaloo; Coral Bay) to 0.10°C/decade (Houtman Abrolhos Islands) during the period 1900–2010.

Warmer-than-average decadal SSTs were associated with significant increases in calcification in massive *Porites* located in the cool southern waters of Western Australia. At the Houtman Abrolhos Islands, increases in SST anomalies resulted in increased calcification rates of 23.5% (Fig. 3). Similar trends occurred at Coral Bay and Tantabiddi, where warmer SST anomalies were associated with 8.7 and 4.9% increases in decadal calcification rates, respectively. Smaller trends for increasing calcification rates were apparent at the northern Clerke and Imperieuse Reefs, where the decadal increase in SST was the least pronounced (Table 1). These positive responses contrasted with massive *Porites* at Bundegi, where above-average decadal SSTs resulted in a declining trend in calcification rates (Table 1).

Annual calcification anomalies at the six locations showed contrasting temporal variability between 1900 and 2010. There was no significant relationship between calcification anomalies and time for corals at the two most northern reefs of Clerke and Imperieuse Reefs (Fig. 4, A and B,

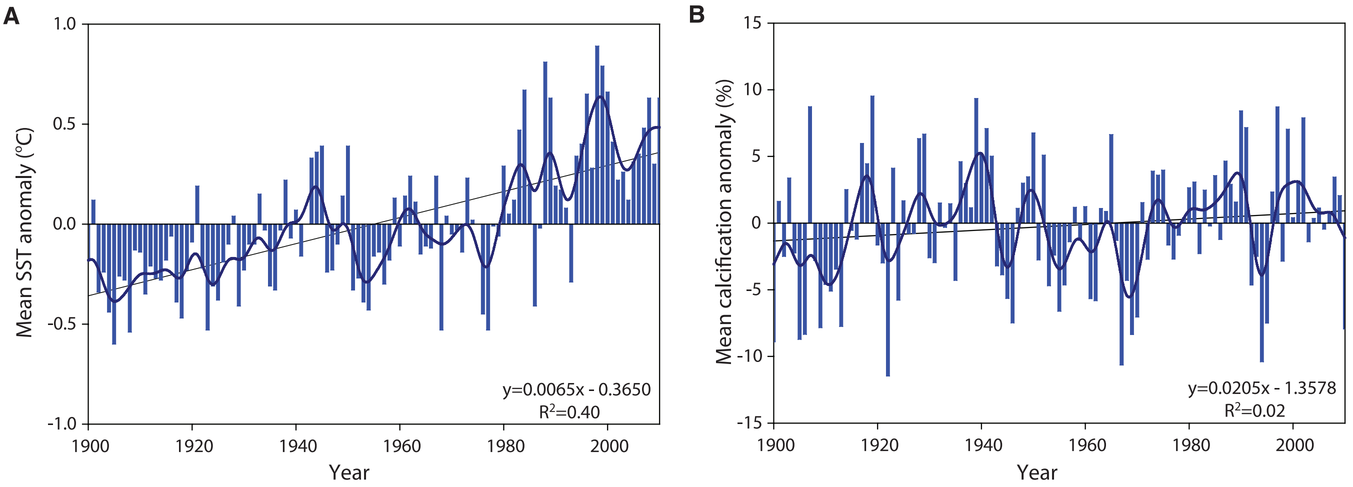
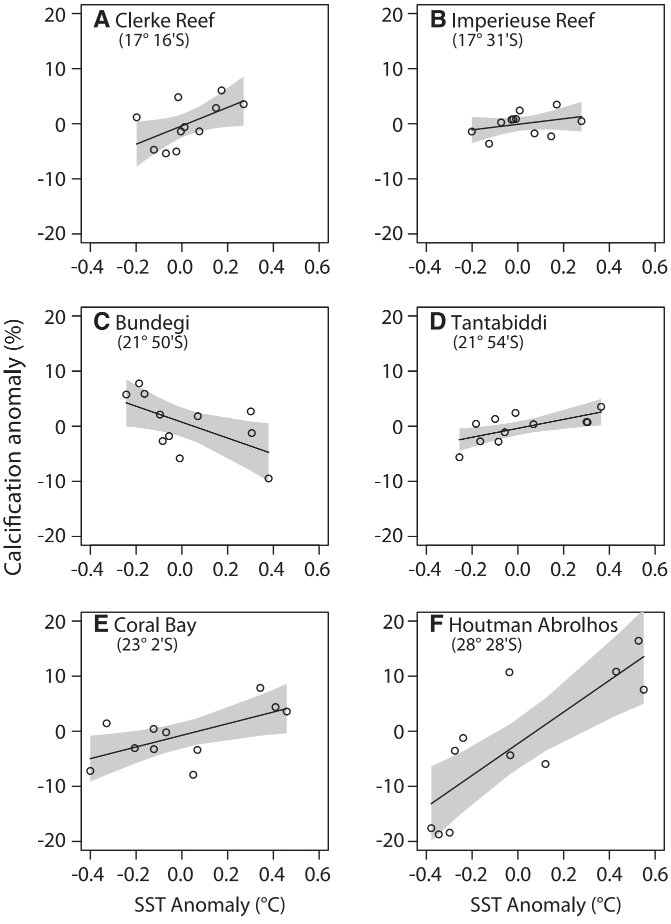


Fig. 2. Annual anomalies in (**A**) average SST (°C from 1900–2010 mean) and (**B**) average calcification (% of 1900–2010 mean) for six coral reef locations in the southeast Indian Ocean, Western Australia. Thick solid line is the 10-year Gaussian filter, and a linear regression is also given.

Fig. 3. Relationships between decadal SST and calcification (cal) anomalies (anom.) for (**A**) Clerke Reef (change in cal anom. is 7.5%; range of SST anom., –0.20 to 0.27; *n* = 5 cores), (**B**) Imperieuse Reef (cal anom., 2.4%; SST anom., –0.20 to 0.28; *n* = 4), (**C**) Bundegi (cal anom., –8.6%; SST anom., –0.39 to 0.38; *n* = 4), (**D**) Tantabiddi (cal anom., 4.9%; SST anom., –0.29 to 0.36; *n* = 7), (**E**) Coral Bay (cal anom., 8.7%; SST anom., –0.40 to 0.46; *n* = 4), and (**F**) Houtman Abrolhos Islands (cal anom., 23.5%; SST anom., –3.8 to 0.55; *n* = 3). Raw data are shown as open circles, solid line is the model fit to the data, and gray area is 95% confidence interval.



and Table 2). For the two locations in the northern Ningaloo Reef, there was a significant decline in calcification rates at Bundegi (Fig. 4C) but no significant change at Tantabiddi (Fig. 4D and Table 2). This contrasted with the two southernmost sampling locations. At Coral Bay, there was a significant increase in calcification rate of 6% over the period 1900–2010 (Fig. 4E; and Table 2). At the Houtman Abrolhos Islands, calcification rates increased significantly, by 23.7% between 1900 and 2010 (Fig. 4F and Table 2). In summary, the two most southerly locations, where recent SST warming was greatest, show a significant increase in calcification rates. This contrasts with the two most northerly locations in the Rowley Shoals, where there was no significant change in calcification rates and a much lower rate of SST warming. Only one location, Bundegi in Exmouth Gulf, showed a significant decline in calcification rates since 1900.

Emerging evidence of declines in coral calcification rates in an era of rapid environmental change is of great concern. On the GBR off eastern Australia, growth rates of massive *Porites* have declined about 14 to 21% (*22*, *23*) since 1990. Although the exact causes are not known, suggestions have been made that large-scale processes, such as ocean acidification, could be a possible driver (*23*, *24*). Others have attributed recent declines in coral growth rates to increasing thermal stress either because of setbacks in growth from coral-bleaching events (*25*) or to exceeding a thermal threshold for sustained calcification rates (*26*, *27*).

Annual density banding represents a valuable tool for retrospective monitoring of calcification rates in massive corals. However, owing to highly variable growth rates (*12*), replication is essential to obtain robust estimates of spatial and temporal variability and change. Our analysis of massive coral growth parameters spanned 11° latitude along Australia's western coast, an area of the southeast Indian Ocean that has warmed significantly during the past century. Overall, we found no widespread and consistent pattern of decline in calcification rates of Western Australian massive corals over time (table S1). Relationships between calcification rates and average SSTs and SST anomalies varied depending on location and were driven by the influence of these parameters on annual extension (table S2) rather than skeletal density (table S3). Where SST warming was minimal (Rowley Shoals; 0.02°C/decade), there was no significant change in calcification rates. This is consistent with Helmle *et al.* (*28*), who found a similar noncorrelation for the massive coral *Montastraea faveolata* in the Florida Keys between 1937 and 1996, when there was no significant SST warming. However, at our two most southerly locations, where a relatively large SST warming has occurred (e.g., 0.10°C/decade at Houtman Abrolhos Islands), we found evi-

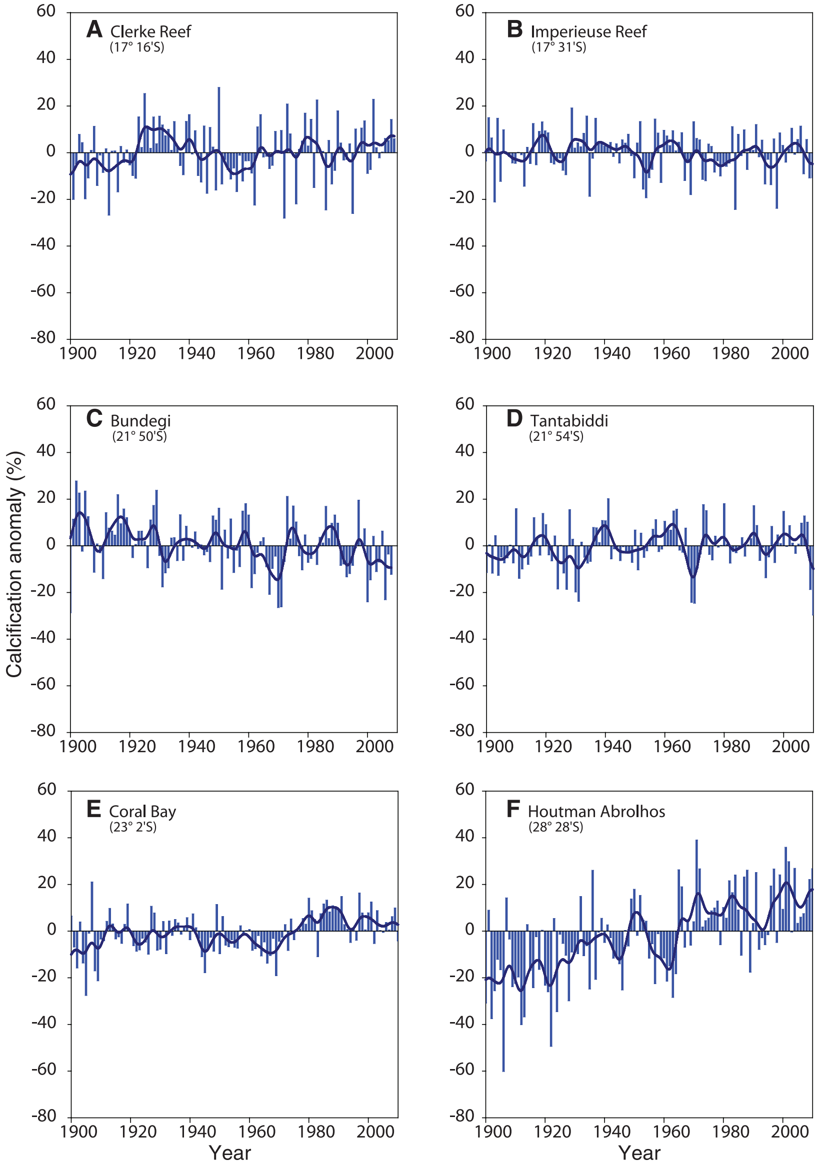


Fig. 4. Average annual calcification anomalies, 1900–2010, for (**A**) Clerke Reef, (**B**) Imperieuse Reef, (**C**) Bundegi, (**D**) Tantabiddi, (**E**) Coral Bay, and (**F**) Houtman Abrolhos Islands. Solid line is the 10-year Gaussian filter.

dence that massive corals have increased their calcification rates. Lough and Barnes (*29*) documented a similar positive correlation, suggesting that calcification rates may, at least initially, increase with global warming. Our findings suggest that the large-scale phenomenon of ocean acidification is not currently limiting calcification on coral reefs uniformly at a global scale. The influence of ocean acidification is expected to occur first at higher latitudes that inherently have lower seawater saturation states with respect to carbonate minerals due to their increased solubility at lower water temperatures (*10*, *30*). However, the significant recent above–long-term–average calcification anomalies recorded at the Houtman Abrolhos Islands lends support to the view that thermal changes are likely to be the principal immediate climate-change threat to the calcification potential of reef-building corals.

Seawater carbon chemistry is a key determinant of coral calcification, and the potential for future anthropogenic-influenced declines in carbonate saturation state, and hence coral calcification, is cause for serious concern (*2*, *4*, *7*). However, we conclude that the rate of change in the thermal environment of coral reefs is currently the primary driver of change in coral calcification rates. Warming SSTs are resulting in (i) increased calcification rates reported here in the southeast Indian Ocean, where marginal reefs have taken advantage of warmer conditions, and (ii) recent declines reported elsewhere for more typical reef environments where thermal optima for calcification have been exceeded or resulted in setbacks in growth as a result of thermally induced bleaching. Whether the former is sustainable as oceans continue to warm is another question.

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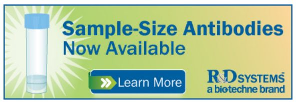

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