

Cycles of coral reef ‘turn-on’, rapid growth and ‘turn-off’ over the past 8,500 years: a context for understanding modern ecological states and trajectories

Running title: Reef growth cycles and ecological states

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Abstract

Human activities threaten reef ecosystems globally, forcing ecological change at rates and scales regarded as unprecedented in the Holocene. These changes are so profound that a cessation of reef accretion (reef ‘turn-off’) and net erosion of reef structures is argued by many as the ultimate and imminent trajectory. Here we use a regional scale reef growth dataset, based on 76 core records (constrained by 211 radiometric dates) from 22 reefs along and across the inner-shelf of the Great Barrier Reef, Australia, to examine the timing of different phases of reef initiation (‘turn-on’), growth and ‘turn-off’ during the Holocene. This dataset delineates two temporally discrete episodes of reef-building over the last 8,500 years: the first associated with the Holocene transgression-early highstand period (~8.5–5.5k calibrated years BP (cal yBP)); the second since ~2.3k cal yBP. During both periods reefs accreted rapidly to sea level before entering late evolutionary states – states naturally characterised by reduced coral cover and low accretion potential – and a clear hiatus occurs between these reef-building episodes for which no records of reef initiation exist. These transitions mimic those projected under current environmental disturbance regimes, but have been driven entirely by natural forcing factors. Our results demonstrate that, even through the late Holocene, reef health and growth has fluctuated through cycles independent of anthropogenic forcing. Consequently, degraded reef states cannot *de facto* be considered to automatically reflect increased anthropogenic stress. Indeed, in many cases degraded or non-accreting reef communities may reflect past reef growth histories (as dictated by reef growth-sea level interactions) as much as contemporary environmental change. Recognising when changes in reef condition reflect these natural ‘turn-on’ - growth - ‘turn-off’ cycles and how they interact with on-going human disturbance is critical for

effective coral reef management and for understanding future reef ecological trajectories.

Introduction

In recent decades coral cover has markedly declined on coral reefs throughout the Indo-Pacific (1-2% per annum; Bruno & Selig, 2007) and Caribbean (80% reduction since the mid-1970s; Gardner *et al.*, 2003), with 60-70 % of coral communities now believed to be directly threatened by anthropogenic activities (Goreau *et al.*, 2000). These changes are considered indicative of deteriorating coral reef 'health' and resilience (Hughes *et al.*, 2003; Bellwood *et al.*, 2004) and have been interpreted as ecological phase shifts – defined, on a reef, as a transition to a state of persistent low coral and high macroalgal cover (Goreau *et al.*, 2000; Bellwood *et al.*, 2004). Such transitions in coral cover can occur under natural disturbance regimes (Done, 1992), but a wide range of anthropogenic stressors are commonly implicated. These include over-fishing, increased sediment and nutrient yields, coral disease, and coral bleaching (Chadwick-Furman, 1996; Porter & Tougas, 2001), all of which have the potential to change the ecological balance on reefs away from calcifying corals and towards fleshy algae and, as a result, to modify reef accretion potential (Perry *et al.*, 2008a).

In terms of contemporary reef ecology and ecological states, one of the most significant recent suggestions has been that ecological changes, at the magnitudes and spatial scales recently reported on reefs, are unprecedented in the Holocene (Bellwood *et al.*, 2004) i.e., that regional declines in reef building, at the scales projected for the near-future, have not occurred over the last ~10,000 years. In addition, most projections of future

reef ecosystem states, under scenarios of both increasing exposure to direct anthropogenic disturbances and to increased stress from changing marine environmental conditions (especially sea surface temperatures and ocean chemistry changes; Kleypas *et al.*, 2001), envisage unparalleled reductions in reef accretion potential and accelerated rates of reef framework disintegration (Hoegh-Guldberg *et al.*, 2007; Veron *et al.*, 2009). These projections are analogous to the conceptual ideas of reef ‘turn-off’ events as originally discussed by Buddemeier and Hopley (1988), whereby reefs cease vertical accretion, lateral accretion is negligible and/or reefs shift to states of net erosion.

However, discussions regarding the recent changes documented for many reefs commonly assume that deteriorating reef ‘health’ and thus accretion potential (ultimately leading to reef ‘turn-off’), can only be a direct consequence of increased anthropogenic stress. Human activities have undoubtedly driven major ecological changes and transitions to states of net reef erosion at some sites (e.g., Eakin, 1996; Edinger *et al.*, 2000; Lewis, 2002) and have clearly led, on many reefs, to ecological transitions of the type discussed above. However, most assessments of changing reef condition fail to consider the additional, but potentially significant, underlying influence a reef’s age and evolutionary state exert on its contemporary ecological status and accretionary potential (Buddemeier & Hopley, 1988; Hopley *et al.*, 2007). For example, reef age (as a measure of the time since reef initiation) and evolutionary state (as a measure of reef structure and accretionary potential with respect to sea level) typically reflect longer-term, geomorphic timescale (Cowell & Thom, 1994) controls such as sea-level history (especially the rate and magnitude of change since reef initiation), coastal evolution, and, fluctuations in climate. Such factors are acknowledged as key controls

on patterns of coral reef development over interglacial – glacial timescales (Montaggioni, 1994), but their potential to influence the tempo of reef-building at timescales meaningful to contemporary reef ecology are poorly documented.

Here we examine regional histories of mid-to late-Holocene reef establishment (‘turn-on’ *sensu* Buddemeier & Hopley, 1988) and growth to provide a longer-term context for interpretations of contemporary reef geomorphic and ecological states and trajectories. Inherent within our assessment is consideration of when different reefs reached sea level and entered states of accretionary stasis or ‘senility’ (as per the morphogenetic evolutionary descriptor of Hopley, 1982). This is equivalent to the ‘turn-off’ phase of Buddemeier & Hopley (1988) when reefs cease to accrete vertically or laterally. Specifically, we utilise reef chronostratigraphic data from the terrigenous sediment-dominated inner-shelf of the Great Barrier Reef (GBR), Australia, as a case site – arguably the only region globally where sufficient reef accretion data exists to examine these issues at appropriate spatial scales. Inner-shelf reefs of the GBR are of particular significance to the debate about present reef ecosystem change because they are widely reported as ‘degraded’ as a function of post-European settlement deteriorations in water quality (McCulloch *et al.*, 2003; Fabricius *et al.*, 2005), associated with increased sediment (Neil *et al.*, 2002) and nutrient yields (Wooldridge *et al.*, 2006) from coastal catchments. Our record includes all available published data augmented by data collected by us between 2006 and 2009, encompassing data from 22 reefs along ~1000 km of the GBR (Fig. 1; see Supplementary Information SI-1). The primary focus is on the northern-central GBR, where the most data exists, but reference is also made to the southern GBR where limited reef growth data are available.

Materials and methods

Study sites: regional setting and characteristics

The inner-shelf of the GBR extends from the coast out to the ~20 m isobath, with the area shallower than ~15 m characteristically covered by a seaward thinning terrigenous sediment wedge (TSW) (Belperio, 1983). The TSW is composed of lowstand soils and fluvial sediments re-worked landwards during the post-glacial marine transgression (PMT), augmented by on-going fluvial inputs (Larcombe & Woolfe, 1999). Wave-driven sediment resuspension of the TSW produces high turbidity which dominates the inner-shelf water condition (Larcombe *et al.*, 1995), and represents an important influence on the spatial and bathymetric extent of reef development (Woolfe & Larcombe, 1998; Smithers & Larcombe, 2003). Despite this, reefs are widely developed across the inner-shelf: fringing reefs occur on inner-shelf high islands on which coral growth extends to ~10-15 m depth (for examples see: Hopley *et al.*, 1983; Johnson & Risk, 1987); some reefs have formed along or near to the margins of mainland-attached intertidal sand flats, where the maximum depth of coral growth is restricted by shallow nearshore bathymetry (<4 m depth) (for examples see: Perry & Smithers, 2006); and other reefs have established in open water inner-shelf settings from substrates in 5-7 m of water depth. The control exerted by the TSW on the location and timing of inner-shelf reef growth is considered by several conceptual models, which emphasise the importance of even small-scale changes to sediment dynamics on reef initiation and growth (see Larcombe & Woolfe, 1999). In this context, sea-level history is viewed as a

primary control on inner-shelf sediment movement and therefore a major control of inner-shelf reef development (discussed below).

Details of the Holocene sea-level history for Eastern Australia remain controversial (see Supplementary Information SI-2), largely because the timing and magnitude of the mid-Holocene highstand is not agreed. For example, one recent re-appraisal of evidence from south-eastern Australia concluded that present sea level was reached between 7900 and 7700 cal yBP and continued to rise 1.0-1.5 m higher to the peak highstand between 7700 and 7400 cal yBP (Sloss *et al.*, 2007). A 2008 review by Lewis *et al.* also concluded the E. Australia highstand was 1-1.5 m above present, but proposed a slightly later peak at ~7000 cal yBP. The most recent evaluation for northern Queensland (Woodroffe, 2009) concluded that the highstand was attained just 5000 cal years ago, and peaked at 2.8 m above present – although the latter is hard to substantiate given the nature of the regional coral microatoll data (discussed in Supplementary Information SI-2).

The precise nature of sea level behaviour post-highstand is also disputed, with three main interpretations for Eastern Australia existing: a) a smooth fall from the highstand to present; b) a prolonged highstand continuing to ~2000 years before present with later fall; and c) either of the above punctuated with episodic oscillations of several metres magnitude (see Lewis *et al.*, 2008 for discussion). Thus even recent datasets remain problematic in terms of precisely constraining the timing and magnitude of sea-level change. However, despite such uncertainties, there is general consensus that the highstand was reached by ~7000 cal yBP or slightly earlier, was around 1-1.5 m above

present, and then fell to be near present for the past ~1000 years. This broad pattern of sea-level change has had two main impacts on inner-shelf reef development.

The first impact is that shoreline position changed markedly through the transgression, and was higher and landward of present during the highstand ~6-7k cal yBP. As sea levels fell post highstand sedimentary coasts in the region prograded seaward – as recorded in numerous chenier and beach ridge sequences (Hayne & Chappell, 2001; Nott *et al.*, 2009), however some of have undergone recent retreat (Smithers & Larcombe, 2003). The second impact is that the seaward edge of the TSW would also have migrated landwards through the transgression, exhuming in the process substrates suitable for reef development. Importantly, however, all sites in this study preserve clear sedimentary evidence of terrigenous sediment influence during reef accretion, with the most proximal inner-shelf reef facies demonstrating accretion under conditions dominated by mud-rich terrigenous sedimentation (see Supplementary Information SI-1).

Reef chronostratigraphic data

In order to examine regional patterns of reef initiation ('turn-on'), growth and 'turn-off' along and across the terrigenous inner-shelf of the GBR we have made use of all available published, as well as new, recently collected, reef growth datasets. The full dataset used in our analyses includes 76 core records constrained by 211 radiometric dates. The cores have been collected from 22 reefs distributed as follows: a) Northern GBR (southern section): Emmagen Reef, Cape Tribulation (Partain & Hopley, 1989); Rykers Reef, Cape Tribulation (Partain & Hopley, 1989); South Myall Reef, Cape

Tribulation (Partain & Hopley, 1989); Low Isles Reef (Frank, 2008); and Yule Point (Chappell *et al.*, 1983); b) Central GBR: Dunk Island (Perry & Smithers, 2010); Lugger Shoal (Perry *et al.*, 2009); Pioneer Bay, Orpheus Island (Chappell *et al.*, 1983; Hopley *et al.*, 1983); Fantome Island (Johnson & Risk, 1987); Paluma Shoals (Smithers & Larcombe, 2003; Perry *et al.*, 2008b); Rattlesnake Island (Hopley *et al.*, 1983); Nelly Bay, Magnetic Island (Lewis, 2005); and Arcadia Bay, Magnetic Island (Chappell *et al.*, 1983); c) Southern GBR: Cockermouth Island (Kleypas, 1996); Scawfell Island (Kleypas, 1996); Penrith Island (Kleypas, 1996); Middle Percy, Percy Islands (Kleypas, 1996); and High Peak (Kleypas, 1996). We also make use of as yet unpublished recently collected data from King Reef (in the northern-central GBR) and Paluma Shoals. We excluded data from Hayman Island because the Holocene record at this site contains no terrigenous material (see Hopley *et al.*, 1983; Kan *et al.*, 1997). In nearly all cases, multiple cores were collected along transects on an across-reef basis, allowing both vertical and lateral reef accretion to be constrained. Exceptions are; 1) Low Isles – where only one core was dated by Frank (2008); 2) Rattlesnake Island – where only one core was collected and described by Hopley *et al.* (1983); and 3) the cores from Middle Percy and High Peak where single or paired cores were recovered by Kleypas (1996). Details of individual sites, core and date chronologies are provided in the Supplementary Information (SI-1).

In order to conform to established definitions of reef ‘turn-on’ and ‘turn-off’ (following Buddemeier & Hopley, 1988) we based our interpretations of the point of reef ‘turn-on’ on the oldest/deepest corals from horizons in core where there is clear evidence of active reef framework accumulation. Specifically, therefore, we excluded dates from

isolated corals within underlying pre-reefal facies. Our estimates of the point of reef ‘turn-off’ are based on dated coral samples from just below the contemporary reef flat surfaces, thus ensuring we did not date or include dates from living corals. In all cases, only radiocarbon dates obtained from coral samples interpreted as either *in-situ* (i.e., in growth position based on orientation and/or basal contact) or *in-site* (i.e., which showed little sign of post-depositional reworking and transport), based on published information or direct observations in new core material, were included in our dataset. We also excluded corals that had clearly been reworked (as evidenced by a high degree of abrasion) that may pre-date the horizons in which they occur, and dates on molluscan material from within the reef matrix as these samples may post-date reef framework deposition. To ensure consistency across the radiocarbon datasets used, both new and previously published conventional radiocarbon dates were (re)calibrated using CALIB Version 5.0.2 and calibration curve Marine04 (<http://calib.qub.ac.uk/marine>; accessed July 2009). We used a weighted mean ΔR value of $+10 \pm 7$ as the best current estimate of variance in the local open water marine reservoir effect for the central Queensland coast (Ulm, 2002). In the supporting text and figures we refer to the 1 sigma calibrated age range for all dated samples and, following Telford *et al.* (2004), the median probability age as a reliable ‘best estimate’ of the calibrated age. To provide a neutral sea level datum across all sites, core data from each reef were (re)plotted relative to the local Lowest Astronomical Tide (LAT) level.

Results

Chronostratigraphic data for the inner-shelf of the northern-central GBR are shown in Fig. 2A. This includes data from both distal (the present inner- to mid-shelf boundary)

and proximal (inside the present extent of the TSW) inner-shelf environments. Within this dataset radiometric dates range from ~8.5k cal yBP to 'modern' and span elevations from -10 m to +2 m LAT. The wide age range suggests reef growth continued throughout the mid-to late-Holocene across the inner-shelf. However, the timing and duration of reef growth was far more structured than the full age-depth dataset suggests. In particular, Fig. 2A includes chronostratigraphic data from two reefs (Fantome Island and Orpheus Island) located along the seaward boundary of the inner shelf (Hopley *et al.*, 1983; Johnson & Risk, 1987). Terrigenous sediment influence has decreased since the early phases of reef growth at these sites (since ~6.5-5k cal yBP) as the TSW migrated landward, and recent phases of accretion have been carbonate dominated. These reefs thus represent 'outliers' in the dataset, and have accretion histories more typical of mid-shelf (clear-water) reefs (Smithers *et al.*, 2006).

Excluding these distal inner-shelf reefs and plotting only reefs that initiated and accreted inside the TSW reveals two temporally discrete chronostratigraphic clusters (Fig. 2B): 1) an older group developed during the late transgression-early highstand (~8.5 to 4.5k cal yBP), with reef initiation constrained to ~8.5 to 5.5k cal yBP (Fig. 2B); and 2) a more recent cohort deposited since ~2.3k cal yBP, with reef initiation confined between ~2.3 and 0.8k cal yBP. Only two dates from Nelly Bay and one date from King Reef plot outside these clusters. Nelly Bay is, however, close to the present seaward margin of the TSW, and the stratigraphic position of these dates and the earliest (initiation) dates at this site are not clear (Lewis, 2005). The youngest date from King Reef is associated with the final stages of lateral reef expansion following the main phase of reef accretion and reef flat emplacement. Interestingly, and despite differences in shelf

width, chronostratigraphic data from the southern GBR also plot into two similar groupings between ~8.7 to 5.5k cal yBP, and since ~3.5k cal yBP (Fig. 3).

Three key periods associated with mid- to late-Holocene inner-shelf reef initiation and growth can therefore be delineated. The first initiation or ‘turn-on’ window is constrained between ~8.7 to 5.5k cal yBP, occurring slightly earlier and from greater depths in the northern and southern GBR (Fig. 4). These reefs all established above non-lithified transgressive sediment substrates (subtidal sands, gravels and muds; see Smithers et al. 2006; Perry & Smithers, 2009) or directly above Pleistocene clays (see Supplementary Information SI-1). All accreted rapidly to sea level before switching to progradational growth modes under conditions of sea-level constraint and small-scale regression. In the northern-central GBR, reef ‘turn-off’ occurred between 6.4 to 4.5k cal yBP (Fig. 4). These reefs are presently in a ‘senile’ (*sensu* Hopley, 1982) evolutionary state. On these reefs live coral cover is highly variable and temporally dynamic (Sweatman *et al.*, 2007), but in all cases appears to comprise an ephemeral living veneer with little accretion potential; reef growth data shows negligible reef accretion over the last ~4,500 years. Only reefs initiating along the offshore margin of the TSW continued to prograde, and they did so free from significant terrigenous influence. The situation in the southern GBR is similar. Some reefs (High Peak, Penrith, Cockermouth West) reached sea level rapidly and ‘turned-off’ over comparable timescales (Fig. 4). Others (Cockermouth South, Scawfell) had more complex growth histories (Fig. 4), although chronostratigraphic data suggests punctuated accretion through the Holocene regression, with the onset of renewed accretion evident only in the past 2-3,000 years.

Discussion

Conceptual ideas about phases of reef ‘turn-on’ and ‘turn-off’ have been widely discussed in the reef geological literature, often being based on long-term evidence for reef demise, as recorded in the geological record as drowning or emergence surfaces within relict (fossil) reef structures, and in Holocene reefs as submerged framework structures (Blanchon *et al.*, 2002; Harris *et al.*, 2008). However, in a very forward thinking paper Buddemeier and Hopley (1988) made a compelling case for the need to consider the causes and mechanisms of reef ‘turn-on’ and ‘turn-off’ events in the context of emerging concerns about increasing anthropogenic disturbance, and of projected large-scale changes to global climate and marine conditions. Integral to their discussions was a consideration of when disturbance and change on reefs (as measured over ecological timescales) truly constituted real ‘turn-off’ phases rather than short-lived ecological hiatus events.

Directly relevant to this is how the terms ‘turn-on’ and ‘turn-off’ are defined and measured. Buddemeier and Hopley (1988) define reef ‘turn-on’ as that point at which “... a substantial coral-algal community capable of developing a significant reef structure that can sustain itself in the ambient environmental conditions [has formed]” (Buddemeier & Hopley (1988) p. 253). Thus it is the point at which a sufficiently robust population of reef-building organisms exists that permit either vertical and/or lateral accumulation of a reef structure. In contrast, reef ‘turn-off’ is defined as a response to states where environmental conditions deteriorate “... into a regime unsuitable for reef development ...even though significant populations of corals and coralline algae may continue to exist” (Buddemeier & Hopley (1988) p. 254). Such transitions may occur

either as a function of extrinsic forcing, for example where environmental disturbances change the balance of the ecosystem from one of net accretion to net erosion (see Perry *et al.*, 2008a for examples), or intrinsic forcing as reef structures reach sea level and further accretion potential is constrained. In these cases it is the lack of additional accommodation space that causes reefs to ‘turn-off’.

Our dataset delineates a relatively distinct ‘window’ or period (between ~8.7 and 5.5k cal yBP) during which inner-shelf coral reefs on the GBR first ‘turned-on’. The timing of reef turn-on at each site is broadly correlated with depth and, given the timing of these turn-on events in relation to the regional sea-level curve, is interpreted as a response to progressive marine inundation of the shelf associated with the post-glacial sea-level rise. Once established these reefs accreted rapidly, biofacies and reef top ages suggesting most lagged slightly behind sea level until they caught up during the mid-Holocene highstand and further vertical accretion halted. Based on the chronostratigraphic datasets presented in this study, average vertical accretion rates for the northern GBR inner-shelf reefs during this period were between 0.3 – 0.5 m/100 years, for the central GBR between 0.3 – 0.65 m/100 years, and for the southern GBR between 0.5 – 0.9 m/100 years. These impressive rates of accretion were achieved despite continued terrigenous sediment influence and accumulation as recorded in the reef sedimentary facies and growth fabrics.

As discussed earlier most of these reefs subsequently shifted to (lateral) progradational growth modes under high, stable and then slowly falling sea levels, before ‘turning-off’, and two main factors probably caused this phase of mid-Holocene inner-shelf reef

demise. The first relates to accommodation space for reef building, the second to changing shoreline positions and inshore sediment dynamics, and both are strongly linked to subtle changes in sea level over the last ~8500 years. Reefs initiating inside the TSW all established in shallow sub-tidal settings before accreting rapidly to sea level within restricted (typically <3-4 m depth) accommodation windows. The onset of the Holocene highstand would have directly restricted vertical accretion (a constraint enforced during the subsequent regression) and thus, where seaward geometries permitted, reefs switched to progradational growth modes. It is of significant interest to note that very similar transitions and markedly suppressed rates of vertical reef accretion are also documented on mid-shelf (Smithers *et al.*, 2006) and outer reefs on the GBR (see fig. 11.3, Hopley *et al.*, 2007). However, for most inner-shelf reefs the typically high turbidity conditions (Larcombe & Woolfe, 1999) may also have constrained progradational vigour, leading to reef ‘turn-off’ as both vertical and lateral accommodation space was restricted (see Perry & Smithers 2010). Dynamic shoreline changes associated with widespread post-highstand shoreline progradation (Hayne & Chappell, 2001; Nott *et al.*, 2009) presumably also directly affected the shallow nearshore environments where inner-shelf reefs could establish. It is also possible that changes in turbidity, water quality, and sedimentation linked to the closure of the Holocene high-energy window (Hopley, 1984) could have affected reef growth rates and stability at around the same time.

Although it is tempting to ascribe such changes to a single environmental cause, it is more probable that the synergistic effects of several factors are involved. For example, Gagan *et al.* (1998) showed that sea surface temperatures were more than 1°C warmer

on the inner central GBR around 5500 years ago, after which declining sea surface temperatures may have reduced calcification (Lough and Barnes, 2000) and thus accretion potential. After the mid-Holocene climatic optimum data from inshore corals show that rainfall in the region became more unreliable (Gagan *et al.*, 1999), and the extremes of drought and flood (and sediment delivery) (Gagan *et al.*, 1996) may have been particularly stressful for inshore corals – as elevated sediment flux from coastal catchments is argued to be today (McCulloch *et al.*, 2003), leading to widespread reef demise. We note, however, that most cores through inshore reefs on the GBR contain high levels of fine-grained terrigenous sediment during periods of active reef accretion, suggesting that changed sediment yields alone were unlikely to have been the sole driver of reef turn-off. Rather, multiple stressors, acting within the clear and overarching constraints of reduced accommodation space, may have been involved (Smithers *et al.*, 2006).

This period of widespread reef ‘turn-off’ was followed by an apparent hiatus (between ~5.5 to 2.3k cal yBP) during which no records of new reef initiation exist and for which the only reliable evidence of on-going reef accretion is restricted to the distal inner-shelf margins (Fig. 4), where the reefs were able to shift to progradation growth modes under conditions of significantly reduced terrigenous sediment influence. It is possible that this ‘hiatus’ simply reflects the present lack of evidence from this period, either because reefs that initiated and accreted through this interval have been eroded away or that they have not yet been found. The latter idea will be tested in future work, but the geographic spread of sites in this study and the number of cores and radiometric dates analysed, provide a high degree of confidence in the broader patterns reported. Given such

confidence it seems most likely that the same conditions that lead to the mid-Holocene period of reef ‘turn-off’ (discussed above) probably inhibited renewed reef initiation through this period.

What is clear is that a second period of inner-shelf reef ‘turn-on’ occurred from ~2.3k cal yBP (Fig. 4). These reefs initiated above a similar range of non-lithified sediment substrates and within similar geomorphic settings – often in close proximity to the older ‘relict’ mid-Holocene reefs (Perry & Smithers, 2010). All initiated in shallow sub-tidal settings, and accreted rapidly to sea level, again in settings dominated by fine-grained terrigenous sediment accumulation. The timing of this second ‘turn-on’ period is harder to explain, but is sufficiently well constrained timewise, to suggest that extrinsic (regional scale) controls were important to this event. Most likely this second ‘turn-on’ event occurred as a function of sea level stabilisation through the late Holocene (see Supplementary Information SI-2), a transition that facilitated the progressive re-opening of potential reefal habitats as further seaward movement of the previously dynamic TSW ceased. Indeed, along some areas of the coast sea-level stabilisation has been followed by periods of shoreline retreat – such as within Halifax Bay (Smithers & Larcombe, 2003) – and thus one can envisage scenarios whereby coral communities were either able to establish on pre-existing sediment substrates, or utilise newly exposed substrates as the coastline retreated. Thus, the potential for reef ‘turn-on’ and ‘turn-off’ has been transitional over millennial timescales, as controlled by subtle changes in sea level.

Interestingly, and despite the relatively young ages, this younger suite of reefs are already at different evolutionary states. Low Isles Reef, Dunk Island (low elevation reef) and Paluma Shoals North are clearly in, or approaching 'senility' having developed wide, well-developed reef flats with relatively low coral cover. The rapid transition to this evolutionary stage can most likely be attributed to rapid vertical accretion and exhaustion of accommodation space – especially as all these reefs initiated in shallow settings from substrates <3 m below LAT; many of these reef flats are quite barren and have clearly ceased accreting. Other 'young' reefs, such as Paluma Shoals South and Lugger Shoal, remain in earlier evolutionary stages, having more recently reached sea level and have incompletely developed reef flats. Recent declines in coral cover on these, or other, 'young' reefs cannot, however, be assumed to solely reflect anthropogenic impacts since many are transforming into less productive states at the end of a natural accretionary cycle. Under present sea-level conditions their ultimate fate will be a 'turn-off' of carbonate accretion (i.e., growth) potential mirroring that seen on inner-shelf reefs in the period 6.5 to 4.5 k cal yBP.

Most near-future sea level projections indicate, however, that sea levels will rise in the order of 0.5-1.0 m by ~2100, rates that are comparable to those experienced during the post-glacial marine transgression. Thus under future scenarios of rising sea levels, and assuming other environmental factors are not limiting, relatively rapid turn-on of vertical reef accretion should be possible for the younger suite of reefs. Re-initiation may also be possible on older (previously sea-level constrained and 'turned-off') reefs, albeit with a longer lead in or lag time, the length of which will reflect the extent to which a reef is affected by the increased mobilization of nearshore sediments produced

by the rising seas. Rising sea levels will also be likely to open up new substrates for potential coral reef initiation, both to landward as coastlines retreat and new substrates are exposed, and on the inner-shelf itself as the TSW once again migrates landwards (conditions mirroring those associated with both phases of inner-shelf reef ‘turn-on’ documented during the Holocene). However, the extent to which coral reefs are actually able to exploit these new accommodation windows and substrates will depend upon how they respond to a host of contemporary extrinsic (anthropogenic-related) environmental factors.

Holocene reef development within the inner-shelf region of the GBR has thus been characterised by distinct cycles of reef ‘turn-on’ and ‘turn-off’, with these cycles of rapid reef growth (separated by a non-reef initiation hiatus period) operating independently of anthropogenic forcing. Of particular significance, from an ecological perspective, is that the products of these ‘turn-on’ and ‘turn-off’ phases have been the formation of reef structures that exist in very different evolutionary states. Those that ‘turned-on and off’ in the period 8.5 to 4.5k cal yBP presently form palimpsest structures that have experienced little or no accretion in the last ~4-5,000 years and are colonised by ephemeral veneers of living coral and associated biota. Examples include the Cape Tribulation reefs, Dunk Island ‘high elevation reef’ (Fig. 5A), King Reef (Fig. 5B), Cockermouth West, Penrith and High Peak (see Fig. 4). Continual ecological turnover and low net carbonate production should thus be the expected norm on these reefs. The present low coral cover on the reef flat surfaces and low accretionary potential certainly should not be immediately attributed to anthropogenic stress.

In contrast, reefs initiating in the last ~2,000 years exist in a range of evolutionary states. Some are already close to ‘senility’ - examples include Dunk Island ‘low elevation reef’ (Fig. 5C) and Paluma Shoals North (Fig. 5D), which have become sea level constrained in the last few 100 years (Fig. 4). Others are still actively accreting – examples include Paluma Shoals South (Fig. 5E) and Lugger Shoal (Fig. 5F), with radiocarbon date chronologies at these sites indicating sea level being achieved only in the last <100 years (Fig. 4). Consequently, it would also seem entirely sensible to incorporate assessments of reef age (evolutionary state) and geomorphic structure into reef management decision-making processes as these factors have an equally important bearing on reef ecosystem state as do prevailing environmental and ecological conditions – indeed they are a major control and influence on these. It is perhaps also worth noting here that those reefs with the highest accretion rates (what many would argue as being the ‘healthiest reefs’, if ‘health’ is defined as a measure of high coral cover and high rates of primary carbonate production) will naturally pass through the different evolutionary stages and reach states of ‘senility’ the fastest. In this context, the youngest and most actively accreting reefs, with the most diverse geomorphic structures and habitats, could provide a valid target for high priority conservation status.

A key finding of this study is that regional scale loss of reef-building potential is not without precedent in the mid- to late- Holocene – in this case with major phases of reef ‘turn-off’ and loss of reef-building potential (analogous to that predicted as the end-point of present ecological change trajectories) being driven entirely by natural processes – most likely a combination of subtle fluctuations in sea-level and associated shifts in shoreline position, potentially augmented by other factors such as sea surface

temperature and inshore water quality. In the context of predicted near-future climatic and sea-level changes a case can be made that even small-scale changes in sea-level (in this case well within the magnitudes of those predicted under most SRES scenarios) and associated changes in shoreline geomorphology and shallow sub-tidal sediment remobilisation can drive regionally significant phases of reef ‘turn-off’ and potentially dictate the timing and location of renewed phases of reef ‘turn-on’. Thus, whilst the timing and longevity of inner-shelf reef growth has in the recent geological past been profoundly influenced by natural processes, the legacy of which is strongly expressed in contemporary reef ecological states, both natural and more widely discussed anthropogenic factors, need to be integrated into considerations of future reef ecological trajectories.

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Supplementary Information

Additional Supporting Information may be found in the online version of this article.

SI – 1. Inner-shelf reef sites and reef chronostratigraphy.

SI – 2. Holocene sea-level history for Eastern Australia

Figure Captions

Fig. 1 Map showing the location of reef sites referred to in this study. Boxed insets show the inner-shelf reef sites discussed in the (1) northern, (2) central, and (3) southern areas of the Great Barrier Reef, Australia. See Supplementary Information for details of core data at each site.

Fig. 2 Age-elevation plots of corals from inner-shelf sites on the central-northern Great Barrier Reef, Australia plotted relative to Lowest Astronomical Tide (LAT) level. A) Plot showing all dates from all sites within the inner-shelf of the northern-central GBR; B) Plot showing only those dates from sites within the proximal inner-shelf (those which initiated inside the terrigenous sediment wedge and continued to accrete under terrigenous sediment influence). This plot also excludes dates from sites where no published chronostratigraphic data exists (only surface microatoll data - Yule Point; and Arcadia Bay, Magnetic Island). Horizontal error bars show the 68% probability range of the calibrated dates. Vertical error bars are plotted at the median probability age point (following Telford *et al.*, 2004) and conservatively shown as 0.25m for *in-situ* corals and 0.5 m for 'in-site' rubble samples. Two discrete age clusters are delineated (circled).

The dark grey circles denote the oldest dates (minimum initiation ages) for different reefs: *SMCT*, South Myall, Cape Tribulation; *RCT*, Rykers Reef, Cape Tribulation; *ECT*, Emmagen Reef, Cape Tribulation; *KR*, King Reef; *NB*, Nelly Bay, *DKH*, Dunk Island – high elevation reef; *LIR*, Low Isles Reef; *PSN*, Paluma Shoals North; *PSS*, Paluma Shoals South; *DKL*, Dunk Island – low elevation reef; *RSI*, Rattlesnake Island; and *LS*, Lugger Shoal. Both data sets are shown relative to a composite sea-level curve for the central GBR region based on the re-calibrated best-fit transgressive data of Larcombe & Woolfe (1999) superimposed on the highstand - sea-level regression plot of Chappell (1983). The grey field is the predicted ‘existence field’ for coastal turbid-zone reefs from Larcombe & Woolfe (1999).

Fig. 3 Age-elevation plots of corals from inner-shelf sites on the southern Great Barrier Reef, Australia plotted relative to Lowest Astronomical Tide (LAT) level. Dates from all sites within the inner-shelf of the southern GBR; Horizontal error bars show the 68% probability range of the calibrated dates. Vertical error bars are plotted at the median probability age point (following Telford *et al.*, 2004) and conservatively shown as 0.25m for *in-situ* corals and 0.5 m for ‘in-site’ rubble samples. Two discrete age clusters are delineated (circled). The dark grey circles denote the oldest dates (minimum initiation ages) for different reefs: *SC*, Scawfell; *CKW*, Cockermouth Island - West; *CKS*, Cockermouth Island – South; *P*, Penrith; *HP*, High Peak; *MP*, Middle Percy. No reliable sea-level curve exists for this area of the GBR.

Fig. 4 Plot showing timescales of reef initiation-accretion-demise for all inner-shelf GBR sites with available chronostratigraphic (core) data. Two distinct reef ‘initiation windows’ can be delineated (grey boxed areas), separated by a ‘hiatus’ period for which no reliable records of inner-shelf reef initiation exist. Only Middle Percy Reef (southern GBR) has its earliest date in this period, but this is not a basal clast and the underlying Holocene reef stratigraphy and the depth to the Pleistocene are not known at this site. The basal dates in most cores are on, or very close, to the underlying Pleistocene substrate and in both ‘initiation windows’ those reefs which initiated and grew inside the terrigenous sediment wedge went through phases of rapid accretion, reef flat development and then ‘turn-off’ over timescales of <2,500 years. Some of the younger suite of reefs (Low Isles Reef, Dunk Island – low elevation reef, Paluma Shoals North) have already moved through this rapid growth phase and are already in/or close to senile evolutionary states. Also shown are the best estimate periods during which Holocene sea levels were rising, were higher than present and then regressing to present levels in Eastern Australia (see SI-2 for detailed discussion).

Fig. 5 Photographs of different reefs on the inner-shelf of the GBR showing variability in contemporary reef flat states that reflect reef age and time since the reefs reached sea level. (A, B) Examples of the mid-Holocene (8.5 to 4.5k yBP) suite of ‘senile’ inner-shelf reefs on the GBR which now exhibit low or no coral cover and are characterised by largely planar, infilled surfaces. (A) Dunk Island ‘high elevation reef’ which reached sea level by ~6.5k yBP and ceased accreting by ~4.5k yBP. (B) King Reef which reached sea level ~5k yBP and ceased accreting by ~4.5k yBP. (C-F) Examples of the late Holocene (since ~2.3k yBP) suite of inner-shelf reefs on the GBR. Dunk Island

'low elevation reef' (C) and Paluma Shoals North (D) are examples of this young suite of reefs that 'turned-on' between 2.5-1.5k yBP and reached sea level in the last few 100 years. These are already in, or are approaching, states of senility, as evidenced by their infilled and relatively planar surfaces. Paluma Shoals South (E) and Lugger Shoal (F) are other examples of this young suite of reefs that 'turned-on' later (in the last <1.5k yBP) and, having only recently reached sea level (in last <100 years), are still actively accreting. Paluma Shoals South is probably approaching a state of complete sea level constraint and will likely soon cease to accrete under present sea level states. Lugger Shoal has not yet reached a state of complete infilling and has a more irregular surface structure.