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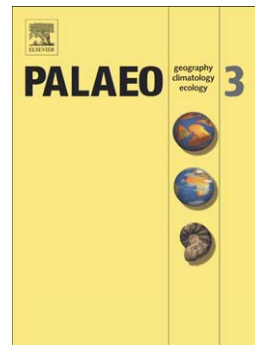
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**Holocene benthic foraminiferal assemblages indicate long-term marginality of reef habitats from Moreton Bay, Australia**

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**Abstract**

Since European settlement (ca. 1824 CE), the subtropical inshore reefs of Moreton Bay have undergone rapid deterioration in water quality from changes in land-use practices, resource exploitation and rapid population growth, spurring marine managers to assess the drivers of ecological shifts. However, the short temporal-scale of most studies is an inadequate baseline for understanding the severity and magnitude of biological response. We present millennial-scale records employing palaeoecological and quantitative multivariate techniques within a concise chronological framework to analyse benthic foraminiferal community structure of reefs in Moreton Bay, Queensland. Well-constrained, U/Th-dated, millennial-scale records from sediment cores were used to document the long-term response of foraminifers to natural environmental variability. The temporal and spatial distribution patterns of foraminifers reveal long-term marginality throughout the ~7400 years of Holocene history, prior to European settlement. While specific faunal response to the effects of relative ENSO-climate and sea level fall are difficult to disentangle, the earlier phases of reef development are already represented by marginal taxa indicating possibly an earlier response to a decline in conditions. Overall, long-term consistency in conditions favoured two types of low diversity reef assemblages: 1) high density of small, heterotrophic and opportunistic species and 2) low density of photosymbiotic foraminiferal assemblages. Comparison of foraminiferal community composition between the Holocene and the present day indicates overlap in species composition supporting long-term marginality, particularly in the Western Bay. Such combined palaeoecological and recent studies can benefit long-term initiatives for monitoring present and future water quality conditions in the Bay's reef habitats.

## 1. Introduction

Water quality in coral reefs is rapidly deteriorating from anthropogenic activities including land-use change, urban and agricultural run-off and eutrophication (Fabricius, 2005). Furthermore, the ability of ecosystems to cope with declining water quality may be undermined by predicted, unavoidable and unprecedented human-induced climate change (Beger et al., 2011; Fabricius, 2005; Gergis and Fowler, 2009; Gooday et al., 2009; Guinotte et al., 2003; Hughes et al., 2003; Pandolfi et al., 2003; Pandolfi et al., 2011). Several countries have enacted legislation including the Clean Water Act and the EU Water Framework Directive (WFD) and Australia's Great Barrier Reef Marine Park Authority (GBRMPA). These agencies promote strategies to: assess ecological status and implement continuous monitoring approaches to achieve 'good' water quality targets within set timeframes; make recommendations for best land-marine management practices, designate marine protected areas (MPAs) and return ecosystems to a pre-impact status (De'ath and Fabricius, 2008; EU-Water-Framework-Directive, 2009; Great-Barrier-Reef-Marine-Park-Authority, 2009). However, the combined effects of natural and anthropogenic stressors have far removed reef ecosystems from their historical baselines (Lotze et al., 2006). A long-term perspective is needed to better understand the ecological processes, which underpin ecological resistance and resilience in subtropical reefs (Beger et al., 2011). Contemporary global studies addressing ecological status are therefore enhanced when they go beyond short temporal scales to consider the age of the reef, its long-term ecological dynamics and the historical range in natural variability prior to significant anthropogenic impacts (Greenstein and Pandolfi, 2008; Lotze et al., 2006; Lybolt et al., 2011; Pandolfi et al., 2003; Roche et al., 2011; Roff et al., 2013; Tager et al., 2010).

Our detailed investigations of the palaeoecological changes in the reef sediments are based on analysis of benthic foraminifers. Their abundance and widespread preservation in marine sediments, short life cycles, high taxonomic diversity, easy collection methods and their sensitivity to environmental conditions, have allowed foraminifers to be commonly applied in palaeoecological and historical reconstructions (Cushman, 1928; Murray, 1991; Natland, 1933; Scott et al., 2005). Increasingly, foraminifers are gaining worldwide recognition as a promising tool: for establishing baseline conditions (Alve et al., 2009); in standard water quality monitoring (Bouchet et al., 2012; Reymond et al., 2012; Sabeau et al., 2009; Schönfeld et al., 2012); and in establishing ecological quality status (EcoQs) (Bouchet et al., 2012). Large benthic foraminifers (LBFs), prominent calcium carbonate sediment producers in tropical/subtropical reefs, live in symbiosis with algae (Hallock, 1981, 1999, 2000). They make excellent bio-indicators of coral reef health (Hallock, 2000) and have been used with the FORAM Index as a simple, cost-effective measure of changes in water quality in reefs (Hallock, 2000; Hallock et al., 2003; Narayan and Pandolfi, 2010; Reymond et al., 2012; Schueth and Frank, 2008; Uthicke and Nobes, 2008).

The dynamic subtropical reefs of Moreton Bay, Queensland, Australia (Figure 1) currently exist under high stress conditions that have brought about substantial ecological degradation (Pandolfi et al., 2003). Since European settlement (ca. 1824 CE), the Bay's catchments have undergone large-scale land use changes, intense logging and severe decline of estuarine vegetation leading to increased erosion of catchment sediments, while within the Bay overexploitation of marine resources has been extensive (e.g. corals for lime production and dugongs for oil), (Capelin et al., 1998; Duke et al., 2003; Neil, 1998). Today, the catchments support the fastest growing urban centre (Brisbane) in Australia. With rapid coastal development and increased

marine traffic, protection of Moreton Bay's critical habitats is more urgent than ever (Chilvers et al., 2005; Duke et al., 2003). Currently, marine management is hindered by a lack of historical information on the Bay's ecological response to natural variability.

We provide the first highly constrained, temporal framework to assess the spatial and temporal distribution patterns of foraminifers and their response to long-term environmental variability in three Holocene reefs located in Moreton Bay (Figure 1). We used foraminiferal fossils preserved within sediment cores taken through the reef structure to test the association between the ecological structure of communities and the timing and magnitude of two global/regional drivers: sea level and ENSO-climatic events. The key questions of interest are: (i) how spatio-temporally different were the benthic foraminiferal assemblages through the Holocene and what do assemblages reveal about mid-Holocene conditions (i.e. was the Bay as degraded during the Holocene as it is today?); and (ii) can we correlate local ecological changes in the foraminiferal assemblages with Holocene global-regional environmental drivers i.e. oscillations in sea level and ENSO.

## **2. Study location and background**

Moreton Bay is a large (1523 km<sup>2</sup>) wedge-shaped, wave-dominated, shallow water (average depth 6.8 m) semi-enclosed estuarine embayment with a large (21,200 km<sup>2</sup>) catchment area, located in South-East Queensland, Australia (27°S, 153°E; Figure 1). It is separated from oceanic waters of the Pacific Ocean to the East by sand-dune barrier islands (Figure 1) (Kelley and Baker, 1984). The mean tidal range is 1.48 m (spring) and 0.85 m (neap). The Pacific Ocean to the east is dominated by the East Australian Current (EAC), which allows tidal exchange of warm tropical waters into the Bay.

The reefs are considered marginal because they occur at high latitude ( $27^{\circ}$ ), in highly variable water temperatures ( $12.5 - 32^{\circ}\text{C}$ ) with low salinity (i.e. 2 to 9‰ during floods) high turbidity and frequent freshwater input (Guinotte et al., 2003; Lybolt et al., 2011; Neil, 1998). Thus, extant coral reef communities of Moreton Bay live in a naturally “stressed” ecosystem (Johnson and Neil, 1998; Lybolt et al., 2011; Neil, 1998).

The Bay’s ecological communities are closely linked to their geological development (Neil, 1998), which began following a Pleistocene ( $\sim 20$  cal ka yBP) postglacial sea level rise and became established when sea level stabilized during the mid-Holocene ( $\sim 7 - 9$  cal ka yBP), at approximately two metres higher than today (Figure 2) (Beaman et al., 1994; Chappell, 1983; Flood, 1984; Lewis et al., 2008; Lovell, 1975a; Sloss et al., 2007). At this time, the Bay was wider,  $\sim 10$  km westward from its present location, deeper, exposed to oceanic flushing, had higher wave energy and lower fluvial-derived catchment impact on water quality compared to today (Lybolt et al., 2011; Neil, 1998; Smith, 1973).

While natural ENSO variability through the mid-Holocene to today is currently debated, the common viewpoint is that optimum conditions prevailed during the mid-Holocene, when ENSO variability is considered to have been greatly reduced (Braconnet et al., 2011; Chiang et al., 2009; Cobb et al., 2013; Donders et al., 2008). Warm air and sea surface temperatures (SST  $\sim 2^{\circ}\text{C}$  higher than today), high rainfall of low intensity and low variability resulted in low, less variable run-off and presumably low turbidity conditions, which would have allowed for the proliferation of fast-growing, branching *Acropora*-coral dominated reefs (Cobb et al., 2013; Lybolt et al., 2011; Neil, 1998). The subsequent onset of the El Niño Southern Oscillation (ENSO) and its intensification (Figure 2), resulted in high frequency, variable rainfall, storm and

drought events, and increased run-off into the Bay (Donders et al., 2008; Lybolt et al., 2011). Furthermore, environmental conditions were exacerbated by gradually falling sea level by approximately two metres to present day levels, during the Late Holocene (Figure 2) (Lewis et al., 2008; Sloss et al., 2007). Naturally, we expected to find a faunal response to these environmental variations influencing the Bay.

Three reef sites were chosen along a west (near-riverine) to central (intermediate) to east (near-oceanic) water quality gradient (Narayan, 2011). Reefs were selected due to their distance away from dredge spoil dump sites; easy accessibility (i.e. outside of the protected 'Green Zone'); and well-studied (Fellegara, 2008; Flood, 1978; Johnson and Neil, 1998; Lovell, 1975b, 1989; Lybolt et al., 2011; Neil, 1998; Slack-Smith, 1959; Wallace et al., 2009; Wells, 1955).

The Wellington Point Reef occurs adjacent to and south of the Brisbane River Delta, where suspended fine sediments from the Brisbane River create a highly turbid environment (Figure 1). More stress tolerant species such as *Favia speciosa* are commonly occur here (Fellegara and Harrison, 2008; Wallace et al., 2009). The foreshores have undergone severe degradation due to land use practices over several decades and since they are easily accessible, they are prone to high human activity from recreational boating and fishing from the heavily utilized Manly Port. This area also receives high pedestrian traffic during low tide. Mid-Holocene, coral outcrops occur along the shoreline and fossil acroporoid coral rubble in the intertidal reef flat provides a suitable substratum for recruitment of coral larvae (Neil, 1998).

SW Peel Island, which was historically used as a leper colony, is the least accessible of the three reefs and can only be accessed by boat (Slack-Smith, 1959). Waters



surrounding the Island are relatively clean and sheltered compared to other western Bay reefs. The SW Peel Island Reef shows high coral richness, diversity and has a large *Favia*-coral dominated community (Fellegara and Harrison, 2008; Wallace et al., 2009). Re-suspension of fine sediments from the western rivers reaches the reefs during major flooding and records indicate that flooding from heavy rainfall has historically impacted coral communities at Peel Island (Slack-Smith, 1959).

The Myora Reef, adjacent to North Stradbroke Island (Figure 1) in the eastern Bay is exposed to oceanic conditions and has comparatively clear water quality (Harrison et al., 1998). Today, Myora Reef has the highest mean coral cover (65%) and supports an assemblage of branching *Acropora*-corals that do not occur elsewhere in the Bay (Fellegara and Harrison, 2008; Harrison et al., 1998).

### 3. Materials and Methods

#### 3.1. Field sampling

Herein we provide the detailed results of eleven age dated cores (Figure 1; Table S1), which were collected using the percussion technique, from 3 recent reef sites and 3 water depths (0, -2 and -4 m) (Dardeau et al., 2000; Lybolt et al., 2011; Roff, 2010; Roff et al., 2013). Reefs were accessed by walking onto the reef flat or by scuba and snorkel, using boats from the Moreton Bay Research Station (UQ), Dunwich, North Stradbroke Island.

Water depth measurements were taken from the top of each core (i.e. depth at which the cores were collected). Depth measurements were corrected for tides (at the time of depth collected) and are accurate to  $\pm 20$  cm. Depth measurements were corrected to the lowest astronomical tide (LAT) (Tables S1 and S2). The LAT inside Moreton Bay is

1.47 m below the mean sea level and the Australian Height Datum (AHD) (Lybolt, 2011). The palaeo-water depths used in this study were calculated using the corrected LAT (from the top of cores), corrected isotopic ages and published, regional sea level curves (Lewis et al., 2008; Sloss et al., 2007).

### *3.2. Laboratory preparation of reef cores*

Cores were cut lengthwise and one half of the cores were archived at the UQ Quaternary Core Facility at 4°C. The ‘working’ half was sliced into 5 cm sections and every second section (i.e. 0-5 cm, 10-15 cm etc.) was analysed. Sediment sections were wet sieved and/or freeze-dried, then dry-sieved through mesh sizes between: 4 mm (to isolate corals) to > 0.063 mm (to isolate foraminifers).

### *3.3. Age dating and palaeo-water depth calculations*

A concise chronological framework was established through isotopic age dating of fossil coral fragments contained within the reef core sections. The chronology was used to determine sediment accumulation rates and palaeo-water depths. The chronologies of the eleven reef cores were constrained by a total of 57 high-precision Uranium-Thorium (U/Th) dates, using either Thermal Ionization Mass Spectrometry (TIMS) or Multi-Collector Inductive-Coupled Plasma Mass Spectrometry (MC-ICPMS) at the Radiogenic Isotopic Facility, The University of Queensland (see online supplementary material for details). Ages were reported as the corrected  $^{230}\text{Th} \pm 2\sigma$  in years before present (before 2010) and are referred to in the paper as calendar years BCE/CE (before common era/common era). Samples were dated following analytical procedures described in the online supplementary material, Lybolt (2011) and other studies (Clark et al., 2012; Lybolt et al., 2011; Roff et al., 2013; Zhao et al., 2009). The U-series ages were calculated using the IsoplotEx v. 2.3 (Ludwig, 2003), decay constants reported by

Cheng et al., (2000) (Cheng et al., 2000) and corrections for the contribution from non-radiogenic (detrital)  $^{230}\text{Th}$  (Lybolt et al., 2011; Yu et al., 2006). Coral isotopic ages are reported here as the corrected  $^{230}\text{Th} \pm 2\sigma$  in years before present (before 2010) (Lybolt et al., 2011). The U/Th results are presented in Supplementary Table S2a.

In addition, 5 complementary AMS Radiocarbon (AMS  $^{14}\text{C}$ ) age dates were obtained from foraminiferal tests, using the AMS facilities at the Institute for Environmental Research, Australian Nuclear Science and Technology Organization (ANSTO in Sydney) (Fink et al., 2004; Stuvier and Polach, 1977) and results can be found in the online supplementary material (Table S2c).

#### *3.4. Sediment composition analysis*

Average grain size was measured using the Udden-Wentworth size classes between  $<4 \Phi$  ( $<0.063$  mm, silt/clay) to  $-4 \Phi$  (4 mm, granule) and analysed using a grain-size cumulative curve (Wentworth, 1922). Loss on ignition (LOI) technique was used to measure sediment composition including organic carbon (TOC), carbonate (TC) and non-carbonate content (Beaudoin, 2003; Heiri et al., 2001). The organic and carbonate content was measured after differential combustion for four hours, in ceramic crucibles, at  $550^\circ\text{C}$  and two hours at  $950^\circ\text{C}$ , respectively. Three replicate samples were measured for nearly all samples.

#### *3.5. Foraminiferal data analysis and taxonomy*

The asymptote on the species accumulation curve determined the minimum number of individual specimens to be collected from each (5 cm) sediment subsample (Figure S1) (Colwell et al., 2004). For this study, 200 benthic foraminifers (where available) were picked from each subsample (0.125 mm and greater) and identified to species level

using Loeblich and Tappan's classification and other regional taxonomies (Albani et al., 2001; Albani, 1974, 1978; Collins, 1958; Hayward et al., 1997; Lobegeier, 1995; Loeblich and Tappan, 1988, 1994; Michie, 1982; Narayan and Pandolfi, 2010; Palmieri, 1976; Riek, 1950; Yassini and Jones, 1995). Figured specimen of the common species discussed here can be found in Plate 1 of Narayan and Pandolfi (2010). A more detailed taxonomic catalogue of Moreton Bay species is currently in preparation.

We calculated the relative abundance (RA) and the frequency of occurrence (FO) of species. Shannon diversity ( $H' \log_2$ ) was calculated and values ranged between 1.5 and 3, reflecting low to high diversity, respectively (Shannon, 1948). We also calculated Margalef richness ( $d'$ ) (Magurran, 1988) and Pielou's evenness ( $J'$ ) (Pielou, 1966, 1979). Indices were calculated for each core subsample using PRIMER-E Version 6.0 software (Clark and Warwick, 2001).

To examine the variability in species composition among the three reef sites, foraminiferal relative abundance data was square-root transformed and the Bray-Curtis similarity index was applied (Bray and Curtis, 1957; Clarke, 1993). The biotic-environmental or BIO-ENV analysis was used to show the 'best' combination of the environmental variables (i.e., time and substrate type) with the highest correlation to the biotic (species composition) data. Differences in species composition among reefs were visualized using a two dimensional, non-metric multidimensional scaling (nMDS) ordination (Clarke and Green, 1988; Clarke et al., 2006). To examine the variation in species composition with reef site and substrate type, a one-way analysis of similarity (ANOSIM) was calculated.

Hierarchical cluster analysis with group average linkage was used to evaluate groupings of the samples and to differentiate foraminiferal assemblages within the reef cores. Similarity percentages (SIMPER) were calculated to determine which taxa contributed the most to the average similarity/dissimilarity at each reef. Statistical analyses were performed using PRIMER-E version 6.0 software (Clark and Warwick, 2001). A Students t-test was used to compare the means of the relative abundance of the different functional groups from the Holocene and recent times.

The FORAM Index (FI) was applied as a general measure of water quality and coral reef health (Hallock, 2000; Hallock et al., 2003; Schueth and Frank, 2008). It is used to compliment the community structure and diversity data. Functional groups (symbiont-bearing (s), opportunistic (o) and other heterotrophic (h) foraminifers) as defined by Hallock et al. (2003) were used to calculate FI:  $FI = (10 \times P_s) + (P_o) + (2 \times P_h)$ , where the proportion of individuals in each of the three functional groups (P) is determined by the total number of individuals in each functional group (N) divided by the total number of individuals in the sample (T):  $P_s = N_s / T$ ;  $P_o = N_o / T$ ; and  $P_h = N_h / T$ . FI values of  $> 4$  correspond to environments with good water quality, whereas values that fall between 2 and 4 indicate marginal conditions and  $< 2$  indicate that water quality is too inhospitable to support symbiont-bearing organisms (Hallock et al., 2003; Schueth and Frank, 2008).

## 4. Results

### 4.1. Reef age, estimated palaeo-water depths

The reef ages ranged between 0.3 to 7.4 cal ka yBP, respectively (Table S2a). Age reversals in two out of 57 (4%) dated sections fell within the range of uncertainty ( $\pm 2\sigma$ ) and were not considered as true reversals (Table S2a). The distribution of coral dates (from reef cores) fell within mostly the oldest three of the four episodes of reef

accretion found by Lybolt et al. 2011 (Lybolt et al., 2011), using coral death assemblage data. In this study, only one reliable date (Core W4b; Table S2a) occurs within Lybolt et al. 2011 (Lybolt et al., 2011) phase 4 and the majority fall within phases 1 to 3 (older than 3.6 cal ka yBP).

The calculated palaeo-water depths of the reef cores ranged between approximately -0.75 m to -7.75 m (Table S2b). Lybolt et al. (2011) found that the correlation between the corrected palaeo-water depth versus radiometric age was highly significant and the resulting coral age dates were negatively correlated with the corrected sea level curve (palaeo-water depth) of Sloss et al. (2007; Figure 6) and Lewis et al. (2008).

#### *4.2. Sediment composition*

A total of eleven sediment cores, 232 core sections and a total of 27.2 metres of unconsolidated Holocene sediments were analysed. Compaction ranged from 4 to 28% and recovery was close to 100% (Table S1). Six of the eleven cores penetrated through Holocene deposits and recovered approximately 0.5 metres of pre-Holocene terrestrial sediments, allowing for examination of reefs since the time of initiation.

Reef substrates were highly influenced by non-carbonate terrestrial sediments and were a mixture of carbonate and non-carbonate sediments (Smithers et al., 2006). Overall, reefal bioclasts were typically smaller than 4 mm, with the exception of a few larger coral clasts. The carbonate content doubled in the upper portion of the sediment cores due to post-depositional exposure to sub-aerial weathering. Seven different substrate types were distinguished based on sedimentology (grain-size, texture) and carbonate composition. These include: (1) medium to coarse grey carbonate shell hash and sand, poorly sorted; (2) medium to coarse brown silty-shelly carbonate sand, poorly sorted;

(3) fine to medium brown silty-shelly carbonate sand, poorly to moderately sorted; (4) fine to coarse reddish brown silty quartz sand with red laterite granules, poorly sorted with bits of shell, wood and few poorly preserved, reworked foraminifers; (5) fine to medium calcareous, foraminiferal-rich shell-hash and carbonate mud, moderate to well sorted; (6) very fine to fine dark grey/brown muddy, mixed silty quartz and carbonate sand; and (7) dark brown palaeosol (“coffee-rock”), very fine to medium silty quartz sand (with some charcoal or wood) with few reworked foraminifers. Substrates 1 and 2 occur at the top of cores, characterize intertidal depths, contain weathered bioclasts of large *Elphidium craticulatum* foraminifers. Substrates 4 and 7 occur at the base of cores and are predominantly siliciclastic terrestrial. They contain poorly preserved (reworked) foraminifers at the erosional contact between basal terrestrial and overlying marine sediments.

The Wellington Point Reef (WP) initiated on basal Tertiary sandstones and Mesozoic basalts (Hekel et al., 1976) during the mid-Holocene (~7.2 cal ka yBP) (Figures 3b and S2a-b). Local sea level drop resulted in erosion and surface exposure of mid-Holocene reefal deposits and underlying (Pleistocene) laterites (Hekel et al., 1976; Palmieri, 1976). (Smithers et al., 2006) Reef substrates ranged from fine-grained calcareous carbonate muds, to fine to medium-grained silty sands and bioclastic material (Figure 3b). The average percent organic carbon content was low, varying between 4 to 10% (Figure 3b). The average carbonate content varied from 3 to 40% and was generally higher (Figure 3b) in the topmost sections of the cores likely due to post-depositional exposure to sub-aerial weathering. The average non-carbonate (siliciclastic) content ranged between 60 to 95% (Figure 3b)

The South-West Peel Island (PI) and Myora (MR) reefs initiated atop of dark-coloured palaeosols from the mid-Holocene (~7.4 cal ka yBP) and late Holocene (~4.5 cal ka yBP), respectively (Figures 3a,c and S2c-f). Substrates ranged from fine-grained calcareous muds, to fine to medium-grained silty sands and bioclastics. The average percent organic carbon content was low, varying between 1 to 12% (Figures 3 and S2). The average carbonate content varied from 1 to 40%. The average non-carbonate content ranged between 60 to 100% with the highest values (>80%) occurring at Myora Reef.

#### 4.3. Taxonomic composition, diversity indices and test preservation

Eighty-five foraminiferal species within 42 genera of the Miliolida and Rotalida orders were identified. Species with the highest frequency of occurrence (FO) are presented in Table 1. The overall Shannon diversity ( $H'_{\log^2}$ ), Margalef richness (d) and Pielou's evenness ( $J'$ ) values were lowest for the WP reefs and highest for the SW Peel Island and Myora reefs (Table 2 and S3; Figure 3).

Preservation of foraminiferal tests ranged from excellent to poor. Loss of taphonomic information occurred mainly by mechanical processes such as abrasion and fragmentation. Fragmentation of the outer test periphery was common in large *Elphidium craticulatum*.

#### 4.4. Community structure

We observed significant differences in overall foraminiferal community structure (one-way ANOSIM  $R = 0.46$ ,  $p = 0.001$ ) among the three reef sites (Table 3), with all pairwise tests showing significant differences (Table 3). The nMDS plot shows partial overlap in the Holocene assemblages from the different reef sites (Figure 4a). However,



assemblages from Wellington Point Reef show greater separation from Myora Reef than either do from the Peel Island assemblages. The influence of two factors, time and substrate, on foraminiferal community composition were assessed using BIO-ENV and the best association occurred between species composition and substrate types at all reefs (ANOSIM  $R = 0.5$ ;  $p = 0.001$ ; Table 5). No strong association between time and species composition was indicated.

The species commonly contributing to similarity within the Holocene reefs (Table 4a) and to (pair-wise) dissimilarity between reefs (Table 4b) include *Elphidium hispidulum*, *Spiroloculina communis* and *Elphidium craticulatum*. We used the RA and hierarchical cluster analysis with group average linkage ( $> 60$  similarity) to differentiate the foraminiferal assemblages (Table 1) and SIMPER (Table 4a and 4b) was used to identify taxa that played a dominant role in the Holocene community composition. Four distinct assemblages were distinguished: Assemblage A (mixed opportunistic-heterotrophic) dominated by *Elphidium hispidulum*; Assemblage B (heterotrophic) dominated by *Quinqueloculina spp.*; Assemblage C (mixed symbiont-bearing and heterotrophic) dominated by *Peneroplis spp.*; and intertidal Assemblage D (mixed heterotrophic-opportunistic) dominated by *Elphidium craticulatum*, and common *Ammonia sp. cf. A. aoteana*.

A combined analysis of the Holocene core assemblages and recent (25 samples) foraminiferal assemblages surveyed by Narayan & Pandolfi (2010) shows some overlap between the present day western Bay reefs and the Holocene, particularly with the Wellington Point site (one-way ANOSIM  $R = 0.29$ ,  $p = 0.02$ ). A cluster of points that shows clear separation from the Holocene and from other recent reef assemblages

includes recent eastern Bay seagrass lagoonal-reef flats, which includes a higher relative abundance of symbiont-bearing taxa (Figure 4b).

#### 4.5. FORAM Index (FI) values

The overall FORAM Index (FI) values for all samples ranged between ~1.0 to 5.7 (Table S3). The FI values for Wellington Point Reef fell into the poor (FI <2) to marginal (2 < FI < 4) categories. The FI values for the southwest Peel Island Reef and Myora Reef ranged from poor (FI <2) to optimal (FI >4). Diversity indices and FORAM index values show a significant but weak correlation with time ( $R^2 = 0.2$ ,  $p = 0.0026$ , with removal of outlier FI = 5.6 in the first phase of reef growth, Phase 1 in Figure 5). A relationship between FI and palaeo-water depth cannot be inferred from this study, without greater sampling of different water depths.

Differences in the relative abundance of the three functional groups (Figure 6) indicate that heterotrophic taxa dominated (~60%) the benthic assemblage during the Holocene, followed by opportunistic (~20-30%) and few symbiont-bearing taxa (~5-10%). The recent assemblage is dominated by opportunistic taxa (~50%) and in contrast, the symbiont-bearing taxa dominated by *Peneroplis* spp. are relatively higher today, especially in eastern Moreton Bay (~15-20%). We found that *Amphistegina*, an important FI indicator of optimal conditions, was not a significant component of the reef cores sediments. Their absence and the dominance of *Peneroplis* spp. is indicative of variable water quality (Nobes and Ulthicke, 2008).

## 5. Discussion

### 5.1. Spatial and temporal patterns in foraminiferal composition among the reefs

The Holocene reefs of western Moreton Bay have been described in previous studies as being markedly different from today, with reef habitats composed of fast-growing *Acropora*-corals and a “rich” assemblage of photosymbionts (Lybolt et al., 2011; Neil, 1998; Palmieri, 1976, 1979). Our chronological study begins ~7.4 cal ka yBP during the mid-Holocene climatic optimum (Donders et al., 2008; Lybolt et al., 2011; Neil, 1998). We expected to see a response by foraminifers to ENSO-deterioration in climate, instead we find that conditions were predominantly and consistently marginal for photosymbiont activity for most of the Holocene timeframe investigated by this study. Below, we discuss spatial and temporal patterns in foraminiferal species composition within the three phases of reef development established by Lybolt et al. (2011).

#### 5.2.1. Phase 1(a): Established reefs and incipient marginality

We record the lowest diversity ( $H'$ ), richness ( $d$ ) and evenness ( $J'$ ) values during the first phase of reef development starting at approximately 7.4 cal ka yBP (Table 2). At the onset of this phase of subtropical reef development, (four) different foraminiferal assemblages are present in the Wellington Point (W) and SW Peel Island reefs (P) and initially signal overall poor to marginal conditions in water quality in the intertidal nearshore (< 2 m) to shallow-subtidal reef habitats (< 5 m).

Phase 1(a) occurs between ~6.8 to 7.4 cal ka yBP at SW Peel Island, where we record a low diversity, opportunistic *Elphidium hispidulum* Assemblage A associated with continuous deposition of fine-grained carbonate muds (Figure 3a). Also during Phase 1, we record a change from carbonate muds to poorly-sorted, medium-coarse grained, shelly carbonate sand deposition (Figure 3a), associated with a change to subtidal Assemblage B (Table 6). This biofacies is characterized by an increase in small,

heterotrophic taxa (*Quinqueloculina* spp., *Miliolinella* spp. and *Triloculina* spp.) indicative of high-energy, normal marine conditions at SW Peel Island (Palmieri, 1976). The change in the biofacies suggests shoaling after 7.3 cal ka yBP, however, sea level remains relatively stable (Sloss et al., 2007) and there is no direct evidence for an increase in siltation during this time for SW Peel Island to strongly implicate the effects of a sea level fall.

At Wellington Point, we record the low diversity, low density, *Elphidium craticulatum* Assemblage (D) during Phase 1. It is associated with a clean, poorly sorted substrate composed of medium to coarse grained carbonate sands and few foraminifers, suggestive of nearshore-intertidal conditions (Lidz and Rose, 1989; Narayan and Pandolfi, 2010; Palmieri, 1976; Reymond et al., 2012) (Figure S2a). The large (up to 4 mm diameter) *E. craticulatum* is a mixotrophic, chloroplast-retaining species tolerant of variability in nutrients, hypo-salinity, high turbidity, low oxygen, low water energy and reduced water circulation (Lopez, 1979; Narayan and Pandolfi, 2010; Palmieri, 1976; Renema, 2008). Holocene Assemblage D resembles the assemblage seen today in the Wellington Point reefs where opportunistic *E. craticulatum* and *Ammonia* spp. are the most abundant components (Narayan and Pandolfi, 2010; Palmieri, 1976).

Assemblages A and D reflect low FI values for Phase 1 and poor to marginal conditions inhospitable for photosymbiont activity (Figure 5) (Hallock et al., 2003). The exception occurs between ~ 7.0 and 7.1 cal ka yBP, when an episodic change to high FI values occurs (Figure 5). This increase is represented by six samples, including a single dated (FI = 5.6 at 7.1 cal ka yBP) and five undated sections with high FI values > 4 (Table S3). The FI values that accompany photosymbiont-bearing *Peneroplis* spp. Assemblage C suggests a short, episodic change (possible improvement) in water quality conditions

(Reymond et al., 2012; Schueth and Frank, 2008). No data is available to interpret conditions in Myora Reef during Phase 1 (Table 6).

### 5.2.2. Phase 2(a): Continuous reef deposition and sub-optimal conditions

The second phase of reef development occurs between 3.3 and 4.9 cal ka yBP. Phase 2(a) is distinguished by continuous deposition of reef-lagoonal carbonate sediments as seen in Wellington Point (Core W2b; Figure 3b) and in Myora Reef (Core M0c; Figure S2e). A thick (250 cm) sequence of fine-grained, foraminiferal-rich, carbonate muds is associated with shallow-subtidal depths, and an increase in species diversity ( $H'_{\log 2} = 2.1 - 4.4$ ) and richness from Phase 1 ( $H'_{\log 2} = 1.9 - 3.7$ ) (Table 2). Despite the increase in diversity, The FORAM index values are initially low (in Wellington Point) and overall marginal (in Peel Island and Myora Reef), due to the influence of mainly small heterotrophic and opportunistic taxa (Figure 5).

### 5.2.3. Phase 3: Water quality gradient and spatial-temporal consistency in Myora Reef

Phase 3 ranges from 0.3 to 1.7 cal ka yBP and follows a rapid episode of reef “turn-off” between approximately 1.7 to 3.3 cal ka yBP (Table 6) (Lybolt et al., 2011; Lybolt, 2011). Turbidity increases and inundates, especially the western Bay reefs, with coarse silty-sand sediments, which likely implicates the combined effects of both sea level fall and/or possibly ENSO-climatic variability during this phase. During Phase 3 we see a strong western-riverine to eastern-near oceanic gradient, similar to the present-day gradient (Narayan and Pandolfi, 2010), become established. At Wellington Point, opportunistic assemblages D and A dominate (similar to today) and the photosymbiont-bearing Assemblage C, seen during Phase 2, disappears. At SW Peel Island, we record an increase in photosymbiotic foraminifers in subtidal depths. Lastly, at Myora Reef we find spatial and temporal consistency in the symbiont Assemblage C.

### 5.3. *Disentangling Holocene drivers: sea level and ENSO-climate*

We detected a response by foraminiferal species composition to spatial differences in water quality among the reefs through the Holocene, which appear to be consistent with a West to East gradient, operating similar to the present day (Narayan and Pandolfi, 2010). The initial onset of poor to marginal water quality conditions and the lowest taxonomic diversity of foraminifers recorded by this study, is already apparent during Phase 1 and early in Phase 2.

While it is difficult to disentangle the cause of declining water quality from a specific regional driver: ENSO-climatic activities can be implicated over sea level fall (Figure 2). There are divergent views regarding the Holocene evolution of ENSO, with the common view that ENSO variability was greatly reduced during the early to mid-Holocene (Braconnet et al., 2011; Chiang et al., 2009; Cobb et al., 2013; Donders et al., 2007).

Palynological findings indicate a step-wise change in the climate regime, which coincides with the timing of reef degradation (Figure 2) (Donders et al., 2007). The mid-Holocene subtropical terrestrial habitats of SE Queensland shifted from a humid, rainforest-dominated ecosystems with high lake levels and low fire frequency to an arid, open environment with drought resistant vegetation, decreased lake levels and increased fire frequency around 5 cal ka yBP (Donders et al., 2007; Donders et al., 2008; Harrison, 1993). A second phase of climatic deterioration and increased aridity followed intensification of ENSO after 3 cal ka yBP (~1000 BCE) and coincides approximately with reef 'gap' 2 (Phase 2b) following Phase 2(a) (Figure 2) (Donders et al., 2007).

Recent findings by Cobb et al. (2013) indicate that the variance of ENSO through the mid- to late Holocene (7 ka to AD 1500) was consistently reduced compared to today and that ENSO variability from the mid-Holocene is statistically indistinguishable from that of the past millennium (Cobb et al., 2013). The findings from this study support the existence of low variance foraminiferal populations and incipient marginality of the reef habitats since 7.4 cal k yBP.

Due to the Bay's semi-enclosed physiography and shallow bathymetry, the drop in sea level of up to two metres that occurred over the past ~7500 years would have negatively affected ecological communities through altered water circulation, increased input of eroded sediments, and increased turbidity in reef habitats (Neil, 1998). Lybolt et al. (2011) record an ~4 m change in the depth distribution of Moreton Bay's coral communities during the Holocene, which currently exceeds the known magnitude of regional sea level fall by a factor of two (Leonard et al., 2013; Lybolt et al., 2011). Therefore, a magnified response by Moreton Bay's foraminiferal assemblages is also predicted.

A sea level high-stand lasted after 2 cal ka yBP (~200 CE) (Sloss et al., 2007). We were unable to distinguish any relationship in species composition patterns to oscillations in sea level. However, the intermingled effects of sea level fall by +/-2.0 m and the intensification of ENSO are both likely implicated for the decline in water quality, increase in terrestrial sediments and variations (mixing) of the biofacies associated with shallowing of the reefs. This is particularly evident in the nearshore Wellington Point Reef, where erosion of lagoonal-reefal sediments and replacement by an intertidal biofacies is indicated during Phase 3 (Figure S2b). Overall, we find a rapid

transition from deposition of very fine-grained muddy carbonate sands (with few shells) to coarse-grained, poorly sorted silty-sand (coarsening upwards), with decreasing age and palaeo-water depth. However, we find that the timing of shallowing occurred much later than 2 cal ka BP (Sloss et al., 2007).

Therefore, the hypothesis that the local ecological changes in reef development are temporally correlated with global and regional drivers of ENSO climate and sea level fall needs to be further tested rigorously, using environmental and geochemical proxy data, over an adequate time-series, and including data from different Eastern Australian reefs.

#### *5.4. Assessing the past, present and future of Moreton Bay's reefs: the importance of symbiont-bearing large benthic foraminifers (LBFs)*

Moreton Bay's Holocene foraminiferal assemblages indicate long-term marginality of reef habitats, well before European settlement and anthropogenic impacts. Our results compliment previous palynological studies and indicate that ENSO activity was the initial driver of declining reef conditions (Phase 1 and 2). Overall, the Wellington Point assemblages indicate poor conditions throughout the Holocene, which are not unlike today. The eastern Bay assemblages indicate marginal to optimal conditions at SW Peel Island and optimal conditions in the Myora Reef. Optimal marine conditions better suited for symbiont-bearing (e.g. assemblage C) showed the greatest consistency during Phase 3 in Myora Reef.

High diversity, high density large benthic foraminiferal (LBF) communities are typical of tropical, carbonate reefs and live under similar conditions to zooxanthellate corals (Renema, 2002). Several interrelated variables including depth, temperature, salinity,



hydrodynamic energy, nutrients, siltation, light intensity and seasonality are important in structuring LBF communities (Cleary and Renema, 2007; Hohenegger et al., 1999; Renema and Trolestra, 2001). An increase in their abundance generally indicates low nutrients and good water quality conditions that are conducive to reef growth (Hallock, 2000; Hallock et al., 2003; Reymond et al., 2012).

Past studies of Holocene age deposits dredged from Mud Island (Allingham and Neil, 1995) and from within the inter-reef channels between other coral islands (Palmieri, 1976; Riek, 1950) all within the western-central Bay and north of Wellington Point (Figure 1), attest to past occurrence of prolific “rich” deposits of large, photosymbiotic foraminifers including fossil *Amphistegina* spp., *Alveolinella quoyi*, *Heterostegina depressa*, *Operculina ammonoides*, *Peneroplis* spp., and *Sorites marginalis*. Such an assemblage would have made the Holocene reefs appear markedly different from today and we expected to encounter this assemblage in our reef cores from Wellington Point. However, we did not encounter such “rich” deposits dominated by symbiont-bearing taxa in any of our reef cores. Instead we encounter low diversity, high density, small, heterotrophic (e.g. *Spiroloculina* spp., *Quinqueloculina* spp. and *Triloculina* spp.); mixotrophic-opportunistic (e.g. *Elphidium craticulatum* and *Elphidium hispidulum*); and low diversity, low density symbiont-bearing (e.g. predominantly *Peneroplis* spp.) species. The recent western Bay reefs are dominated by similar assemblages, which are tolerant of stressful conditions, such as episodic high turbidity, high nutrient, low oxygen and variable salinity (Narayan and Pandolfi, 2010; Palmieri, 1976).

So what became of the “rich” foraminiferal community dominated by LBFs? Fossil LBFs (*Amphistegina* spp., *Alveolinella quoyii*, *Heterostegina depressa*, and *Operculina ammonoides*) were in very low abundance and only found near the base of the cores at

Myora Reef. Taphonomic signals of test discolouration by iron-oxide staining (Palmieri, 1976) suggest weathering and erosion (Yordanova and Hohenegger, 2002) from possibly older (than 7.4 cal ka yBP ) Holocene age deposits than what we encountered in Phase 1. Therefore, one possibility for the low abundance/absence of LBFs is that they were associated with older Holocene deposits than what we encountered in our reef cores in this study. Possible future high-precision dating of the “rich” reef deposits surrounding Mud Island may help to constrain the timeframe within which photosymbionts dominated in the western Bay reefs and to establish a true baseline for reefal conditions.

Secondly, amphisteginids, alveolinids, house diatom endosymbionts, whereas peneroplids house rhodophytic algae (Cleary and Renema, 2007). Differences in the symbionts use of the light spectrum (longer wave-lengths of rhodophytes vs. shorter wave-length of diatoms) results in differences in the LBFs depth distribution. The amphisteginids and alveolinids occur in deeper waters than peneroplids, to avoid extreme light intensity (Cleary and Renema, 2007; Renema and Trolestra, 2001). Today, extant LBFs are uncommon in the western Bay reefs (Narayan and Pandolfi, 2010; Palmieri, 1976) but have been encountered in the tidal flats at water depths greater than 10 m in the eastern Bay (e.g. off south-western Moreton Island) and from reef slopes adjacent to Peel Island (Narayan and Pandolfi, 2010).

Low diversity, low density photosymbiotic assemblages are not atypical of marginal reefs and reefs influenced by ENSO climatic patterns (Kelmo and Hallock, 2013). Our Holocene symbiont-bearing assemblages were dominated by *Peneroplis* spp., which are tolerant of a broad range of light intensity from extreme (80-100% surface irradiance) to weak (5-15% surface irradiance) (Hohenegger et al., 1999). *Peneroplis* spp. are also

reliable indicators of optimal conditions in the recent reefs of Moreton Bay and in the GBR (Narayan and Pandolfi, 2010; Reymond et al., 2012). In recent samples from Wellington Point, *Peneroplis* spp. are found only rarely (~2%) on the reef flats and often as epiphytes on seagrass. Previous studies report their occurrence from channels between Green and St. Helena islands (Figure 1) and along the reef slopes east of Green Island (Narayan and Pandolfi, 2010; Palmieri, 1976).

### 5.5. Recent coral community shifts

Corals, taxa that also possess photosymbionts, clearly show spatial and temporal distribution patterns that suggest a gradual shift from intertidal reef flats into subsequently deeper reef slope environments during the Holocene (Lybolt et al., 2011). Fast-growing *Acropora* corals dominated in the Holocene reefs, including Wellington Point Reef (Johnson and Neil, 1998; Lybolt et al., 2011; Wells, 1955). In contrast, slow-growing, massive favid-corals dominate the Bay's reefs today (Johnson and Neil, 1998; Lybolt et al., 2011). The recent corals exist under high turbidity conditions due to siltation from rivers and organic-rich mangrove muds and increased sediment input following storm events (Flood, 1978; Neil, 1998). At Myora Reef, water quality is high due to reduced siltation, deeper water depths, higher water energy and greater oceanic circulation compared to the other western Bay reefs (Johnson and Neil, 1998; Lybolt et al., 2011; Neil, 1998) (Lybolt et al., 2011; Neil, 1998; Wells, 1955). The highest mean coral cover and a colony of branching *Acropora*-corals has been reported here and is unknown elsewhere in the Bay (Fellegara and Harrison, 2008; Harrison et al., 1998).

Lybolt et al. (2011) argue that the unprecedented shift from the Holocene branching *Acropora*-dominated to the massive-favid-dominated subtidal communities occurred relatively recently and was anthropogenically-driven by increased land-clearing and

subsequent sediment input into the Bay, following European settlement of 1842 CE (Capelin et al., 1998; Lybolt et al., 2011). Similarly, Roff et al. (2013) find a recent collapse of *Acropora* in the inshore Pelorus Reef on the Great Barrier Reef as a result of chronic increases in sediment flux and nutrient loading following European settlement in the region (1870 CE). Both studies support remarkable long-term resilience to marginality and ephemeral conditions by the *Acropora*-coral community structure in inshore reefs, over millennial and centennial time-scales, respectively (Lybolt et al. 2011; Roff et al. 2013).

We find a disparity between the foraminiferal assemblages and the FI with the Holocene *Acropora*-dominated coral communities. The Holocene foraminiferal record suggests an earlier sensitivity to deteriorating conditions and declining water quality than the *Acropora*-corals, particularly in western Moreton Bay. It is the opportunistic and heterotrophic foraminiferal assemblages, and not the photosymbiotic assemblages that are best associated with the Holocene *Acropora* community in the western Wellington Point Reef (Phase 1). If photosymbiotic foraminiferal communities once dominated in the reefs of (western) Moreton Bay, they did so prior to the timeframe investigated by this study, which was instead dominated by heterotrophic taxa. Their absence in the reef cores suggests an earlier response to the onset of marginal conditions or ecosystem degradation than the *Acropora*-coral community.

## 6. Conclusions

Within the timeframe investigated, Holocene spatio-temporal differences in foraminiferal species composition overlap with recent differences among the reefs and suggest an overall persistent west (riverine-influenced) to east (oceanic-influenced) gradient in water quality. This gradient may have strengthened after the second phase

of reef growth. The species composition in the recent reefs, which is dominated by opportunistic taxa, suggests marginal to poor water quality conditions (Narayan and Pandolfi, 2010; Palmieri, 1976).

The natural drivers influencing the evolution of Moreton Bay are difficult to disentangle throughout the Holocene. The timing of the changes in the foraminiferal community structure suggests that there is temporal correlation with existing palynological studies to implicate the onset of ENSO climatic events, which lead to community change prior to Phase 1 and, which likely resulted in the decline (i.e. *Peneroplis* spp.) and/or dramatic disappearance of the large benthic foraminifers (LBFs) from the western Bay reefs. Future studies that aim to correlate palaeoecological, palaeoclimate and geochemical time-series data, over the time frame represented by this study, can contribute towards an improved correlation between regional events and local changes in reef development.

The FORAM Index (FI) was originally used in the Caribbean as a rapid and cost-effective approach to assess water quality, which supports reef growth. The disparity between the Holocene foraminiferal assemblages, the FI and the *Acropora*-dominated coral communities requires further testing of the FI in marginal reefs. Herein, the spatio-temporal consistency in the foraminiferal assemblages (mainly heterotrophic taxa) and low FI values ( $2 < FI < 4$ ) overwhelmingly indicate that marginal conditions were maintained throughout the Holocene timeframe of this study. Increases in the relative abundance of photosymbionts, mainly *Peneroplis* spp., consistently correlated with high FI values to suggest that optimal water quality conditions were ephemeral throughout the Holocene. Optimal conditions better suited for photosymbionts showed greatest consistency during Phase 3 in the Myora Reef and in the Recent, in the eastern Bay.

Poor water quality conditions recorded by this study were already present during Phase 1 (and early in Phase 2) of reef development. Future application of the FI will benefit from calibration of taxa with natural environmental conditions, typical of marginal reefs. The FI can be used as a general tool, complimentary to palaeoecological community structure and diversity data where detailed investigations of recent environmental conditions have been established.

Photosymbionts are important water quality indicators. However, they were not a major component in the Holocene reefs for the time-frame investigated by this study.

Photosymbionts are extremely sensitive to changes in the environment and may have responded earlier to deterioration in water quality than the *Acropora* corals. More specifically, we find that the photosymbiotic assemblage (dominated by *Peneroplis* spp.) occurred sporadically with slightly higher densities in the eastern Bay reefs, had their greatest abundance during Phase 3 in Myora Reef, and generally displayed a positive correlation with FI values to indicate an improvement in conditions to favour photosymbiont growth. Also, an improvement in conditions from the past cannot be hypothesized unless a clear baseline (prior to 7.4 cal ka yBP) of environmental conditions including Holocene ENSO-climatic variance for Moreton Bay is established.

Moreton Bay's reef communities have experienced long-term marginality in water quality from natural variations, prior to European settlement. This study contributes towards an understanding of the history of ecological conditions in Moreton Bay's reef habitats prior to the significant localized anthropogenic impacts that followed European settlement. Long-term studies that incorporate palaeoecological and recent datasets are useful tools, which can help scientists and marine resource managers better address the

potential repercussions that future predicted human-induced climate and sea level change will have on coastal habitats and their ecological communities.

#### **Appendix A. Supplementary data**

Supplementary data (Tables S1 to S3; Figures S1 to S2) for this article can be found online.

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Figure 1.

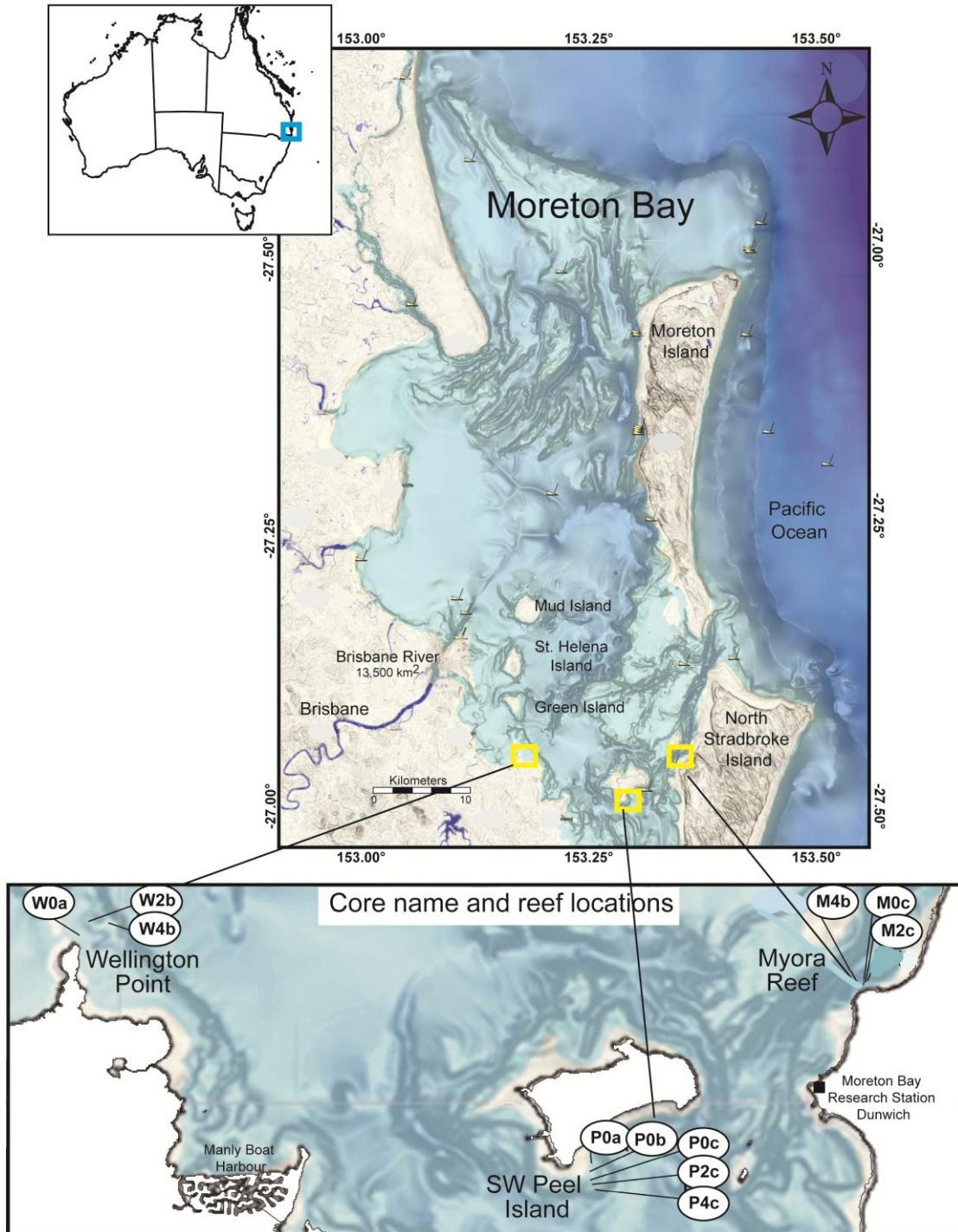
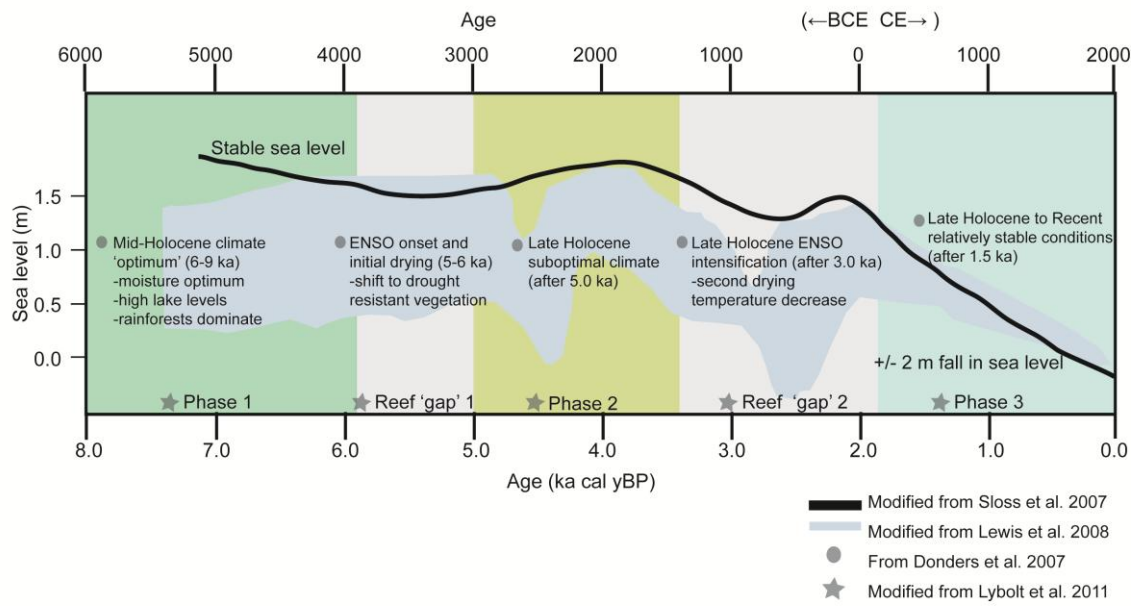


Figure 2



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Figure 3 (a-b)

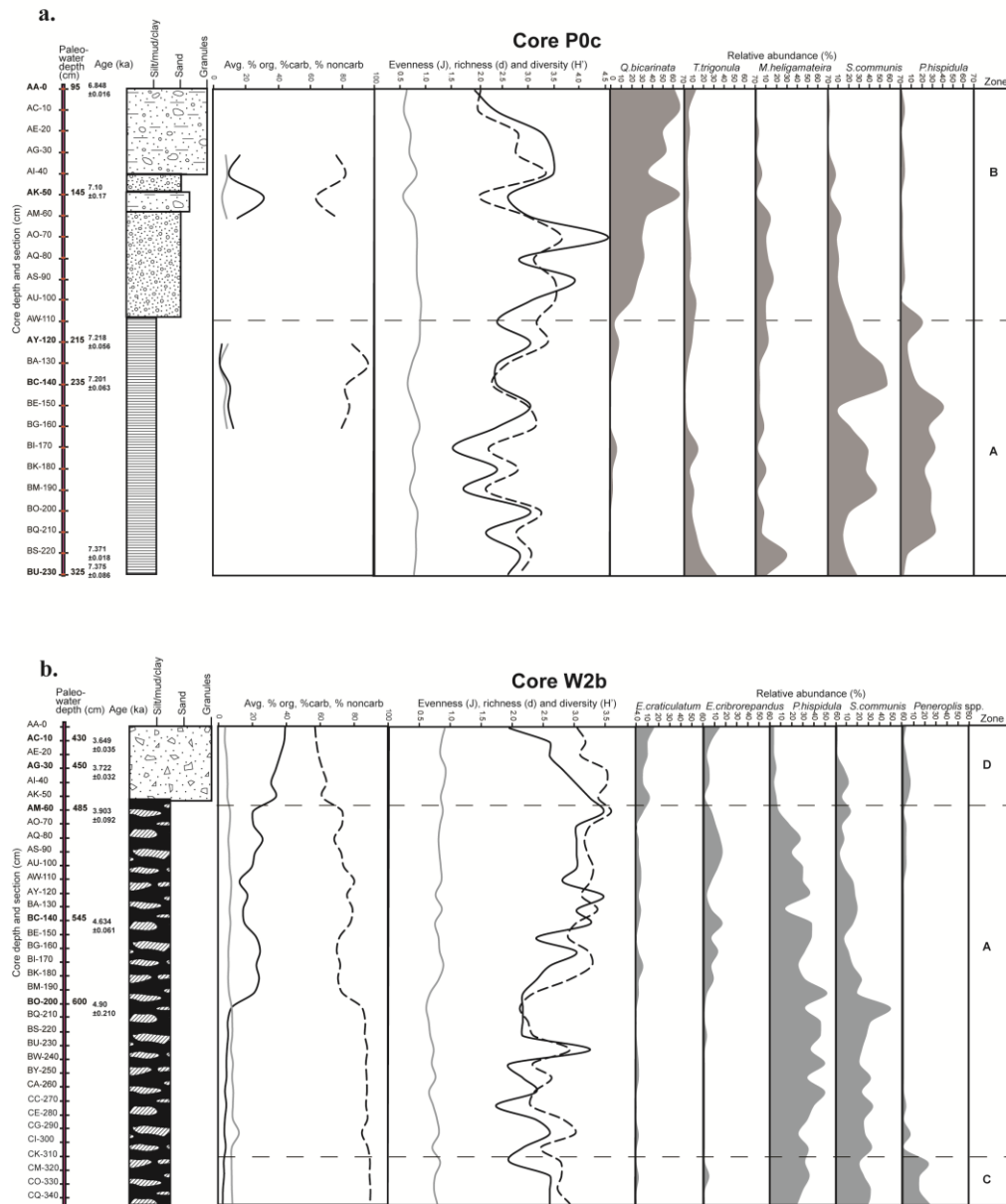


Figure 3 (c)

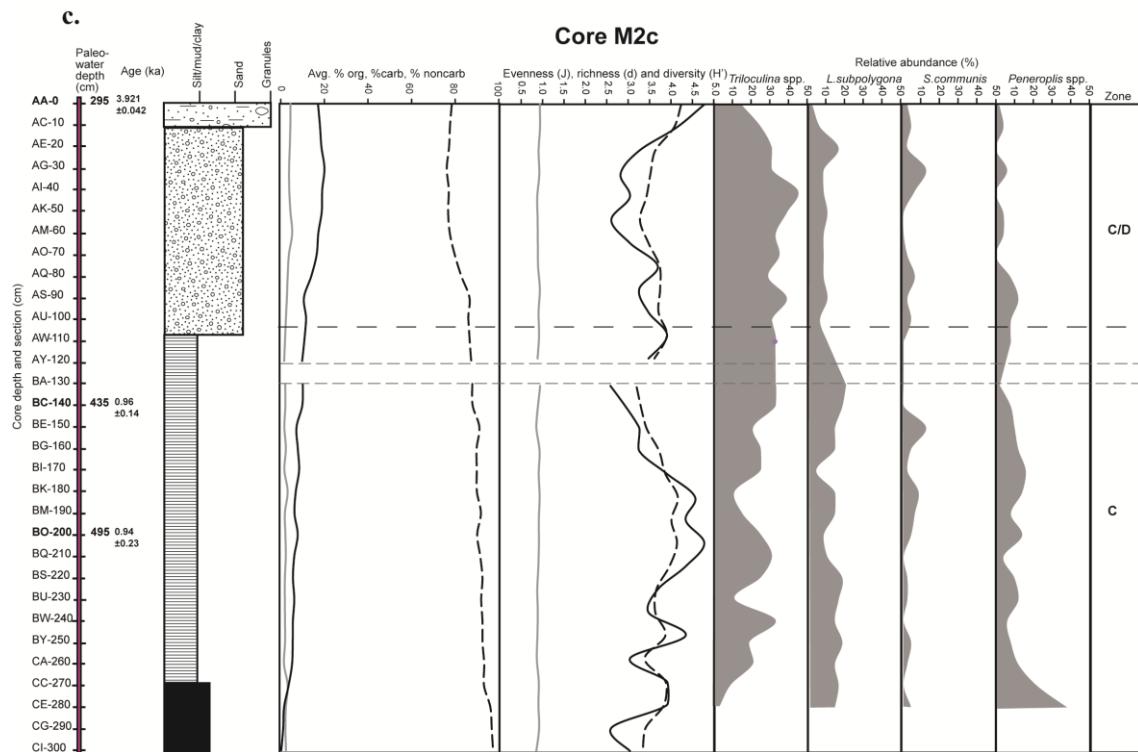
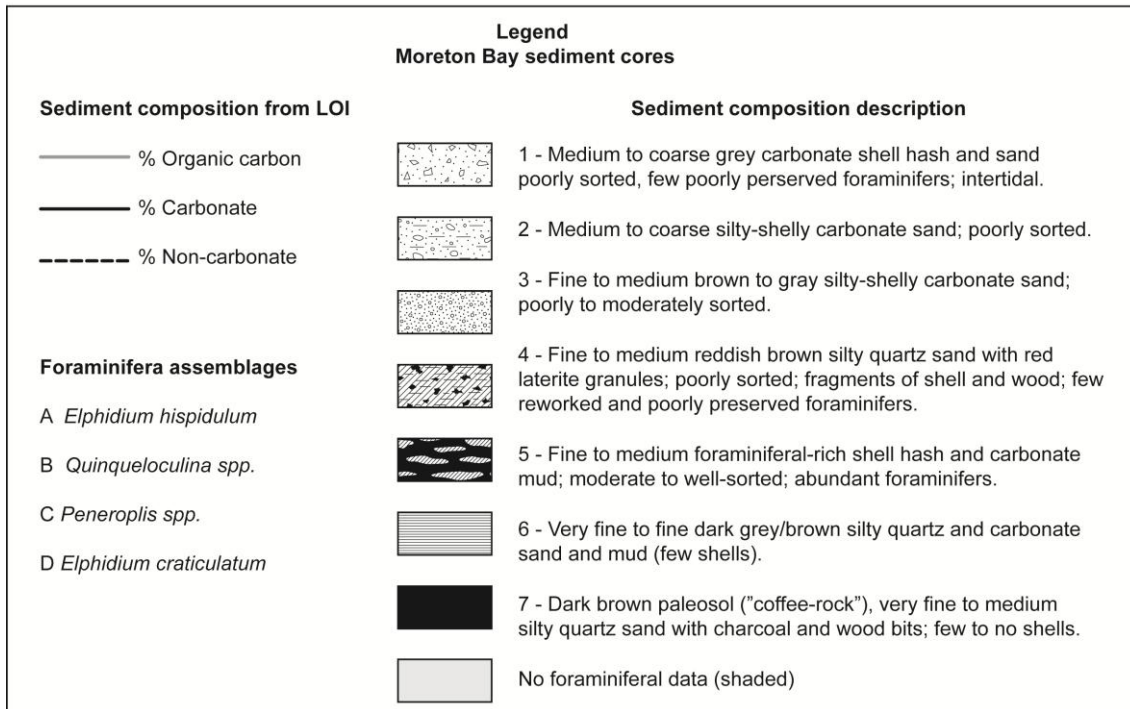


Figure 3 Legend



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Figure 4 (a and b)

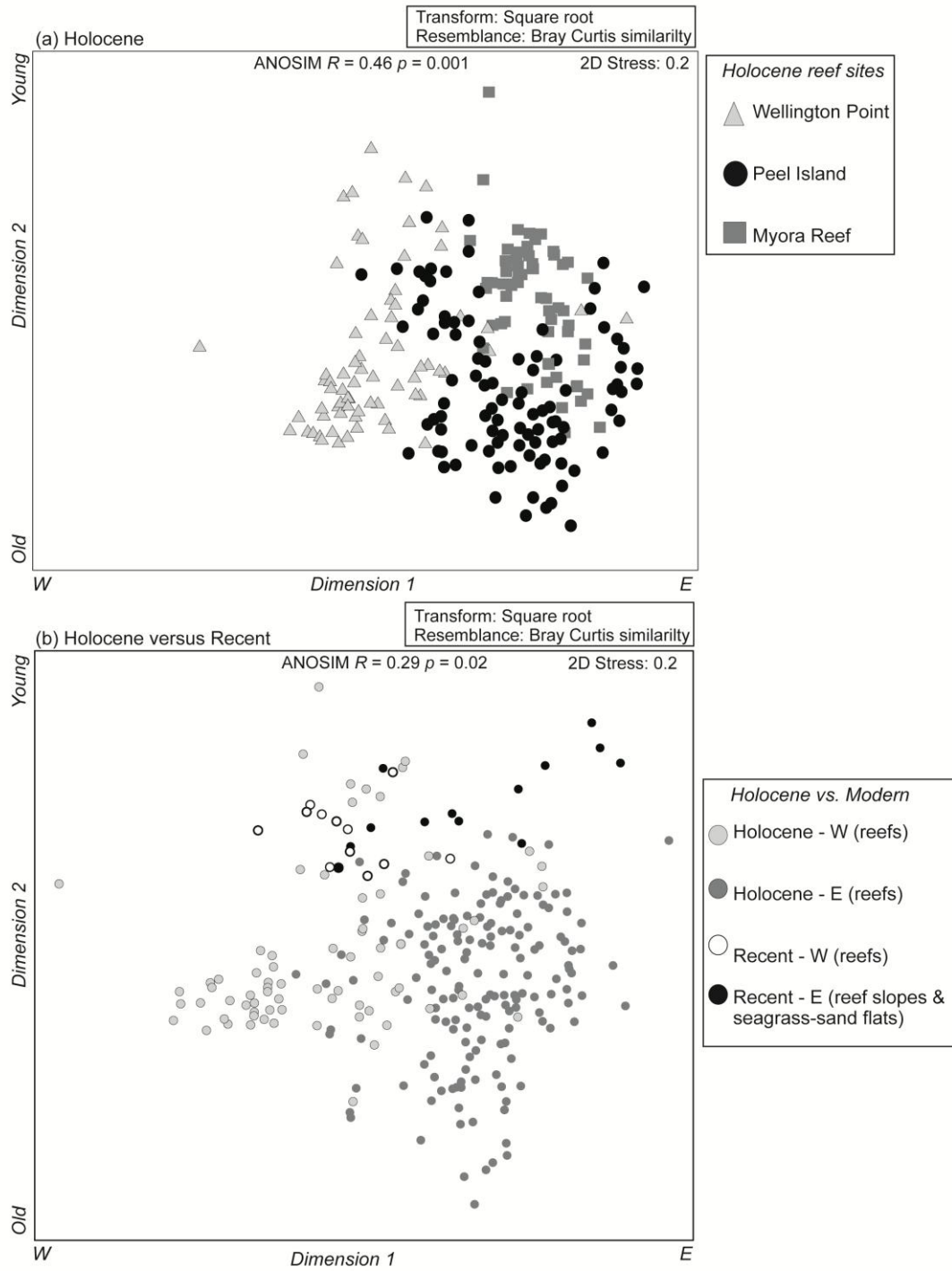


Figure 5

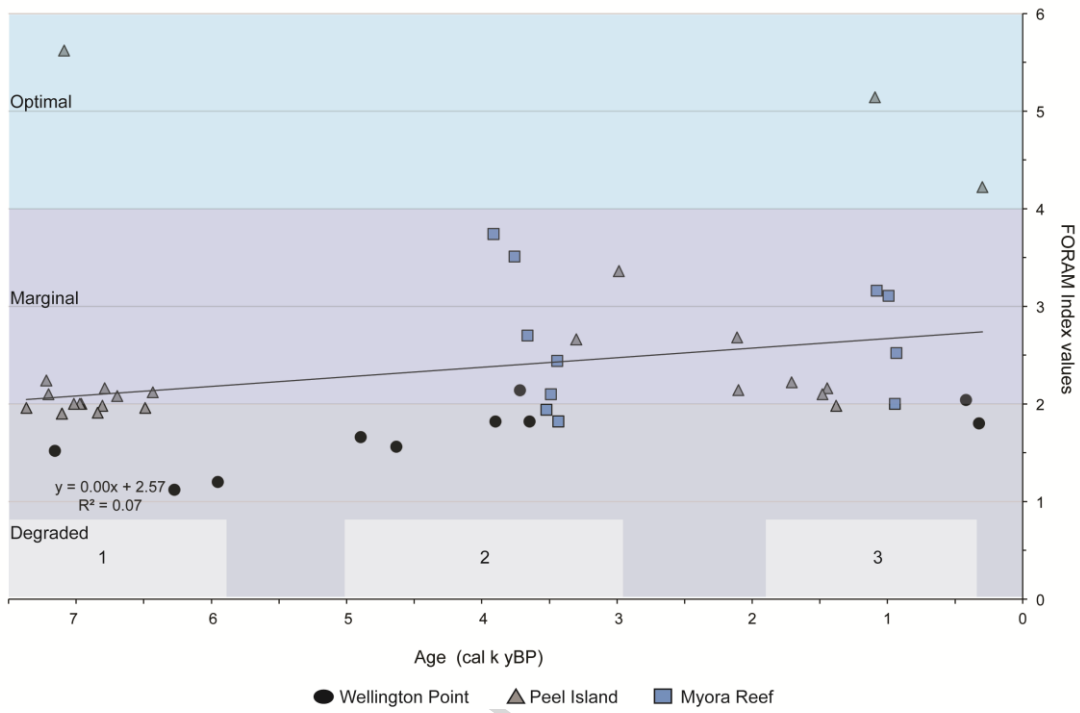
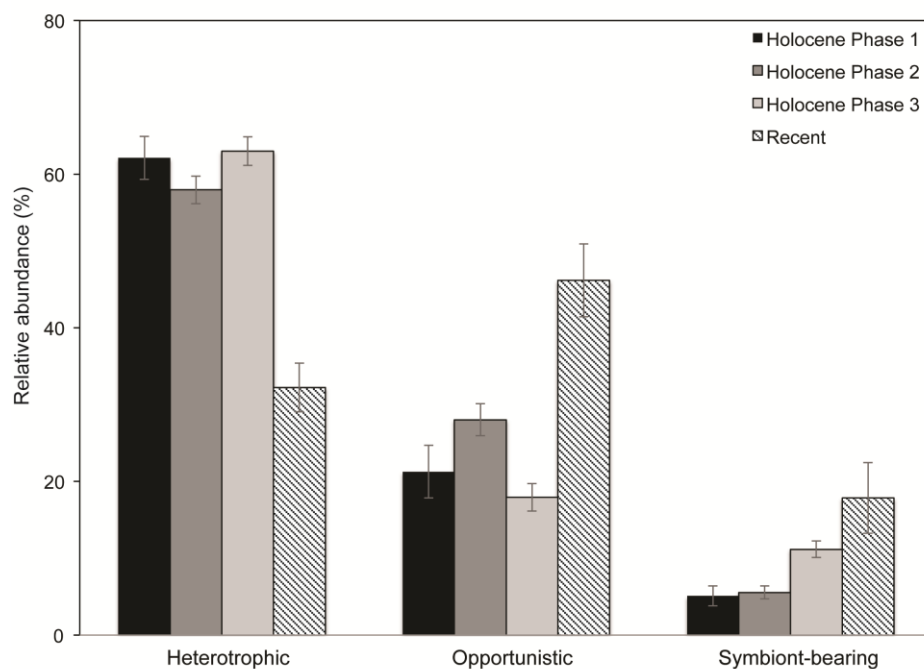


Figure 6



Functional groups	Pairwise Phase comparisons	t-test	p-value	df
Heterotrophic	H1 and H2	1.2231	0.2237	118
	H1 and H3	0.2768	0.7823	177
	H1 and R	6.1499	< 0.0001	86
	H2 and H3	1.7084	0.0894	167
	H2 and R	7.5506	< 0.0001	78
	H3 and R	7.2339	< 0.0001	137
Opportunistic	H1 and H2	1.6259	0.1067	116
	H1 and H3	0.9456	0.3456	175
	H1 and R	4.0035	0.0001	86
	H2 and H3	3.3964	0.0009	167
	H2 and R	4.0745	0.0001	78
	H3 and R	6.3657	< 0.0001	137
Symbiotic	H1 and H2	0.2941	0.7692	116
	H1 and H3	3.5148	0.0006	175
	H1 and R	3.6095	0.0005	86
	H2 and H3	3.4113	0.0008	167
	H2 and R	3.7052	0.0004	78
	H3 and R	2.1416	0.0340	137



### List of Figures

Figure 1. Location of Moreton Bay in South-East Queensland, Australia. The city and port of Brisbane is located near the mouth of the Brisbane River. The location of the three study reefs (Wellington Point, SW Peel Island and Myora reefs) are shown with the location of replicate cores collected from each site depicted in the enlarged panel below. Sediment core names (i.e. W0a) are indicated by reef site i.e. (W = Wellington Point, P = SW Peel Island and M = Myora), depth (0, 2, 4 metres) and core replicate (a, b, c). Seafloor map of Moreton Bay 1:250,000, GDA 94, Zone 56 modified from Australian Government, Maritime Safety Queensland (data sources EPA, NRW DPI&F, HWP, MSQ).

Figure 2. The range of variation in climate and relative sea level influencing the eastern Australian coast during the Holocene. The El Nino Southern Oscillation (ENSO) in the eastern equatorial Pacific (EEP), which was diminished during the mid-Holocene, increased in variability after 5 cal ka yBP (~3000 BCE and intensified at about 3 cal ka yBP (~1000 BCE), respectively (Neil, 1998; Loubere et al., 2003; Donders et al., 2008; Cobb et al., 2013). Relative sea level fall from approximately 1.5 to 2 metres above present day level occurred during the late Holocene (2 cal ka yBP) (Sloss et al., 2007; Lewis et al., 2008).

Figure 3. Composite diagrams of: (a) SW Peel Island Core P0c (b) Wellington Point Core W2b and (c) Myora Reef Core M0c (from the oldest to youngest phases). Core heights are adjusted relative to the Lowest Astronomical tide (LAT). The corrected radiometric U-Series ( $^{230}\text{Th}$ ) coral ages and their corresponding palaeo-water depths (based on Sloss et al. 2007) are provided for the dated (bold) sections. The composite diagrams for 6 other reef cores are provided in Supplementary Figure S2 (a-f).

Figure 4. The non-metric multi-dimensional scaling (nMDS) ordination of the relative abundance of the foraminiferal taxa in the Holocene and recent assemblages of Moreton Bay. (a) Foraminiferal assemblages from the three Holocene reef sites (across all Phases of reef development) and the overall differences (ANOSIM,  $p = 0.001$ ; Table 3) in species composition maintained among the three Holocene reefs investigated. (b) The combined analysis of the Holocene (232 samples) and present day (25 samples) foraminiferal death assemblage surveyed by Narayan and Pandolfi (2010). The Holocene-West sites include Wellington Point and the Holocene-East sites include SW Peel Island and Myora Reef. The recent samples include Western Bay reef flat and reef slope near (Wellington Point, Green and St. Helena's Island) and the Eastern Bay sites of Peel Island and the seagrass sand flats North-West of Peel Island (Narayan and Pandolfi, 2010). The latter sites (top right cluster of five points) show separation from other recent and Holocene reef sites on the ordination plot above and differ in having a greater abundance of symbiont-bearing foraminiferal taxa.

Figure 5. The FORAM Index (FI) values plotted against the 43 coral aged-dated sections for the three phases of reef growth at Wellington Point, SW Peel Island and Myora Reef.

Figure 6. The relative abundance of three functional groups of foraminifera the three phases of Holocene reef growth (H1-H34) in comparison to the recent (R) assemblage surveyed by Narayan and Pandolfi (2010). Error bars are the standard error of the mean (H1  $n = 65$ ; H2  $n = 55$ ; H3  $n = 114$ ; and R  $n = 25$ ). The t-test, p-values and degrees of freedom (df) are shown for pairwise comparisons (shaded comparisons are not significant).

Table 1. The frequency of occurrence (FO) of foraminifer species from Wellington Point (71 samples), SW Peel Island (100 samples) and Myora Reef (61 samples), Moreton Bay, Queensland, Australia. Taxa with greater than 50% FO (in all reefs) are indicated in bold typeface. The Foraminifera Suborders include Miliolina (M) and Rotaliina (R); the wall structures includes hyaline (Hy) and porcelain (P); and the functional groups include opportunistic (O), symbiont-bearing (S) and other heterotrophic (H). FO is calculated as the ratio between the number of samples where the species occurred ( $p$ ) and the total number of samples ( $P$ ):  $FO = p \times 100/P$ .

Foraminifera species	Suborder	Functional Group	All Reefs	Wellington Pt	SW Peel Island	Myora Reef
<i>Alveolinella quoyi</i>	M/P	S	3	0	0	12
<i>Ammonia</i> sp. cf. <i>A. aoteana</i>	R/Hy	O	20	13	18	31
<i>Amphistegina radiata</i>	R/Hy	S	7	0	7	15
<i>Amphistegina lobifera</i>	R/Hy	S	1	0	1	2
<i>Cymbaloporeta bradyi</i>	R/Hy	H	17	23	17	12
<i>Edentostomina cultrata</i>	M/P	H	15	32	10	3
<b><i>Elphidium crispum</i></b>	R/Hy	O	57	35	76	51
<b><i>Elphidium craticulatum</i></b>	R/Hy	O	59	59	49	75
<b><i>Elphidium hispidulum</i></b>	R/Hy	O	73	100	59	66
<i>Eponides cribrorrepandus</i>	R/Hy	H	14	34	3	10
<i>Heterostegina depressa</i>	R/Hy	S	1	0	3	0
<i>Lachlanella subpolygona</i>	M/P	H	31	10	13	85
<i>Miliolinella heligmateira</i>	M/P	H	41	14	70	26
<i>Miliolinella labiosa</i>	M/P	H	32	9	52	25
<i>Operculina ammonoides</i>	R/Hy	S	2	1	4	0
<i>Pararotalia venusta</i>	R/Hy	O	12	25	1	15
<b><i>Peneroplis pertusus</i></b>	M/P	S	57	30	61	71
<i>Peneroplis planatus</i>	M/P	S	43	33	31	72

Foraminifera species	Suborder	Functional Group	All Reefs	Wellington Pt	SW Peel Island	Myora Reef
<i>Planispirinella exigua</i>	M/P	H	19	47	7	7
<i>Planorbulina acervalis</i>	R/Hy	H	5	11	0	5
<i>Poroeponides lateralis</i>	R/Hy	H	9	16	3	10
<b><i>Pseudomassilina macilenta</i></b>	M/P	H	54	63	33	79
<b><i>Quinqueloculina bicarinata</i></b>	M/P	H	53	13	63	84
<b><i>Quinqueloculina distorta</i></b>	M/P	H	61	47	71	62
<i>Quinqueloculina neostriatula</i>	M/P	H	30	3	25	69
<i>Quinqueloculina philippinensis</i>	M/P	H	28	39	36	2
<b><i>Quinqueloculina pittensis</i></b>	M/P	O	60	66	49	72
<i>Spirolina acicularis</i>	M/P	S	5	0	1	18
<i>Spirolina arietina</i>	M/P	S	2	1	3	0
<b><i>Spiroloculina communis</i></b>	M/P	H	79	83	82	69
<b><i>Spiroloculina corrugata</i></b>	M/P	H	59	47	70	54
<i>Spiroloculina rugosa</i>	M/P	H	29	59	22	3
<i>Sorites marginalis</i>	M/P	S	0.4	0	0	2
<i>Triloculina oblonga</i>	M/P	H	47	11	51	83
<i>Triloculina terquemiana</i>	M/P	H	41	14	42	72
<i>Triloculina tricarinata</i>	M/P	H	35	13	18	87
<b><i>Triloculina trigonula</i></b>	M/P	H	79	48	95	89
<i>Vertebralina striata</i>	M/P	H	28	23	42	10

Table 2. The range in Shannon diversity ( $H' \log_2$ ), Margalef richness ( $d$ ), Pielou evenness ( $J'$ ) and the FORAM Index values of the Holocene reefs, for individual reef cores, and for the major phases of reef development (Lybolt et al. 2011). Additional results for each core section can be found in Supplementary Table S3. Names of reefs are indicated by reef site (W = Wellington Point, P = SW Peel Island, M = Myora Reef), depth (0, 2, 4 m) and replicate (a, b, c).

Reef	Reef core	Diversity ( $H'$ )	Richness ( $d$ )	Evenness ( $J'$ )	FORAM Index
Wellington Pt	<i>All times</i>	1.2 – 3.5	0.9 – 3.5	0.53 – 0.92	
	W0a	1.2 – 3.1	0.9 – 1.7	0.53 – 0.87	1.1 – 1.5
	W2b	2.1 – 3.6	1.9 – 3.4	0.61 – 0.92	1.5 – 3.7
	W4b	1.9 – 3.3	1.3 – 3.0	0.69 – 0.85	1.5 – 2.9
SW Peel Island	<i>All times</i>	1.9 – 4.1	1.3 – 4.7	0.55 – 0.94	
	P0a	1.9 – 3.3	1.3 – 2.6	0.68 – 0.91	1.9 – 2.2
	P0b	2.0 – 3.6	1.7 – 3.5	0.61 – 0.90	1.9 – 5.6
	P0c	2.0 – 3.6	1.5 – 4.6	0.55 – 0.90	1.7 – 2.2
	P2c	2.7 – 4.1	3.0 – 4.7	0.76 – 0.94	1.9 – 3.4
	P4c	2.8 – 4.1	2.1 – 4.3	0.76 – 0.94	2.1 – 5.7
Myora Reef	<i>All times</i>	2.6 – 4.4	2.4 – 6.3	0.73 – 0.93	
	M0c	2.6 – 4.4	2.4 – 6.3	0.73 – 0.93	1.8 – 3.7
	M2c	3.3 – 4.2	2.6 – 4.8	0.86 – 0.94	2.0 – 5.0
	M4b	3.5 – 4.3	3.3 – 5.2	0.80 – 0.92	1.9 – 4.2
Reef (sub)phase	Age range (cal k yBP)	Diversity $H' (\log_2)$	Richness ( $d$ )	Evenness ( $J'$ )	FORAM Index
Phase 1a	6.8 to 7.4	1.9 – 3.7	1.5 – 4.6	0.64 – 0.90	1.7 – 5.6
Phase 1b	4.9 to 6.8	---	---	---	---
Phase 2a	3.3 to 4.9	2.1 – 4.4	1.9 – 6.3	0.61 – 0.93	1.5 – 3.7
Phase 2b	1.7 to 3.3	---	---	---	---
Phase 3	0.3 to 1.7	1.9 – 4.3	2.2 – 5.2	0.74 – 0.94	1.6 – 4.4

Table 3. One-way ANOSIM of the three inshore reef sites based on the Bray-Curtis similarity index.

<b>Pair-wise comparisons</b>	<b>R-value</b>	<b>P-value</b>
<i>All reefs (global test)</i>	0.46	0.001
SW Peel Island and Myora Reef	0.32	0.001
SW Peel Island and Wellington Point	0.45	0.001
Myora Reef and Wellington Point	0.66	0.001

Table 4a. Similarity percentage analysis (SIMPER) of the foraminiferal species composition, showing the species that contribute most to similarities within each Holocene reef site. SIMPER analysis values included are: total similarity (T. Sim), average abundances (Av. Abund), average similarity (Av. Sim) of a species within each reef site, ratio of average similarity and standard deviation (Sim:SD) and percent contribution of species (%) to total similarity at an approximately 90% cut-off. (Reefs: W = Wellington Point; P = SW Peel Island; M = Myora Reef).

Reef	T. Sim	Species contributing to similarity within reefs	Av. Abund	Av. Sim	Sim:SD	% Con.
W	42.9	<i>Elphidium hispidulum</i>	29.2	20.4	1.6	47.5
		<i>Spiroloculina communis</i>	15.1	8.8	1.0	20.6
		<i>Elphidium craticulatum</i>	11.8	2.9	0.4	5.7
		<i>Spiroloculina rugosa</i>	3.5	1.6	0.7	3.6
		<i>Pseudomassilina macilenta</i>	3.3	1.5	0.6	3.4
		<i>Triloculina trigonula</i>	5.3	1.4	0.4	3.3
		<i>Quinqueloculina pittensis</i>	3.1	1.2	0.7	2.8
		<i>Quinqueloculina distorta</i>	3.3	0.9	0.4	2.0
		<i>Planispirinella exigua</i>	2.4	0.7	0.4	1.7
P	34.5	<i>Triloculina trigonula</i>	13.1	7.6	1.3	22.0
		<i>Spiroloculina communis</i>	12.3	5.8	0.8	16.7
		<i>Quinqueloculina bicarinata</i>	11.2	3.0	0.4	8.8
		<i>Miliolinella heligmateira</i>	7.7	2.7	0.7	7.9
		<i>Peneroplis pertusus</i>	7.0	2.3	0.5	6.6
		<i>Elphidium hispidulum</i>	6.5	1.9	0.5	5.6
		<i>Elphidium crispum</i>	3.4	1.7	0.9	4.8
		<i>Quinqueloculina distorta</i>	3.8	1.6	0.7	4.6
		<i>Spiroloculina corrugata</i>	3.2	1.3	0.7	3.7
		<i>Quinqueloculina pittensis</i>	2.9	0.8	0.5	2.4
		<i>Miliolinella labiosa</i>	2.5	0.8	0.5	2.3
		<i>Triloculina oblonga</i>	2.3	0.8	0.5	2.2
		<i>Elphidium craticulatum</i>	2.7	0.7	0.4	2.1
<i>Quinqueloculina philippinensis</i>	2.6	0.5	0.3	1.4		
M	43.0	<i>Triloculina trigonula</i>	13.00	6.7	1.0	15.5
		<i>Triloculina tricarinata</i>	11.7	6.6	1.1	15.4
		<i>Lachlanella subpolygona</i>	8.0	4.8	1.1	11.1
		<i>Pseudomassilina macilenta</i>	4.7	2.4	0.9	5.6
		<i>Peneroplis planatus</i>	4.9	2.1	0.7	5.0
		<i>Quinqueloculina bicarinata</i>	3.8	2.1	1.1	4.8
		<i>Elphidium craticulatum</i>	3.8	1.8	0.8	4.2
		<i>Triloculina oblonga</i>	2.9	1.7	1.2	4.1
		<i>Peneroplis pertusus</i>	3.9	1.7	0.7	4.0
		<i>Quinqueloculina distorta</i>	4.3	1.6	0.6	3.8
		<i>Triloculina terquemiana</i>	3.6	1.6	0.8	3.6
		<i>Spiroloculina communis</i>	3.9	1.5	0.7	3.5
		<i>Quinqueloculina pittensis</i>	3.2	1.5	0.8	3.4
		<i>Quinqueloculina neostriatula</i>	3.4	1.5	0.7	3.4
		<i>Elphidium hispidulum</i>	2.5	1.1	0.7	2.6
		<i>Elphidium crispum</i>	1.9	0.5	0.5	1.5

Table 4b. Pair-wise dissimilarity analysis of the foraminiferal species composition data among the three Holocene reef sites: Wellington Point (W), SW Peel Island (P) and Myora Reef (M). SIMPER analysis values included are: total dissimilarity (T. Diss), average abundances (Av. Abund), average dissimilarity (Av. Diss) between two different times and reef sites, ratio of average similarity and standard deviation (Diss:SD) and percent contribution of species (%) to total dissimilarity at an approximately 50% cut-off.

Reef	T. Diss	Species contributing to dissimilarity between reefs	Av. Abund (1)	Av. Abund (2)	Av. Diss	Diss:SD	%
W and P	75.2	<i>Elphidium hispidulum</i>	6.5	29.2	12.4	1.5	16.4
		<i>Spiroloculina communis</i>	12.3	15.1	6.6	1.3	8.8
		<i>Elphidium craticulatum</i>	2.7	11.8	6.1	0.7	8.1
		<i>Triloculina trigonula</i>	13.1	5.3	5.9	1.3	7.8
		<i>Quinqueloculina bicarinata</i>	11.2	0.3	5.6	0.6	7.4
		<i>Peneroplis pertusus</i>	7.0	1.1	3.5	0.7	4.6
W and M	80.7	<i>Elphidium hispidulum</i>	2.5	29.2	13.4	1.6	16.6
		<i>Spiroloculina communis</i>	3.9	15.1	6.6	1.4	8.2
		<i>Elphidium craticulatum</i>	3.8	11.8	6.1	0.7	7.6
		<i>Triloculina trigonula</i>	13.0	5.3	6.1	1.1	7.5
		<i>Triloculina tricarinata</i>	11.7	0.3	5.7	1.3	7.1
		<i>Lachlanella subpolygona</i>	8.0	0.6	3.9	1.4	4.8
P and M	71.6	<i>Triloculina trigonula</i>	13.1	13.0	5.8	1.2	8.2
		<i>Triloculina tricarinata</i>	0.6	11.7	5.7	1.3	7.9
		<i>Quinqueloculina bicarinata</i>	11.2	3.8	5.6	0.7	7.8
		<i>Spiroloculina communis</i>	12.3	3.9	5.5	1.0	7.7
		<i>Lachlanella subpolygona</i>	0.7	8.0	3.9	1.4	5.4
		<i>Peneroplis pertusus</i>	7.0	3.9	3.6	0.8	5.1
		<i>Elphidium hispidulum</i>	6.5	2.5	3.3	0.8	4.6
<i>Miliolinella heligmateira</i>	6.7	1.4	3.3	0.9	4.6		



Table 5. Comparison of the differences in foraminiferal species composition among substrate types using one-way ANOSIM (using Bray-Curtis similarity index) from all reefs and from each of the three reef sites ( $R$  = ANOSIM test statistic). The different substrate types are indicated below (\*).

<b>Pair-wise comparisons</b>	<b><math>R</math>-value</b>	<b><math>P</math>-value</b>
<i>All reefs - substrates</i>	0.50	0.001
<i>Wellington Pt. - substrates</i>	0.49	0.001
1 and 4	0.35	0.001
1 and 5	0.62	0.001
4 and 5	0.26	0.007
<i>SW Peel Island - substrates</i>	0.55	0.001
2 and 3	0.40	0.001
2 and 4	0.50	0.013
2 and 6	0.75	0.001
3 and 4	0.40	0.003
3 and 6	0.46	0.001
4 and 6	0.90	0.001
<i>Myora Reef - substrates</i>	0.14	0.006
2 and 3	0.62	0.009
2 and 6	-0.12	0.750
2 and 7	0.92	0.100
3 and 6	0.06	0.044
3 and 7	0.77	0.001
5 and 7	0.43	0.009

\*

1. Reef carbonate - medium to coarse grey carbonate shell hash and sand (clean), poorly sorted (top of the core);
2. Reef carbonate - medium to coarse silty-shelly carbonate sand, poorly sorted (top of the core);
3. Reef carbonate - fine to medium brown silty-shelly carbonate sand, poorly to moderately sorted;
4. Siliciclastic/terrestrial - fine to coarse reddish brown silty quartz sand with red laterite granules, poorly sorted with bits of shell and wood and few reworked poorly preserved reworked foraminifers (base of the core);
5. Reef carbonate - fine to medium foraminiferal-rich shell-hash and carbonate mud;
6. Mixed- very fine to fine dark grey/brown mixed silty quartz and carbonate sand;
7. Siliciclastic/terrestrial - Dark brown palaeosol ("coffee-rock") very fine to medium silty quartz sand (with some charcoal or wood) with few reworked foraminifers (base of the core).

Table 6. Summary of the temporal (reef phases) and spatial (depth-related) patterns in the foraminiferal assemblages (\*A to D), following the three phases of reef growth and two reef 'gaps' from Lybolt et al. (2011). Shaded areas indicate episodes of non-reef deposition and blank (white) areas contain no available foraminifera data (\*\*I, SS and DS indicate water depths).

Reef Phase	Subphase	Approximate Age range (cal k y BP)	Reference cores	Moreton Bay Reefs (W → E)								
				Wellington Point			SW Peel Island			Myora Reef		
				I	S	D	I	SS	DS	I	S	D
			*Water depths →		S	S					S	S
3	3	0.3 to 1.7	W4b, (P2c, P4c?), M2c, M4b	D	D	A	B	A/B / C	A / C	C / D	C	C
2	2b	1.7 to 3.3 (reef "gap")										
	2a	3.3 to 4.9	W2b, M0c	D ?	A	C	-	--	--	D	C	C
1	1b	4.9 to 6.8 (reef "gap")										
	1a	6.8 to 7.4	W0a, P0a, P0b, P0c	D	--	--	B	A/C / A	--	--	--	--

\* A = Mixed opportunistic-heterotrophic assemblage dominated by *Elphidium hispidulum*; B = Heterotrophic assemblage dominated by *Quinqueloculina spp.* including *Q. bicarinata*; C = Mixed symbiont-bearing and heterotrophic assemblage dominated by *Peneroplis spp.*; and D = Mixed heterotrophic-opportunistic assemblage dominated by *Elphidium craticulatum*.

\*\* I = intertidal (< 2 m); SS = shallow-subtidal (> 2 m and < 5 m); DS = "deep"-subtidal (> 5 m).

**Highlights:**

- 1 The first concise chronological framework for the Holocene reefs of Moreton Bay.
- 2 Historical environmental conditions in Moreton Bay prior to European settlement.
- 3 Foraminifera indicate long-term marginality throughout ~7400 year timeframe.
- 4 Moreton Bay's Holocene inshore reefs were dominated by low diversity assemblages.
- 5 Long-term resilience of ecological communities to marginality.