

# Transitions in coral reef accretion rates linked to intrinsic ecological shifts on turbid-zone nearshore reefs

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## ABSTRACT

Nearshore coral communities within turbid settings are typically perceived to have limited reef-building capacity. However, several recent studies have reported reef growth over millennial time scales within such environments and have hypothesized that depth-variable community assemblages may act as equally important controls on reef growth as they do in clear-water settings. Here, we explicitly test this idea using a newly compiled chronostratigraphic record (31 cores, 142 radiometric dates) from seven proximal (but discrete) nearshore coral reefs located along the central Great Barrier Reef (Australia). Uniquely, these reefs span distinct stages of geomorphological maturity, as reflected in their elevations below sea level. Integrated age-depth and ecological data sets indicate that contemporary coral assemblage shifts, associated with changing light availability and wave exposure as reefs shallowed, coincided with transitions in accretion rates at equivalent core depths. Reef initiation followed a regional ~1 m drop in sea level (1200–800 calibrated yr B.P.) which would have lowered the photic floor and exposed new substrate for coral recruitment by winnowing away fine seafloor sediments. We propose that a two-way feedback mechanism exists where past growth history influences current reef morphology and ecology, ultimately driving future reef accumulation and morphological change. These findings provide the first empirical evidence that nearshore reef growth trajectories are intrinsically driven by changes in coral community structure as reefs move toward sea level, a finding of direct significance for predicting the impacts of extrinsically driven ecological change (e.g., coral-algal phase shifts) on reef growth potential within the wider coastal zone on the Great Barrier Reef.

## INTRODUCTION

Coral communities that form within highly turbid nearshore habitats (i.e., shallow-water mesophotic settings; *sensu* Morgan et al., 2016) are widely considered to be marginal environments for long-term reef building. The negative impacts associated with low-light and high-sedimentation conditions on coral calcification and reef ecological health are reported to be exacerbated by elevated terrigenous sediment and nutrient inputs due to coastal catchment land-use change (De'ath and Fabricius, 2010). However, coral community responses and reef-building capacity under declining water quality are likely a function of the magnitude of localized sedimentation regime shifts against the long-term background (or “natural”) environmental conditions under which the corals established. This is supported by core-based chronostratigraphic reconstructions from several nearshore sites (<10 m water depth) within the central region of Australia's Great Barrier Reef, which indicate that reefs within this zone have rapidly accreted (2–7.8 mm yr<sup>-1</sup>) and supported diverse coral assemblages under conditions of terrigenous sediment influence throughout the mid- to late Holocene (Perry et al., 2012). Furthermore,

recent research has shown high contemporary coral cover on these reefs (Morgan et al., 2016), most notably of the key reef-building taxa (branching *Acropora* spp.) that have reportedly declined in abundance at sites further offshore (e.g., Pelorus Island; Roff et al., 2012).

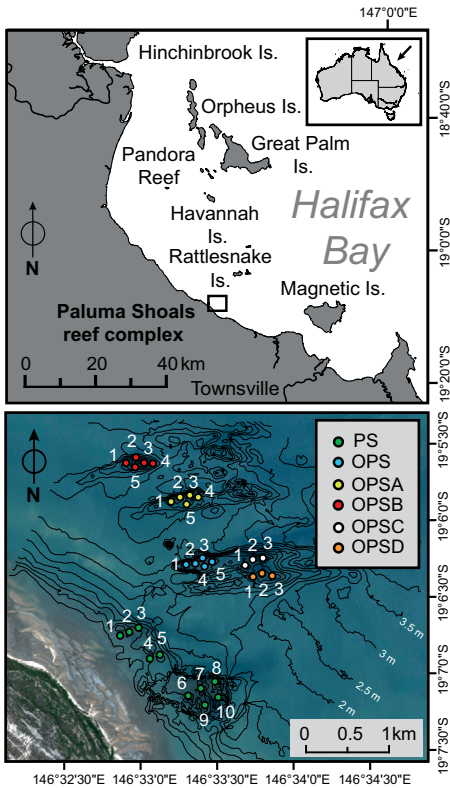
On the basis of this recent work, Morgan et al. (2016) hypothesized that depth-constrained transitions in coral taxa and morphologies may act as equally important controls on long-term reef-building rates and styles in turbid environments as they do within clear-water reef settings, even despite the narrow depth ranges (<5 m depth), reduced coral diversity, and the atypical environmental conditions (i.e., low light and high turbidity) under which they form. Here, we test this hypothesis using a newly compiled chronostratigraphic record based on 31 reef cores and 142 radiometric dates, and use this to examine the growth histories of seven proximal (but discrete) reefs (i.e., reefs that grew under near-identical environmental conditions) that are currently at different depths below sea level. This record, which for the first time spans the full spectrum of reef developmental stages, is examined together with recent field data on contemporary nearshore coral assemblages to provide

insights into an intrinsic two-way relationship whereby past reef-growth history drives transitions in reef ecology, and which ultimately influence reef-building capacity and morphology. Our findings confirm that on these turbid nearshore reefs, reef morphology not only underpins habitat availability and ecological dynamics (e.g., the coral taxa and growth morphologies present), but also ultimately influences rates of vertical growth as the reefs mature. Importantly, these findings have wider relevance across other similarly low-impacted (located further from river inputs and/or coastal development) nearshore sites on the Great Barrier Reef where comparable ecological patterns have been reported (Browne et al., 2010).

## FIELD SETTING AND METHOD

We compiled a core record from seven proximal nearshore reefs that form the Paluma Shoals reef complex (PSRC) located ~3 km from the coast within Halifax Bay, central Great Barrier Reef (Fig. 1; 19.1145°S, 146.5497°W). Reef surfaces span a range of water depths (–0.6 to +0.5 m relative to lowest astronomical tide [LAT]), sitting atop subtle (1–2 m elevation) rhythmically spaced arcuate ridges (see Morgan et al., 2016). These reefs experience episodic high turbidity (up to 385 mg L<sup>-1</sup>) caused by wave-driven resuspension of seafloor terrigenous sediment (Browne et al., 2013b), and periods of chronic turbidity following sustained southeast-northwest trade winds. Coral cover (June 2014) across the structures is high (mean: 38% ± 24%; Morgan et al., 2016), and coral assemblages are highly depth stratified as light attenuates rapidly through the turbid water. Our core record includes 16 new cores and 72 radiometric dates collected from four previously unsampled submerged reefs (–0.6 to –0.4 m LAT) (offshore Paluma Shoals A, B, C, and D [OPSA, OPSB, OPSC, and OPSD]; Fig. 1; Table DR1 in the GSA Data Repository<sup>1</sup>). These cores represent the first records of early-stage nearshore reef development and augment

<sup>1</sup>GSA Data Repository item 2016335, methods and Tables DR1 and DR2, is available online at [www.geosociety.org/pubs/ft2016.htm](http://www.geosociety.org/pubs/ft2016.htm) or on request from [editing@geosociety.org](mailto:editing@geosociety.org).



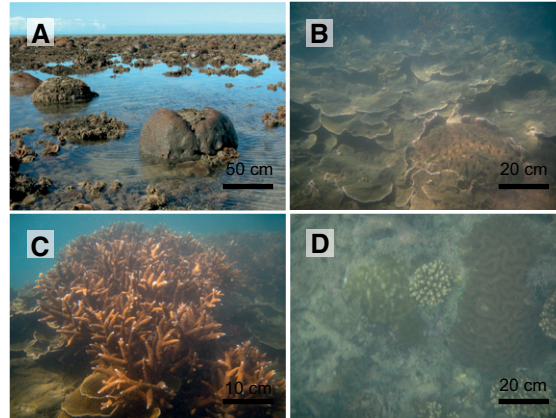
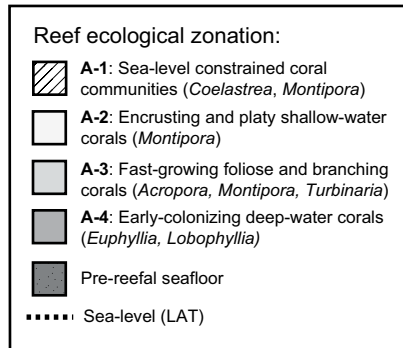
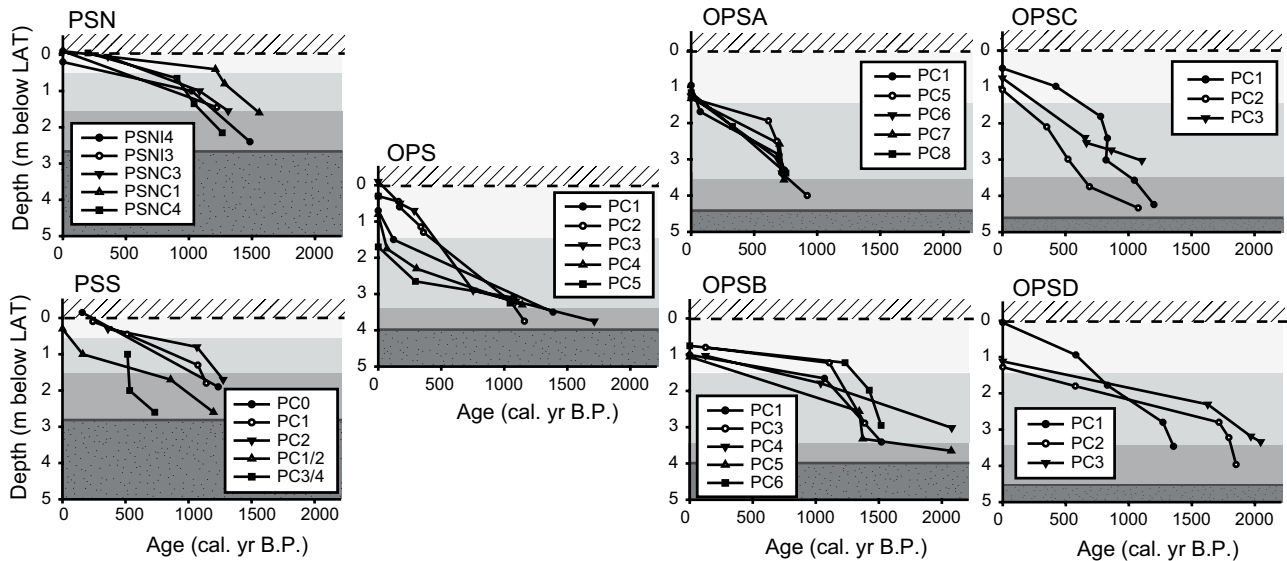
**Figure 1. Paluma Shoals reef complex located within Halifax Bay, central Great Barrier Reef, Australia. Approximate core locations are shown for each reef site. PS—Paluma Shoals; OPS(A–D)—offshore Paluma Shoals (A–D).**

an existing record of 15 cores (70 radiometric dates) collected during earlier investigations (Paluma Shoals north [PSN] and south [PSS], Palmer et al., 2010; offshore Paluma Shoals [OPS], Perry et al., 2013; Fig. 1). Together they provide a unique data set spanning the full spectrum of nearshore reef developmental stages from incipient reef growth through to full sea-level emplacement. All cores (collected using percussion techniques with 100% recovery of undisturbed core material) penetrated the entire Holocene reef sequence, terminating in pre-reefal sedimentary units, and were logged to record biosedimentary facies information. *In situ* coral material was selected for accelerator mass spectrometry radiocarbon dating to determine reef chronology (see the Data Repository for methodology). Recent depth-calibrated ecological data sets of the study area (Morgan et al., 2016) were used to determine coral community

distribution which were then applied to corresponding core depths. Previously, a poor understanding of nearshore ecological communities meant that such comparisons were not possible.

## RESULTS

Core records collected from across the PSRC show that all reefs initiated directly on Pleistocene clays or intertidal marine sands and lithic gravels ca. 2000–700 calibrated (cal.) yr B.P. in contemporary water depths of between –1.5 m LAT (PSN) and –4.3 m LAT (OPSC) (Fig. 2). Three of the seven reef structures within PSRC (PSN, PSS, OPS) have recently become sea-level constrained (since <450 cal. yr B.P.), as indicated by the development of extensive semi-emergent reef flats. Terrigenous muds were volumetrically important within the reef framework throughout all the cores, suggesting that naturally high levels of mud deposition were occurring long before reported increased anthropogenic sediment inputs following European settlement (ca. A.D. 1862). Mean accretion rate across all reefs that compose the PSRC was  $4.5 \pm 3.3 \text{ mm yr}^{-1}$ , but there was variability between the different stages of reef geomorphic maturity (Fig. 3A), and each stage was associated with



**Figure 2. Age-depth profiles from 31 cores (142 radiocarbon dates) collected across Paluma Shoals reef complex, Great Barrier Reef, Australia. PSN, PSS—Paluma Shoals north and south; OPS(A–D)—offshore Paluma Shoals (A–D); LAT—lowest astronomical tide; cal.—calibrated. Shaded zones correspond to depth-variable contemporary coral assemblages reported for these reefs: zone A-1 (photo A); zone A-2 (photo B); zone A-3 (photo C); zone A-4 (photo D).**

distinctive coral communities (see Table DR2). Several reef structures, specifically those initiating further offshore in deeper waters (e.g., OPSB, OPSD), show two main phases of growth with an apparent unconformity separating an older phase of reef initiation ca. 2000 cal. yr B.P. from a more recent period of rapid vertical accretion over the past ~1000 yr (Fig. 2).

Depth-variable transitions in accretion rates coincide with reported zonation patterns of contemporary nearshore corals (Morgan et al., 2016), specifically changes in total coral cover and the dominant coral taxa and morphologies with depth (Figs. 2 and 3B). Accretion rates following initiation were slow (mean:  $1.5 \pm 0.5$  mm yr<sup>-1</sup>). Contemporary corals that occur within this depth range consist of isolated slow-growing and stress-tolerant taxa (e.g., *Euphyllia* sp., *Lobophyllia* sp.; Fig. 2D). Maximum vertical accretion occurred typically between 2 and 3 m below LAT (mean:  $6.0 \pm 3.7$  mm yr<sup>-1</sup>). At comparable depths within the contemporary ecological record we observe a shift toward higher coral

cover (mean:  $40\% \pm 36\%$  cover) and fast-growing and/or structurally complex branching and foliose coral morphotypes (e.g., *Acropora* spp., *Turbinaria* spp.), as light penetration and near-bed sediment resuspension increases with reef shallowing (Fig. 2C). As accommodation space fills and reefs approach sea level (<1.5 m below LAT), rates of accretion decrease (mean:  $3.2 \pm 2.8$  mm yr<sup>-1</sup>; Figs. 2 and 3B). This transition corresponds with a decrease in contemporary coral cover (to 25%) and a change in coral community structure to low-profile encrusting coral taxa (e.g., *Montipora* spp.; Fig. 2B), indicating greater hydrodynamic stress as reefs reach wave base. Once reefs are sea-level constrained (e.g., PSS and PSN), mean accretion rates are lower (mean:  $1.4 \pm 1.0$  mm yr<sup>-1</sup>), potentially as a combined consequence of reduced coral cover (18% cover) and a shift toward massive (*Coelastrea* sp. [formerly *Goniastrea* sp.]) and encrusting taxa (*Montipora* spp.), as well as increased sediment redistribution and export from the reef surface by waves (Fig. 2A).

## DISCUSSION

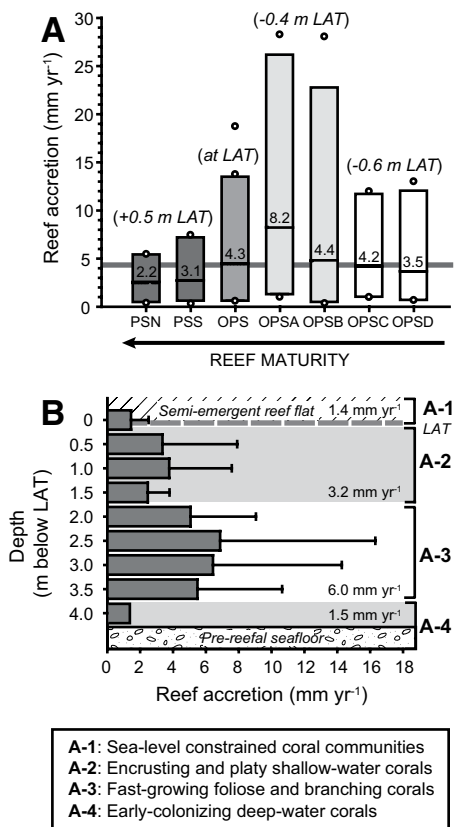
Our findings suggest that these nearshore coral reefs exhibit high structural complexity and coral cover that diminishes naturally during reef development as accommodation space fills and the reefs shallow toward sea level (Figs. 2 and 3). Most significantly, our results provide the first empirical evidence that changes in nearshore coral communities through time may be just as critical as drivers of vertical reef growth as within clear-water settings, despite fundamental differences in the environmental conditions under which they form and the diversity of corals which inhabit them. Reef accretion rates from core records collected across the wider PSRC were relatively high (mean:  $4.5 \pm 3.3$  mm yr<sup>-1</sup>), with maximum accretion calculated at 26 mm yr<sup>-1</sup> (Fig. 3). These values demonstrate the capacity for rapid reef building under conditions of high sedimentation across multiple reefs and generally exceed those reported for many clear-water (i.e., perceived more optimal) reefs. Importantly, these reefs also continue to actively accrete, and therefore exhibit higher modern rates of accretion than those clear-water reefs that have ceased vertical growth since attaining sea level (Hopley et al., 2007). This disparity in growth chronologies between the two settings has strong implications for predicting future trajectories of reef development and ecological change. Those reefs located within evolving nearshore environments, which preliminary satellite and field analysis suggests extend beyond PSRC, are likely to experience natural (and predictable) depth-related transitions in coral assemblages and vertical reef accretion as they continue to fill their accommodation space and move closer to sea level.

Our core records also point to critical ecological-sedimentary interactions during reef

development. During the earliest stages of initiation, contemporary seafloor surfaces are dominated by sediment-tolerant corals (e.g., *Galaxea* sp., *Lobophyllia* sp., *Euphyllia* sp.), resulting in slow accretion rates (mean:  $1.5 \pm 0.5$  mm yr<sup>-1</sup>). These corals rely primarily on heterotrophic feeding for energy acquisition under high sedimentation and thus may exhibit slower growth and calcification (Anthony and Fabricius, 2000). Over time, and as corals become elevated above the seafloor with greater access to light, corals can increasingly utilize both autotrophic and heterotrophic feeding mechanisms (Anthony and Fabricius, 2000) allowing for structurally complex genera (e.g., *Montipora* spp., *Turbinaria* spp.) to dominate. Fast-growing corals are abundant on submerged reef surfaces (1.5–3.5 m below LAT; reefs OPSA–OPSD), at depths coincident with an increase in calculated accretion rates (mean:  $6.0 \pm 3.7$  mm yr<sup>-1</sup>) in the core record. However, once accommodation space is near filled and reefs become semi-emergent, increased tidal exposure, solar irradiance, and wave energy restrict coral assemblages to low-profile and slow-calcifying genera (e.g., *Coelastrea* sp., encrusting *Montipora* spp.), leading to slower vertical growth (mean:  $1.4 \pm 1.0$  mm yr<sup>-1</sup>). These patterns are likely transferable across other low-impacted sites within the wider nearshore zone of the Great Barrier Reef where similar descriptions of ecological community types have been reported (Browne et al., 2010).

Direct parallels between coral assemblages and reef accretion are evident within our core records. However, secondary extrinsic factors must also be considered. As reefs move toward sea level throughout maturity, they increasingly interact with wave base. Reef surface hydrodynamics increases the redistribution and export of fine terrigenous sediment from the reef framework (Browne et al., 2013a), which is an important component of the reef matrix, as well as intensifies physical framework erosional processes. Therefore, in addition to depth-variable changes in coral cover and taxa, reef preservation will also likely vary across similar environmental gradients because of differences in external forces in relation to sea level. Deeper reefal assemblages associated with higher coral cover and higher-rate calcifying taxa will have resultant elevated rates of carbonate production, but also lower sediment export and/or erosion, thus enhancing *in situ* preservation. In contrast, shallow material associated with low coral cover and greater sediment export (through increased hydrodynamic activity as the reef shallows) will be less well preserved. These interacting factors compound changes in coral community structure to ultimately influence net accretion rates and vertical reef growth.

Nearshore areas are clearly capable of supporting high coral cover that is acclimated to low-light and high-sedimentation conditions



**Figure 3. A: Accretion rates across reefs that form the Paluma Shoals reef complex, Great Barrier Reef, Australia. PSN, PSS—Paluma Shoals north and south; OPS(A–D)—offshore Paluma Shoals (A–D). Maximum, minimum, and mean accretion values are presented. B: Mean (standard deviation) accretion rates at core depths below lowest astronomical tide (LAT). Alternately shaded zones (with mean accretion rates) correspond to depth-variable contemporary coral assemblages (zones A-1 to A-4; see Figs. 2A–2D).**

(Browne et al., 2010; Morgan et al., 2016). Within the PSRC, the marked reduction in light availability with depth as a result of naturally high turbidity restricts reef building to a shallow zone that extends to ~4 m below LAT, preventing further seaward expansion. Reef start-up within PSRC occurred between 700 and 2000 cal. yr B.P. in contemporary water depths of up to 4.3 m below LAT, coinciding with a rapid regional 1 m drop in sea level at 1200–800 cal. yr B.P. (Lewis et al., 2015). Based on the temporal context of reef start-up, and given the strong depth limitations on nearshore reef growth, it is likely that this lower sea level dramatically increased light penetration to the seafloor, i.e., moving ridge crests into the active photic zone, allowing for coral recruitment (e.g., *Euphyllia* sp., *Galaxea* sp.). The winnowing of fine seafloor sediment as wave base was translated further seaward would have exposed new initiation substrates (e.g., lithic sands and gravels as seen within the basal units of cores at PSRC) for coral recruitment and early reef building.

## CONCLUSIONS

Past histories of reef development are a well-recognized and fundamental control on contemporary ecological communities because they underpin habitat availability and local environmental conditions (e.g., depth, submergence time, wave energy, sediment resuspension, and export). Here we show that despite inhabiting marginal coastal environments, nearshore reefs experience similar intrinsic controls on reef initiation and vertical growth (albeit over a vertically compressed depth range) to those in traditional clear-water settings. We recognize a strong two-way feedback where reef growth and the position of reefs below sea level govern the abundance and diversity of coral taxa as well as sediment export and reef disassembly. These in turn influence rates of vertical accretion and reef structural complexity as reefs mature. These findings, derived from detailed core and

ecological data sets, have implications for determining the trajectories of nearshore reefs, as although natural depth-related changes in ecology are expected, disruptions from other external pressures (e.g., increased sedimentation) may strongly influence future reef development. The intrinsic mechanisms of reef growth and change under high terrigenous sediment influence provide an insight into natural long-term ecological dynamics (coral cover and coral genera abundance and distribution) of highly turbid nearshore reefs, and support recent suggestions that nearshore reefs may act as important refugia from climate-related bleaching events (Cacciapaglia and van Woesik, 2015).

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## REFERENCES CITED

Anthony, K.R.N., and Fabricius, K.E., 2000, Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity: *Journal of Experimental Marine Biology and Ecology*, v. 252, p. 221–253, doi:10.1016/S0022-0981(00)00237-9.

Browne, N.K., Smithers, S.G., and Perry, C.T., 2010, Geomorphology and community structure of Middle Reef, central Great Barrier Reef, Australia: An inner-shelf turbid zone reef subject to episodic mortality events: *Coral Reefs*, v. 29, p. 683–689, doi:10.1007/s00338-010-0640-3.

Browne, N.K., Smithers, S.G., and Perry, C.T., 2013a, Carbonate and terrigenous sediment budgets for two inshore turbid reefs on the central Great Barrier Reef: *Marine Geology*, v. 346, p. 101–123, doi:10.1016/j.margeo.2013.08.011.

Browne, N.K., Smithers, S.G., and Perry, C.T., 2013b, Spatial and temporal variations in turbidity on two inshore turbid reefs on the Great Barrier Reef, Australia: *Coral Reefs*, v. 32, p. 195–210, doi:10.1007/s00338-012-0965-1.

Cacciapaglia, C., and van Woesik, R., 2015, Reef-coral refugia in a rapidly changing ocean: *Global Change Biology*, v. 21, p. 2272–2282, doi:10.1111/gcb.12851.

De'ath, G., and Fabricius, K., 2010, Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef: *Ecological Applications*, v. 20, p. 840–850, doi:10.1890/08-2023.1.

Hopley, D., Smithers, S., and Parnell, K., 2007, *The Geomorphology of the Great Barrier Reef: Development, Diversity and Change*: Cambridge, UK, Cambridge University Press, 532 p., doi:10.1017/CBO9780511535543.

Lewis, S.E., Wüst, R.A.J., Webster, J.M., Collins, J., Wright, S.A., and Jacobsen, G., 2015, Rapid relative sea-level fall along north-eastern Australia between 1200 and 800 cal. yr BP: An appraisal of the oyster evidence: *Marine Geology*, v. 370, p. 20–30, doi:10.1016/j.margeo.2015.09.014.

Morgan, K.M., Perry, C.T., Smithers, S.G., Johnson, J.A., and Daniell, J.J., 2016, Evidence of extensive reef development and high coral cover in nearshore environments: Implications for understanding coral adaptation in turbid settings: *Scientific Reports*, v. 6, 29616, doi:10.1038/srep29616.

Palmer, S.E., Perry, C.T., Smithers, S.G., and Gulliver, P., 2010, Internal structure and accretionary history of a nearshore, turbid-zone coral reef: Paluma Shoals, central Great Barrier Reef, Australia: *Marine Geology*, v. 276, p. 14–29, doi:10.1016/j.margeo.2010.07.002.

Perry, C.T., Smithers, S.G., Gulliver, P., and Browne, N.K., 2012, Evidence of very rapid reef accretion and reef growth under high turbidity and terrigenous sedimentation: *Geology*, v. 40, p. 719–722, doi:10.1130/G33261.1.

Perry, C.T., Smithers, S.G., and Gulliver, P., 2013, Rapid vertical accretion on a “young” shore-detached turbid zone reef: Offshore Paluma Shoals, central Great Barrier Reef, Australia: *Coral Reefs*, v. 32, p. 1143–1148, doi:10.1007/s00338-013-1063-8.

Roff, G., Clark, T.R., Reymond, C.E., Zhao, J.X., Feng, Y., McCook, L.J., Done, T.J., and Pandolfi, J.M., 2012, Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore Great Barrier Reef, following European settlement: *Proceedings of the Royal Society B: Biological Sciences*, v. 280, 20122100, doi:10.1098/rspb.2012.2100.

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