

Reef shallowing is a critical control on benthic foraminiferal assemblage composition on nearshore turbid coral reefs

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ABSTRACT

Declining water quality represents a major threat to the coral reefs of Australia's Great Barrier Reef (GBR). Due to their close proximity to river point sources, reefs situated on the inner-shelf of the GBR are widely perceived to be most susceptible to the increased discharge of nutrients and sediments from coastal catchments, many of which have been modified since European settlement. However, the impact and magnitude of water quality change on the GBR's inner-shelf reefs remains unclear. Much of the uncertainty can be attributed to a paucity of long-term records with which to assess ecological and environmental change over appropriate reef-building timescales. Here, we present benthic foraminiferal palaeo-records from three proximal nearshore turbid-zone reefs located within the central region of the GBR. Bayesian age-depth modelling was used to identify the core intervals corresponding to the timing of European settlement in the region (c. 1850 CE), enabling the investigation of: (1) the composition and variability of benthic foraminiferal assemblages during reef shallowing towards sea level; and (2) whether any signal of increased nutrient and sediment inputs, as the result of historical land-use change, can be discerned on the most nearshore reefs of the central GBR. Multivariate analyses identified two assemblage groups, delineated by a significant increase in the relative abundance of *Pararotalia* spp. up-core. Our results suggest that post-European settlement associated increases in nutrient and sediment inputs are unlikely to have driven the observed shifts in benthic foraminiferal assemblage composition. Rather, we interpret changes in the composition of benthic foraminiferal assemblages as being linked to changes in hydrodynamic energy, light availability and the carbonate content of reef-matrix sediments during reef shallowing towards sea level. Our findings support the hypothesis that nearshore turbid-zone reefs have a higher resistance to increased nutrient and sediment inputs than those located further offshore, towards the inner/mid-shelf boundary of the GBR.

1. Introduction

Benthic foraminifera are valuable biological indicators (or bioindicators) of environmental change, particularly with respect to sea level (e.g., Gehrels, 2000; Woodroffe, 2009a) and water quality (e.g., Alve, 1995; Frontalini and Coccioni, 2011). The utility of benthic foraminifera as bioindicators is largely due to their high taxonomic diversity and abundance; narrow ecological specificity; excellent preservation potential; and relatively short life spans (Coccioni, 2000; Schönfeld et al., 2012). Due to their ability to capture both long-term and short-term environmental change, the application of benthic foraminifera as bioindicators in tropical coral reef environments is a subject of growing interest (Renema, 2018).

Deteriorating water quality is considered a major threat to the

ecological health of Australia's Great Barrier Reef (GBR). Due to their close proximity to river point sources, coral reefs on the inner continental shelf of the GBR are widely perceived to be most susceptible to reduced water quality discharged from coastal catchments, many of which have been modified following European settlement (c. 1850 CE) (Lewis et al., 2007; Brodie et al., 2012; De'ath et al., 2012; Schaffelke et al., 2012). Since European settlement of coastal catchments in the mid-nineteenth century, the annual delivery of nutrients and sediments to the GBR lagoon is estimated to have increased by up to nine and five times, respectively (Kroon et al., 2012). Consequently, reported collapses of hard coral communities have been attributed to regional deteriorations in water quality (Roff et al., 2013; Clark et al., 2017), and are often associated with increased macro-algal cover on reefs (De'ath and Fabricius, 2010), Crown-of-Thorns seastar (*Acanthaster planci*) outbreaks (Brodie

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et al., 2017), and coral disease (Haapkylä et al., 2011). Despite the widely held perception that inner-shelf reefs are most susceptible to increased nutrient and sediment delivery, the impact of reported changes in water quality on the GBR remains unclear (Ryan et al., 2016a). This uncertainty persists because few long-term datasets are available with which to assess both ecological and environmental change over appropriate reef-building timescales (i.e. centennial to millennial; Pandolfi, 2002). Uncertainty of the impact of altered sediment regimes (i.e., changes in suspended sediment concentrations and sedimentation rates) on inner-shelf reef communities is also exacerbated by the ongoing debate concerning the extent to which increased terrestrial sediment inputs have altered the naturally high sedimentary background conditions that have characterised the zone for the last ~6000 years (Larcombe and Woolfe, 1999a; Orpin and Ridd, 2012).

Core-based records have provided valuable insights into the key controls on reef initiation and subsequent development on the inner-shelf of the GBR (see Hopley et al., 2007; Perry and Smithers, 2011; Browne et al., 2012a for reviews). Importantly, palaeoecological reconstructions from reef cores have confirmed the long-term persistence of hard coral assemblages within the most nearshore turbid settings of the central GBR (i.e., landward of the 10 m isobath; hereafter referred to as the 'nearshore turbid-zone'), where large volumes of terrigenous sediments are available for resuspension and deposition within the reef structure (Hopley et al., 2007; Browne et al., 2012a). Supported by a progressively expanding evidence base (e.g., Perry et al., 2008, 2009, 2011; Roche et al., 2011; Roff et al., 2013; Ryan et al., 2016b; Clark et al., 2017; Johnson et al., 2017), there is an emerging hypothesis that corals growing within the nearshore turbid-zone of the GBR are more resistant to increased nutrient and sediment inputs than those located further offshore, towards the inner/mid-shelf boundary (i.e., seaward of the 10 m isobath; hereafter referred to as the 'inshore zone'), where episodic pulses of sediment and nutrient inputs may exert a more deleterious impact on coral reef communities (Larcombe et al., 2001; Perry et al., 2008; Morgan et al., 2016a). Whilst there is an expanding body of evidence to support this hypothesis, relatively few have utilised benthic foraminifera as bioindicators for the investigation of past environmental change within nearshore turbid-zone reef settings on the GBR (but see Uthicke et al., 2012; Reymond et al., 2013; Narayan et al., 2015).

Here, we present detailed benthic foraminiferal assemblage records reconstructed from a nearshore turbid-zone reef complex within Halifax Bay, central GBR (Australia). Specifically, reef core records were recovered with the aim of investigating (1) the composition and variability of benthic foraminiferal assemblages during reef shallowing towards sea level; and (2) whether any signal of increased nutrient and sediment input, as the result of historical land-use change, can be discerned on the most nearshore reefs of the central GBR.

2. Study site and environmental setting

Halifax Bay is a shallow (< 20 m water depth) semi-protected embayment situated within the central region of Australia's GBR (Larcombe et al., 2001), immediately north of Australia's most populous tropical city, Townsville (Fig. 1). The seafloor of Halifax Bay is characterised by the presence of an 'inshore sediment prism' (ISP). The ISP comprises a wedge of mixed terrigenous sediments reworked shoreward during the post-glacial marine transgression (~10,500–7000 calibrated years before present; cal. yr BP), together with those delivered by floods from coastal catchments since sea level stabilised ~6000 years (yr) ago (Hopley et al., 2007). Collectively, the Black, Bohle and Ross Rivers deliver an estimated 144 kt yr⁻¹ of sediment, 2 kt yr⁻¹ of total nitrogen, and 16 t yr⁻¹ of total phosphorus to the southern sections of Halifax Bay (Kroon et al., 2012) (Fig. 1). Coral skeletons from Halifax Bay also geochemically preserve records of flood events from the Burdekin River, located ~100 km to the south (Lewis et al., 2007; Lough et al., 2015). These studies therefore demonstrate that water quality in Halifax Bay may also be influenced by flood plumes associated with coastal river catchments further afield.

The landwards edge of the ISP is detached from the mainland in Halifax Bay, separated by a narrow corridor of low sedimentation that is maintained through the resuspension of fine-grained sediments by wind-driven waves (Larcombe and Woolfe, 1999b; Larcombe et al., 2001; Smithers et al., 2006). Nearshore turbid-zone reefs have developed in this low sedimentation corridor, in areas where waves and currents have exhumed substrates suitable for colonisation by hard corals (i.e., transgressive alluvial clays and lithic sands/gravels) (Larcombe et al., 2001).

The Paluma Shoals reef complex (PSRC) is a collection of nearshore turbid-zone reefs confined between the ISP and the shoreline within Halifax Bay (Fig. 1). The PSRC consists of seven discrete reefs located within an area of ~16 km², extending from the shoreline to approximately 3 km offshore (Fig. 1). Recent surveys show that the reefs in the PSRC are at different stages of 'geomorphological maturity' (sensu Hopley, 1982), and that reef growth is concentrated above a series of shore-normal, ridge-like bedforms up to ~2 km long and 200 m wide (Morgan et al., 2016a). Live coral cover across the reef structures in the PSRC is high for the central region of the GBR (mean ~40%, June, 2014) (Morgan et al., 2016a). Core-based studies have also revealed the reefs in the PSRC to have initiated relatively recently (i.e., between ~2000 and 700 cal. yr BP) and to have been built by temporally persistent assemblages of coral taxa adapted to turbid water conditions, notably *Acropora* spp. (~45%), *Montipora* spp. (~25%) and *Turbinaria* spp. (~10%) (Smithers and Larcombe, 2003; Perry et al., 2008, 2013; Palmer et al., 2010; Morgan et al., 2016b; Johnson et al., 2017). Average rates of vertical reef accretion in the PSRC are variable and closely correspond to observed depth-stratification patterns in coral taxa, ranging from 1.4 ± 1.0 mm yr⁻¹ (reef elevation: 0 to 0.5 m above present lowest astronomical tide; LAT) to 6.0 ± 3.7 mm yr⁻¹ (reef elevation: 2 to 3 m below present LAT) (Morgan et al., 2016b).

3. Materials and methods

3.1. Reef cores

Palaeoecological records of benthic foraminiferal assemblages were derived from three radiometrically-dated cores that captured the entire reef growth sequence at several reefs within the PSRC (see Perry et al., 2013; Morgan et al., 2016b). Specifically, a single core was selected for analysis from the 'mature' reef of Offshore Paluma Shoals (OPS; OPS-PC2) that is emergent at LAT; and the 'juvenile' reefs of Offshore Paluma Shoals-C (OPS-C; OPS-C-PC1) and Offshore Paluma Shoals-D (OPS-D; OPS-D-PC1) that are both fully submerged at LAT (Fig. 1). By analysing core records from three proximal reefs with different growth histories, as interpreted from their current stage of geomorphological maturity, our aim was to ensure the independence of core records for the investigation of both depth- and time-related changes in benthic foraminiferal assemblage composition.

All cores were recovered using percussion methods (see Smithers and Larcombe, 2003 for full methods) and terminated in mottled clay (Table 1), which is widely interpreted to be Late Pleistocene in age (Hopley et al., 2007). Core elevations were normalised to present LAT datum using field measurements (Table 1), and an existing digital elevation model of seafloor bathymetry (Morgan et al., 2016a). Core compaction was calculated (assuming uniform compaction) using recovered core length and penetration measurements (Table 1). Prior to detailed analyses, cores were longitudinally split, photographed and logged.

3.2. Core chronologies and age-depth modelling

Chronologies were developed for each core based on 18 previously published radiocarbon dates (Perry et al., 2013; Morgan et al., 2016b) (Fig. 2). Age-depth models were developed using a flexible Bayesian approach in the R-package 'bacon', version 2.2 (Blaauw and Christen, 2011; R Development Core Team, 2014) (see Supplementary material 1

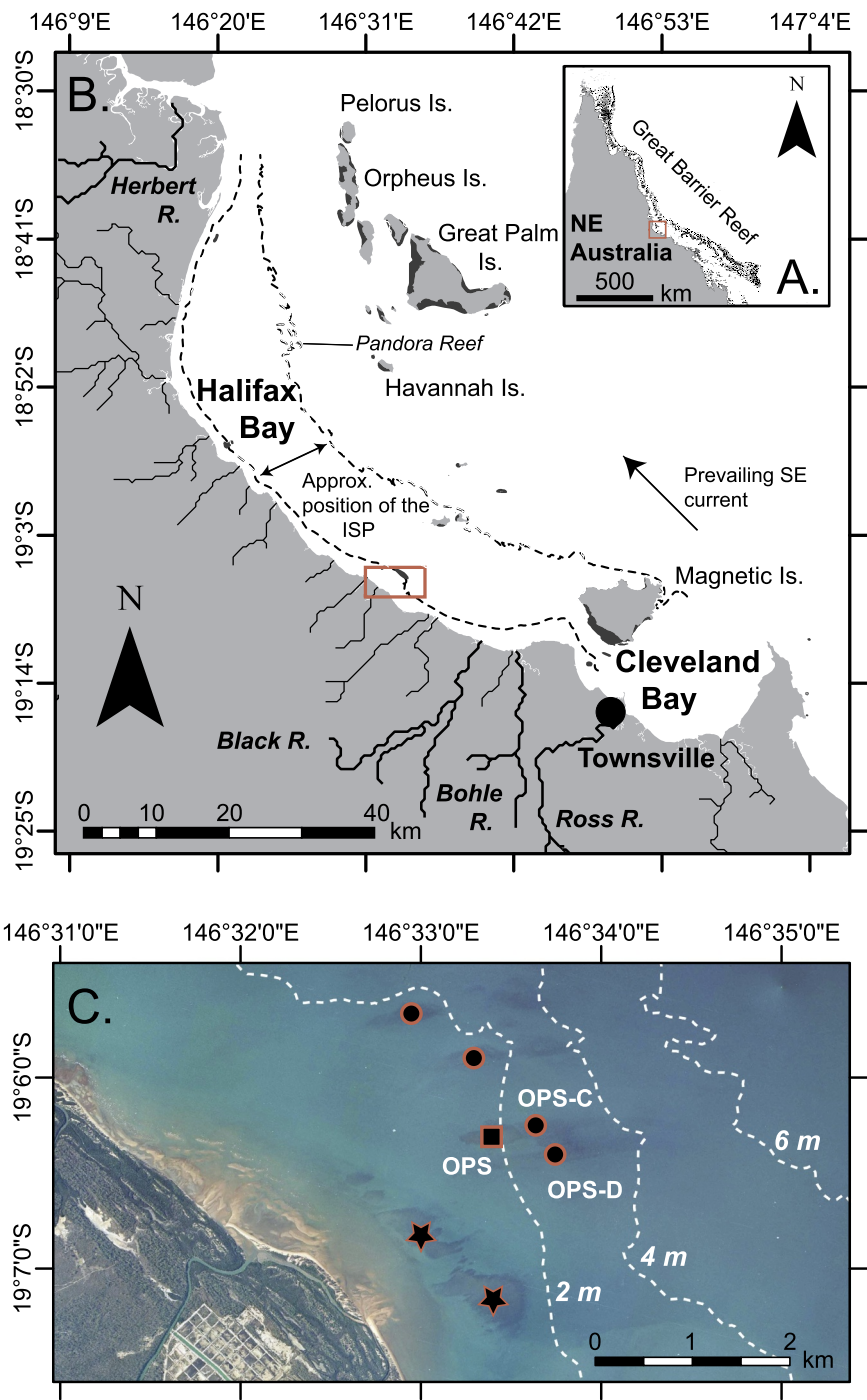


Table 1
Details of percussion cores recovered from the Paluma Shoals reef complex.

Core	Depth, relative to LAT (m)	Core length (m)	Penetration (m)	Compaction (%)
OPS-PC2	−0.2	3.5	4.0	24
OPS-C-PC1	−0.4	2.8	5.0	44
OPS-D-PC1	−0.7	2.5	4.5	44

for further details). This approach utilised radiocarbon dates obtained for coral material in the cores to approximate sediment age, assuming comparable rates of sedimentation and vertical reef accretion. Sedimentation rates determined by ^{210}Pb and ^{137}Cs radionuclide dating methods in coral reef environments elsewhere on the inner-shelf of the

GBR have been calculated at between 2 and 6 mm yr^{-1} over the last ~ 100 years (Uthicke et al., 2012). Importantly, these sedimentation rates are consistent with those estimated in this study for the period following ~ 100 cal. yr BP (i.e., 2.4 to 3.4 mm yr^{-1}) (Fig. 2).

3.3. Core sampling and foraminiferal analysis

The age-depth models were used to identify the most probable depth intervals corresponding to the advent of European settlement (c. 1850 CE, or 100 cal. yr BP; Lewis et al., 2007) as recorded in the three cores (Fig. 2). To adequately represent both pre- and post-European settlement foraminiferal assemblages, three samples were collected at 10 cm (uncompacted) intervals from the upper core sections post-dating the interpreted European settlement interval, and at a resolution of

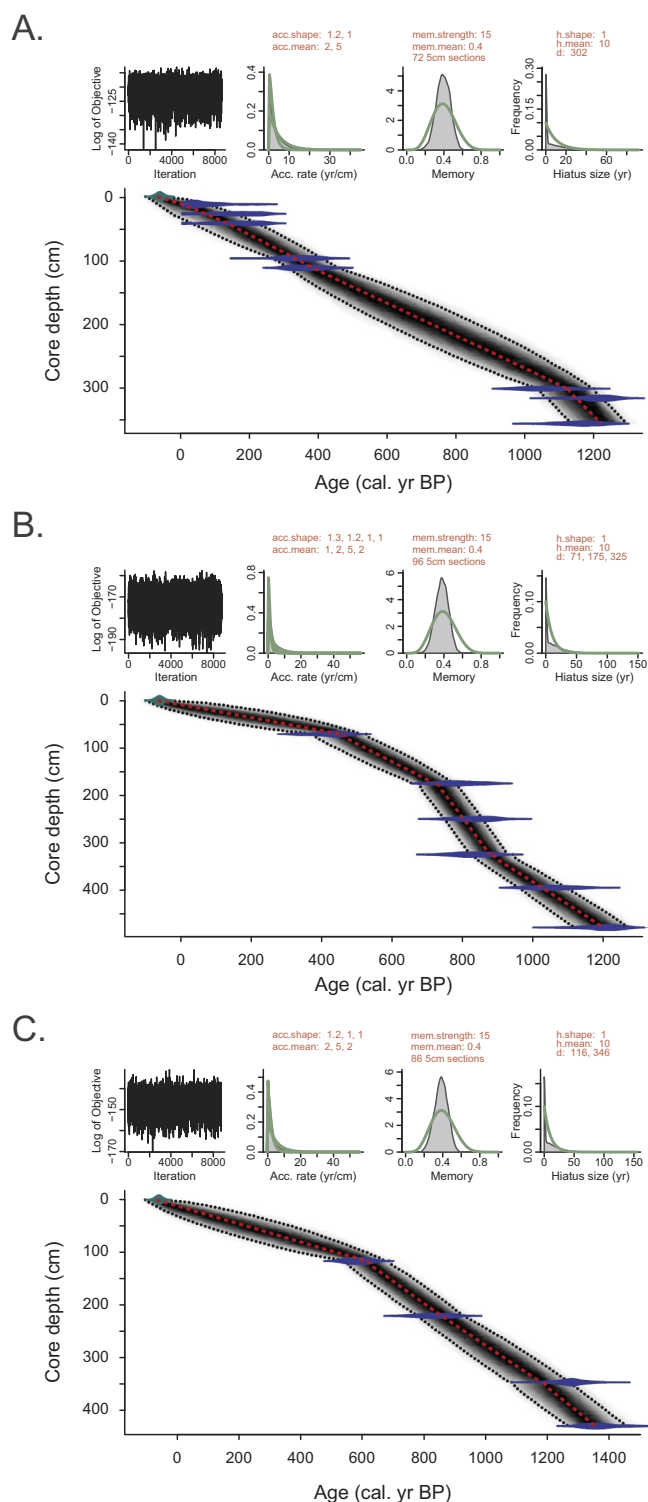


Fig. 2. Bayesian age-depth models produced using available radiocarbon dates (see Morgan et al., 2016b) for the individual cores of A. Offshore Paluma Shoals (OPS)-PC2; B. OPS-C-PC1; and C. OPS-D-PC1. Plots show the calibrated radiocarbon ages (blue) and the age-depth model (grey shading). The darker areas of the model indicate the more likely calibrated ages. The model 95% confidence is represented by dotted lines, whilst the single 'best' model (based on the weighted mean age of each depth interval) is marked by the red curve. The upper panels depict the Markov Chain Monte Carlo iterations (left panel); the prior (green curves) and posterior (grey curves) distributions for the accumulation rate (middle panel) and memory (right panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

20 cm (uncompacted) below this interval. Core samples intended for foraminiferal analysis were collected from one half of each core split. Paired samples (~30 g dry mass) were collected for sedimentary analyses from the corresponding half of each core split. Samples for sedimentary analyses were split to a ratio of 1:3 (carbonate content analysis: mud content analysis). The proportions of carbonate and mud-sized material (i.e., < 63 μ m size fractions) were determined for each sample following the methods detailed in Perry et al. (2011).

Samples for foraminiferal analysis were wet sieved to remove the < 63 μ m sediment fractions. After sieving, samples were oven dried (60 °C for 24 h) before further sieving to remove any residual mud and sediments > 4 mm. A 1 cm³ split was obtained from the retained sediment fractions (i.e., between 63 μ m and 4 mm) from each sample using a riffle splitter. Foraminiferal assemblages were characterised for each sample split by counting and identifying a total of 300 tests (Schönfeld et al., 2012), creating a multivariate dataset containing 66 samples and over 19,000 individual specimens. Following Schueth and Frank (2008) and Uthicke et al. (2010), only well-preserved tests (i.e., those exhibiting minimal abrasion, bioerosion, or dissolution; see Berkeley et al., 2007, 2009) were counted to avoid preservational bias and to represent those specimens most likely to have been deposited in situ.

Foraminiferal tests were dry picked and identified to the lowest taxonomic level under a stereomicroscope and using published taxonomies (Collins, 1958; McCulloch, 1977; Haig, 1988; Jones, 1994; Leoblich and Tappan, 1994; Hayward et al., 1997). All taxonomic names were validated, and established synonymies updated, using the World Registry of Marine Species (WoRMS) online database (www.marinespecies.org/) (Schönfeld et al., 2012). Where samples contained < 300 individual specimens, a second sample split was taken and specimens counted until the target number was attained. Counts of 300 were achieved from the first sample in 80% of cases ($n = 53$ samples).

All identified genera were separated into three widely accepted functional groups based upon their known ecologies (sensu Hallock et al., 2003): (1) 'symbiont-bearing' taxa, with endosymbiotic relationships that typically occupy similar environments to hard coral; (2) stress-tolerant 'opportunistic' taxa, tolerant of stressful and hypoxic conditions; and (3) 'other small-heterotrophic' taxa, that proliferate in response to nutrient enrichment. To maintain consistency with previous studies, functional classifications of individual foraminiferal genera followed Nobes and Uthicke (2008), Uthicke et al. (2010), Raymond et al. (2013), Fajemila et al. (2015), and Narayan et al. (2015). The proportion of each functional group, calculated as the ratio of the total number of specimens counted ($n = 300$), was used to derive an index value based upon the Foraminifera in Reef Assessment and Monitoring (FoRAM) Index (FI) for each sample (Hallock et al., 2003; Hallock, 2012) (see Supplementary material 2). Following Corliss and Chen (1988), foraminifera were also divided into nine morphological classifications to establish the proportion of epifaunal and infaunal taxa within each sample.

3.4. Statistical analysis

3.4.1. Benthic foraminiferal abundance and sampling effort

All statistical analyses were performed at the genus level. Whilst we recognise that genus level analysis may result in the loss of potentially valuable species-level information, it ensures that reliable comparisons can be made between separate investigations (Hallock et al., 2003). Taxonomic grouping was most notable within the genera of *Quinqueloculina* (13 species identified), and *Elphidium* (6 species identified). All other genera contained less than five identified species, with ~70% of all genera containing only one species (see Supplementary material 3).

Foraminiferal counts were converted to relative abundance by dividing the frequency of occurrence of each taxon by the total number of identified tests within a sample. Individual-based rarefaction and extrapolation analyses were performed in EstimateS v. 9.1 (Colwell, 2013) to assess the extent to which the sampling strategy captured sample taxonomic richness. Samples were randomised (resampled) 100 times,

with curve extrapolations constrained to double the sample reference number. Individual-based rarefaction curves confirmed sampling completeness to be approaching saturation at a specimen count of 300 for each site (see Supplementary Fig. S2). We are therefore confident that the adopted sampling strategy provides a representative record of benthic foraminiferal assemblage composition within each sample.

3.4.2. Foraminiferal assemblages

All relative abundance data were square-root transformed to reduce data asymmetry prior to further analyses (Legendre and Birks, 2012). To identify the major foraminiferal assemblage zones present within each core, and to facilitate determination of compositional change, constrained incremental-sum-squares clustering (CONISS) were performed using Bray-Curtis dissimilarity matrices (Grimm, 1987). The number of significant assemblage zones present within each core was determined by the comparison of CONISS results to a 'broken-stick' model (Bennett, 1996). Analyses were performed in the R packages 'rioja' and 'vegan' (R Development Core Team, 2014; Juggins, 2016; Oksanen et al., 2017).

To explore trends in the composition of the CONISS-derived assemblage zones, a principle component analysis (PCA) was undertaken, with similarity percentage (SIMPER) analysis (using Bray-Curtis dissimilarity) employed to identify the taxa contributing most to inter-group dissimilarities (Clarke, 1993). A detrended correspondence analysis (DCA) was conducted prior to the PCA to estimate the underlying gradient length of the data. As the length of the DCA axes were < 2.5 standard deviations (SD), the linear-based model of PCA was considered appropriate for the analysis of the foraminiferal assemblage data (Legendre and Birks, 2012). Ordination (DCA and PCA) and SIMPER analyses were performed in PAST, version 3 (Hammer et al., 2001).

4. Results

4.1. Core stratigraphy and foraminiferal taxonomy

Reef-matrix sediments from the PSRC were characterised by poorly sorted muddy sands of a mixed carbonate-terrigenous composition (Fig. 3). Mud content within the sediment matrices was variable but persistent throughout each reef sequence (mean mud content: $34 \pm 16\%$; mean $\pm$ SD) (Fig. 3). Carbonate content of the matrix sediments was also variable throughout each reef sequence (mean carbonate content: $65 \pm 15\%$) (Fig. 3). Despite the variability in both carbonate and mud contents, similar up-core trends were evident within each core. Notably, carbonate content increased, whilst conversely, mud content decreased. This trend is particularly evident within shallow core depths (typically < 50 cm below present LAT) and has previously been interpreted as a signal of reef shallowing towards sea level (Perry et al., 2011, 2012; Ryan et al., 2016b).

Taxonomic analysis identified 133 benthic foraminiferal species belonging to 85 genera within the PSRC palaeoecological inventory (Table 2; see Supplementary material 3 and Supplementary Fig. S1). Average genus richness within each sample ranged from 34 ± 6 (OPS-PC2) to 40 ± 4 (OPS-C-PC1). Overall, the palaeoecological inventory included an assortment of benthic foraminifera from seven Orders of Foraminifera (Table 2), including Lagenida (1%), Lituolida (< 1%), Miliolida (40%), Robertinida (< 1%), Rotaliida (54%), Spirillinida (< 1%) and Textulariida (4%).

The most abundant genera within the Order Rotaliida were *Elphidium* spp. (16%), *Pararotalia* spp. (14%), *Ammonia* spp. (6%), *Siphoninoides* spp. (3%), and *Eponides* spp. (2%). Within the Order Miliolida, important contributions were made by *Quinqueloculina* spp. (21%), *Planispirinella* spp. (3%), *Peneroplis* spp. (2%), and *Hauerina* spp. (2%). Foraminiferal specimens identified within the Order Textulariida were mainly of the genera *Textularia* spp. (3%) and *Sahulita* spp. (1%).

4.2. Foraminiferal assemblages

The broken-stick model separated samples into two discrete assemblage zones within each core sequence, based upon the expected and measured variations of the CONISS analyses (Fig. 3). These results were confirmed by PCA, which explained ~85% of the total between-group variance along its first two axes and showed little to no overlap between the CONISS-derived assemblage zones (Fig. 4A). The PCA also separated the foraminiferal assemblage zones into two disparate groups along axis 1 (~70% variance explained). The significance of this separation was confirmed by an ANOVA (Welch's $F_{(5, 60)} = 63.3$, $p < 0.001$) and Games-Howell post hoc tests, performed in SPSS, version 23 (IBM Corp, 2015) (Supplementary Table S1). Assemblages associated with 'Group 1' (i.e., assemblage zones C_A, D_A, and O_A) were more homogenous than those of 'Group 2' (i.e., assemblage zones C_B, D_B, and O_B), as demonstrated by the degree of overlap between the CONISS-derived assemblage zones (Fig. 4A). This trend is particularly pronounced along axis 2 (~15% variance explained) (Fig. 4A). The foraminiferal taxa contributing most to the difference between 'Group 1' and 'Group 2' were identified by SIMPER analysis, which confirmed the results of the PCA (Fig. 4; Table 3). Notably, the SIMPER analysis identified *Pararotalia* as the primary taxon contributing to the overall dissimilarity between 'Group 1' and 'Group 2' (Table 3).

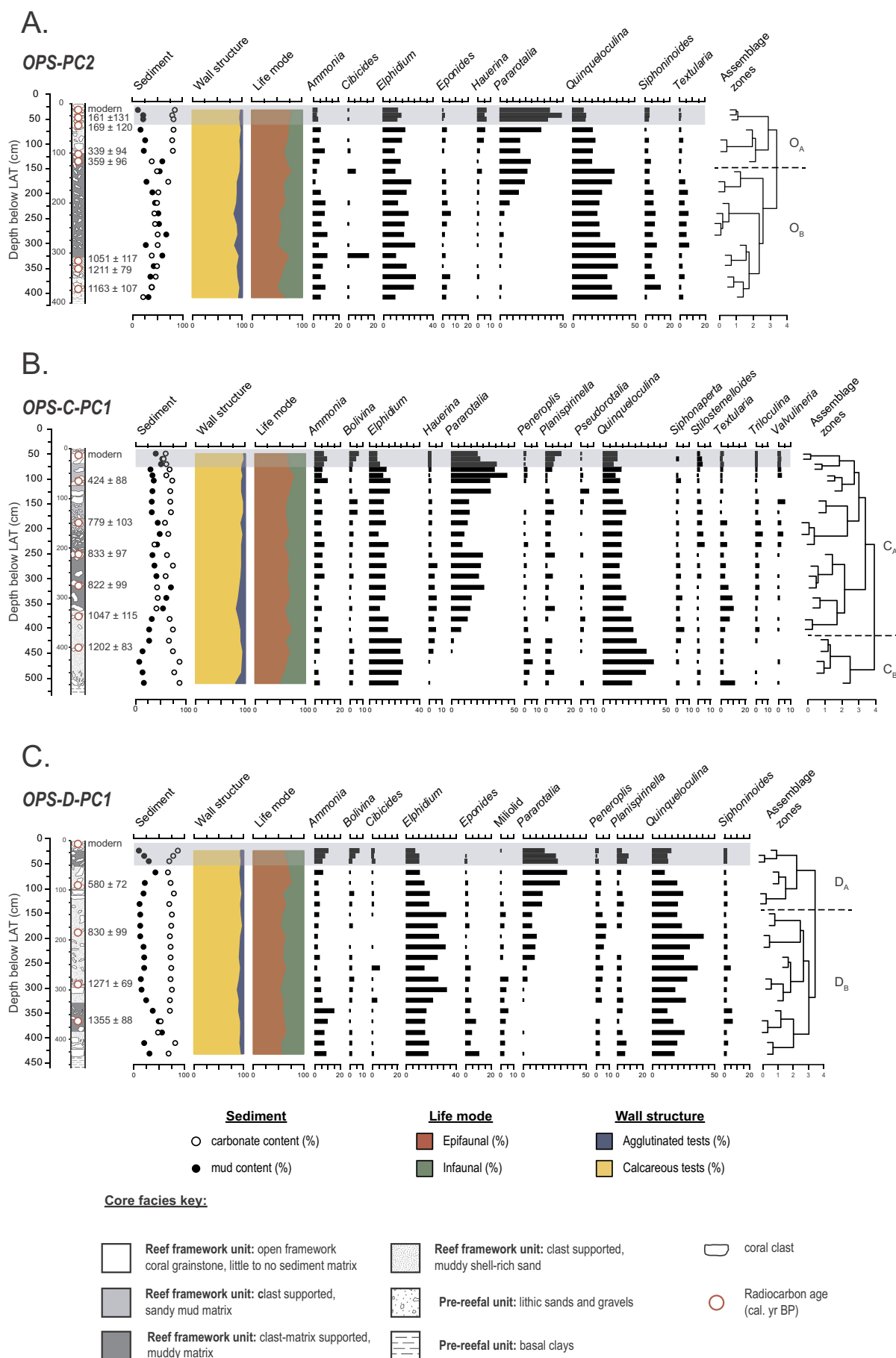
To investigate the degree to which *Pararotalia* influenced the multivariate analyses, the taxon was removed from the ecological dataset and an additional PCA performed using the recalculated relative abundance data (Fig. 4B). The results of this additional PCA revealed a high degree of overlap between the CONISS derived assemblage zones (~60% of between-group variance explained), confirming *Pararotalia* abundance to be the principle driver of the observed dissimilarity between the delineated assemblage groups.

Within each core sequence, 'Group 1' occurred exclusively above 'Group 2', occupying a depth range between ~0 and 4 m below present LAT (Figs. 3 and 4). 'Group 1' was dominated by *Pararotalia*, *Quinqueloculina*, and *Elphidium* (Table 3). Other important contributions (i.e., contributions ~5%) to this assemblage group were also made by *Ammonia*, *Planispirinella*, *Hauerina* and *Textularia* (Table 3). The underlying 'Group 2' occupied a depth range between ~2 and 5 m below present LAT (Figs. 3 and 4) and was dominated by high abundances of *Quinqueloculina* and *Elphidium* (typically > 50%, collectively). Other important contributions to 'Group 2' were made by *Ammonia*, *Siphoninoides*, *Pararotalia*, *Peneroplis*, *Textularia*, *Eponides* and *Planispirinella* (Table 3).

Significant changes in foraminiferal assemblage composition, as identified by CONISS analysis and broken-stick models, were found to pre-date European settlement within each core (Fig. 3). Exploratory analysis (using untransformed relative abundance data) of those taxa identified as contributing most to between group dissimilarities (Table 3) revealed almost half to exhibit significant monotonic relationships with core depth, normalised to present LAT (Fig. 5; Supplementary Table S2). Cumulatively, these taxa accounted for approximately 33% of the total dissimilarity observed between 'Group 1' and 'Group 2' (Table 3).

4.3. ForAM Index

Overall, calculated sample FI values averaged 1.9 (range: 1.5 to 2.4; Fig. 3), reflecting the consistently low abundance of foraminifera traditionally classified as 'symbiont-bearing' within the foraminiferal assemblages of the PSRC (mean sample abundance: $3 \pm 2\%$). Instead, the benthic foraminiferal assemblages of the PSRC were dominated by foraminifera traditionally classified as 'opportunistic' (mean abundance: $39 \pm 10\%$) and 'other small-heterotrophic' (mean abundance: $58 \pm 10\%$) (Table 2). A total of nine symbiont-bearing taxa were identified (Table 2), with contributions to the overall palaeoecological inventory primarily made by *Peneroplis* (~2%). All other symbiont-



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Fig. 3. Stratigraphic diagrams for A. Offshore Paluma Shoals (OPS)-PC2; B. OPS-C-PC1; and C. OPS-D-PC1. Foraminiferal abundance is presented as relative abundance. Only the foraminifera with abundances of > 5% (for at least one sample) are displayed. The results of constrained incremental sum of squares (CONISS) are displayed to the right of the stratigraphic diagrams, with the significant assemblage zone indicated by the dashed lined, as determined by 'broken-stick' models. The grey shading represents core sections corresponding to post-European settlement (i.e., < 1850 CE), as determined by Bayesian age-depth modelling (see Fig. 2). The median probability ages of the available radiocarbon dates (see Morgan et al., 2016b) are presented in calibrated years before present (cal. yr BP $\pm$ 1 σ). The term 'modern' denotes ages associated with dates post-dating 1950 CE (0 cal. yr BP).

bearing taxa accounted for < 1% of the overall palaeoecological inventory.

5. Discussion

5.1. Drivers of change in nearshore turbid-zone foraminiferal assemblages

Benthic foraminiferal assemblages within the PSRC were largely dominated by calcareous epifaunal taxa characteristic of shallow and warm marine environments (Fig. 3) (Debenay, 1988; Langer, 1993; Murray, 1991, 2006; Sen Gupta, 1999; Debenay and Payri, 2010). Foraminiferal assemblages were also similar to those from other subtidal inner-shelf settings in (sub)tropical northeastern Australia (e.g., Woodroffe, 2009b; Horton et al., 2007; Uthicke et al., 2012; Raymond et al., 2013; Narayan and Pandolfi, 2010), as well as turbid reef settings elsewhere in the Indo-Pacific (e.g., Langer and Lipps, 2003). Based upon available sea-level curves for the GBR region, reef development within the PSRC likely initiated in palaeo-water depths of up to, but not exceeding, 1 m above present-day elevations (Woodroffe, 2009a; Lewis et al., 2013, 2015). The palaeo-records presented in this study therefore represent foraminiferal assemblages that developed in water depths of less than ~6 m.

In the absence of a comprehensive understanding of the palaeoecological significance of mixing (e.g., infaunal test production and bioturbation) and taphonomic (e.g., abrasion, bioerosion and dissolution) processes within nearshore turbid reef settings, the degree to which living foraminiferal assemblages are preserved within the fossil record of the PSRC is somewhat uncertain (Berkeley et al., 2008, 2009). Discerning the influence of other processes (i.e., differential core compaction, non-uniform sedimentation and episodic events) on the fossil record is also problematic (Berkeley et al., 2014). However, past

studies suggest that limited bioturbation and reef-matrix sediment mixing occurs in nearshore turbid-zone reef settings on the central GBR (Smithers and Larcombe, 2003; Palmer et al., 2010). Attempts to reduce preservational bias were also made by constraining analyses to only well-preserved foraminiferal specimens (Schueth and Frank, 2008; Uthicke et al., 2010). Hence, we are confident that the records presented in this study provide a reliable history of past foraminiferal assemblage composition within the PSRC.

Multivariate analysis identified two assemblage groupings within the palaeo-records of the PSRC (Fig. 4). The depths and timings at which significant changes in foraminiferal assemblage composition occurred varied between cores (OPS-PC2: ~140 cm below present LAT, ~410 $\pm$ 170 cal. yr BP; OPS-C-PC1: ~420 cm below present LAT, ~1140 $\pm$ 145 cal. yr BP; OPS-D-PC1: ~130 cm below present LAT, ~620 $\pm$ 140 cal. yr BP) (Figs. 2 and 3). The occurrence of compositional shifts in foraminiferal assemblages throughout the Late Holocene suggests that the transitions are independent of time and instead associated with depth. Thus, the delineated shifts in foraminiferal assemblage composition are unlikely to have been driven by increased regional nutrient and sediment runoff associated with post-European settlement land-use practices. Rather, we interpret the foraminiferal assemblage shifts as being intrinsically-driven and influenced by variations in the abiotic environment during reef shallowing towards sea level (notably changes in hydrodynamic energy, light availability and substrate type).

Hydrodynamic energy is widely regarded as one of the most important depth-related factors controlling the distribution of benthic foraminifera within shallow-water environments. This is because hydrodynamic energy is a strong controlling factor of substrate type, food availability, and photosynthetically active radiation (PAR) availability

Table 2
Benthic foraminiferal genera identified from the recovered reef cores.

Palaeoecological inventory			
Lagenida	<i>Nodobacularella</i> (H)	<i>Anomalinoidea</i> (H)	<i>Nonionoides</i> (O)
<i>Fissurina</i> (H)	<i>Parahauerinoides</i> (H)	<i>Bolivina</i> (O)	<i>Operculina</i> (S)
<i>Gladulina</i> (H)	<i>Peneroplis</i> (S)	<i>Bulimina</i> (O)	<i>Pararotalia</i> (O)
<i>Lagena</i> (H)	<i>Planispirinella</i> (H)	<i>Calcarina</i> (S)	<i>Pegidia</i> (H)
<i>Procerolagena</i> (H)	<i>Pseudomassilina</i> (H)	<i>Cancris</i> (H)	<i>Planogypsina</i> (H)
<i>Pyrulina</i> (H)	<i>Pseudotriloculina</i> (H)	<i>Chrysalidina</i> (H)	<i>Poreponides</i> (H)
<i>Sigmoidella</i> (H)	<i>Pyrgo</i> (H)	<i>Cibicides</i> (H)	<i>Pseudorotalia</i> (H)
<i>Unidens</i> ^a (H)	<i>Quinqueloculina</i> (H)	<i>Cibicidoides</i> (H)	<i>Rectobolivina</i> (H)
Lituolida	<i>Schlumbergerina</i> (H)	<i>Conorbella</i> (H)	<i>Reussella</i> (O)
<i>Latentoverneuilina</i> (H)	<i>Sigmoihauerina</i> (H)	<i>Cyclocibicides</i> (H)	<i>Rosalina</i> (H)
<i>Placopsilina</i> (H)	<i>Sigmoilopsis</i> (H)	<i>Cymbaloporeta</i> (H)	<i>Sagrinella</i> (H)
<i>Reophax</i> (H)	<i>Siphonaperta</i> (H)	<i>Discorbis</i> (H)	<i>Sestronophora</i> (H)
Miliolida	<i>Sorites</i> (S)	<i>Elphidium</i> (O)	<i>Stilostomelloides</i> (H)
<i>Adelosina</i> (H)	<i>Spiroculina</i> (H)	<i>Epistominella</i> (H)	<i>Siphoninoides</i> (H)
<i>Articulina</i> (H)	<i>Triloculina</i> (H)	<i>Eponides</i> (H)	<i>Valvulineria</i> (H)
<i>Coscinospira</i> (S)	<i>Triloculinella</i> (H)	<i>Floresina</i> (H)	Spirillinida
<i>Cycloforina</i> (H)	<i>Vertebralina</i> (H)	<i>Glabratella</i> (H)	<i>Spirillina</i> (H)
<i>Edentostomina</i> (H)	<i>Wiesnerella</i> (H)	<i>Haynesina</i> (H)	Textulariida
<i>Euthymonacha</i> (H)	Robertinida	<i>Heterostegina</i> (S)	<i>Clavulina</i> (H)
<i>Fischerinella</i> (H)	<i>Hoeglundina</i> (H)	<i>Lobatula</i> (H)	<i>Pseudoclavulina</i>
<i>Hauerina</i> (H)	<i>Lamarckina</i> (H)	<i>Melonis</i> (H)	<i>Sahulina</i> (H)
<i>Miliolid</i> ^b (H)	Rotaliida	<i>Murrayinella</i> (H)	<i>Textularia</i> (H)
<i>Miliolinella</i> (H)	<i>Ammonia</i> (O)	<i>Neonorbina</i> (H)	
<i>Monalysidium</i> (S)	<i>Amphistegina</i> (S)	<i>Nonionella</i> (H)	

Foraminiferal functional groups: 'symbiont-bearing' (S); 'opportunistic' (O); and 'other small-heterotrophic' (H).

^a Unidentified foraminifera (Jones, 1994).

^b Unidentified Miliolid (Jones, 1994) see [Supplementary material 3](#) for species list.

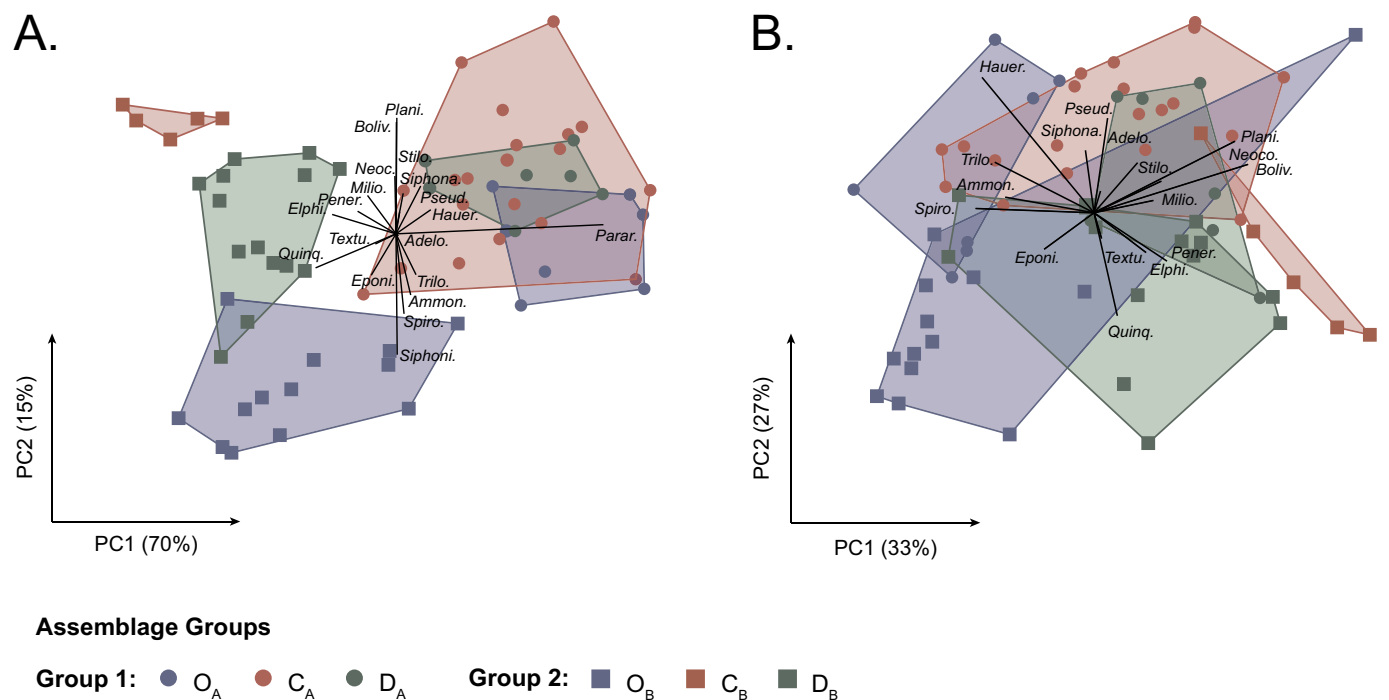


Fig. 4. Principle component analysis (PCA) biplots of foraminiferal assemblages from all analysed core samples from the Paluma Shoals reef complex. PCA tests were performed on relative abundance data, calculated from A. the inclusion of all genera-level abundance data; and B. the exclusion of *Pararotalia* spp. from the established ecological dataset. Both ordinations are based on between-group variance within a variance-covariance matrix. Convex hulls (dotted lines) denote the samples from the individual assemblage zones delineated by constrained incremental sum of squares (see Fig. 3). Those assemblage zones comprising ‘Group 1’ are denoted by green convex hulls, whilst those comprising ‘Group 2’ are represented by blue convex hulls. Vectors represent the foraminiferal taxa, with the length indicating the loadings for each taxon. For presentation purposes, only taxa accounting for > 1% of the total number of foraminifera identified within this study are shown: *Adelo.* = *Adelosina*, *Ammon.* = *Ammonia*, *Boliv.* = *Bolivina*, *Elphi.* = *Elphidium*, *Eponi.* = *Eponides*, *Hauer.* = *Hauerina*, *Milio.* = unidentified Miliid (Jones, 1994), *Neoc.* = *Neonorbina*, *Parar.* = *Pararotalia*, *Pener.* = *Peneroplis*, *Plani.* = *Planispirinella*, *Pseud.* = *Pseudorotalia*, *Quinq.* = *Quinqueloculina*, *Siphona.* = *Siphonaperta*, *Siphono.* = *Siphoninoides*, *Spiro.* = *Spirulina*, *Stilo.* = *Stilostomelloides*, *Textu.* = *Textularia*, *Trilo.* = *Triloculina*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Similarity percentage (SIMPER) analysis.

Average dissimilarity: 38.1%					
Genus	Av. dissim.	Contrib. (%)	Cumulative (%)	Group 1 (%)	Group 2 (%)
<i>Pararotalia</i> ^b	3.5	9.3	9.3	24.0 (10.5)	3.6 (4.8)
<i>Quinqueloculina</i> ^b	1.5	4.0	13.3	15.2 (5.7)	26.5 (7.4)
<i>Elphidium</i> ^b	1.2	3.3	16.6	12.1 (3.5)	21.1 (6.1)
<i>Planispirinella</i>	1.0	2.7	19.2	3.6 (2.9)	2.6 (1.9)
<i>Hauerina</i>	1.0	2.6	21.8	2.8 (2.1)	0.8 (1.0)
<i>Pseudorotalia</i>	0.9	2.4	24.2	1.4 (1.7)	0.9 (1.2)
<i>Peneroplis</i> ^b	0.9	2.3	26.5	1.4 (1.0)	3.3 (1.9)
<i>Bolivina</i>	0.8	2.2	28.7	2.0 (2.0)	1.2 (1.1)
<i>Eponides</i> ^b	0.8	2.2	30.8	1.4 (1.1)	2.9 (2.3)
<i>Miliid</i> ^{a,b}	0.8	2.1	32.9	1.4 (1.4)	2.0 (1.6)
<i>Siphoninoides</i>	0.8	2.0	35.0	2.3 (1.2)	3.8 (3.0)
<i>Siphonaperta</i>	0.8	2.0	37.0	1.4 (1.3)	0.8 (0.9)
<i>Textularia</i> ^b	0.8	2.0	39.0	2.7 (2.4)	3.0 (2.3)
<i>Cibicides</i> ^b	0.7	2.0	41.0	0.9 (1.1)	1.1 (3.0)
<i>Valvulineria</i> ^b	0.7	2.0	42.9	1.2 (1.3)	0.3 (0.4)
<i>Ammonia</i>	0.7	1.9	44.9	5.4 (2.2)	5.8 (3.4)
<i>Rosalina</i>	0.7	1.9	46.7	0.5 (0.8)	1.0 (1.2)
<i>Triloculina</i> ^b	0.7	1.7	48.5	0.7 (0.8)	0.3 (0.6)
<i>Parahauerinoides</i> ^b	0.7	1.7	50.2	0.4 (0.4)	1.1 (1.0)

SIMPER analysis was performed between the two assemblage groups identified by Principle Components Analysis (see Fig. 4). Taxa (square-root transformed) cumulatively accounting for ~50% of the dissimilarity are displayed with their average dissimilarities (Av. dissim.), and relative contributions to dissimilarity (Contrib.). The average relative abundance (untransformed) of the listed taxa within each of the two assemblage groups is also presented (± SD).

^a Unidentified Miliolid (Jones, 1994).

^b Taxa with a significant monotonic relationship with core depth (corrected to present lowest astronomical tide) (see Table S2).

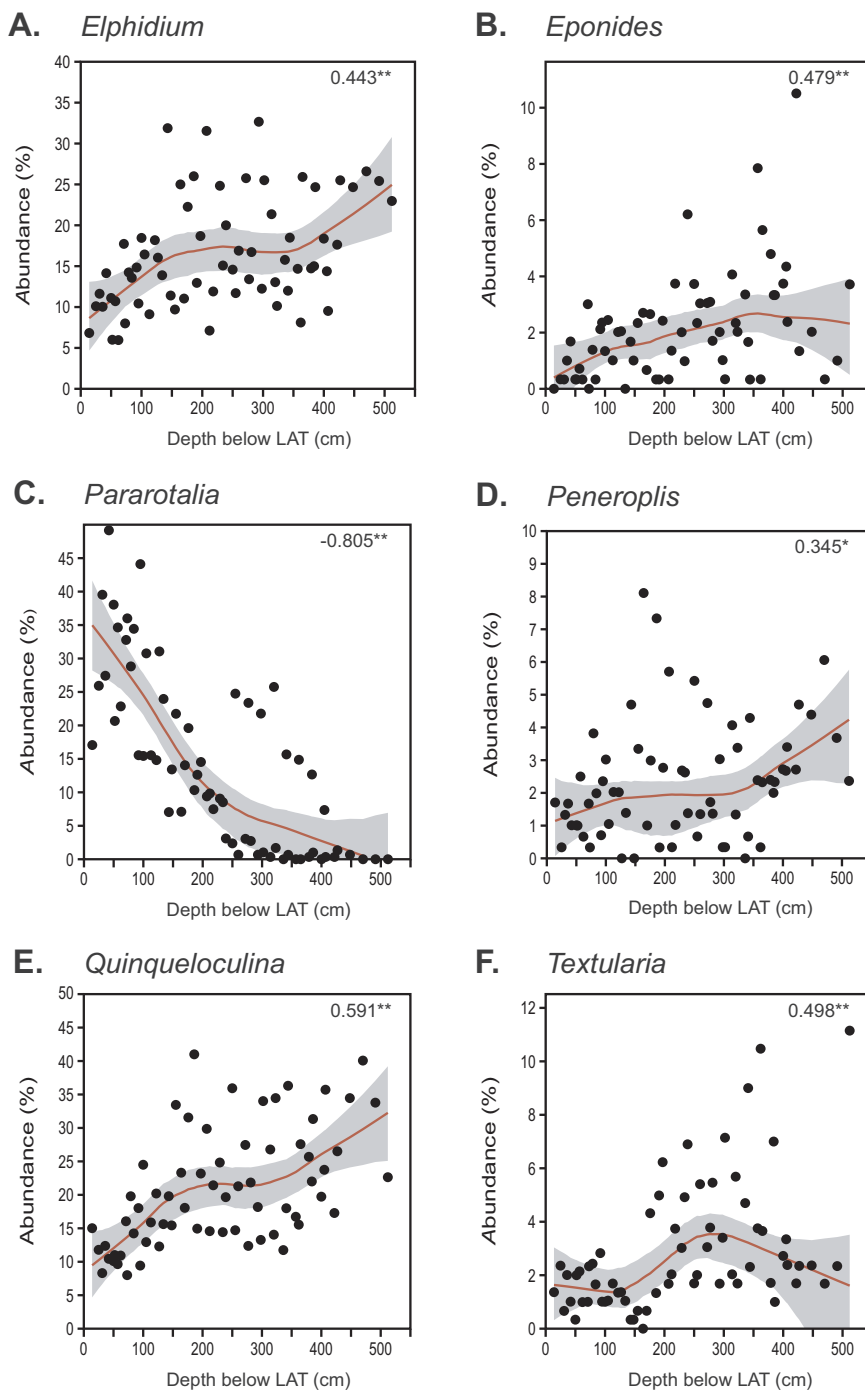


Fig. 5. Scatterplots showing the down-core distribution of untransformed foraminiferal abundance for A. *Elphidium* spp.; B. *Eponides* spp.; C. *Pararotalia* spp.; D. *Peneroplis* spp.; E. *Quinqueloculina* spp.; and F. *Textularia* spp. All presented core depths have been corrected to present lowest astronomical tide (LAT). Locally weighted regressions (LOESS) with a smoothing factor of 0.5 are fitted to the abundance plots (red line), with the 95% confidence intervals, as determined by bootstrapping, represented by the shaded area. Spearman's rho coefficients are presented for each taxa, with significance level denoted by the asterisk (* = $p < 0.05$, ** = $p < 0.005$). Of the taxa tested, only those accounting for > 1% of the total number of foraminifera identified within this study are shown. The full results of the Spearman's rank correlation analysis are provided in Supplementary Table S2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Hohenegger et al., 1999; Hohenegger, 2004; Murray, 2006; Cleary and Renema, 2007; Reymond et al., 2013). Previous studies have demonstrated considerable spatial variability in abiotic environmental factors within the PSRC, including (1) light availability, controlled by suspended sediment concentrations (Larcombe et al., 2001; Browne et al., 2013; Morgan et al., 2017); (2) rates of sedimentation (Browne et al., 2012b); and (3) sediment type (Browne et al., 2012b). Given the known variability of key environmental controlling factors within the PSRC, the vertical distribution of key nearshore foraminiferal taxa (Fig. 5; Supplementary Table S2) and the delineated assemblage groups (Figs. 3 and 4) likely reflect spatio-temporal variations in benthic habitat availability, as influenced by prevailing hydrodynamics. Inter-reef scale variations in hydrodynamic activity may also explain the observed heterogeneity in the composition of 'Group 2' (Fig. 4A) by controlling

for a wider range of habitats below the mean wave base elevation (Renema, 2008).

Whilst some studies provide compelling evidence for the high resistance potential of inner-shelf foraminiferal assemblages to historical increases in nutrient and sediment delivery in (sub)tropical northeast Australia (Reymond et al., 2013; Narayan et al., 2015; this study), others suggest the contrary. Notably, perturbations in historical foraminiferal assemblages are reported from nearshore reef settings in the Whitsundays region (Uthicke et al., 2012), approximately 300 km south of the PSRC. Background suspended sediment concentrations in the Whitsundays region typically do not exceed 5 mg L^{-1} and are therefore considerably lower than experienced within the PSRC, where suspended sediment concentrations are regularly $> 20 \text{ mg L}^{-1}$ (Schaffelke et al., 2012; Browne et al., 2013; Thompson et al., 2014). Current

evidence therefore supports the emerging hypothesis that coral reefs are more resistant to historical increases in nutrient and sediment inputs where they have initiated and developed under high terrigenous sediment influence (Larcombe and Woolfe, 1999a; Morgan et al., 2016a, 2017; Johnson et al., 2017).

5.2. Distribution of functional groups across the inner-shelf of the GBR

The consistently low abundance of taxa traditionally classified as 'symbiont-bearing' in previous studies from the GBR region (sensu Nobes and Uthicke, 2008; Uthicke et al., 2010; Raymond et al., 2013; Narayan et al., 2015) is one of the most distinguishable features of the PSRC foraminiferal assemblages (Fig. 3). On the GBR, the abundance of symbiont-bearing taxa is positively correlated to distance from the mainland and is primarily controlled by cross-shelf variations in nutrient availability and turbidity (Fig. 6; Uthicke and Nobes, 2008). Photosynthesis by endosymbionts (i.e., algae, diatoms, and dinoflagellates) is crucial for the efficient recycling of nutrients and calcification in symbiont-bearing foraminifera (Lee and Hallock, 1987). The low abundance of symbiont-bearing foraminifera recorded within the PSRC is therefore likely indicative of prevailing environmental conditions of low PAR availability, as the result of light attenuation by suspended sediments (Morgan et al., 2017). The prevalence of low PAR availability throughout the growth history of the PSRC is strongly supported by the continuous presence of terrigenous muds within the reef sediment matrix of the cores (Fig. 3). The prevalence of muddy substrate is also likely to inhibit the abundance of symbiont-bearing foraminifera within the PSRC, many of which prefer coarser and firmer substrates (Hohenegger et al., 1999; Renema, 2006, 2008; Renema and Troelstra, 2001).

Peneroplis spp. was the only symbiont-bearing taxon to make notable contributions to the overall composition of foraminiferal assemblages within the PSRC (Fig. 3; Table 3). In mixed terrigenous-carbonate shelf settings in Indonesia, *Peneroplis* is often affiliated with sandy substrates in sheltered environments (Renema and Troelstra, 2001; Cleary and Renema, 2007; Renema, 2008). However, *Peneroplis* can also be abundant within inshore reef settings on the GBR, under conditions characterised by low PAR availability and fine-grained sediment (Nobes et al., 2008; Uthicke et al., 2010). As *Peneroplis* host Rhodophycean symbionts (Renema and Troelstra, 2001), it may therefore be reasonably inferred that Rhodophyta-bearing foraminifera are better adapted to more marginal reef-associated conditions than those taxa with different host-symbiont associations (e.g., Chlorophyta, diatoms, and dinoflagellates) (Uthicke et al., 2010).

The prevalence of *Elphidium* over *Ammonia* throughout the analysed core sequences suggests that the benthic environment within the PSRC is not oxygen depleted and that food supply is variable (Fig. 3) (Hallock, 2012; Narayan and Pandolfi, 2010; Sen Gupta et al., 1996). Food supply is an important factor influencing foraminiferal microhabitat availability (Jorissen et al., 1995). For example, in mud-rich sediments, organic matter is readily trapped within interstitial sediment pore spaces and is utilised by heterotrophic foraminifera as a food source (Jorissen et al., 1995; Barbosa et al., 2009). Geochemical analyses of bulk sediment samples from reef cores recovered from Havannah Island and Pandora Reef (see Fig. 1) have shown organic sediments within Halifax Bay to be primarily derived from terrestrial sources and plants with C₄ metabolic pathways, namely Poaceae (Raymond et al., 2013). These findings, coupled with the consistently higher abundance of *Elphidium* over *Ammonia* reported in this study, thus highlight the important role of fluvially-derived sediment in structuring benthic foraminiferal assemblages within nearshore turbid-zone reef settings on the GBR.

5.3. Using the FoRAM Index to characterise turbid nearshore environmental quality

The FI has been applied extensively across a range of reef settings for the assessment of water quality, with respect to environmental suitability for coral growth and reef development (Hallock, 2012;

Renema, 2018). Indeed, the FI has been shown to provide an effective measure of water quality and sediment organic enrichment on the GBR (Schueth and Frank, 2008; Uthicke and Nobes, 2008; Narayan and Pandolfi, 2010; Uthicke et al., 2010; Fabricius et al., 2012). In this study, FI values derived from core samples suggest that the reefs of the PSRC reefs established under 'suboptimal/marginal' environmental conditions (Fig. 7). These findings are consistent with previous studies utilising the FI within nearshore turbid-zone reef settings elsewhere on the GBR and in (sub)tropical northeast Australia (Uthicke et al., 2012; Narayan et al., 2015).

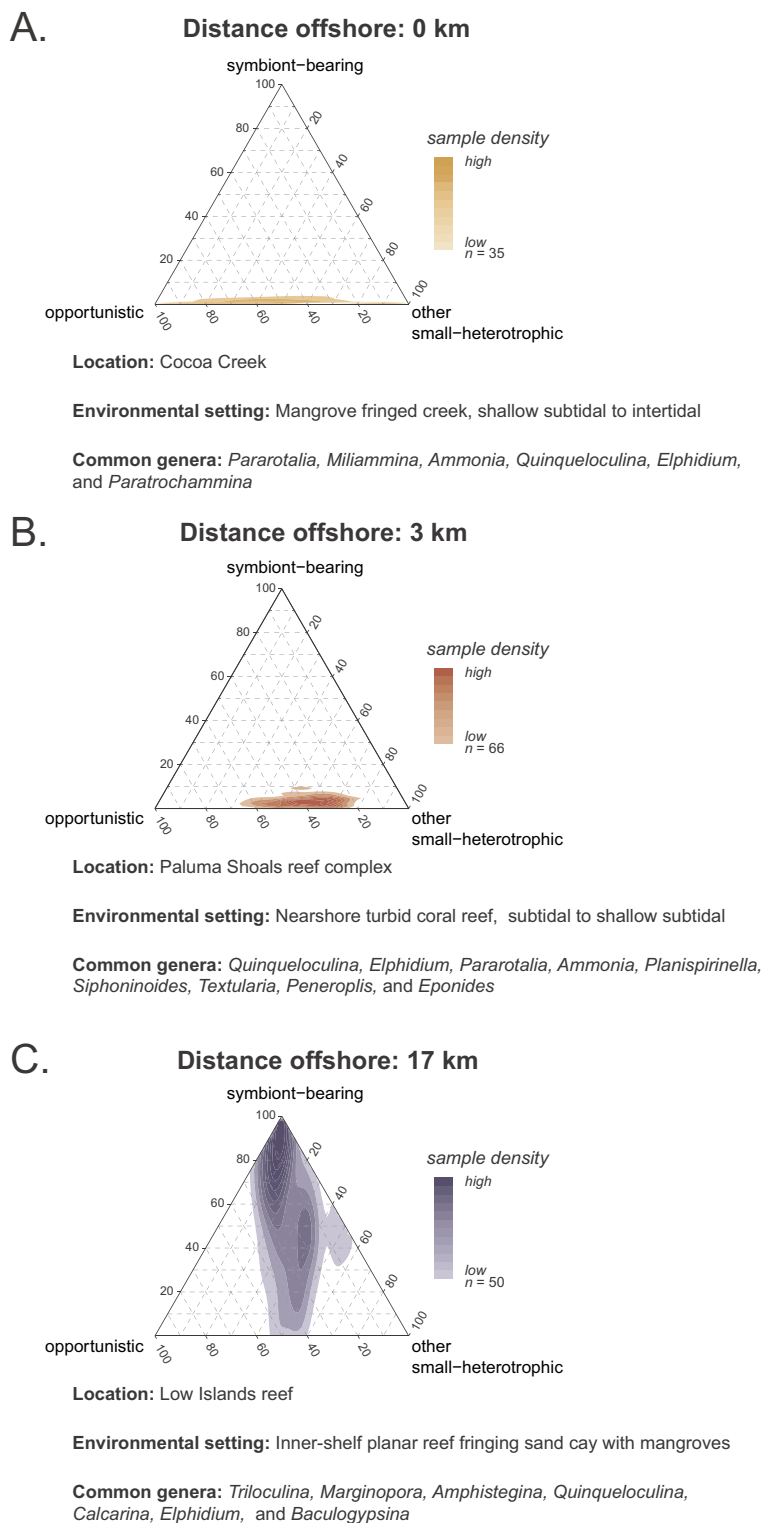
Over 70% of the analysed samples were indicative of environmental conditions considered to be 'suboptimal' for reef growth (Fig. 7). Under 'suboptimal' conditions (i.e., FI < 2), higher nutrient fluxes and particulate food supply, coupled with increasing turbidity and associated reductions in PAR availability, limit the development of mixotrophic-dominated benthic communities (i.e., 'symbiont-bearing' foraminifera and zooxanthellate corals) (Hallock et al., 2003; Carnahan et al., 2009).

In their original article, Hallock et al. (2003) recognised the requirement for the refinement of the FI to local conditions outside of the Caribbean. In this respect, a taxon of particular interest within nearshore turbid-zone settings on the central GBR is *Pararotalia* spp., which contributed most to the observed dissimilarities between the two assemblage groups delineated in this study (Fig. 4; Table 3). To maintain consistency with previous investigations (see Schueth and Frank, 2008; Uthicke et al., 2010; Raymond et al., 2013; Narayan et al., 2015), *Pararotalia* spp. were classified as 'opportunistic' (Table 2). This classification was made despite the fact that *Pararotalia* spp. are known to host a consortium of endosymbionts (Schmidt et al., 2015, 2018). By reclassifying *Pararotalia* spp. as 'symbiont-bearing', revised FI values revealed approximately 70% of samples as being indicative of conditions considered 'marginal' for reef growth (Fig. 7; see Supplementary material 2). Interestingly, the recalculated FI values are indicative of 'optimal' environmental conditions (i.e., FI > 4), at least temporarily, within the upper core sequences (i.e., shallower than 1 m below present LAT; Fig. 7). This trend is consistent with measured increases in light availability and carbonate content of the reef-matrix sediment towards sea level (Fig. 3; Morgan et al., 2017).

As a shallow epiphytic taxon, *Pararotalia* spp. attach to algae, feeding on microflora, and are common within muddy inner-shelf settings (Murray, 2006; Narayan and Pandolfi, 2010; Horton et al., 2007). In this study, the vertical distribution of *Pararotalia* spp. was notably constrained to depths shallower than ~4 m below present LAT, where it exhibited a significant and strongly negative relationship with core depth (Fig. 5). This apparent depth threshold is close to that of the regional maximum photic depth within coastal environments on the GBR (Fabricius et al., 2016), suggesting PAR availability to be an important control on the vertical distribution of *Pararotalia* spp. The presence of a suitable algal substrate may also be influenced by PAR availability. Thus, the vertical distribution of *Pararotalia* spp. may be further constrained to shallow water depths, where PAR availability is higher and sedimentary conditions more favourable for algal growth (Guest et al., 2016).

Recent genotyping and culturing experiments of endosymbiotic algae have provided evidence to support the existence of symbiont shuffling in *Pararotalia calcariformata* in the Mediterranean Sea as an adaptive mechanism to environmental change (Schmidt et al., 2018). Similar mechanisms have also been reported in the symbiont-bearing foraminifera *Amphistegina lobifera* from the GBR, in which inner-shelf populations exhibit an increased acclimation/adaptive capacity to environmental stress compared to those from mid- and outer-shelf locations (Prazeres et al., 2016). The ability to regulate symbiont density and to host a diversity of endosymbionts may therefore explain the apparent success of *Pararotalia* spp. within the nearshore turbid-zone reef setting of the PSRC.

The appropriate functional classification of foraminiferal taxa is crucial for determining FI values that are representative of prevailing environmental conditions. This is particularly true with respect to the



Distance offshore

Fig. 6. Ternary diagrams showing the relative contributions of functional groups to overall foraminiferal assemblage composition at three inner-shelf reef sites distributed along an offshore gradient. Data are presented as sample density plots for A. contemporary assemblage data from Cocoa Creek ($n = 35$; Woodroffe et al., 2005; Woodroffe, 2009b), Cleveland Bay (approximately 50 km south of the Paluma Shoals reef complex); B. the Paluma Shoals reef complex, data are based on the palaeoecological assemblages presented in this study ($n = 66$); and C. contemporary assemblage data from Low Island Reef ($n = 50$; Schueth and Frank, 2008), northern Great Barrier Reef (approximately 300 km north of the Paluma Shoals reef complex). Presented foraminifera represent those accounting for > 70% of the total dataset at each location and are listed in rank order of abundance.

classification of 'opportunistic' and 'symbiont-bearing' foraminifera. Furthermore, high numbers of a single 'symbiont-bearing' taxon have also been reported as biasing the FI towards higher values that were not reflective of the true ecological status of the reefs in question (Uthicke and Nobes, 2008). Given the current ambiguity concerning the functional classification of certain Indo-Pacific taxa, further study of the biology and ecology of benthic foraminifera is clearly warranted to refine the FI across region-specific nearshore turbid settings. This

requirement was recently emphasised by Renema (2018) who noted that the FI index does not currently account for differences in species preferences within 'symbiont-bearing' assemblages for either coral- or macroalgal-dominated environments. For example, observations of Calcarinidae on Indonesian reefs have shown the abundance of *Calcarina* spp. to increase with macroalgal cover (Renema, 2010). Given this behaviour, it may be argued that some species of *Calcarina* (e.g., *Calcarina mayori*) are more closely aligned to the 'opportunistic'

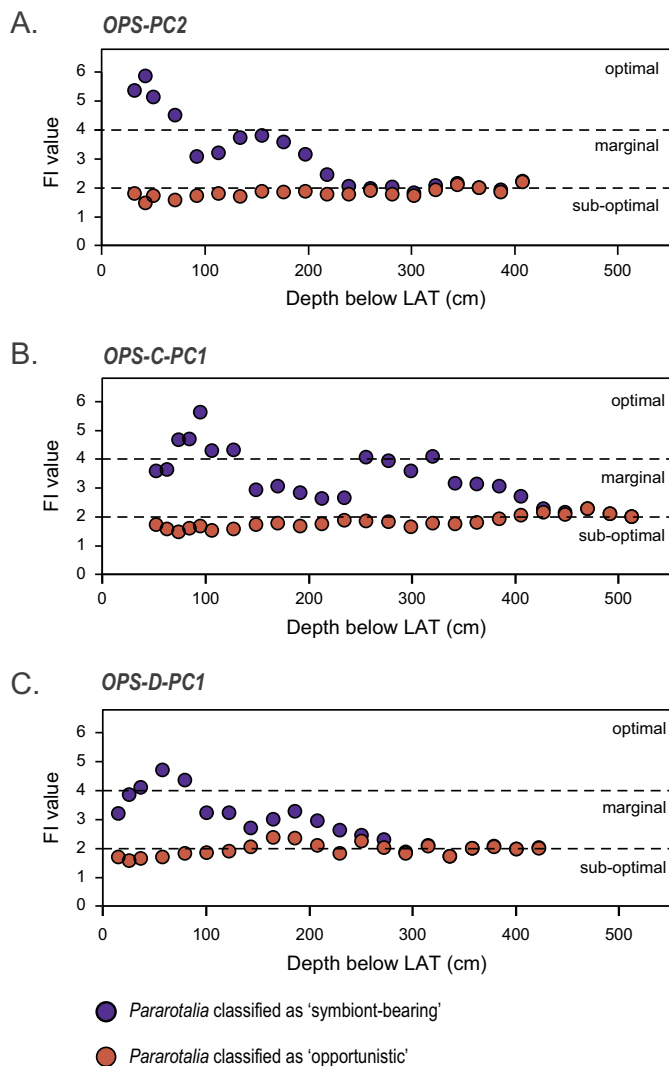


Fig. 7. FORAM Index (FI) values for each of the analysed core samples from A. Offshore Paluma Shoals (OPS)-PC2; B. OPS-C-PC1; and C. OPS-D-PC1. Samples are presented relative to the inferred environmental conditions considered to be 'optimal' ($FI > 4$), 'marginal' ($2 > FI < 4$), and 'suboptimal' ($FI < 2$) for reef growth (sensu Hallock et al., 2003). FI values derived from the classification of *Pararotalia* spp. as 'opportunistic' are represented by red circles. FI values derived from the classification of *Pararotalia* spp. as 'symbiont-bearing' are represented by blue circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

functional group than the other taxa classified as 'symbiont-bearing' taxa within this study (for the purposes of deriving FI values, at least).

A further genus of interest is that of *Elphidium*, which contains a number of kleptoplastic species that profit from photosynthetic products derived from chloroplasts sequestered from their food source (mainly diatoms) (Lopez, 1979; Renema and Troelstra, 2001; Renema, 2008). Whilst some species of *Elphidium* (e.g., *Elphidium craticulatum*) cannot be regarded as true 'symbiont-bearing' taxa, as they are less dependent on autotrophic production than diatom or dinoflagellate-bearing species, they are nonetheless well adapted to nearshore turbid-zone settings on the central GBR (this study; Woodroffe et al., 2009; Lewis et al., 2012; Raymond et al., 2013). Thus, *Elphidium* spp. may not necessarily behave as intended for the 'opportunistic' grouping of the FI (Carnahan et al., 2009). Without further experimental and field studies at the species-level, difficulties in the appropriate functional classification of benthic foraminifera for the purposes of utilising the FORAM index within the Indo-Pacific region will remain. To this end, the

following recommendations made by Uthicke and Nobes (2008) for the further refinement of the FI may prove useful: (1) individual species to be weighted differently; and (2) the inclusion of a weighting factor based on the diversity of 'symbiont-bearing' taxa.

6. Conclusions

Palaeoecological records established from reef cores recovered from the PSRC enabled the investigation of long-term foraminiferal assemblage composition and variability within a nearshore turbid-zone reef setting on the central GBR. Each reef core penetrated the entire Holocene reef sequence, capturing a ~1200 year history of reef growth under the high influence of terrigenous sediments. No discernible evidence of compositional change within the foraminiferal assemblages of the PSRC was found relative to post-European settlement land-use change. Rather, identified transitions in benthic foraminiferal assemblages are interpreted as reflecting intrinsically-driven changes in hydrodynamic energy, light availability and the carbonate content of reef-matrix sediments during reef shallowing towards sea level. This study also demonstrates the high resistance potential of nearshore turbid reefs and their associated communities under increased nutrient and sediment inputs, as the result of historical land-use change. To this end, the foraminiferal assemblages presented in this study provide valuable baseline records for future assessments and the monitoring of ecological and environmental change within similar geomorphic settings on the GBR and elsewhere in the Indo-Pacific.

Data availability

Supplementary information to this article can be found under Supplementary materials 1–3.

Datasets concerning the radiometric data and associated methodologies used in this article can be found under GSA Data Repository item 2016335, 2016, available at www.geosociety.org/pubs/ft2016.htm.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2019.109240>.

References

- Alve, E., 1995. Benthic foraminiferal responses to estuarine pollution: a review. J. Foraminif. Res. 25, 190–203. <https://doi.org/10.2113/jsfr.25.3.190>.
- Barbosa, C.F., Prazeres, M., Ferreira, B.P., Seonane, J.C.S., 2009. Foraminiferal assemblages and reef check census in coral reef health monitoring of East Brazilian margin. Mar. Micropaleontol. 73, 62–69. <https://doi.org/10.1016/j.marmicro.2009.07.002>.
- Beaman, R.J., 2010. Project 3DGBR: a high-resolution depth model for the Great Barrier Reef and Coral Sea. Marine and Tropical Sciences Research Facility (MTSRF) Project 2.5i.1a Final Report, MTSRF, Cairns, Australia. p. 13, plus Appendix 1. <http://www.mtsrf.gov.au>.

- deepreef.org/publications/reports/67-3dgr-final-report.html.
- Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *New Phytol.* 132, 155–170. <https://doi.org/10.1111/j.1469-8137.1996.tb04521.x>.
- Berkeley, A., Perry, C.T., Smithers, S.G., Horton, B.P., Taylor, K.G., 2007. A review of the ecological and taphonomic controls on foraminiferal assemblage development in intertidal environments. *Earth Sci. Rev.* 83, 205–230. <https://doi.org/10.1016/j.earscirev.2007.04.003>.
- Berkeley, A., Perry, C.T., Smithers, S.G., Horton, B.P., 2008. The spatial and vertical distribution of living (stained) benthic foraminifera from a tropical, intertidal environment, north Queensland, Australia. *Mar. Micropaleontol.* 69, 240–261. <https://doi.org/10.1016/j.marmicro.2008.08.002>.
- Berkeley, A., Perry, C.T., Smithers, S.G., 2009. Taphonomic signatures and patterns of test degradation on tropical, intertidal benthic foraminifera. *Mar. Micropaleontol.* 73, 148–163. <https://doi.org/10.1016/j.marmicro.2009.08.002>.
- Berkeley, A., Perry, C.T., Smithers, S.G., Hoon, S., 2014. Towards a formal description of foraminiferal assemblage formation in shallow-water environments: qualitative and quantitative concepts. *Mar. Micropaleontol.* 112, 27–38. <https://doi.org/10.1016/j.marmicro.2014.08.005>.
- Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Anal.* 6, 457–474. <https://doi.org/10.1214/11-BA618>.
- Brodie, J.E., Kroon, F.J., Schaffelke, B., Wolanski, E.C., Lewis, S.E., Devlin, M.J., Bohner, I.C., Bainbridge, Z.T., Waterhouse, J., Davis, A.M., 2012. Terrestrial pollutant runoff to the Great Barrier Reef: an update of issues, priorities and management responses. *Mar. Pollut. Bull.* 65, 81–100. <https://doi.org/10.1016/j.marpolbul.2011.12.012>.
- Brodie, J., Devlin, M., Lewis, S., 2017. Potential enhanced survivorship of crown of thorns starfish larvae due to near-annual nutrient enrichment during secondary outbreaks on the central mid-shelf of the Great Barrier Reef, Australia. *Diversity* 9, 17. <https://doi.org/10.3390/d9010017>.
- Browne, N.K., Smithers, S.G., Perry, C.T., 2012a. Coral reefs of the turbid inner-shelf of the Great Barrier Reef, Australia: an environmental and geomorphic perspective on their occurrence, composition and growth. *Earth Sci. Rev.* 115, 1–20. <https://doi.org/10.1016/j.earscirev.2012.06.006>.
- Browne, N.K., Smithers, S.G., Perry, C.T., Ridd, P.V., 2012b. A field-based technique for measuring sediment flux on coral reefs: application to turbid reefs on the Great Barrier Reef. *J. Coast. Res.* 28, 1247–1262. <https://doi.org/10.2112/JCOASTRES-D-11-00171.1>.
- Browne, N.K., Smithers, S.G., Perry, C.T., 2013. Spatial and temporal variations in turbidity on two inshore turbid reefs on the Great Barrier Reef, Australia. *Coral Reefs* 32, 195–210. <https://doi.org/10.1016/j.marenvres.2012.02.005>.
- Carnahan, E.A., Hoare, A.M., Hallock, P., Lidz, B.H., Reich, C.D., 2009. Foraminiferal assemblages in Biscayne Bay, Florida, USA: responses to urban and agricultural influence in a subtropical estuary. *Mar. Pollut. Bull.* 59, 221–233. <https://doi.org/10.1016/j.marpolbul.2009.08.008>.
- Clark, T.R., Roff, G., Zhao, J.-x., Feng, Y.-x., Done, T.J., McCook, L.J., Pandolfi, J.M., 2017. U-Th dating reveals regional-scale decline of branching *Acropora* corals on the Great Barrier Reef over the past century. *Proc. Natl. Acad. Sci.* 114, 201705351.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143. <https://doi.org/10.1073/pnas.1705351114>.
- Cleary, D.F.R., Renema, W., 2007. Relating species traits of foraminifera to environmental variables in the Spermonde Archipelago, Indonesia. *Mar. Ecol. Prog. Ser.* 334, 73–82. <https://doi.org/10.3354/meps334073>.
- Cocconi, R., 2000. Benthic foraminifera as bioindicators of heavy metal pollution: a case study from the Goro lagoon (Italy). In: Martin, R.E. (Ed.), *Environmental Micropaleontology: The Application of Microfossils to Environmental Geology*. Springer, New York, pp. 71–104.
- Collins, A.C., 1958. Great Barrier Reef Expedition 1928–29. Scientific Reports Volume VI. No.6. Foraminifera. British Museum (Natural History), UK.
- Colwell, R.K., 2013. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, version 9.1.0. User's Guide and publication. <http://www.viceroy.eeb.uconn.edu/estimates>
- Corliss, B.H., Chen, C., 1988. Morphotype patterns of Norwegian Sea deep-sea benthic foraminifera and ecological implications. *Geology* 16, 716–719. [https://doi.org/10.1130/0091-7613\(1988\)016<0716:MPONSD>2.3.CO;2](https://doi.org/10.1130/0091-7613(1988)016<0716:MPONSD>2.3.CO;2).
- De'ath, G., Fabricius, K., 2010. Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecol. Appl.* 20, 840–850. <https://doi.org/10.1890/08-2023.1>.
- De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M., 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Natl. Acad. Sci.* 109, 17995–17999. <https://doi.org/10.1073/pnas.1208909109>.
- Debenay, J.P., 1988. Recent foraminifera tracers of oceanic water movements in the southwestern lagoon of New Caledonia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 65, 59–72. [https://doi.org/10.1016/0031-0182\(88\)90112-5](https://doi.org/10.1016/0031-0182(88)90112-5).
- Debenay, J.P., Payri, C.E., 2010. Epiphytic foraminiferal assemblages on macroalgae in reefal environments of New Caledonia. *J. Foraminif. Res.* 40, 36–60. <https://doi.org/10.2113/jsjfr.40.1.36>.
- Fabricius, K.E., Cooper, T.F., Humphrey, C., Uthicke, S., De'ath, G., Davidson, J., LeGrand, H., Thompson, A., Schaffelke, B., 2012. A bioindicator system for water quality on inshore coral reefs of the Great Barrier Reef. *Mar. Pollut. Bull.* 65, 320–332. <https://doi.org/10.1016/j.marpolbul.2011.09.004>.
- Fabricius, K.E., Logan, M., Weeks, S.J., Lewis, S.E., Brodie, J., 2016. Changes in water clarity in response to river discharges on the Great Barrier Reef continental shelf: 2002–2013. *Estuar. Coast. Shelf Sci.* 173, A1–A15. <https://doi.org/10.1016/j.ecss.2016.03.001>.
- Fajemila, O., Langer, M.R., Lipps, J.H., 2015. Spatial patterns in the distribution, diversity and abundance of benthic foraminifera around Moorea (Society Archipelago, French Polynesia). *PLoS ONE* 10, e0145752. <https://doi.org/10.1371/journal.pone.0145752>.
- Frontalini, F., Cocconi, R., 2011. Benthic foraminifera as bioindicators of pollution: a review of Italian research over the last three decades. *Rev. Micropaleontol.* 54, 115–127. <https://doi.org/10.1016/j.revmic.2011.03.001>.
- Gehrels, W.R., 2000. Using foraminiferal transfer functions to produce high-resolution sea-level records from salt-marsh deposits, Maine, USA. *The Holocene* 10, 367–376. <https://doi.org/10.1191/095968300670746884>.
- Grimm, E.C., 1987. CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Comput. Geosci.* 13, 13–35. [https://doi.org/10.1016/0098-3004\(87\)90022-7](https://doi.org/10.1016/0098-3004(87)90022-7).
- Guest, J.R., Tun, K., Low, J., Vergès, A., Marzini, E.M., Campbell, A.H., Bauman, A.G., Feary, D.A., Chou, L.M., Steinberg, P.D., 2016. 27 years of benthic and coral community dynamics on turbid, highly urbanised reefs off Singapore. *Sci. Rep.* 6, 36260. <https://doi.org/10.1038/srep36260>.
- Haapkyä, J., Unsworth, R.K.F., Flavell, M., Bourne, D.G., Schaffelke, B., Willis, B.L., 2011. Seasonal rainfall and runoff promote coral disease on inshore reef. *PLoS One* 6, e16893. <https://doi.org/10.1371/journal.pone.0016893>.
- Haig, D.W., 1988. Milioid foraminifera from inner neritic sand and mud facies of the Papuan lagoon, New Guinea. *J. Foraminif. Res.* 18, 203–236.
- Hallock, P., 2012. The ForAM Index revisited: uses, challenges, and limitations. In: *Proceedings of the 12th International Coral Reef Symposium*. Australia, Cairns.
- Hallock, P., Lidz, B.H., Cockey-Burkhard, E.M., Donnelly, K.B., 2003. Foraminifera as bioindicators in coral reef assessment and monitoring: the FORAM Index. *Environ. Monit. Assess.* 81, 221–238. <https://doi.org/10.1023/A:1021337310386>.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 1–9.
- Hayward, B.W., Hollis, C.J., Grenfell, 1997. Recent Elphidiidae (Foraminifera) of the south-west Pacific and fossil Elphidiidae of New Zealand. *Institute of Geological & Nuclear Sciences Monograph* 16. Lower Hutt, New Zealand, Institute of Geological & Nuclear Sciences Limited, pp. 170.
- Hohenegger, J., 2004. Depth coenoclines and environmental considerations of western Pacific larger foraminifera. *J. Foraminif. Res.* 34, 9–33. <https://doi.org/10.2113/0340009>.
- Hohenegger, J., Yordanova, E., Nakano, Y., Tatzreiter, F., 1999. Habitats of larger foraminifera on the upper reef slope of Sesoko Island, Okinawa, Japan. *Mar. Micropaleontol.* 36, 109–168. [https://doi.org/10.1016/S0377-8398\(98\)00030-9](https://doi.org/10.1016/S0377-8398(98)00030-9).
- Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. John Wiley & Sons, USA, pp. 453.
- Hopley, D., Smithers, S.G., Parnell, K.E., 2007. *The Geomorphology of the Great Barrier Reef: Development, Diversity and Change*. Cambridge University Press, New York, pp. 345.
- Horton, B.P., Culver, S.J., Hardbatt, M.I.J., Larcombe, P., Milne, G.A., Morigi, C., Whittaker, J.E., Woodroffe, S.A., 2007. Reconstructing Holocene sea-level change for the central Great Barrier Reef (Australia) using subtidal foraminifera. *J. Foraminif. Res.* 37, 327–343. <https://doi.org/10.2113/jsjfr.37.4.327>.
- IBM Corp., 2015. IBM SPSS Statistics for Windows. Version 23.0. (Armonk, New York).
- Johnson, J.A., Perry, C.T., Smithers, S.G., Morgan, K.M., Santodomingo, N., Johnson, K.G., 2017. Palaeoecological records of coral community development on a turbid, nearshore reef complex: baselines for assessing ecological change. *Coral Reefs* 36, 685–700. <https://doi.org/10.1007/s00338-017-1561-1>.
- Jones, R.W., 1994. *The Challenger Foraminifera*. Oxford University Press, UK, pp. 416.
- Jorissen, F.J., de Stigter, H.C., Widmark, J.G.V., 1995. A conceptual model explaining benthic foraminiferal microhabitats. *Mar. Micropaleontol.* 26, 3–15. [https://doi.org/10.1016/0377-8398\(95\)00047-X](https://doi.org/10.1016/0377-8398(95)00047-X).
- Juggins, S., 2016. Rioja: analysis of Quaternary science data. Functions for the analysis of Quaternary science data, including constrained clustering, WA, WAPLS, IKFA, MLRC and MAT transfer functions, and stratigraphic diagrams. R package version 0.9-9. <https://cran.r-project.org/web/packages/rioja/>
- Kroon, F.J., Kuhnert, P.M., Henderson, B.L., Wilkinson, S.N., Kinsey-Henderson, A., Abbott, B., Brodie, J.E., Turner, R.D.R., 2012. River loads of suspended solids, nitrogen, phosphorus and herbicides delivered to the Great Barrier Reef lagoon. *Mar. Pollut. Bull.* 65, 167–181. <https://doi.org/10.1016/j.marpolbul.2011.10.018>.
- Langer, M.R., 1993. Epiphytic Foraminifera. *Mar. Micropaleontol.* 20, 235–265. [https://doi.org/10.1016/0377-8398\(93\)90035-V](https://doi.org/10.1016/0377-8398(93)90035-V).
- Langer, M.R., Lipps, J.H., 2003. Foraminiferal distribution and diversity, Madang Reef and Lagoon, Papua New Guinea. *Coral Reefs* 22, 143–154. <https://doi.org/10.1007/s00338-003-0298-1>.
- Larcombe, P., Woolfe, K.J., 1999a. Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. *Coral Reefs* 18, 163–169. <https://doi.org/10.1007/s003380050174>.
- Larcombe, P., Woolfe, K.J., 1999b. Terrigenous sediments as influences upon Holocene coral reefs, central Great Barrier Reef, Australia. *Aust. J. Earth Sci.* 46, 141–154. <https://doi.org/10.1046/j.1440-0952.1999.00694.x>.
- Larcombe, P., Costen, A., Woolfe, K.J., 2001. The hydrodynamic and sedimentary setting of nearshore coral reefs, central Great Barrier Reef shelf, Australia: Paluma Shoals, a case study. *Sedimentology* 48, 811–835. <https://doi.org/10.1046/j.1365-3091.2001.00396.x>.
- Lee, J.J., Hallock, P., 1987. Algal symbiosis as the driving force in the evolution of larger foraminifera. *Ann. N. Y. Acad. Sci.* 503, 330–347. <https://doi.org/10.1111/j.1749-6632.1987.tb040619.x>.
- Legendre, P., Birks, H.J.B., 2012. From classical to canonical ordination. Birks HJB, Lotter AF, Juggins S, Smol JP (eds). *Tracking Environmental Change Using Lake Sediments, Volume 5: Data Handling and Numerical Techniques*. Springer, Netherlands, pp. 201–248.

- Leoblich, A.R., Tappan, H., 1994. Foraminifera of the Sahul Shelf and Timor Sea. Cushman Foundation Special Publication No. 31. p. 661.
- Lewis, S.E., Shields, G.A., Kamber, B.S., Lough, J.M., 2007. A multi-trace element coral record of land-use changes in the Burdekin River catchment, NE Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 246, 471–487.
- Lewis, S.E., Wüst, R.A.J., Webster, J.M., Shields, G.A., Renema, W., Lough, J.M., Jacobsen, G., 2012. Development of an inshore fringing coral reef using textural, compositional and stratigraphic data from Magnetic Island, Great Barrier Reef, Australia. *Mar. Geol.* 299–302, 18–32. doi: <https://doi.org/10.1016/j.margeo.2012.01.003>.
- Lewis, S.E., Sloss, C.R., Murray-Wallace, C.V., Woodroffe, C.D., Smithers, S.G., 2013. Post-glacial sea-level changes around the Australian margin: a review. *Quat. Sci. Rev.* 74, 115–138. <https://doi.org/10.1016/j.palaeo.2006.10.021>.
- Lewis, S.E., Wüst, R.A.J., Webster, J.M., Collins, J., Wright, S.A., 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. *Mar. Geol.* 370, 20–30. <https://doi.org/10.1016/j.margeo.2015.09.014>.
- Lopez, E., 1979. Algal chloroplasts in the protoplasm of three species of benthic foraminifera: taxonomic affinity, viability and persistence. *Mar. Biol.* 53, 201–211. <https://doi.org/10.1007/BF00952427>.
- Lough, J.M., Lewis, S.E., Cantin, N.E., 2015. Freshwater impacts in the central Great Barrier Reef: 1648–2011. *Coral Reefs* 34, 739–751. <https://doi.org/10.1007/s00338-015-1297-8>.
- McCulloch, I., 1977. Qualitative Observations on Recent Foraminiferal Tests With Emphasis on the Eastern Pacific. In: Part 1–3. University of Southern California, Los Angeles.
- Morgan, K.M., Perry, C.T., Smithers, S.G., Johnson, J.A., Daniell, J.J., 2016a. Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. *Sci. Rep.* 6, 29616. <https://doi.org/10.1038/srep29616>.
- Morgan, K.M., Perry, C.T., Smithers, S.G., Johnson, J.A., Gulliver, P., 2016b. Transitions in coral reef accretion rates linked to intrinsic ecological shifts on turbid-zone nearshore reefs. *Geology* 44, 995–998. <https://doi.org/10.1130/G38610.1>.
- Morgan, K.M., Perry, C.T., Johnson, J.A., Smithers, S.G., 2017. Nearshore turbid-zone corals exhibit high bleaching tolerance on the Great Barrier Reef following the 2016 warming event. *Front. Mar. Sci.* 4, 224. <https://doi.org/10.3389/fmars.2017.00224>.
- Murray, J.W., 1991. *Ecology and Palaeoecology of Benthic Foraminifera*. Longman Group, UK, pp. 354.
- Murray, J.W., 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, UK, pp. 440.
- Narayan, Y.R., Pandolfi, J.M., 2010. Benthic foraminiferal assemblages from Moreton Bay, South-East Queensland, Australia: applications in monitoring water and substrate quality in subtropical estuarine environments. *Mar. Pollut. Bull.* 60, 2062–2078. <https://doi.org/10.1016/j.marpolbul.2010.07.012>.
- Narayan, Y.R., Lybolt, M., Zhao, J.-x., Feng, Y., Pandolfi, J.M., 2015. Holocene benthic foraminiferal assemblages indicate long-term marginality of reef habitats from Moreton bay, Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 420, 49–64. <https://doi.org/10.1016/j.palaeo.2014.12.010>.
- Nobes, K., Uthicke, S., 2008. Benthic Foraminifera of the Great Barrier Reef: A Guide to Species Potentially Useful as Water Quality Indicators. Report to the Marine and Tropical Sciences Research Facility. Reef and Rainforest Research Centre Limited, Cairns, pp. 44.
- Nobes, K., Uthicke, S., Henderson, R., 2008. Is light the limiting factor for the distribution of benthic symbiont bearing foraminifera on the Great Barrier Reef? *J. Exp. Mar. Biol. Ecol.* 363, 48–57. <https://doi.org/10.1016/j.jembe.2008.06.015>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2017. *Vegan: community ecology package. Ordination methods, diversity analysis and other functions for community and vegetation ecologists. R-package version 2.0*. <https://cran.r-project.org/web/packages/vegan>.
- Orpin, A.R., Ridd, P.V., 2012. Exposure of inshore corals to suspended sediments due to wave-resuspension and river plumes in the central Great Barrier Reef: a reappraisal. *Cont. Shelf Res.* 47, 55–67. <https://doi.org/10.1016/j.csr.2012.06.013>.
- Palmer, S.E., Perry, C.T., Smithers, S.G., Gulliver, P., 2010. Internal structure and accretionary history of a nearshore, turbid-zone coral reef: Paluma Shoals, central Great Barrier Reef, Australia. *Mar. Geol.* 276, 14–29. <https://doi.org/10.1016/j.margeo.2010.07.002>.
- Pandolfi, J.M., 2002. Coral community dynamics at multiple scales. *Coral Reefs* 21, 13–23. <https://doi.org/10.1007/s00338-001-0204-7>.
- Perry, C.T., Smithers, S.G., 2011. Cycles of coral reef 'turn-on', rapid growth and 'turn-off' over the past 8500 years: a context for understanding modern ecological states and trajectories. *Glob. Chang. Biol.* 17, 76–86. <https://doi.org/10.1111/j.1365-2486.2010.02181.x>.
- Perry, C.T., Smithers, S.G., Palmer, S.E., Larcombe, P., Johnson, K.G., 2008. 1200 year paleoecological record of coral community development from the terrigenous inner shelf of the Great Barrier Reef. *Geology* 36, 691–694. <https://doi.org/10.1130/G24907A.1>.
- Perry, C.T., Smithers, S.G., Johnson, K.G., 2009. Long-term coral community records from Lugga Shoal on the terrigenous inner-shelf of the Great Barrier Reef, Australia. *Coral Reefs* 28, 941–948. <https://doi.org/10.1007/s00338-009-0528-2>.
- Perry, C.T., Smithers, S.G., Roche, R.C., Wassenburg, J., 2011. Recurrent patterns of coral community and sediment facies development through successive phases of Holocene inner-shelf reef growth and decline. *Mar. Geol.* 289, 60–71. <https://doi.org/10.1016/j.margeo.2011.09.012>.
- Perry, C.T., Smithers, S.G., Gulliver, P., Browne, N.K., 2012. Evidence of very rapid reef accretion and reef growth under high turbidity and terrigenous sedimentation. *Geology* 40, 719–722. <https://doi.org/10.1130/G33261.1>.
- Perry, C.T., Smithers, S.G., Gulliver, P., 2013. Rapid vertical accretion on a 'young' shore-detached turbid zone reef: Offshore Paluma Shoals, central Great Barrier Reef, Australia. *Coral Reefs* 32, 1143–1148. <https://doi.org/10.1007/s00338-013-1063-8>.
- Prazeres, M., Uthicke, S., Pandolfi, J.M., 2016. Influence of local habitat on the physiological responses of large benthic foraminifera to temperature and nutrient stress. *Sci. Rep.* 6, 21936. <https://doi.org/10.1038/srep21936>.
- R Development Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Renema, W., 2006. Habitat variable determining the occurrence of large benthic foraminifera in the Berau area (East Kalimantan, Indonesia). *Coral Reefs* 25, 351–359. <https://doi.org/10.1007/s00338-006-0119-4>.
- Renema, W., 2008. Habitat selective factors influencing the distribution of larger benthic foraminiferal assemblages over the Kepulauan Seribu, Mar. Micropaleontol. 68, 286–298. <https://doi.org/10.1016/j.marmicro.2008.06.002>.
- Renema, W., 2010. Is increased calcarinid (foraminifera) abundance indicating a larger role for macro-algae in Indonesian Plio-Pleistocene coral reefs? *Coral Reefs* 29, 165–173. <https://doi.org/10.1007/s00338-009-0568-7>.
- Renema, W., 2018. Terrestrial influence as a key driver of spatial variability in large benthic foraminiferal assemblage composition in the Central Indo-Pacific. *Earth Sci. Rev.* 177, 514–544. <https://doi.org/10.1016/j.earscirev.2017.12.013>.
- Renema, W., Troelstra, S.R., 2001. Larger foraminifera distribution on a mesophotic carbonate shelf in SW Sulawesi (Indonesia). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 175, 125–146. <https://doi.org/10.1016/j.earscirev.2017.12.013>.
- Reymond, C.E., Roff, G., Chivas, A.R., Zhao, J.-x., Pandolfi, J.M., 2013. Millennium-scale records of benthic foraminiferal communities from the central Great Barrier Reef reveal spatial differences and temporal consistency. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 374, 52–61. <https://doi.org/10.1016/j.palaeo.2013.01.001>.
- Roche, R.C., Perry, C.T., Johnson, K.G., Sultana, K., Smithers, S.G., Thompson, A.A., 2011. Mid-Holocene coral community data as baselines for understanding contemporary reef ecological states. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299, 159–167. <https://doi.org/10.1016/j.palaeo.2010.10.043>.
- Roff, G., Clark, T.R., Reymond, C.E., Zhao, J.-x., Feng, Y., McCook, L.J., Done, T.J., Pandolfi, J.M., 2013. Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore Great Barrier Reef, following European settlement. *Proc. R. Soc. B* 280, 20122100. <https://doi.org/10.1098/rspb.2012.2100>.
- Ryan, E.J., Lewis, S.E., Smithers, S.G., Clark, T.R., Zhao, J.-x., 2016a. Multi-scale records of reef development and condition provide context for contemporary changes on inshore reefs. *Glob. Planet. Chang.* 146, 162–178. <https://doi.org/10.1016/j.gloplacha.2016.10.007>.
- Ryan, E.J., Smithers, S.G., Lewis, S.E., Clark, T.R., Zhao, J.-x., 2016b. Chronostratigraphy of Bramston Reef reveals a long-term record of fringing reef growth under muddy conditions in central Great Barrier Reef. *Palaeogeography, Palaeoclimatology, Palaeoecology* 441, 734–747. doi: <https://doi.org/10.1016/j.palaeo.2015.10.016>.
- Schaffelke, B., Carleton, J., Skuza, M., Zagorskis, I., Furnas, M.J., 2012. Water quality in the inshore Great Barrier Reef lagoon: implications for long-term monitoring and management. *Mar. Pollut. Bull.* 65, 249–260. <https://doi.org/10.1016/j.marpolbul.2011.10.031>.
- Schmidt, C., Morard, R., Almogi-Labin, A., Weinmann, A.E., Titelboim, D., Abramovich, S., Kucera, M., 2015. Recent invasion of the symbiont-bearing foraminifera *Pararotalia* into the Eastern Mediterranean facilitated by the ongoing warming trend. *PLoS One* 10, e0132917. <https://doi.org/10.1371/journal.pone.0132917>.
- Schmidt, C., Morard, R., Romero, O., Kucera, M., 2018. Diverse internal symbiont community in the endosymbiotic foraminifera *Pararotalia calcariformata*: implications for symbiont shuffling under thermal stress. *Front. Microbiol.* 9, 2018. <https://doi.org/10.3389/fmicb.2018.02018>.
- Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., Spezzaferri, S., Abramovich, S., Almogi-Labin, A., du Chatelet, E.A., Barras, C., Bergamin, L., Bicchì, E., Bouchet, V., Cearreta, A., Di Bella, L., Dijkstra, N., Disaro, S.T., Ferraro, L., Frontalini, F., Gennari, G., Golikova, E., Haynert, K., Hess, S., Husum, K., Martins, V., McGann, M., Oron, S., Romano, E., Sousa, S.M., Tsujimoto, A., 2012. The FOBIMO (Foraminiferal Bio-Monitoring) initiative – towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies. *Mar. Micropaleontol.* 94–95, 1–13. <https://doi.org/10.1016/j.marmicro.2012.06.001>.
- Schuetz, J.D., Frank, T.D., 2008. Reef foraminifera as bioindicators of coral reef health: Low Isles Reef, northern Great Barrier Reef, Australia. *J. Foraminif. Res.* 38, 11–22.
- Sen Gupta, B.K., 1999. Foraminifera in marginal marine environments. In: Sen Gupta, B.K. (Ed.), *Modern Foraminifera*. Kluwer Academic Publishers, UK, pp. 141–159.
- Sen Gupta, B.K., Turner, E.R., Rabalais, N.N., 1996. Seasonal oxygen depletion in continental-shelf waters of Louisiana: historical records of benthic foraminifera. *Geology* 24, 227–230. [https://doi.org/10.1130/0091-7613\(1996\)024<0227:SODICS>2.3.CO;2](https://doi.org/10.1130/0091-7613(1996)024<0227:SODICS>2.3.CO;2).
- Smithers, S.G., Larcombe, P., 2003. Late Holocene initiation and growth of a nearshore turbid-zone coral reef: Paluma Shoals, central Great Barrier Reef, Australia. *Coral Reefs* 22, 499–505. <https://doi.org/10.1007/s00338-003-0344-z>.
- Smithers, S.G., Hopley, D., Parnell, K.E., 2006. Fringing and nearshore coral reefs of the Great Barrier Reef: episodic Holocene development and future prospects. *J. Coast. Res.* 22, 175–187. <https://doi.org/10.2112/05A-0013.1>.
- Thompson, A., Schroeder, T., Brando, V.E., Schaffelke, B., 2014. Coral community responses to declining water quality: Whitsunday Islands, Great Barrier Reef, Australia. *Coral Reefs* 33, 923–938. <https://doi.org/10.1007/s00338-014-1201-y>.
- Uthicke, S., Nobes, K., 2008. Benthic foraminifera as ecological indicators for water quality on the Great Barrier Reef. *Estuar. Coast. Shelf Sci.* 78, 763–773. <https://doi.org/10.1016/j.ecss.2008.02.014>.
- Uthicke, S., Thompson, A., Schaffelke, B., 2010. Effectiveness of benthic foraminiferal and coral assemblages as water quality indicators on inshore reefs of the Great Barrier Reef, Australia. *Coral Reefs* 29, 209–225. <https://doi.org/10.1007/s00338-009-009-0>.

- 0574-9.
- Uthicke, S., Patel, F., Ditchburn, R., 2012. Elevated land runoff after European settlement perturbs persistent foraminiferal assemblages on the Great Barrier Reef. *Ecology* 93, 111–121. <https://doi.org/10.2307/23144026>.
- Woodroffe, S.A., 2009a. Testing models of mid to late Holocene sea-level change, North Queensland, Australia. *Quat. Sci. Rev.* 28, 2474–2488. <https://doi.org/10.1016/j.quascirev.2009.05.004>.
- Woodroffe, S.A., 2009b. Recognising subtidal foraminiferal assemblages: implications for quantitative sea-level reconstructions using a foraminifera-based transfer function. *J. Quat. Sci.* 24, 215–223. <https://doi.org/10.1002/jqs.1230>.
- Woodroffe, S.A., Horton, B.P., Larcombe, P., Whittaker, J.E., 2005. Intertidal mangrove foraminifera from the central Great Barrier Reef shelf, Australia: implications for sea-level reconstruction. *J. Foraminif. Res.* 35, 259–270. <https://doi.org/10.2113/35.3.259>.