

Instability in a marginal coral reef: the shift from natural variability to a human-dominated seascape

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As global climate change drives the demise of tropical reef ecosystems, attention is turning to the suitability of refuge habitat. For the Great Barrier Reef, are there historically stable southern refugia where corals from the north might migrate as climate changes? To address this question, we present a precise chronology of marginal coral reef development from Moreton Bay, southeast Queensland, Australia. Our chronology shows that reef growth was episodic, responding to natural environmental variation throughout the Holocene, and that Moreton Bay was inhospitable to corals for about half of the past 7000 years. The only significant change in coral species composition occurred between ~200 and ~50 years ago, following anthropogenic alterations of the bay and its catchments. Natural historical instability of reefs, coupled with environmental degradation since European colonization, suggests that Moreton Bay offers limited potential as refuge habitat for reef species on human time scales.

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The general demise of tropical coral reefs globally is attributed to overfishing, climate change, and pollution (Hughes *et al.* 2003; Pandolfi *et al.* 2003). Climate change-induced range shifts of coral reefs from the tropics to the “marginal” subtropics are well documented on geological time scales (Hughes *et al.* 2003; Greenstein and Pandolfi 2008). These range shifts allow subtropical reefs to be viewed as potential refuge habitats as “classical” reefs, ie tropical reefs in near-ideal environments, decline on account of climate change (Guinotte *et al.* 2003; Riegl and Piller 2003; Precht and Aronson 2004). Moreton Bay, in southeast Queensland, Australia, is specifically proposed as a subtropical refuge for Great Barrier Reef (GBR) corals threatened by climate change (Hughes 2007; Wallace 2009). Though extensively debated (Ricciardi and Simberloff 2009), some researchers even advocate human intervention in “assisted colonization” or “managed relocation” to accelerate species range shifts (Hoegh-Guldberg *et al.* 2008). However, any such intervention must take into account the historical range of variation in ecosystem dynamics of the target refuge. Here, we investigate the historical range of variation in coral reef growth and coral community composition, in order to evaluate whether Moreton Bay can function as a suitable long-term refuge for tropical species on human time scales.

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Marginal reefs occur where environmental conditions (ie temperature, salinity, nutrients, turbidity, aragonite saturation, local anthropogenic impacts), biodiversity, and/or ecosystem function depart substantially from those associated with classical reefs (Guinotte *et al.* 2003; Perry and Larcombe 2003; Macdonald *et al.* 2005). Aragonite saturation affects an organism's ability to secrete and maintain an aragonite skeleton, a high-strength form of calcium carbonate in coral, bivalve, and other marine organisms' skeletons. In eastern Australia, subtropical marginal reefs extend along the coastline well south of the GBR. Prominent among these are the subtropical coral communities of Moreton Bay (Figure 1).

Moreton Bay is the southernmost marginal reef that seems to have the most desirable attributes of a GBR coral refuge. South of Moreton Bay, the subtropical and temperate coast of Australia is narrow and much less suitable for corals, with submerged areas comprising approximately 29% rock and 67% sand (Galloway 1984). Although reefs occasionally initiate on mobile sediments in lower energy environments (Perry *et al.* 2008), this is unlikely in the wave-dominated settings that characterize most of Australia's coastline south of the GBR (Short and Woodroffe 2009). Because there is relatively little classical reef growth on existing rocky headlands in east Australia's tropical or subtropical settings, there is little reason to consider rocky headlands to be desirable as coral reef refugia. Extant habitat in the shallow protected waters of Moreton Bay may present an ideal potential coral refuge because of the bay's geomorphology and history of coral reef growth during a variety of sea levels and climate conditions.

Previous studies of the marginal reefs of Moreton Bay have proposed that changes in temperature, sea level, El Niño–Southern Oscillation (ENSO) intensity, and sedimentation led to natural reef declines sometime between

3000 and 8000 years ago (Johnson and Neil 1998), prior to major anthropogenic disturbance. Further decline, resulting from over-exploitation and water-quality degradation, has been indicated since European settlement began in 1824 (Neil 1998; Pandolfi *et al.* 2003). Here, for the first time, we present a detailed account of the historical range of variation of Moreton Bay's reefs, which will be critical for evaluating refuge potential.

The goal of this study is to describe the historical dimensions of ecosystem dynamics and provide some context for the future dynamics of climate-induced range shifts, be they natural or human-assisted. We present a precise chronology, which shows that reef growth in Moreton Bay was episodic, responding to environmental variation during the Holocene. The variation in reef growth correlates with regional and global drivers, including sea-level change and the onset of the modern ENSO regime. Even before the recent anthropogenic degradation of Moreton Bay habitats, analysis of the historical range of variation shows an ephemeral coral habitat, unsuitable as a refuge for GBR species in the face of predicted climate change.

Methods

Study site

Compared with their tropical counterparts, coral communities of Australia's subtropics experience a relatively extreme range of temperatures and available light, occur near the geographic limit of reef development, and are extensively degraded. They fulfill all working definitions of "marginal reefs" (Guinotte *et al.* 2003). Moreton Bay is an ideal location to study the historical range of variation because the bay acts to magnify the impact of stressors, making ecological responses readily detectable (see Neil 1998). The tidal range is 2.71 m at highest astronomical tide, and the datum for all depths in this study is modern lowest astronomical tide. The volume of the bay is approximately equal to the volume of three spring tides. Living coral assemblages are dominated by massive *Favia*, *Goniastrea*, and *Goniopora* colonies at all but a few localities (Wallace *et al.* 2009). Fossil coral assemblages are dominated by branching or tabular *Acropora* colonies (Lovell 1989; Johnson and Neil 1998).

Sampling

Coral colonies were sampled from death assemblages (the dead corals amongst living corals at the reef surface;

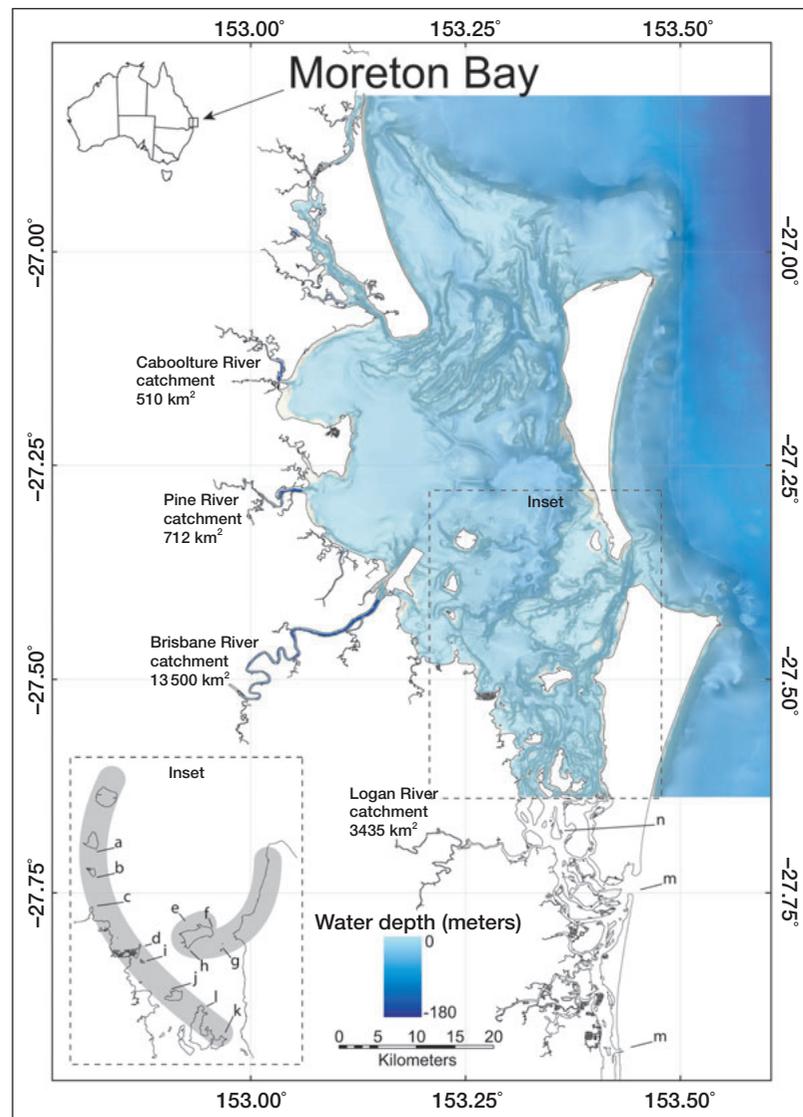


Figure 1. Locality and sampling area for Moreton Bay, Queensland, Australia. Bathymetry depicts a network of tidal and river channels amidst generally shallow waters. Inset: Gray bands show the areas of major Holocene reef growth. Locations of sample sites are indicated by labels "a" to "l" (corresponding to WebTable 1). "m" = historically ephemeral inlets; "n" = modern tidal node.

Figure 1, inset). However, samples from intertidal and supratidal areas were collected up to several tens of meters away from the nearest living corals (Figure 2). Whole colonies were haphazardly collected from the death assemblage for 42 of 57 samples. To test for an age bias related to colony morphology, we chose 15 additional samples targeting whole colonies of massive and columnar growth forms in a narrow depth range. This subset is excluded from analyses of community composition because the subset was not collected haphazardly with respect to morphology. Depth measurements were corrected for tide state and are accurate to ± 20 cm (WebTable 1). The distribution of sample depths is normal (significant normal quantile test for non-normality at $\alpha = 0.01$, critical value = 0.97, $r = 0.99$). The taphonomic condition of typical specimens (ie the state of post-



Figure 2. Typical Moreton Bay sampling sites. (a) Shallower site at low tide (location “k” in Figure 1). For scale, note the person walking on the sand ridge. (b–d) Deeper sites (location “g” in Figure 1). (b–c) Though uncommon, live branching *Acropora* species are present in most localities in Figure 1. Note unconsolidated, silt-covered rubble among living corals.

mortem degradation) ranged from moderately bioeroded to pristine (Figure 3). We determined the ages of all coral colonies from nearly pristine aragonite skeletal material by thermal ionization mass spectrometry U-series dating techniques, conducted at the University of Queensland’s Radiogenic Isotope Facility using standard procedures and instrumentation (Yu *et al.* 2006; WebTable 1).

Data analysis

An appropriate bin size for analyses of coral ages was derived from the second standard deviation of the age determination errors ($\pm 2\sigma$ throughout) (WebTable 1). The average $\pm 2\sigma$ error for all 57 samples is 83 years; thus, if the difference in the age of two samples is greater than 166 years, we can be reasonably certain that they are from different times. For convenience, 166 years is rounded up to 200 years, and there are thirty-five 200-year bins between the oldest and youngest corals. The number and sequence of filled versus empty bins were tested by comparison with a binomial probability mass function after Aronson *et al.* (2002) and non-parametric runs test, respectively. Coral assemblage changes between branching (pooled branching and tabular) and massive (pooled massive and columnar) morphologies were tested by Fisher’s exact test. These analyses (1) excluded corals that were not collected haphazardly, (2) ordered the

remainder by age, and (3) tested for differences among quartiles and among the four episodes evident in Figure 4.

Results

Three notable patterns emerged from the 57 coral samples from Moreton Bay. First, development of coral communities was episodic through time. Second, there was a depth-related shift through time, with younger corals observed at progressively deeper sites than older corals. Third, an abrupt change in coral dominance, from branching *Acropora* to massive *Favia* corals, occurred.

Episodic coral growth

Rather than being randomly or evenly distributed in time, coral reefs occurred episodically (Figure 4, a and d). There were four clearly distinguishable episodes with corals (nineteen of thirty-five 200-year bins), separated by at least three clearly distinguishable periods without corals (sixteen bins) during the past 7000 years.

We tested for sampling adequacy by investigating whether age-dating additional samples would fill the empty periods between episodes of coral growth. The expected number of empty bins after 57 random samples was seven. The observed number of empty bins was 16, which was significantly greater than random processes would generate (binomial analysis, $P = 0.003$). The observed number of empty bins was so great that only 27 dated corals were needed to confirm that the distribution of empty bins was non-random.

We also tested for randomness in the sequence of periods with and without samples. A non-parametric runs test (Siegel 1956) found that the sequence of filled and empty bins was significantly different from a random sequence (one-tailed, $P = 0.005$). Thus, the episodic occurrence of corals through time was significantly non-random and very likely an accurate representation of episodic reef growth, rather than the result of chance or sampling error.

Shift in water depth

There was a significant negative correlation between coral age and water depth ($r^2 = 0.65$, analysis of variance [ANOVA], $F = 101.89$, $P < 0.001$) (Figure 4a). Our next step was to correct the modern depths by scaling them relative to paleo sea level. The two best sea-level curves for the region are Sloss *et al.* (2007) and Lewis *et al.*

(2008), which integrate and correct many earlier datasets (Figure 4, b and c). Correlations between corrected paleo depth versus age were also highly significant, following Sloss *et al.* (2007) ($r^2 = 0.37$, ANOVA, $P < 0.001$) or Lewis *et al.* (2008) ($r^2 = 0.47$, ANOVA, $P < 0.001$). The modern coral depth distribution is significantly different from the historical distribution, even when corrected for sea-level change (two-tailed heteroscedastic t test, $P < 0.001$). Thus, the 2-m sea-level fall is insufficient to explain the 4-m depth changes in coral distribution during the Holocene.

Shift in coral dominance

The only significant change in the composition of coral assemblages occurred between ~200 and ~50 years ago (the boundaries are 1842 ± 11 and 1956 ± 9 common era [CE]). Branching *Acropora* corals dominated assemblages from 7000 to 200 years ago, and since that time assemblages were dominated by massive corals such as *Favia* (Figure 4e; WebTable 1). We looked for changes in coral dominance both among episodes and independently of episodes (quartiles), to test the commonly accepted hypothesis for tropical reefs that coral assemblages in the same locality are similar through time (Edinger *et al.* 2001). Coral assemblages were indistinguishable among all tests (Fisher's exact test, two-tailed, $P > 0.5$) except for tests including the youngest corals (Fisher's exact test, two-tailed, $P < 0.05$ [episodes] and $P < 0.02$ [quartiles]). The youngest coral community is significantly different than its predecessors over the past 7000 years.

Potential biases

We examined potential biases that could falsely create these three features of episodic coral growth, shift in depth, and shift in dominance (Table 1). None were statistically significant. Although the living coral assemblages exhibit clear correlations with water quality (Johnson and Neil 1998), the death assemblages do not, which implies that bay-wide gradients in water quality did not structure the historical coral assemblages (Table 1).

Post-depositional transport can create age patterns that result from physical rather than biological processes. It is extremely unlikely that post-depositional transport contributes to the age–depth correlation. First, our sampling includes reefs with varying magnitudes of fetch (uninterrupted distance for wind-driven wave development) from different directions (Figure 1, inset). Our analyses found no spatial or fetch-related pattern in the age distribution. Second, physical disturbance should include up- or down-slope transport. Evidence of transport in this dataset would include corals older than 2300 before common era

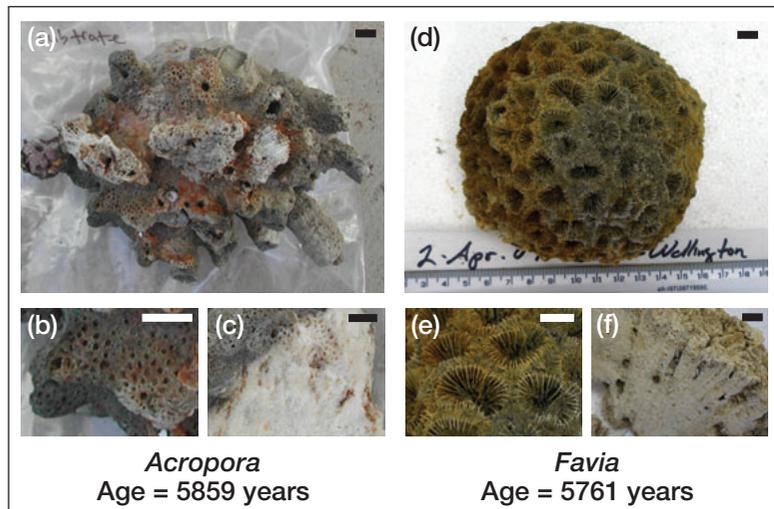


Figure 3. Two death assemblage samples illustrating typical size and state of preservation. (a–c) Branching *Acropora* sp, sample name 50908-7b. Red surface is the remnant of a living encrusting sponge. (b) Moderate bioerosion of external features. (c) Nearly pristine interior skeleton. (d–f) Massive *Favia* sp, sample name IW20. (e) Nearly pristine exterior skeleton. (f) Moderate bioerosion of interior skeleton. Scale bars represent 1 cm.

(BCE) found in deep water or corals younger than 800 BCE found in shallow water, but there is no evidence of either of these occurrences (Figure 4a). None of these plausible biases influenced the correlation between death assemblage age and depth.

Discussion

By applying the concept of historical range of variation to the marginal reefs of Moreton Bay, we have shown that – over millennial time scales – natural reef growth in the bay was episodic and shifted toward deeper water. We first discuss these natural changes and their mechanisms, before examining the more recent anthropogenic impacts and the future potential for Moreton Bay habitats to provide refuge for northern reefs in the face of global climate change.

Episodic coral growth

The absence of corals between episodes exemplifies a natural fluctuation between multiple stable states. Two ecosystem states – coral-dominated and non-coral-dominated – persisted on time scales from centuries up to about two millennia. Episodic patterns are known on tropical marginal reefs (Smithers *et al.* 2006), but episodes on subtropical reefs are poorly known (Hongo and Kayanne 2009). Relative to conditions in the tropics, the environmental conditions on subtropical marginal reefs include more extreme variations in light, temperature, salinity, aragonite saturation, and population connectivity. Because of these edge effects, an environmental driver that does not cause multiple states in the tropics could cause multiple states in the subtropics, simply because of

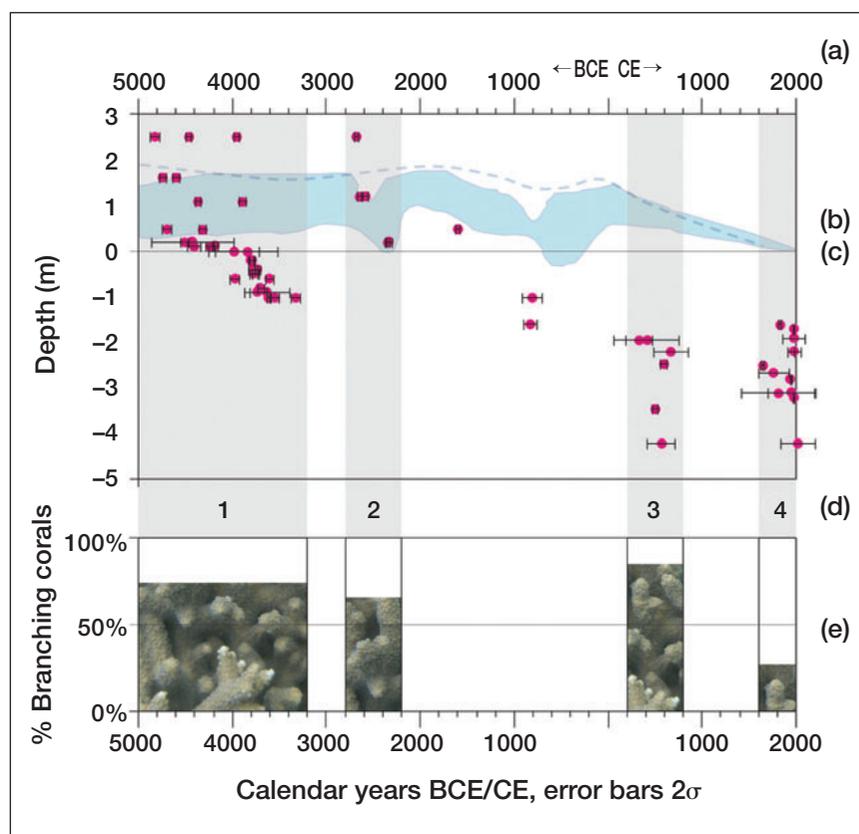


Figure 4. Age, depth, and community composition of coral death assemblages from Moreton Bay, Queensland, Australia. (a) Scatter plot of coral death assemblage age versus depth relative to lowest astronomical tide, uncorrected for paleo sea level. (b–c) Sea-level fluctuations after Lewis *et al.* (2008) (shaded blue area) and Sloss *et al.* (2007) (dashed blue line). (d) Statistically significant episodes of coral growth. (e) Coral community composition depicted as percent branching corals versus other corals.

the harsher setting. Our finding of at least five shifts between states demonstrates reversible phase-shifts in the historical record.

Shift in water depth

Episodes of coral growth occur in progressively deeper water over time. Although this might be attributed to reef deposition during sea-level fall, the magnitude of the depth change exceeds the magnitude of sea-level change by a factor of two (Figure 4, a–c). The upper depth range of the earlier episodes 1–2 was intertidal (corrected for paleo sea level), but the later episodes 3–4 did not leave deposits in the upper subtidal zone. Two commonly accepted hypotheses for classical tropical reefs are rejected for these marginal reefs. First, accommodation space does not limit modern reef growth in Moreton Bay. Second, when corrected for sea-level change, the modern depth distribution is significantly deeper than the historical depth distribution. Although there is a history of intertidal accretion, this zone is no longer suitable coral substrate, and the younger episodes do not extend into the shallows. This is clear evidence of mechanisms, acting since 2300 BCE, to prevent coral accretion in the shallows.

Mechanisms

Sea level in the region exhibited minor oscillations throughout the Holocene, after a mid-Holocene high of 2 m above present (Figure 4, b and c). Generally, falling sea level negatively affects reefs and rising sea level acts conversely. Ecological responses to small sea-level changes are detectable in a semi-enclosed system like Moreton Bay because the enclosure tends to magnify changes. Falling sea level allows thermal anomalies to be more frequent and more extreme because the heat capacity in semi-enclosed systems is reduced. Fluvial discharges are displaced seaward as sea level falls, and impacts of fluvial discharges intensify because they are discharged into a reduced volume of water. Furthermore, falling sea level reduces tidal flushing because water circulates less efficiently in restricted depths and because oceanic inlets are restricted or closed, particularly at the southern end of the bay (“m” sites in Figure 1; Neil 1998). Fluvial inputs are therefore not only more concentrated, but their residence time is also increased. Finally, decreased sea levels bring the floating, hypersaline wedge of flood plumes into direct contact with proportionally more of the benthos. This was probably

not an issue for the region until the onset of modern ENSO conditions, about 3500 BCE, and particularly at peak ENSO intensity, about 700 BCE (Donders *et al.* 2008). We think this mechanism is the main driver of the observed change in coral depth distribution. A hypersaline wedge, lethal to shallow corals, results from little vertical mixing during and after floods. Widespread coral mortality in Moreton Bay followed precisely these conditions after three recent floods, in 1956, 1974, and 1996 (Lovell 1989; Johnson and Neil 1998).

Shift in coral dominance

The modern coral assemblage in Moreton Bay is dominated by massive *Cyphastraea*, *Favia*, and *Goniopora* spp (Johnson and Neil 1998). This community assemblage is unprecedented in the historical record, which is dominated at all other times by branching *Acropora* corals (Wells 1955; Flood 1978; Figure 4e; WebTable 1). Not only are historical episodes of reef growth dominated by branching *Acropora*, but the modern episode also started out that way. The oldest corals in the modern episode are branching or foliose and range from 1653–1842 CE, whereas all of the recent corals are massive (WebTable

Table 1. Results of investigations into factors that could bias the three principal findings for reef growth in Moreton Bay

Potential bias	Mechanism	Premise	Prediction	Analytical results			
				Multiple R	r ²	Test statistic	Effect?
Living coral density	Increased contribution of young corals to DA	Greater density of living corals would contribute a greater number of young skeletons to the DA	DA age is negatively correlated with living coral density	0.24	<0.1	†F = 3.24 P = 0.08	No
Terrigenous stressors	Decreased contribution of young corals to DA	Terrigenous stressors would decrease from west to east because all fluvial inputs of note enter from the western side of the bay (Figure 1)	DA age is negatively correlated with distance from mainland	0.02	<0.1	†F = 0.02 P = 0.90	No
Tidal flushing	Decreased contribution of young corals to DA	Stressors associated with restricted flushing would decrease from south to north because oceanic flood tides enter from the north, following deep channels (Figure 1)	DA age is positively correlated with distance from oceanic inlets	0.11	<0.1	†F = 0.66 P = 0.42	No
Coral morphology	Increased contribution of young massive corals to DA	Contribution of massive corals to DA is strongly dependent on depth-restricted massive-dominated LA	Massive coral DA age is distinct from branching coral DA age when collected randomly	-	-	‡F = 5.08 P = 0.03	Yes
	Underrepresentation of old massive corals in old branching-dominated DA	Testing the ages of 15 non-randomly collected massive corals from ± 1m of the branching-dominated DA should remove the influence of the massive-dominated LA	Massive coral DA age is indistinguishable from branching coral DA age when collected non-randomly	-	-	‡F = 0.22 P = 0.64	No

Notes: DA = coral death assemblage; LA = coral life assemblage; † = linear regression model; ‡ = ANOVA.

1). This skewed distribution is clearly non-random (Fisher's exact test, two-tailed, $P < 0.01$), and the timing of the shift suggests a mechanism between 1842 and 1956. European settlement began around 1824 and by 1880 the Brisbane River catchment was largely deforested, livestock numbered ~300 000, and soil depletion was cited as a serious concern by settlers (Neil 1998). These impacts would have increased inputs of nutrients and sediments that are known to alter coral community composition and decrease the abundance of branching *Acropora* corals (Edinger *et al.* 1998). Coral communities dominated by massive corals are very recent phenomena, and almost certainly a result of rapid anthropogenic change.

Placed in the context of the historical range of variation, a "healthier" version of the modern, massive-coral-dominated assemblage is an inappropriate management goal. Instead, any sign of branching *Acropora* recovery and return to dominance signals historically relevant management success.

Using historical range of variation to assess potential refugia

Ecologists and reef managers are tempted to consider the potential for subtropical marginal reefs to serve as coral refugia from the impacts of global climate change

(Hughes *et al.* 2003; Greenstein and Pandolfi 2008; Hoegh-Guldberg *et al.* 2008). A good refuge should be capable of maintaining immigrant organisms for the projected duration of impacts. Although Moreton Bay appears to be a good candidate, it has poor refuge potential for four reasons. First, Moreton Bay is highly sensitive to anthropogenic change, given that impacts attributable to fewer than 20 000 European settlers (Neil 1998) had profound effects on coral assemblages. Second, as a consequence of this sensitivity, the area currently supports few vibrant communities of branching *Acropora*, which are the dominant structural components of the GBR. Third, the restriction of corals from the shallows is a non-linear response that dramatically reduced the quantity of substrate suitable for corals. Finally, this subtropical habitat was conducive to reef growth only about 50% of the time over the past 7000 years, and only once were reefs stable on millennial time scales. Even if modern anthropogenic impacts were removed from Moreton Bay, the suitability of this habitat as a coral refuge comes down to a coin toss. This is a strong argument against conservation strategies for corals that rely on range shifts or assisted colonization from the GBR to Moreton Bay, as suggested by Hughes (2007) and Wallace (2009), and implied by Hoegh-Guldberg *et al.* (2008). Our case study of Moreton Bay

cautions against the use of such conservation strategies, without consideration of the long-term historical range of variation in the ecosystem.

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