# One Tree Reef lagoon, a relic of the pre-colonial Great Barrier Reef



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This thesis is written using the format required for submission to the journal *Coral Reefs* with exceptions that the abstract is restricted to 200 words, figures are embedded into the body as opposed to being contained in separate files, figure and table captions appear with relevant figures as opposed to being contained at the end of body text and spacing is 1.5x, all as requested by Macquarie University under their Master of Research thesis format instructions. The aims have been placed earlier in the discussion than specified by Coral Reefs.

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All other research described in this report is my own original work.

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#### Abstract

Coral reefs are in decline worldwide due to local/regional (e.g., water quality and fishing) and global stressors (e.g., ocean warming and acidification). Palaeoecological studies help differentiate the effects of anthropogenic versus natural stressors, assist ecological interpretations of fluctuations in dynamic systems, and decipher the impact of future changes. Benthic Foraminifera are valuable proxies for monitoring coral reef condition. This project utilises Foraminifera preserved in a sediment core from the One Tree Reef (OTR) lagoon on the southern Great Barrier Reef (GBR) to quantify potential ecological changes associated with European colonisation (late 1700's) and industrialisation of Australia (1950's). Previous work focuses on foraminiferal assemblages from near shore reefs, but analysis of outer reef systems is lacking. OTR is located some 100 km from the mainland, removed from most local and regional stressors likely to drive changes in the foraminiferal assemblages. Richness, diversity and changes in foraminiferal assemblages over time using standard ecological indices and foraminifera assemblages over the last four centuries. These Foraminifera assemblages suggest that the OTR lagoon may contain a living example of a pre-colonial GBR lagoon ecosystem.

Keywords: "Small benthic Foraminifera", "lagoon sediment core", 'Conservation Palaeobiology", "Anthropogenic change".

# Introduction

Tropical coral reefs are diverse and economically valuable environments providing essential ecosystem services and often identified as biodiversity hotspots due to their high productivity, species diversity and abundance (Moberg and Folke 1999). Calcifying organisms such as corals, calcareous algae, molluscs and Foraminifera are important for modern reef functioning, 3D structural complexity and sedimentary budgets (Fabricius et al. 2012; Dawson et al. 2014; Förderer et al. 2018). Globally, climate change threatens reef survival, through rising water temperatures and ocean acidification, which may adversely impact organismal calcification rates and coral reef building capacity (Schmidt et al. 2014; Kornder et al. 2018). On a local or regional basis, reef ecosystems, especially those located adjacent to the mainland, are adversely impacted by localised anthropogenic activities. Land clearing and coastal development, tourism, pollution and eutrophication all reduce water quality, which is critical to the survival of many reef organisms (Pandolfi et al. 2003; Fabricius et al. 2016; Fontanier et al. 2018). Globally, even reef systems that are considered least stressed like the Great Barrier Reef (GBR), show significant degradation predating the 1900's and impacting the survival of key biota (Pandolfi et al. 2003). These combined stressors not only threaten the continued survival of coral reefs communities but can be difficult to discriminate and isolate in ecological assessments. Written environmental records of reef condition rarely predate the last 50 years, and reef coverage has declined worldwide from 60% to 20% during this time (Pandolfi et al. 2003; Brodie and Waterhouse 2012). Palaeoecological studies, in contrast, provide evidence of climatic, environmental and depositional fluctuations predating anthropogenic influence, and may assist in isolating cause and effect, uncovering natural variation and enable better determination of reference or natural environmental states (Willis and Birks 2006).

Foraminifera are important elements of GBR reef, inter-reef (between reef and other non-reefal areas) and shelf faunas (Maxwell 1968; Mathews et al. 2007). Live Foraminifera that produce a calcareous test (i.e., shell) are common proxies for investigating and monitoring fluctuations in marine environments, caused by varying drivers over differing time intervals (Hallock et al. 2003; Barras et al. 2014; Zeppilli et al. 2015; Musco et al. 2017; Bouchet et al. 2018). Foraminifera preserved in sediment cores have been used successfully to investigate past environmental conditions since the late twentieth century and more recently are being used to monitor changes in Holocene water quality (Haynes 1981; Karlsen et al. 2000). After allowing for the influence of taphonomic factors sediment cores can provide an opportunity to examine past community dynamics (e.g. biodiversity, abundance and overturn) preserved sequentially in stratigraphic layers. It is important to consider the influence of time averaging and taphonomic signals such as bioturbation, diagenesis and erosion which may

alter preserved assemblage composition when comparing recent and fossilised foraminiferal assemblages (Glenn-Sullivan and Evans 2001). By dating core layers researchers can relate faunal occurrence with events and other records. Palaeoecological data can be used to quantify past changes, which improves our understanding of impacts and the extent of future stressors on the GBR and inhabitants such as Foraminifera.

## Aims

This project aimed to quantify shifts in foraminiferal assemblages from pre-colonial through to modern times, by identifying and analysing Foraminifera preserved in a dated lagoonal sediment core from One Tree Reef (OTR) (Kosnik et al. 2015). The project sought to identify any changes, and their timing, in the diversity, composition and abundance of the OTR foraminiferal assemblage relative to the colonisation and industrialisation of Australia. Understanding historical changes on an outer reef will improve our understanding of the geographic extent of anthropogenic impacts on the GBR.

Further, this study has contributed to an increased knowledge of the diversity and ecology of Foraminifera within the GBR, by expanding the geographic areas and the environments studied.

#### **Great Barrier Reef**

A World Heritage Area, the GBR is the world's largest coral reef system, with approximately 3,000 reefs and 950 islands, located in the Great Barrier Reef Marine Park in an area exceeding 344 000 km<sup>2</sup> (Day 2002; Schaffelke et al. 2017). The GBR has undergone structural and compositional changes in response to changes in sea-level and variations in sediment flux over the last 30 kyr but has existed in its current structural form for approximately 10 kyr (Webster et al. 2018). While research emphasis is often on reef biotypes, they only represent 5 % of the GBR as a whole and the majority of the GBR is composed of inter-reef zones (Mathews et al. 2007). These non-reef areas are far less studied than the reefs within the GBR (Mathews et al. 2007).

Generally, the GBR high energy, near shore zone extends from the coast to 22.5 km out on the continental shelf and to 9 m in water depth (Maxwell 1968). The inner shelf zones extend out to 37 km from the coast. Both these areas tend to be dominated by terrigenous sand derived from quartzose (Maxwell 1968). Herein, the term inner reef refers to those situated around the near shore or inner continental shelf zones, dominated by terrigenous facies. Outer reefs are located in the area from the inner shelf to the continental shelf edge, in deeper water dominated by carbonate facies (Maxwell 1968).

#### Local anthropogenic impacts

In addition to its rich and diverse ecosystem, the GBR provides an opportunity to investigate the anthropogenic impacts on reef systems through the use of pre-colonial/palaeontological reference data. European settlement resulted in a change in fishing regime, rapid land clearing, increased runoff and drastic modification of reef coastal zones followed by development and industrialisation (Whitehouse 1991; Hill et al. 2000; Kroon et al. 2012; Reside et al. 2017). While indigenous people lived in Australia prior to the current sea level, there is no evidence their activities caused large scale environmental disturbance to reef systems (Jackson et al. 2001). Following British settlement in Sydney in 1788, European colonisers spread through the continent adapting the landscape to European agricultural practices, with populations concentrated in coastal zones and river catchments (Bradshaw 2012). Colonisation of QLD occurred in the early 1800's, followed in the 1900's by the period of worldwide industrialisation. It is estimated that over 60% of pre-settlement land cover had been cleared from the Fitzroy Basin by 1999, with 95% of the area used for grazing and agriculture (Packett et al. 2009). Today the city of Gladstone, which sits on the southern edge of the GBR, is one of the Australia's largest industrially developed areas and ports (Van Beers et al. 2007). In addition the Fitzroy River Basin is one of the largest catchments in Eastern Australia, delivering flow from five major rivers to the GBR (Douglas et al. 2010).

Regular monitoring of coral cover and reef condition began along the reef in the 1980's as part of the GBR Long-term Reef Monitoring Program by the Australian Institute of Marine Science, but there is strong palaeobiological evidence that the GBR has been deteriorating since the mid 1800's following European colonisation of the region (Pandolfi et al. 2003; Clark et al. 2017). The level of degradation is greater on the inner GBR than on the outer reefs and areas to the South of the GBR such as Moreton Bay are severely degraded (Pandolfi et al. 2003; Lybolt et al. 2011). Large scale land clearing and development in river catchments has resulted in significant increases (up to eight-fold) in sediment run off since European settlement in the 1800's (Mcculloch et al. 2003; Fabricius et al. 2016). Some of the highest rates of land clearing in Australia since the 1970's has been in southeast Queensland (Bradshaw 2012). Water quality in the GBR is linked to a number of spatial factors such as distance from the mainland, reef placement and water depth along with seasonal variations, due to changes in river run-off delivery to the reef (Furnas et al. 2005). Studies undertaken between 2006 and 2011 show a significant short-term decline in GBR water clarity, linked to increased sedimentation, especially after flooding events (Fabricius et al. 2016). Palaeoecological reconstructions using sediment cores from the central GBR demonstrate a reorganisation of longstanding stable coral communities following European colonisation and increases in sediment delivery to the reef (Roff et al. 2013). In its latest Outlook Report, the GBR Marine Park Authority advised that overall reef habitats were in poor condition, particularly seagrass meadows and shallow, inshore reefs (GBRMPA 2019).

Increases in terrigenous sedimentation damage seagrasses by reducing light availability, most notably in inshore zones of the GBR (Brodie et al. 2012). Sediment plumes also carry fertiliser and agricultural chemicals, which further decrease water quality, most notably near shore and river mouths (Mercurio et al. 2015). Herbicides and anti-fouling chemicals, such as Diuron, inhibit photosynthesis in autotrophs, including some photosymbiont-bearing Larger Benthic Foraminifera (LBF) (Van Dam et al. 2012). During wet-seasons and floods, river discharges carry sediment further onto the reef and the concentrations of nutrients and chemicals can exceed ecological guideline values, particularly in coastal areas (Lewis et al. 2009). Generally, plumes stay within 50 km of the coast (Mathews et al. 2007). Flooding of the Fitzroy River in 2010 due to cyclonic rain caused an extra-large flood plume, which extended 70 km north and resulted in 100% coral mortality in shallow inner reef systems due to lowered salinity from sediment loaded floodwaters (Jones and Berkelmans 2014).

#### Natural stressors

Cyclones are a regular and increasing occurrence responsible for generating strong winds and waves in the GBR region and a primary source of natural disturbance in coral reefs (Devlin et al. 2001). Since 1858 there have been 207 recorded cyclones along the Queensland coast (Gallina and Sidle 2018). Severe weather events can leave a record in sedimentary deposits and result in mixing of sedimentary layers. Sediment cores examined from the deep sea surrounding Madagascar show distinct terrestrial layers corresponding to surges of terrigenous input following storm events (Fontanier et al. 2018).

#### **Global factors**

Reef extinction events in the geological past have been linked to ocean acidification, changes in sealevel and global warming, all effects being reported as impacting reef systems today (Kiessling and Sampson 2011: Webster et al. 2018). Since the late 1700's pH has decreased, with pH decreasing 0.1 pH units or 26%, while sea surface temperature on the GBR has risen by 0.8 °C since the late 1900's, with the rate of increase accelerating since the 1950's; both trends are expected to continue (Hoegh-Guldberg et al. 2007; Schaffelke et al. 2017). In 1998, 2010 and 2015/2016 large scale mass bleaching occurred worldwide in tropical reefs, including the GBR, in response to thermal stress resulting from rising sea temperatures (Hughes et al. 2017). Formal monitoring of ocean acidification of the GBR is still being developed, although geochemical proxies suggest a coral bleaching event in the 1940's, since which time pH on the GBR is estimated to have declined by between 0.2 - 0.3 units (Wei et al. 2009). Hard coral cover on the GBR has declined to an average of 13.8 % (28% in 1985) in response to these global factors combined with cyclonic events and predation by Crown of Thorns starfish (COTS) (De'ath et al. 2010). Outbreaks of COTS have been associated with declining water quality on the GBR (De'ath et al. 2010).

It is likely that these changes, combined with localised anthropogenic stressors, have already reduced the condition of other autotrophic and calcifying organisms and caused shifts in biodiversity on the GBR (Schaffelke et al. 2017).

#### Foraminifera

There are approximately 9,000 extant species of Foraminifera, found at all depths across all marine environments globally (Gooday and Jorissen 2012; Morard et al. 2018; Hayward et al. 2019). Foraminifera are predominantly microscopic, unicellular protists, with the majority of identified species in shallow water carbonate shelves secreting carbonate shells or "tests", of which the most ancestral forms can be found in sedimentary deposits dating back to the Cambrian Period (Tappan and Loeblich 1988). Most modern Foraminifera species (~90%) live in and on the benthos while a smaller number of species, but a far larger biomass, float in the water column as planktic forms that eventually fall as "oceanic snow" accumulating in the deep sea (Jones 2013). Benthic forms can be epifaunal, infaunal or encrusting and some live as epiphytes on marine plants (Murray 2006). The common test types are agglutinated or calcareous and the calcareous species can be further divided into subgroups based on the chemical composition (such as the amount of magnesium incorporated) and morphology. They are generally identified as possessing either a hyaline (or perforate) calcareous test, or a porcelaneous (or imperforate) calcareous test, which appear different under a microscope based on the ultrastructure and arrangement of crystal layers (Fig. 1) (Tappan and Loeblich 1988). Historically tests were used to classify species, the Order Miliolida all have porcelaneous tests, whilst taxa in the Order Rotaliida have hyaline tests. Foraminifera tests shapes vary from simple unilocular structures to complex forms with multiple divided chambers.

Foraminifera are common stratigraphic markers and widely accepted as biological proxies to assess changes in marine environments over time due to their diversity, sensitivity, abundance, short lifespan, preservation potential and the ease of sampling (Zeppilli et al. 2015; Musco et al. 2017). The carbonate tests constructed by key foraminiferal groups are an important source of sediment in reef lagoons, coral cays and islands and they are integral components in pelagic and benthic marine



**Fig. 1.** Key benthic foraminifera from the GBR showing different test compositions. Scale bars = 1.0 mm unless otherwise specified. Images (except c) made with Micro Macro Digital Imaging System (Dun Inc) with image stacking applied using Zerene software. a) *Marginopora vertebralis* Quoy & Gaimard, 1830, b) *Peneroplis planatus* (Fichtel & Moll, 1798). Scale bar for  $c - d = 100 \mu m c$ ) *Quinqueloculina bosciana* d'Orbigny, 1839, d) *Elphidium macellum* (Fichtel & Moll, 1798), e) *Elphidium craticulatum* (Fichtel & Moll, 1798), f) *Calcarina capricornia* (Mamo, 2016)

ecosystems (Lipps and Valentine 1970; Yamano et al. 2000; Langer 2008; Doo et al. 2017). Whilst foraminifera may be found in all marine realms, some species are found only within extremely narrow ecological parameters and environmental ranges associated with specific water temperatures, depths, turbidity, turbulence and salinity, and sedimentary environments (Jones 2013). There is a strong relationship between these environmental variables, habitat heterogeneity and species distribution (Förderer et al. 2018). Further, it has been shown that some epiphytic species are associated with specific types of sea-grasses or algae (Langer 1993; Hallock 2012).

The strong correlation between species and environmental parameters means that coastal, estuarine and inner shelf facies are often dominated by specific benthic assemblages while the relative abundance of planktonic species increase ten-fold as you move from the neritic to the abyssal zone (Fig. 2) (Armstrong and Brasier 2013). Foraminifera exhibit morphological characteristics that can be used to infer lifestyle and ecological preferences. Infaunal species tend to be elongate, round or

cylindrical or have planispiral coiling whilst epifaunal taxa often have plano-convex or biconvex shapes with trochospiral coiling (Corliss and Chen 1988). In total contrast to these generalised morphological distinctions, some benthic forms also have planktic life stages such as *Bolivina variabilis* (Williamson, 1858) (Banner et al. 1985; Seears et al. 2012).



**Fig. 2.** Foraminifera assemblage associations with water depth and conditions. Foraminifera assemblages vary with depth, latitude, temperature and salinity. (Image adapted from Armstrong and Brasier, 2005, Fig 15.9)

Large benthic Foraminifera (LBF) is an informal grouping of symbiont bearing, large complex tests that thrive in the photic zone of low nutrient, warm tropical waters where they are fundamental components of tropical reef systems (Förderer et al. 2018). LBF occur in 11 (> 8%) of known families of extant Foraminifera, the majority hosting diatoms, chlorophytes, rhodophyte, cyanobacteria and dinoflagellates as endosymbionts (Lee 2006). LBF taxa show specific sensitivity to nutrification and elevated seawater temperatures. Research by Uthicke and Altenrath (2010) demonstrated reduced growth rates in Amphistegina radiata (Fichtel and Moll, 1798) and Heterostegina depressa d'Orbigny, 1826 corresponding with increased levels of terrigenous runoff. In laboratory tests, A. radiata and H. depressa also lost their diatom endosymbionts in temperatures exceeding 31 °C causing bleaching, while Calcarina mayori Cushman, 1924 did not (Schmidt et al. 2011). The effects of increased temperature and nutrients, combined with lower light conditions, reduced survivorship and fecundity of Amphistegina lobifera Larsen, 1976, with populations from GBR inner shelf zones more resistant to higher temperature and nitrate levels, indicating the resistance of inner shelf populations to some stressors (Prazeres et al. 2017). Due to their dependence on algal endosymbionts and response to rises in sea surface temperatures, pollution and water quality, LBF are excellent indicators of water quality and can be used as early warning species for coral mortality events

(Hallock et al. 2003; Marques et al. 2017; Spezzaferri et al. 2018). LBF are important elements of the carbonate production cycle of tropical systems and reefs representing up to 95% of the carbonate sands in the West Pacific and East Indian Oceans (Hohenegger 2006). They are responsible for between 3.9-5.4% of the annual carbonate production on OTR (Doo et al. 2017).

Small benthic Foraminifera (SBF), non-symbiotic benthic species, are diverse and abundant in marine environments but have been less studied than LBF, particularly in tropical reef environments (Uthicke and Nobes 2008). In comparison to LBF, there are many times more genera of SBF and some have been identified as environmental and pollution indicators. Increased eutrophication or anoxia of shallow marine areas has been linked to increases in opportunistic SBF genera such as *Ammonia* Brunnich, 1771 and decreases in the cosmopolitan genus *Elphidium* Montfort 1808, in studies conducted in Europe, Asia and the USA (Yasuhara et al. 2012). Deformities, test dissolution and dwarfism in both LBF and SBF have been reported in marine environments subjected to heavy metal pollution, acidification and eutrophication (Hallock et al. 2003; Yasuhara et al. 2012; Marques et al. 2017; Martin and Nesbitt 2017).

Reduced water quality, caused by increased turbidity or nutrients, results in decreased LBF and increased SBF abundance in tropical reef environments (Hallock et al. 2003; Uthicke and Nobes 2008). There has been considerable research conducted in Europe and USA using benthic forms as proxies for changes in water quality. Multiple indices have been devised to monitor foraminifera changes over time and/or geographic gradients based on proportions of ecological functional groups or fluctuations in diversity (Hallock et al. 2003; Mateu-Vicens et al. 2014; Dimiza et al. 2016; Bouchet et al. 2018; Jorissen et al. 2018; Alve et al. 2019). The most broadly utilised index is the FORAM (Foraminifera in Reef Assessment and Monitoring) Index (FI), upon which most of the other indices are based. The FI assesses the relative proportions of LBF against two categories of SBF, small heterotrophic species and opportunistic species (Hallock et al. 2003). An FI = 4 implies 25% of the assemblage is LBF and FI > 4 indicates water quality that is suitable for coral growth; FI < 2is unsuitable and between these two ranges the environment is marginal for coral growth (Hallock et al. 2003) Low or declining FIs and/or densities of Foraminifera accompanied by changes in assemblages have been reported in reefs near urbanised and heavily populated sites around the world, including nearshore sites on the GBR and in Moreton Bay reflecting poor water quality (Schueth and Frank 2008; Uthicke and Nobes 2008; Fujita et al. 2009; Narayan and Pandolfi 2010; Osawa et al. 2010; Uthicke et al. 2010; Fabricius et al. 2012; Parsaian et al. 2018). Changes in Foraminifera assemblages have also been demonstrated over short time periods. Researchers reported increased dominance of SFB and declines in LBF in Foraminifera assemblages in coastal waters off Florida over a 30 year period, attributed to increased levels of dissolved nutrients in the water (Cockey et al. 1996). While the FI has been successfully applied in a variety of areas, Hallock et al. (2003) highlighted that some modification may be required to adapt the FI in certain regions. Work with the FI in the Central Indo-Pacific has indicated that for effective use the index may require calibration to account for regional taxonomic variations (Renema 2018). Renema (2018) reported high numbers of some species of LBF, in poor quality waters.

Standard diversity indices can be misleading when analysing changes in foraminiferal assemblages to assess changes in water quality. An increase in Foraminifera diversity and richness does not necessarily indicate improved water conditions (Hallock 2012). Species richness in oligotrophic waters may be consistently lower than that of nutrient enriched waters, simply due to the fact that there are less LBF taxa than SBF (Hallock 2012).

#### **Benthic Foraminifera of the GBR**

Study of GBR Foraminifera commenced in the 1940's with the majority of research undertaken as geological and ecological studies to improve understanding of reef functioning and formation and to investigate potential for fossil fuels and minerals (Lloyd 1961; Mamo 2016). The GBR is a collection of diverse ecosystems including coastal marshlands, inshore reefs, outer reefs and seagrass meadows (Kerrigan et al. 2010). The study of foraminifer has concentrated within specific regions and has generally focused on surface collections rather than sediment cores. Most research has examined LBF and inner reef zones, rather than from lagoonal environments. Spatial heterogeneity of Foraminifera likely reflects both regional groupings and differences in microhabitats (Uthicke and Nobes 2008).

Studies of GBR foraminifer indicate that their proportion in sediment samples increases away from the mainland, with offshore reefs generally supporting a greater diversity and abundance of LBF than inshore reefs (Scoffin and Tudhope 1985; Nobes et al. 2008; Uthicke and Nobes 2008). Foraminiferal assemblages in dated sediment cores show that this pattern has persisted over thousands of years in the central GBR, predating European settlement (Uthicke et al. 2012; Reymond et al. 2013).

When Foraminifera die their tests contribute to the creation of marine sediments. Benthic Foraminifera are important for the creation of carbonate sediment in tropical shallow water environments and net sediment accumulation is affected by dissolution, abrasion and test destruction (Hallock 1981). Islands such as Raine Island in the northern GBR rely on LBF for up to 63% of the island sediment budget, predominantly derived from three genera of LBF, *Baculogypsina* Sacco,

1893 (75%), *Marginopora* Quoy and Gaimard in Blainville, 1830 and *Amphistegina* d'Orbigny (Dawson et al. 2014). This contrasts with Heron Island in the south (in the Capricorn Group) and Green Island in the central GBR, both formed on platform reefs where the dominant genus found on the reef flat is *Calcarina* d'Orbigny, 1826 (Jell et al. 1965; Yamano et al. 2000; Lobegeier 2002). Foraminifera account for less than 12% of the Heron Island sediment budget, however, contribute to ~30% of the sediment on Green Island and 50% to the reef flat (Maxwell et al. 1964; Yamano et al. 2000). However, it is in the inter-reef areas, which represents over 95 % of the surface area of the GBR, that benthic foraminifera are most numerous (Maxwell 1968; Mathews et al. 2007). LBF on the outer GBR shelf represent 33% of shelf edge facies and up to 40% of sedimentary grains in the inter-reef zones consisting of taxa such as *Operculina* d'Orbigny, 1826, *Amphistegina, Marginopora, Alveolinella* H. Douville, 1907 and *Cycloclypeus* W. B. Carpenter, 1856 (Scoffin and Tudhope 1985).

A recent taxonomic assessment using surficial samples identified 133 foraminiferal species in the Capricorn Group of the GBR (Mamo 2016). The majority of these species (46%) were Miliolida with 34% assigned to the Rotaliida. The dominant foraminiferal taxon recovered from surficial sediment in the interior of OTR lagoons ( $36\% \pm 5.6\%$ , mean  $\pm$  SD), Heron Lagoon ( $43\% \pm 7\%$ , mean  $\pm$  SD) and Wistari Lagoon ( $43\% \pm 4\%$ , mean  $\pm$  SD) was *Quinqueloculina* (Mamo 2016). *Calcarina* was the dominant taxa on Heron reef flat, reaching relative abundance of 88% in some transects and averaging  $66\% \pm 19\%$  (mean  $\pm$  SD) across all samples (Mamo 2016). In contrast Sykes reef flat was dominated by *Baculogypsina*, which represented  $53.25\% \pm 17\%$  (mean  $\pm$  SD) of all taxa sampled (Mamo 2016). Heron reef lagoon was reported in 1965 to have no live Foraminifera present and tests composed less than 1% of overall lagoonal sediment (Jell et al. 1965). Mamo (2016) reported low numbers (n < 10) of live taxa from samples within the lagoons of the Capricorn Group, including OTR, predominantly encrusting *Millettiana milletti* (Heron-Allen & Earland, 1915) and *Cymbaloporetta bradyi* (Cushman, 1915).

#### Impact of anthropogenic change on Foraminifera in the GBR.

There are surprisingly few studies that have investigated changes in the distribution and abundance of Foraminifera on the GBR over time, either from a palaeontological perspective using sediment cores, or from an ongoing monitoring perspective. Intermittent temporal sampling was undertaken to incorporate the FI as part of the Governments Reef Water Quality Protection Plan from 2007 to 2014 (Thompson et al. 2014). Water quality monitoring showed a decline in the FI across monitored inshore reefs in the GBR regions of the Wet Tropics, Burdekin, Mackay Whitsunday and Fitzroy (Thompson et al. 2014) This decline accompanies increases in dissolved organic carbon, nitrogen and turbidity through the study. The FI = 2 for the inner Mackay Whitsunday Region indicates

communities that are almost exclusively SBF and not conducive to coral growth.

Three previous studies have utilised sediment cores to examine changes in Foraminifera over time in relation to investigating anthropogenic change on the GBR. Using 11 sediment cores obtained along a water quality gradient in Whitsundays inshore fringing reefs (central GBR) Uthicke et al. (2012) identified a decline in LBF over the last 55 years and a rise in opportunistic SBF in reefs closest to the mainland (Uthicke et al. 2012). Assemblages were grouped into six time-intervals corresponding to modern (< 55 yr) and then older bands (55-150, 150-500, 500-1000, 100-1500 and >1500 yr). The study reported a clear difference between the impact on inner, intermediate and outer reef locations when comparing pre- and post-European settlement time intervals. These assemblages had previously been stable for thousands of years. Uthicke et al. 2012 demonstrated that the severity of the impact declined with increasing distance from the coast, and away from the influence of higher levels of dissolved nutrients, with LBFs still dominating the most outer reef zones. The FI was approximately three times higher in outer zones (FI = 6.36) compared to FI = 2.3 in inner reef zones suggesting better quality conditions in outer reef zones. Uthicke et al. (2012) hypothesised that the changes were locally driven and resulted from increased terrestrial run off and pollution following European colonisation since there was little perturbation in the assemblages on outer reef zones over time.

The Burdekin River delivers the highest sediment loads to the central GBR; the result of over three quarters of the vegetation in the catchment area having been cleared since European settlement (Reymond et al. 2013). In addition to delivering sediment, freshwater outflow to the reef lowers salinity of inner and mid shelf waters (Lough et al. 2015). Eight sediment cores from Halifax Bay ~ 130 km north of the river mouth examined by Reymond et al. (2013) at Pandora Reef and Havannah Reef (10 km further to the east), showed distinctly different assemblages of Foraminifera. However, in contrast to Uthicke et al. (2012), they reported no significant change in assemblage diversity indices over 1,000 years for either reef. Pandora was consistently dominated by more opportunistic SBF taxa than Havannah and associated with higher terrestrial runoff. No taxon count data or FI were published so it is not possible to directly compare this work with other researchers.

From the same Halifax Bay region, Johnson et al. (2019), obtained three cores from the inshore (0 - 3 km from shoreline) Paluma Shoals to examine changes in foraminiferal assemblages over time. Similar to the results reported by Reymond et al. 2013, Johnson et al. (2019) found no change in assemblages or in the FI over time in relation to European colonisation and land use changes. All foraminiferal assemblages were dominated by SBF (98%), and the FI ranged from 1.5 to 2.4, with 70% of the samples indicating environmental conditions not conducive to coral growth. The sole LBF

to contribute significantly to any assemblage was *Peneropolis*, which has been associated with reduced light conditions, small grain size and high organic matter (Uthicke et al. 2010). Johnson et al. (2019) proposed that this region has been under the influence of consistently higher rates of terrigenous sedimentation compared to the area studied by Uthicke et al (2012).

Differences across the 3 studies may reflect geographically distinct regions and variation in the distribution of foraminifer across these areas, as well as being the result of using different methods. Both reefs assessed in Reymond et al (2013), sit within the confines of Halifax Bay and could be inferred to have been subjected to the same historical sediment load as that proposed by Johnson et al (2019). Both areas were described as having low coral cover  $11.4\% \pm 1.8\%$  (mean  $\pm$  SD) and  $14.1\% \pm 3\%$  (mean  $\pm$  SD) in 2009 (Uthick et al. 2010). This contrast with the study by Uthicke et al. (2012) where samples were taken along a water quality gradient, with Daydream Island having  $47\% \pm 3\%$  (mean  $\pm$  SD) coral cover (Uthick et al. 2012). Halifax Bay is an area that is high terrigenous (100% terrigenous) to transitional (40 - 60% carbonate) facies, while the Whitsunday Islands are in an impure (60-80%) to high (80-100%) carbonate environment (Maxwell 1968). The River delivers flood plumes into the Bay which also reduce salinity. Reymond et al. (2013) sampled every 50 years and obtained 200 count from 5cm of sediment that had been sieved using a 125 µm sieve. Uthicke et al. (2012) subsampled 10 cm core sections after being 63 µm sieved and picked all foraminifer and compared grouped time intervals. All three papers classified different genera as opportunistic for the calculation of the FI and the number of taxa designated opportunistic varied from five to ten.

It has been demonstrated that documenting fluctuations and faunal overturn in foraminiferal assemblages over time can be linked with natural and/or anthropogenic stressors using sediment cores (Hallock 2012). Work on the GBR and Moreton Bay (~ 300 km south of GBR) shows that the FI can be applied to assess changes and gradients in water quality (Narayan and Pandolfi 2010; Uthicke et al. 2012; Reymond et al. 2013). European colonisation of QLD commenced in the early 1800s and as such, sediment cores that predate these time periods, may provide an indication of the pre-impacted natural population or reference conditions. While threats to the GBR cover a spectrum of stressors, this thesis concentrates on impacts on OTR within the Capricorn Group. (Davies 1976; Jell and Flood 1977).

OTR is on the outer shelf, distant from the impacts related to mainland development and has had little local human modification. Due to the distance from shore and the relatively untouched environment, changes in Foraminifera assemblages over time are not expected on OTR. It is expected that OTR will provide an indication of the extent of the influence of global anthropogenic change on the GBR.

# **Material and Methods**

#### Study site.

One Tree Reef (OTR) is a lagoonal platform reef, one of 14 reefs that comprise the Capricorn Group in the southern GBR (23° 30' S, 152° 06' E). OTR, composed solely of carbonate sediment, is situated approximately 100 km east of Gladstone, Queensland and 10 km west of the continental shelf edge (Fig. 3) (Davies 1976; Jell and Flood 1977; Mamo 2016). On the GBR outer shelf up to 99% of sediment is biogenically derived calcium carbonate and benthic Foraminifera are among the most important producers (Scoffin and Tudhope 1985). The reef area is 12.7 km<sup>2</sup> and has a small vegetated, coral shingle cay (0.075 km<sup>2</sup>) located in the southeastern corner on which The University of Sydney established a scientific research station in 1971 (Jell and Flood 1977). Other than this low impact scientific facility the area is a designated Scientific Research Zone, with human access restricted in comparison to similar reefs on the GBR. OTR's limited modification and distance from the mainland make a perfect model for a natural reference site for the outer, southern GBR.



**Fig. 3**. Location map of One Tree Reef. a) position from Australian mainland and within the Capricorn Group, showing 40 m depth bathymetric contour line; b) One Tree Reef, with the core position marked by a red arrow. First, Second and Third lagoons are identified, and the island is circled in red. Scale bar = 1 km. (Map in a) adapted from Barret and Webster 2012, Fig.1; (Map in b) adapted from Landsat image supplied by Heron Island Research Station.

OTR has three shallow lagoons, separated from each other by reef framework that is exposed at low tide. The largest lagoon is 10 km<sup>2</sup> in area and is referred to as First Lagoon (Fig. 3). OTR is fully rimmed; at low tide the three lagoons pool above mean sea-level, separated from the open ocean for approximately 6 h daily (Fig. 3) (Davies 1976; Chazottes et al. 2017). Combined with a maze of reticulate reef systems within First Lagoon, this creates a complex water circulation system (Frith and Mason 1986). Water moves from the windward to leeward direction in the lagoon (Frith 1983).

The inner reef system, consisting of micro-atolls and patch reefs, forms a network through First Lagoon and contribute *in situ* bioclastic sediment in addition to that transported from the reef crest. Distance from the coast means that OTR sediments are wholly bioclastic, composed of autochthonous carbonate (Davies 1976). The sediment grain size decreases from the south eastern end of First Lagoon to the northern part of the lagoon and at the time of core collection evidence of bioturbation was reported to be low (Kosnik et al. 2015).

#### The core and dating methods

A 1.6 m long, 80 mm diameter percussive hand core was obtained in September 2012 from the north western end of First Lagoon (23.49677° S, 152.06587° E) (Fig. 3) (Kosnik et al. 2015). At the time of collection water depth was 4.5 m (see methods in Kosnik et al., 2015). During collection the core compressed 2 cm, as such all measurements reflect compressed length. The core was split longitudinally, half stored for archival purposes and the other half used for detailed sampling as part of this thesis and other research. The sediment retrieved from the core is composed of a homogenously fine grained bioclastic calcareous material with median grain size of 85  $\mu$ m (Kosnik et al. 2015). Texture and colour is consistent throughout; there is no evidence of terrestrial derived sediment or visible changes in grain size or texture.

Kosnik et al. (2015) sampled 1.0 cm intervals every 5 cm (down to 56-57 cm depth interval) for lead -210 (<sup>210</sup>Pb) dating at the Australian Nuclear Science and Technology Organisation (ANSTO) Environmental Radioactivity Measurement Centre. The 47- 48 cm interval was excluded due to low levels of lead. <sup>210</sup>Pb dating has been applied since the 1970's for estimating the age of recent marine sediment and has confirmed that the carbonate sediments in the core are in stratigraphical order (Koide et al. 1972; Kosnik et al. 2015). The <sup>210</sup>Pb dating method has been shown to be accurate up to 150 years and used to create age/depths curves as the rate of <sup>210</sup>Pb natural decay is known (Appleby and Oldfield 1978).

Measurement of the <sup>210</sup>Pb rate of decay enables the estimation of a chronology and sedimentation rates producing age/depths curves using two models based on the assumptions of either a constant initial concentration (CIC) or a constant rate of supply (CRS). For the purpose of this analysis the more conservative CIC model has been used to correlate depth with age, which dates the base of the core at ~ 400 ya (Table 1). The sedimentation rate is estimated at 3.9 mm pa, with translates to an age range of ~2.5 yrs per cm of sediment through the core. Age uncertainty for the core layers using the CIC model range from 5 – 26 years (Table 1), which is greater than the time-averaging of layers.

The age estimates from the CIC model have less uncertainty than those from the CRS model, although the models ages overlap in the 19<sup>th</sup> and 20<sup>th</sup> century (Table 1). The CRS model predicts future ages for the top layer of the core. While age correlations using either model agree in the mid years, there is notable variation in the oldest and youngest age estimates. For the purposes of this study core layers were selected with the criterion that they fall within the period ranges using either age model, but CIC model ages will be used hence forth (Fig. 4).

**Table 1.** Ages and uncertainties using <sup>210</sup>Pb under CRS and CIC models for layers picked. Mid mm = mid-point of the 1 cm layer picked. Age Fit is the model age estimate, lower and upper are the 95% CI range for the model estimates. Uncertainty is the 95% CI associated with the model estimate. Pre-colonial = pink, colonial = green, modern=blue.

Mid mm	<sup>210</sup> I	Pb ages und	ler CIC (Y	ears AD)	<sup>210</sup> Pb ages under CRS			
	Age Fit	Lower	Upper	Uncertainty	Age Fit	Lower	Upper	Uncertainty
25	2004	2008	2000	7	2022	2052	1991	60
75	1991	1995	1988	7	2005	2034	1977	57
125	1978	1981	1975	6	1989	2017	1962	55
325	1927	1929	1925	5	1925	1954	1896	57
375	1914	1917	1912	5	1909	1939	1879	60
605	1855	1859	1851	8	1835	1877	1794	83
1105	1726	1735	1718	17	1674	1750	1599	151
1405	1649	1661	1637	24	1578	1676	1480	196
1505	1623	1636	1611	26	1546	1651	1440	211

The complete core is ~1.6 m long, sectioned into 1 cm intervals. The length of the core was divided into three distinct sampling intervals where the layer age uncertainty falls entirely within the: Modern (post 1945 [< 240 mm]), Colonial (1945 – 1788 [260 mm - 840 mm]) and Pre-colonial (pre 1788 [> 895 mm]). Five sample layers were selected from each time interval using a stratified random number generator (R version 3.6.1), but time only allowed the full preparation of the first 9 samples (3 from each time interval) (R Core Team 2019). Selected core layers (Table 1) were weighed using a Metler Toledo scale (0.01 mg resolution) to obtain gross weights before transferred to beakers and soaked for 20 min in tap water to breakup clumps of sediment



**Fig. 4** Estimated ages of using CRS model plotted against estimated ages using CIC model. Colour codes indicate the three time periods modern, colonial and pre-colonial. Samples picked are marked as circles. Horizontal lines are age uncertainties under CIC model, vertical lines are age uncertainties under CRS model. The blue dotted line shows the intercept of 2012, the core collection date. The black dotted line is the unity line indicating perfect agreement between the two models.

Sample layers were wet sieved using tap water, using stacked sieves:  $250 \mu m$ ,  $125 \mu m$  and  $63 \mu m$  to separate into three size fractions, to ease picking and enable comparison with published work by other researchers. Between each sample the sieves were cleaned thoroughly with tap water and placed in a Soniclean for 3 min to reduce contamination risk between samples.

Sediment fractions were dried at ambient temperature and then weighed. Size fractions were split into smaller aliquots using a Carpco sample splitter until a manageable sized sediment sample was achieved. Care was taken to clean the splitter and the containers between each fraction and layer, and sequential splitting was undertaken to minimise contamination between samples.

A pilot study using samples from an undated OTR core indicated that 250 mg of sediment contained approximately 100 - 200 Foraminifera. To get ~ 250 mg samples each size fraction was split four times. Half of the 4<sup>th</sup> split was designated split A, the other half of the 4<sup>th</sup> split was split a 5<sup>th</sup> time to obtain splits B1 and B2. Initially B1 fractions were picked from each layer, however after examination it became clear that the dated core had a greater proportion of > 63  $\mu$ m sediment than the pilot samples. B1 split was then split again into C1 and C2 for the > 63  $\mu$ m fraction. B1 splits (~ 250mg) were exhaustively picked for the > 250  $\mu$ m and 250 - 125  $\mu$ m fractions. Due to the larger volume of 63 -125  $\mu$ m sediment and the associated large number of Foraminifera, the C1 split (~ 150 mg) was picked for the 63 -125  $\mu$ m fraction.

The Foraminifera in the 63 - 125  $\mu$ m fractions are difficult to identify using a stereomicroscope so taxonomic identification was completed by examination of taxa under scanning electron microscope (SEM). As such only the first three layers (110 – 111 cm, 2 – 3 cm and 60 – 61 cm) had the 63 - 125  $\mu$ m fractions picked. Only the > 250  $\mu$ m and 250 - 125  $\mu$ m fractions were picked for the remaining six layers. The picked 63 - 125  $\mu$ m fractions provide an indication of whether there are trends that should be investigated further in this size fraction. When using the >125  $\mu$ m fraction for a research project, the additional study of a smaller number of samples in the 63 - 125  $\mu$ m fraction enables estimation of whether reliance on the larger fraction has introduced a size bias (Sen Gupta et al. 1987).

All sediment samples were exhaustively picked, rather than arbitrarily selecting a subsample abundance target to facilitate comparison of species richness and abundance through time. All foraminiferal tests were picked, regardless of condition or whether they appeared juvenile or mature. Sample sizes were such that juveniles and damaged tests could be excluded from later analysis and still retain ~ 200 identified specimens per sediment layer. This process may exclude some rare taxa, however, a count of between 150-300 individuals is standard protocol for subsample size to assess changes in species diversity and composition over time and obtain census data (Hallock et al. 2003; Murray 2006; Schönfeld 2012). Genus level identification has been completed to enable the tracking of patterns and fluctuations in community compositions through the core.

Samples were picked in a random order to minimise bias through the core due to increased skill at detecting and identifying specimens over time. All specimens were picked using an Olympus SZ40

stereomicroscope using 20 x oculars applying standard picking techniques (Murray 2006). Specimen counts were recorded, sorted and transferred to labelled, welled microscope slides. Raw specimen counts for each layer and fraction were entered into a spreadsheet and assigned to a genus/species for further analysis (Appendix 1). Approximately 25% of specimens were mounted on carbon coated aluminium stubs and gold sputter coated (EMTECHK 550 Gold Spotter Coater) and then imaged using an electron microscope (JEOL 648 0LA) for identification. Images were then prepared using Pixelmator Pro Version 1.4 Hummingbird. Specimens detailed in Appendix 3 have been provided Macquarie University Palaeontological Catalogue (MPAL) numbers and all specimens are housed in the collections of Palaeobiology Research Lab, Macquarie University.

#### Specimen identification

Where possible specimens were identified to species level, but the large number of SBF in samples meant that some taxa could only be identified to genus level. Some genera, such as *Quinqueloculina* have 938 known species, so species level identification was not feasible in the time (Hayward et al. 2019). However, tracking key changes in Foraminifera assemblage over time at genus level changes is well established (Hallock et al. 2003; Uthicke et al. 2010). Species identification can be inconsistent across researchers due to splitting and lumping practices but generic composition has been demonstrated to provide a more conservative resolution for monitoring assemblage changes over time (Hallock et al. 2003). For palaeoecological data to be useful in assisting conservation biology, taxonomic resolution is important (Willis and Birks 2006). While there may be information loss by concentrating on generic rather than species level identification, the likelihood of consistent identification increases both within the study and as a comparison between published research. The use of genera thus enables meaningful comparison with other research data.

When tests are in a poor condition it is often possible to allocate them to a genus or a family, but not to a species. Where it was not possible to allocate a specimen to a genus due to the amount of test damage they were assigned to "unidentified porcelaneous" or "unidentified hyaline" categories. No specific ranking of taphonomic condition was undertaken, however if the external features of the test were unable to be assessed due to breakage or abrasion, or the aperture was completely removed from the Miliolids, then the specimen was designated "unidentified". Some tests, even in poor condition, can still be identified due to distinctive features, such as the shape or for example the intricate test decoration of *Spiroloculina foveolata* Egger, 1893.

A recent comprehensive taxonomic monograph (Mamo 2016) identified 133 species of benthic Foraminifera from the Capricorn Group. This monograph was used as the primary source for specimen identification. While identifications were cross checked using primarily taxonomic works (Jones and Brady 1994; Hayward 1999; Parker 2009; Debenay 2012; Lei et al. 2017; Förderer and Langer 2018) and the World Foraminifera Database (Hayward et al. 2019) to verify current taxonomic status, Mamo (2016) was relied upon through analysis to ensure that comparisons could be made with that body of work and in consideration of the fact that this taxonomy is the most recent specialised taxonomy for the GBR. In the small number of cases where species recombinations have been proposed, the combination used in Mamo (2016) has been used in analysis.

Specimens were allocated to one of nine functional morphology groups or "morphogroups", which can then be applied, based on assumptions of linkages between morphology and lifestyle, to categorise taxa into epifaunal and infaunal groups (Corliss and Chen 1988). Morphogroups lump genera based solely on the morphology of the test, rather than using taxonomic assignments. Broad groupings of forms with similar morphologies have been used to infer information about palaeoenvironments and microhabitats (Alperin et al. 2011). Classification and analysis independent of taxonomic constraints can be valuable in situations where there is uncertain taxonomy, which can be complex in the case of SBF (Alperin et al. 2011).

Epifaunal groups, those that live on the sediment, plants or hard surfaces are allocated to either; rounded trochospiral, plano-convex trochospiral, milioline and biconvex trochospiral. Morphology that is allocated to the infaunal grouping includes; rounded planispiral, flattened ovoid, tapered and cylindrical, spherical and flattened tapered (Corliss and Chen 1988). To confirm definitions of morphology with groupings the descriptions and terminology applied by Debenay (2012) were used, as initial descriptions of taxa commence with test shape and this enabled the application of a consistent standard of examination (Debenay 2012). LBF taxa such as *Peneroplis* and *Sorites*, which are not within the scope of Corliss and Chen 1988, were allocated to the epifaunal, milioline group.

Foraminifera were also classified into ecological functional groups (symbiont-bearing, opportunistic, sensitive or other small heterotrophic benthic Foraminifera) following Hallock et al. (2003) and Dimiza et al. (2016) to allow calculation and application of foraminiferal indices. While symbiont bearing taxa are identified with reasonable accuracy, the classification of small benthic genera is less well known. Different papers allocate different taxa to the opportunistic grouping. To enable calculation of Foraminifera specific indices the allocations used in the original papers were applied. Where there was disagreement, or past research had not determined the ecological category, it was

generally in relation to rarer taxa. As such these genera were allocated to the heterotrophic group. Additionally, both indices have had genus level identification applied.

# **Statistical Analysis**

Statistical and assemblage analysis was conducted at genus level. Initially all fractions and all specimens were examined individually to understand differences between and within the three fractions principally to discern the impact of not examining the >63 - 125  $\mu$ m fraction for all layers. After this initial analysis, all further analysis was conducted on the >125  $\mu$ m fraction only (analytically combining the 125 – 250  $\mu$ m and > 250  $\mu$ m fractions). For subsequent analysis of diversity and Foraminifera specific indices unidentified, juvenile and broken specimens were removed and only taxa allocated to a genus were considered.

Data were not normally distributed, therefore significance of variance in means of all indices among layers was tested using a Wilcoxon signed-rank test (R's "wilcox.test" function) and among the three time periods; pre-colonial, colonial and modern, using the non-parametric Kruskal-Wallis rank sum test (R's "kruskal.test" function). Both the difference between layers and time intervals were assessed to increase the opportunity of detecting any changes in assemblages. Analyses were undertaken in R 3.6.1 with additional packages detailed below (R Core Team 2019). An alpha level of 0.05 was applied to all statistical tests. A link to the specimen count file and the R script used in analysis and for figures is found in Appendix 1.

## **Diversity and Abundance**

Total count (T), genus richness (S) and relative abundance (RA = the total of each genus (n) / total specimens (T)\*100) were calculated for each sample. Shannon-Wiener Index (H), Simpsons (D), and Fisher's Alpha ( $\alpha$ ) were calculated using the 'diversity' function in the R 'vegan' package (Oksanen et al. 2019). These are commonly used indices in foraminiferal research, each with underlying assumptions or limitations (Stephenson et al. 2015). It is noted that the Shannon-Wiener index assumes that all species in a community are represented, Simpsons is a measure of dominance and Fisher's Alpha is not strongly influenced by sample size (Magurran 2013). The three indices are calculated to provide a comprehensive assessment of alpha diversity. The Chao 1, an estimator of unseen species or true richness based on actual counts, was calculated with the 'specpool' and 'estimateR' functions in 'vegan' (Oksanen et al. 2019).

### Assemblage Analysis

Cluster analysis is a common method used in ecology to allocate samples and/or species into groups, based on similarities or dissimilarities between samples (van Tongeren 1995). Agglomerative, hierarchical methodology has been chosen here, which groups single objects into clusters and then ranks them hierarchically using R's 'hclust' function (R Core Team 2019). Q-mode hierarchical cluster analysis, starting with a Bray Curtis dissimilarity matrix of the relative abundance data (using the vegan's 'vegdist' function), before applying the Ward error sum of squares hierarchical clustering method was plotted (Oksanen et al. 2019). Several other methodologies were tested, however, Ward's method minimises the within cluster variance by creating clusters with the smallest sum of squares (Murtagh and Legendre 2011). By undertaking analysis of the relative abundance, variance in the data due to differences in sediment weight were avoided.

A one-way analysis of similarities (ANOSIM) was conducted to assess the null hypothesis ( $H_0$ ) of no difference in taxonomic composition between time intervals using vegan's 'ANOSIM' functi (Oksanen et al. 2019). A community analysis of deviance using the command 'mvabund' was undertaken to test for significant changes at a community level across time intervals using the R package mvabund to analyse multivariate abundance data (Wang et al. 2012).

Nonmetric Multidimensional scaling (NMDS) was undertaken using the 'vegan' package methods 'metaMDS' function to identify patterns or changes in the composition of foraminiferal assemblages (Oksanen 2015). NMDS uses rank order (distances) for ordination and can be used with nonlinear species data (Oksanen 2007). With this command data is square root transformed before being Wisconsin double standardised to create a Bray-Curtis dissimilarity matrix for depicting gradients (Oksanen et al. 2019). A NMDS model was established using the configuration with the lowest stress value. A regression model was fitted to check the goodness of fit between the data and the ordination.

A plot of polar coordinates was produce using the R package 'EcoIndR' applying the 'DER' function (Guisande et al. 2017). This algorithm calculates 39 indices before scaling the indices from 0 to 1. Once the indices are standardised, polar coordinates for all samples and all possible combinations are calculated and Euclidean distances are calculated so as to maximise dispersion among all the samples. This plot was included as it provides another method of examining the relationship among assemblages. The plot can be derived using specified indices, or the algorithm will apply the indices. The algorithm applies up to five indices from the list of 39: two of rarity, 14 of heterogeneity, seven of evenness, two of taxonomic diversity, eighteen of phylogenetic diversity and six of functional

diversity. Two plots were created, one using indices chosen from the list and one using allocated indices. The same general configuration was obtained, so the chosen indices have been used for this report. The indices applied were Rarity, Simpson, Pielous Eveness and Taxonomic diversity. The details of the indices are attached in Appendix 4.

#### Foraminifera specific indices

The FORAM index (FI) and the Foram Stress Index (FSI) were calculated to assess whether there was evidence of changes in water quality over time, although neither index is designed to reflect all types of environmental change, such as chemical pollution (Hallock et al. 2003; Dimiza et al. 2016). Both indices are calculated based on the weighting of allocated genera to ecological categories but differ in the assignment of categories. The FI was designed for reef environments, specifically to indicate whether the system was supportive of coral growth. It relies on three categories, photosymbiont-bearing, opportunistic and other small heterotrophic foraminifers (Formulas below).

An assemblage with FI > 4 indicates low nutrient water that supports coral reef growth, while FI < 2 represents unsuitable conditions for photosynthesising taxa such as coral and by extrapolation indicate nutrient rich or poor water quality (Hallock et al. 2003). Hallock (2003) specifies two genera as opportunistic *Elphidium* and *Ammonia*, and then identifies several families, which have opportunistic genera. However, a review of five papers (Uthicke and Nobes 2008; Narayan and Pandolfi 2010; Uthicke et al. 2010; Reymond et al. 2013; Fajemila and Langer 2017), four based on studies from the GBR, shows that different researchers allocate different taxa to the "opportunistic" group. To facilitate comparison with the greatest number of sites on the GBR the allocation applied by Uthicke et al. (2012) has been followed, such that only *Elphidium* and *Ammonia* are treated as opportunistic herein.

The FSI can be used in assessing soft-bottom environments such as lagoons and divides the benthic Foraminifera assemblage into sensitive and stress tolerant taxa. In a natural or pristine environment, the FSI will be between nine and ten, whilst a heavily polluted environment would range between FSI = 1 to 2 with an azoic environment indicated by FSI< 1. The FSI was designed using live specimens rather than fossilised specimens, however, is likely to still provide strong signals of change over time in an assemblage. To ensure consistency with the authors intent, for the calculation of the FSI, *Elphidium* was treated as stress sensitive as per Dimiza et al. (2016). Taxa allocations to stress tolerant follow Dimiza et al. (2016): *Ammonia; Melonis* Montford, 1808; *Bolivina; Bulimina* d'Orbigny 1826; *Textularia* Defrance, 1824; *Globocassidulina* Voloshinova, 1960.

For the FSI symbiont bearing and heterotrophic groups were allocated to the sensitive grouping. $FI = (10 \cdot P_{sym}) + (P_{opp}) + (2 \cdot P_{het})$  $FSI = (10 \cdot P_{sen}) + (P_{str})$ Where  $P_{sym}$  = proportion of symbiont-bearing taxa $P_{opp}$  = proportion of opportunistic taxa $P_{sen}$  = proportion of sensitive taxa $P_{str}$  = proportion of stress-tolerant taxa $P_{het}$  = proportion of heterotrophic or other small benthic taxa

The ratio of infaunal taxa to epifaunal taxa was calculated for each layer and analysed over time based on morphological assignment of the test shape.

# Results

#### Sediment

After washing and sieving to remove mud, most of the remaining sediment was in the 63 - 125  $\mu$ m fraction, averaging 31% of the weight of the sediment across all layers. The > 250  $\mu$ m fraction was consistently the size fraction with the least sediment, accounting for an average of 14% of total sediment weight. In excess of 4,200 specimens of Foraminifera, broken and complete, were picked from the nine samples across all size fractions.

The density of Foraminifera tests per mg of sediment, was variable across fractions and layers, ranging from 0.11 Foraminifera per mg in the 1405 mm (1649 AD) (>250  $\mu$ m fraction) to a maximum of 2.11 Foraminifera per mg in the 75 mm layer (1991 AD) (125 - 250  $\mu$ m fraction) (Table 1.). As well as being the smallest component of total sediment the > 250  $\mu$ m fraction consistently had the lowest number of preserved tests falling to ~ 0.1 Foraminifera per mg of sediment in the 1600's.

Variance in the number of tests/mg of sediment reduces when the size fractions are combined, although the same layers remain representative of peak and minimum abundance. Across all samples the highest density of Foraminifera occurs in the 125 - 250  $\mu$ m fraction, with the exception of the layer 2-3 mm (2004 AD), where the highest number of tests were found in the 63 - 125  $\mu$ m fraction (Fig. 5). Excluding the 63 - 125  $\mu$ m fraction, the average number of tests per mg across combined layers was 0.99  $\pm$  0.31 tests/mg (mean  $\pm$  SD). The peak density remains in 75 cm (1991 AD) with 2.48 tests/mg; minimum in 1405 mm (1649 AD) with 1.18 tests per mg. The number of Foraminifera per mg of sediment fluctuates significantly through layers of the core but does not follow a long-term trend of increasing or declining density over time (V = 45, p = 0.004) (Fig. 5). The bottom three layers, the oldest sections of the core, show a decline in the Foraminifera per mg, from 605 mm (1855 AD), however, the oldest core layer 1505 mm (1623 AD) has higher density of tests than the youngest core layer 25 mm (2004 AD) for the 2 larger size fractions. When layers are combined into time intervals there was no significant difference in foraminifera per mg of sediment (chi-squared = 2, df = 2, p = 0.37).

#### Unidentifiable tests

All layers contained large numbers of unidentifiable tests. Unidentifiable tests were a combination of juveniles, too undeveloped to be taxonomically assigned, and damaged tests. The highest percentage of specimens that were unidentifiable were in the 63 - 125  $\mu$ m fractions, reaching 41% in the 25 mm layer (2004 AD) (Fig. 5). Even when ~ 50% of the 63 -125  $\mu$ m taxa were examined under SEM for

Layer Weight (mg)				ght (mg)	) Foraminifera				
	Core depth (mm)	Age AD	Sieve size (um)	Initial	Picked	Total	Unid	Unid %	Total Foram per mg.
	20-30	2004	63	9791.4	139.46	222	92	41	1.59
			125	6636.6	253.91	244	66	27	0.96
			250	5305.7	195.05	59	1	2	0.3
	70-80	1991	125	8126	250.51	529	117	22	2.11
			250	5236.9	140.13	50	5	10	0.36
	120-130	1978	125	7960.1	262.72	298	28	9	1.13
			250	4301	137.64	34	4	12	0.25
	320-330	1927	125	9526.5	324.68	661	187	28	2.04
			250	5559.5	210.75	75	6	8	0.36
	370-380	1914	125	8883.4	288.22	455	63	14	1.58
			250	5467.6	176.6	36	2	6	0.2
	600-610	1855	63	11492.3	219.51	167	38	23	0.76
			125	4927.8	163.19	307	70	23	1.88
			250	3940.1	112.02	25	3	12	0.22
	1100-1110	1726	63	11525.8	176.61	206	72	35	1.17
			125	4677.8	134.9	210	38	18	1.56
			250	4168.5	112.67	21	1	5	0.19
	1400-1410	1649	125	7528.2	239.65	257	61	24	1.07
			250	5999.9	190.83	21	0	0	0.11
	1500-1510	1623	125	8228.35	327.33	342	69	20	1.04
			250	8416.97	230.31	29	4	14	0.13

**Table 2.** Sediment weight for picked layers and fractions. Total Foraminifera abundance and foraminiferal abundance per mg of sediment, including unidentifiable taxa ('Unid') and percentage of unidentifiable ('Unid %') for each fraction. Depth is correlated with age as per Table 1, methods. Colours as per Fig. 4.

1105 mm (1726 AD) and 25 cm (2004 AD) layers the number of unidentifiable taxa remained high. The > 250  $\mu$ m fractions consistently had the lowest number of unidentifiable taxa predominantly resulting from test damage, with just 2% of specimens being juvenile. Excluding the 63 - 125  $\mu$ m



**Fig. 5.** Total Foraminifera picked. Panel a) raw count by all fractions over time, panel b) Foraminifera picked per mg of sediment for each fraction over time, panel c) Unidentifiable Foraminifera for each fraction over time. Colours as per Fig. 4.

fractions, to enable comparison across all layers, the 125 mm (1978 AD) layer had the lowest number of unidentifiable specimens, mostly damaged tests, representing 9.6% of the total count for that layer. Over 25% of the tests from the 325 mm (1927 AD) and 25 mm (2004 AD) layers were too damaged to be assigned to a genus. Overall, an average of 19.2% of all specimens counted were allocated to either juvenile or damaged test categories, and there significant difference in the was no unidentifiable tests across the three time intervals for the >125 µm fractions (chisquared = 1.16, df = 2, p-value = 0.56).

#### Genera

Across all samples and fractions, excluding unidentified taxa, 3,139 specimens allocated to 105 species within 65 genera and 42 families were identified in the nine sediment layers investigated, the orders assigned to Textularida, Miliolida, Rotaliida, Lagenida, Spirillinida, Robertinida and Lituolida (Appendix 1). Seventeen genera (26%) were recovered less than three times (< 0.1% of the total specimen count) and 50 genera (77%) are classified as rare, occurring 1% or less in the overall counts (n < 31). There are 11 genera occurring once through the core and six doubletons, but 1405 mm (1649 AD) layer had no singletons or doubletons. All layers had at least one planktic specimen, predominantly

*Globigerina* d'Orbigny, 1826. Two layers held slightly higher numbers of planktonic Foraminifera with 1927 AD and 1991 AD, each reaching 2% of identified taxa.

	Pre - colonial			Colonial			Modern			Kruskal-Wallis
Years AD	1623	1649	1726	1855	1914	1927	1978	1991	2004	
Richness	20	15	23	28	16	28	16	25	25	$\chi^2 = 2.07, p=0.35$
Abundance	32	21	48	82	39	68	31	55	41	$\chi^2 = 2.76, p=0.25$
Shannon (H)	2.9	2.6	3.0	2.9	2.5	3.1	2.5	3.0	3.1	$\chi^2 = 0.62, p=0.73$
Fisher's $\alpha$	22.8	23.5	17.3	15.0	10.1	17.8	13.3	17.6	27.2	$\chi^2 = 1.87, p=0.39$
Simpson (D)	0.94	0.92	0.94	0.92	0.89	0.94	0.9	0.93	0.95	$\chi^2 = 0.62, p=0.73$

**Table 3.** Rare taxa (n < 1% of total) for picked layers. Layers grouped into time intervals with test for significant difference (df = 2) among, pre-colonial, colonial, modern. Colours as per Fig. 4.

Multiple species were identified from the two most dominant genera; 13 species of *Quinqueloculina* and 7 species of *Elphidium*. An additional 3 variations of *Quinqueloculina* could not be identified to a described species. They are undescribed species, or a morphological variation of a named species.

# The >63 µm fraction

Thirty genera were identified in the 63 - 125  $\mu$ m fraction, with only a single genus (*Asanonella* Huang, 1965) at 600 mm depth (1855 AD) not also identified in the coarser sediment fractions. All other genera found in the 63 - 125 um fraction were also represented in > 125  $\mu$ m samples. All of the 63 - 125  $\mu$ m fractions had lower generic richness (S) than the >125  $\mu$ m fraction (after damaged and juvenile taxa are removed), peaking at 20 genera (Tables 4 and 5). The average Shannon (H) and Simpson (D) indices are similar to the larger size fractions, Fishers-alpha ( $\alpha$ ) was consistently lower than the larger grain fractions (Tables 4 and 5).

**Table 4**. Diversity and Richness indices for  $> 63 - 125 \mu m$  fraction. Layers grouped into time intervals with test for significant difference among, pre-colonial, colonial, modern. Colours as per Fig. 4.

	Pre-colonial, 1726	Colonial, 1855	Modern, 2004	Kruskal-Wallis (df = 2)
Richness	19	20	19	$\chi^2 = 2, p=0.37$
Abundance	116	103	103	$\chi^2 = 2, p=0.37$
Shannon (H)	2.14	2.07	2.03	$\chi^2 = 2 p = 0.37$
Fisher's $\alpha$	6.46	7.4	6.85	$\chi^2 = 2, p=0.37$
Simpson (D)	0.82	0.78	0.78	$\chi^2 = 2 p = 0.37$

The dominant taxon in the 63 - 125  $\mu$ m size fraction is *Quinqueloculina*, which varies in dominance from 41% in 605 mm (1855 AD), 30% in 25 mm (2004 AD), to 18% in 1105 mm (1726 AD). Smaller taxa, such as *Bolivina* and *Glabratella* Dorreen, 1948, are more dominant in this size fraction than in the coarser fractions. The relative abundance of Bolivinitidae was higher in the 63 -125  $\mu$ m fractions than in larger fractions reaching 21% in 1105 mm (1726 AD) and 18% in 25 mm (2004 AD) layers. There was no significant difference between the richness or abundance of taxa, or diversity within the 63 -125  $\mu$ m fractions in the time intervals (Table 4). The 63  $\mu$ m - 125  $\mu$ m fraction is not included in further analyses.

## 125 µm and 250 µm fractions

After removing unidentifiable, damaged and the 63  $\mu$ m – 125  $\mu$ m fraction there remained ~ 200 specimens per layer (Table 5). The mean generic richness through the core was 34 ± 5.4 genera (mean ± SD). Rarefaction curves, for both layers and the separate fractions indicate that there are unsampled taxa, which would likely be sampled with a larger sample, there is little sign of levelling off of the rarefaction curves (Fig. 6). X and Y axis starting points have been increased to enable better display, the rarefaction curves do not cross prior to 20 and 10 respectively.



**Fig. 6.** Rarefaction curves. For combined layers, x and y axis have been logged and the axis adjusted for display. Time intervals colour coded, Modern in pink, Colonial in green, and Pre-colonial in blue.



**Fig. 7.** Chaol estimator for layers with fractions combined. Panel a) number of observed genera graphed against Chaol estimated richness. Vertical bars are standard error bars. b) proportion of estimated genera found in each layer. Blue dotted line is 100% sampling of the estimated richness. Vertical bars are standard error bars. Time intervals indicated as in Fig. 4.



Year (AD)

**Fig. 8.** Diversity and the relative abundance of genera over time for all layers (>125  $\mu$ m fractions). Panel a) Shannon-Wiener diversity index b) Simpsons – D index, c) Fisher's alpha d) Foram Stress Index e) Relative abundance of benthic genera with a total abundance of >1% of the total count (> 31 individuals). Time intervals indicated as in Fig 4 for panels a - d.
When size fractions are combined, peak genus richness occurs in 1927 AD (325 mm) (S = 43), with lowest richness in 1978 AD (125 mm) and 1914 AD (375 mm) (S = 2 9). Mean richness through the core is  $34 \pm 5.4$  (mean  $\pm$  SD). There is a significant difference in richness across the nine core layers (V = 45, p = 0.009). When layers are grouped into time intervals, there is no significant difference in richness among the three time intervals (chi-squared = 2.19, df = 2, p = 0.3).

*Quinqueloculina* contributed 49% of total specimen count and was the dominant genus in all of the layers (Appendix 3, Plate1). Relative abundance (RA) of *Quinqueloculina* varied between 34% and 53% for individual layers. The next most abundant genera were *Elphidium* (14%) and *Bolivina* (5%) across all layers (Appendix 3, Plate 2 and Plate 4). Declines in *Quinqueloculina* generally corresponded with an increase in *Bolivina*. Only six genera made up at least 5% of any layer's assemblage and this group accounted for between 61% (605 cm = 1855 AD) and 78% (125 cm = 1978 AD) of assemblages in the core (Appendix 2).

	Pre - colonial			Colonial			Modern			Kruskal-
										Wallis
Years AD	1623	1649	1726	1855	1914	1927	1978	1991	2004	
Foraminifera	289	213	190	254	403	517	293	429	229	n/a
Richness	35	30	30	40	31	43	29	40	33	$\chi^2 = 2.19$ ,
										p=0.3
Shannon (H)	2.05	2.12	2.39	2.77	2.19	2.42	1.95	2.54	2.34	$\chi^2 = 1.87$ ,
										p=0.39
Fisher's $\alpha$	10.43	9.52	10.02	13.34	7.83	11.14	7.99	10.79	10.57	$\chi^2 = 0.8,$
										p=0.67
Simpson (D)	0.71	0.75	0.80	0.86	0.76	0.78	0.69	0.84	0.78	$\chi^2 = 0.8,$
										p=0.67
Foram Index	2.52	2.43	2.57	2.31	2.38	2.36	2.07	2.27	2.40	$\chi^2 = 5.6,$
										p=0.06
FSI	9.78	9.62	9.62	9.47	9.78	9.37	9.72	8.8	9.49	$\chi^2 = 1.69$ ,
										p=0.43

**Table 5.** Ecological indices for >125  $\mu$ m fractions. Diversity and Richness indices and the Foram Index and the Foram Stress Index (FSI). All taxa except unidentified specimens. Layers grouped into time intervals, with test for significant difference among, pre-colonial, colonial, modern (df = 2). Colours as per Fig. 4.

In addition to the three most abundant taxa, mentioned above, they included *Cibicidoides* Thalmann, 1939, *Sorites* Ehrenberg, 1839 and *Abditodentrix* Patterson, 1985 (Appendix 3, Plate 2 and Plate 4). Porcelaneous taxa accounted for 60% of all specimens (Appendix 3, Plate 1 and 3). Agglutinated specimens were extremely rare, with only 0.3% of the total count (Appendix 3, Plate 5). Large benthic Foraminifera (LBF) or symbiont bearing taxa rarely exceeded 5% in sampled layers and were represented by 5 genera: *Amphistegina*; *Calcarina*; *Neorotalia* Bermudez, 1952; *Peneroplis* Montfort 1808; and *Sorites*. All specimens of *Sorites* were either broken or juvenile but could be readily identified.

The variance in means of all diversity indices showed significant differences among the layers. Layer richness varied significantly (V = 45, p = 0.009), but there was no significant differences amongst the three time intervals, pre-colonial, colonial and modern (Chi square = 2.19, p = 0.33 df = 2). Shannon diversity (H) varied through time and while there was significant difference in H among layers (V = 45, p = 0.004), there was no significant across the three time intervals (Chi square = 1.87, p = 0.39, df = 2). Likewise, a significant difference existed among layers for Fishers Alpha, (V = 45, p = 0.004) and the Simpson D (V = 45, p = 0.004), but not for the three time intervals (Chi square = 0.8, p = 0.67, df = 2).

The FI index was calculated for each of the nine layers, using the methods described by Hallock et al. (2003). There were few genera of symbiont-bearing foraminifer, only *Amphistegina* (n = 4), *Calcarina* (n = 8), *Neorotalia* (n = 5), *Peneroplis* (n = 10) and *Sorites* (n = 100) in the core layers. The most common opportunistic taxa was *Elphidium* (n = 339). Low levels of symbiont bearing taxa and domination of heterotrophic groups, resulted in FI of 2 across all layers, varying between a low of 2.07 in 1978 AD (125 mm), and a peak of 2.57 in 1726 AD (1105 mm). Variations in the FI among the three time periods were not significant (Chi-squared = 5.6, p = 0.06, df = 2) (Table 5). The number of symbiont bearing taxa was lowest in the colonial times, compared to both the modern and the precolonial intervals.

The FSI index removes the weighting from the symbiont bearing taxa and focusses instead on changes in the assemblage of SBF, which dominate this core (Dimiza et al. 2016). The value of the FSI is strongly influenced by the presence of *Elphidium* and treatment of *Elphidium*. Authors of the FSI do not classify *Elphidium* as stress tolerant (Dimiza et al. 2016), while the FI classify *Elphidium* as opportunistic (Hallock et al. 2003). The FSI is stable over time, recording a slight decline in 1991 (FSI = 8.8), corresponding with the highest RA of *Bolivina* and the lowest RA of *Quinqueloculina* in the core (Fig. 8). The FSI range of 9.78 (1505 mm = 1623 AD) to 8.8 (75 mm = 1991 AD) would indicate an area with high water quality. There was no significant variation in the FSI over the three time intervals (Chi square = 1.69, p = 0.43, df = 2).



**Fig. 9** Morphogroups. Foraminifera tests (>125  $\mu$ m fractions) allocated to morphogroups and then split into epifaunal (above the black line) and infaunal for all sampled layers of the core.

The microhabitats of testate benthic Foraminifera were estimated by examining test morphology. On average 72% of taxa in the lagoon through time are epifaunal, predominantly milioline and planoconvex forms (Fig. 9). While there was a decline in 2004 AD (25 mm) from 76% epifaunal to 65% in 1991 AD (75 mm), epifaunal levels increased again by 1978 AD (125 mm). There is no shift in the domination of the core assemblage from a predominantly epifaunal one to one that is dominated by infaunal taxa.

#### Assemblage analysis

There are no significant differences in foraminiferal assemblages among the three time periods (ANOSIM, R = 0.03, p = 0.36). This was confirmed using a MVABUND, which confirmed no significant change in foraminiferal assemblages among the three time periods (LRT = 190.2, p = 0.118). Univariate tests for each genus showed no significant changes among the three time intervals for any individual taxa (p > 0.05).



**Fig. 10.** Dendrogram derived from Q-mode Hierarchical Cluster Analysis. Distance matrix established using Bray Curtis and aggregation using Wards sum of squares method with relative abundance data for all benthic taxa. The y-axis demonstrates the dissimilarity among sample clusters. Clusters are tighter on the left. Time intervals colour coded, modern in pink, colonial in green, and pre-colonial in blue.

Q-mode hierarchical cluster analysis was undertaken to establish whether there were any groupings of samples and the degree of similarity in communities through the core. Different methods of clustering and distance matrix calculation will achieve different dendrograms, each with distinct clusters reflecting the data groupings. Using the Ward sum of squares method the correlation between the original Bray Curtis distance matrix and the cluster matrix is 0.74, higher than with complete and similar to average conglomeration methods and each yield the same dendrogram (Fig. 10). Different methodologies were tried with lower correlations and did not cluster samples with respect to age, or to the age intervals, modern, colonial or pre-colonial. Even after reducing the number of taxa

examined to those composing at least 1% of the total count, the same clusters are returned. Within clusters the old and young layers have consistently been mixed and grouped together indicating, as diversity indices suggest, variation in layers through the core.

Samples cluster into three groups with 1991 AD (75 mm) and 1855 AD (605 mm) tightly clustered in the first arm of the dendrogram (Fig. 10). These years both have the highest species richness, H and Simpson indices. Both 1991 AD and 1855 AD were the years with the lowest RA of *Quinqueloculina*.



**Fig. 11.** Nonmetric Multidimensional scaling (NMDS) of all benthic taxa excluding rare (taxa <1% of total count). Using Bray Curtis dissimilarity matrix. Time intervals colour coded, modern in pink, colonial in green, and pre-colonial in blue.

NMDS of all taxa representing greater than 1% of total count again shows similar grouping of 1991 AD and 1855 AD to the cluster analysis (Fig. 11). Stress analysis of the NMDS has a non-metric fit of  $R^2 = 0.994$  (linear fit  $R^2 = 0.965$ ) for the ordination distances with the observed dissimilarity (Stress = 0.08). NMDS demonstrates the greater influence of *Sorites* on the two oldest / deepest layers 1623

AD and 1649 AD. Pearsons tests for correlation on both axis showed no significant relationship between the years and either axis (MDS1, t = 1.71, df = 7, p = 0.13: MDS2, t = 1.95, df = 7, p = 0.09). Kruskal-Wallis tests for correlation between the axis and three time intervals also showed no significant relationships (MDS1, chi-squared = 4.36, df = 2, p = 0.11: MDS2, chi-squared = 2.49 df = 2, p = 0.29). NMDS shows no significant temporal trend.



**Fig. 12.** Plot of polar coordinates for rarity, heterogeneity, evenness and taxonomic diversity. The area of the convex hull is based on the mean Euclidean distance of the polar coordinates for the indices. The size of the layer circles indicates the species richness, while the colour of the circle highlights the size of the polar value. The indices applied were calculated by the program and include: Rarity, Simpson, Pielou evenness, Taxonomic diversity (D).

On the basis of the polar coordinates plot, the layers are spread out, with some pairing between 1991 AD and 1855 AD, and 1914 AD with 1649, and AD 1726 AD with 2004 AD (Fig. 12). However, the layers have grouped differently than in the cluster dendrogram and the NMDS because the algorithm

has applied a combination of measures for rarity, heterogeneity evenness and taxonomic diversity. The sediment layers are grouped based on their similarities and differences across these four classes of indices. Again, no clustering on the basis of the three time intervals is evident.

#### **Comparison with Mamo (2016) surface samples**

To better understand the results obtained within this study, a comparison was made using the Foraminifera Appendix A, supplementary data from Mamo (2016). Mamo undertook surface sampling from multiple sites on Heron Reef, Sykes Reef, Wistari Reef and OTR in the Capricorn Group over a two-year period from 2007 to 2009. Lagoon samples from Heron, Wistari and OTR were obtained using a Petite Ponar Dredge to collect approximately 300 g of sediment from which 400 tests were picked after splitting and sieving ( > 63  $\mu$ m fraction) each sample. Mamo collected nine samples from the interior of First Lagoon of OTR (sites NE: 36, 1, 38, 25, 8 and sites SW: 33, 43, 34, 54) (Appendix 5). From these nine collection sites, which are most similar to the environment and location sampled here, Dr Mamo collected 3,384 specimens (23 living and 3,561 dead).

	Site 1	Site 8	Site 25	Site 33	Site 34	Site 36	Site 38	Site 43	Site 54	Kruskal-Wallis, df = 1
Richness	25	23	21	30	24	21	26	29	22	$\chi^2 = 11.34, p=0.0008$
Shannon (H)	2.23	2.1	1.85	2.26	2.18	2.30	2.34	2.44	2.23	$\chi^2 = 0.56, p=0.45$
Fisher's $\alpha$	5.93	5.31	4.74	7.53	5.62	4.74	6.25	7.19	5.02	$\chi^2 = 12.8, p=0.0003$
Simpson (D)	0.81	0.81	0.73	0.81	0.81	0.84	0.82	0.85	0.83	$\chi^2 = 2.85, p=0.09$
Foram Index	2.73	2.26	2.17	2.41	2.16	2.64	2.49	2.13	4.92	$\chi^2 = 0.4, p=0.51$
FSI	10	9.82	9.96	9.89	9.82	9.98	9.66	9.66	9.91	χ <sup>2</sup> =9.32, p=0.002

**Table 6.** Mamo's diversity and richness indices and the Foram Index and the Foram Stress Index Statistics for nine Mamo (2016) inner lagoon samples, with test for significant difference between Mamo (2016) samples and OTR core samples using Kruskal-Wallis.

Across the nine sites sampled in the OTR lagoon, Mamo reported 51 genera. Genus richness (S) ranged from 21 to 30 across the nine sampling locations with a mean of  $24.5 \pm 3.3$  (mean  $\pm$  SD) compared to the core  $34 \pm 5.4$  (mean  $\pm$  SD). Fishers Alpha and genus richness were significantly higher in core samples than in the surface samples, possibly reflecting the accumulation of tests over time. The Shannon-Wiener diversity (H) was similar to that of the core data (core mean H =  $2.3 \pm 0.26$ ) averaging H =  $2.2 \pm 0.17$  (mean  $\pm$  SD) over all sampling sites. There is no significant difference from the H or D for the core and the surface sites (Table 6). As with the core samples,

*Quinqueloculina* was the dominant genus at all sites and averaged 36% of each sample. There were however a greater number of abundant other genera, *Elphidium* 10%, *Adelosina* d'Orbigny, 1826, 12% and *Siphonaperta* Vella, 1957, 9% while *Bolivina* only represented 1% of total counts. As such there were fewer singletons (n=8) and doubletons (n=4). When small miliolids are combined (*Adelosina, Hauerina, Miliolinella* Wiesner, 1931, *Quinqueloculina, Spiroloculina* d'Orbigny, 1826, *Triloculina* d'Orbigny, 1826) excluding the LBF, they dominate all sites, with the exception of site 54 (41%), reaching 75% at one sample site.

One site, site 54, from Mamo (2016) differed from both the core samples and the other surface samples with *Calcarina* representing 26% of the total. The high level of *Calcarina* at site 54 resulted in an of FI = 4.92 while other sites had similar FI's as the core, varying between FI = 2.13 and FI = 2.73. Site 54 is on the edge of the reef flat where LBF are reported in high numbers. Without this site there is no significant difference between the FI of the core samples and the FI of the surface samples (chi-squared = 0.08, df = 1, p = 0.77). The FSI for all surface sites was high, between 9.66 and 10, overall significantly higher than in the core layers (Chi-squared = 9.32, df = 1, p = 0.002).

## Discussion

The main aim of this study was to identify any changes in OTR lagoon foraminiferal assemblages associated with colonial and modern time intervals and to determine if any of these changes were responses to anthropogenic stressors. OTR was chosen as a study site due to its remote location from the mainland and protected status. While foraminifera from cores have been examined from several inshore GBR reefs, to gain an understanding of the spatial extent of temporal change, fluctuations in ecological conditions should be understood with reference to local conditions and should be based on measurements of impact across multiple locations (Alve et al. 2009). Differences in assemblages in a core may reflect both specific regional and/or microhabitat characteristics (Uthicke and Nobes 2008). Ecosystems are not fixed conditions in time so natural variability is to be expected, and it is difficult to separate natural variation from variation resulting from disturbances (Willis and Birks 2006). The density of foraminifera on the OTR reef flat has been shown to be patchy, both in terms of taxa distribution and spatial biomass (Doo et al. 2017). Analysis of foraminiferal assemblages within three time intervals, pre-colonial, colonial and modern was undertaken to minimise the impact of short term noise. These analyses suggest that the foraminifer assemblage of OTR's First Lagoon represents a pre-colonial assemblage and that it has remained relatively stable over the last  $\sim 400$ years.

#### Grain size

Sediment through the core is consistently dominated by the < 125  $\mu$ m fraction (Table 2). The sediment grain size has a median grain size of 85  $\mu$ m (Kosnik et al. 2015). This is consistent with environmental conditions and past studies, which have shown a fining of sediment toward the NW end of First Lagoon (Davies 1976). The core records no evidence of terrigenous sediment as a result of extreme weather events such as Cyclone Joy in 1991 AD (75 mm), which resulted in a flood plume that reached Heron Island reef flat (Devlin et al. 2001).

The >63  $\mu$ m, >125  $\mu$ m and >150  $\mu$ m sediment fractions are most commonly used in benthic foraminiferal analysis (Bergamin and Romano 2016). The Foraminiferal Bio-Monitoring (FOBIMO) initiative, which attempts to establish a protocol for the use of (live) benthic Foraminifera in monitoring marine ecosystems in Europe, suggests that given the additional time and skill required for assessing the >63  $\mu$ m, the >125  $\mu$ m is generally preferable, unless conditions are expected to be anoxic (Schönfeld et al. 2012). There were no expectations, or reports, of anoxia in the OTR lagoon. Analysis within lagoonal environments in the Maldives reefs relied on the >125  $\mu$ m fraction (Parker and Gischler 2011). Analysis on ten lagoons in French Polynesia using fine (> 50  $\mu$ m) and coarse (> 500  $\mu$ m) fractions noted, that with the exception of two attached species, most species were present in both size fractions (Bicchi et al. 2002).

Both the FI and the FSI reported herein are based on analysis of the >125  $\mu$ m sediment fraction (Hallock 2000; Dimiza et al. 2016). It is possible that, in some environments, the >63  $\mu$ m fraction may be needed to detect small opportunistic species and their response to changes in the levels of organic input when calculating the FI. Using the >125  $\mu$ m fraction may fail to retain some SBF that have been identified as environmentally indicative taxa that are important for correct usage of the FI, but is, however, preferable to the 150  $\mu$ m (Hallock et al. 2003). If using the >125  $\mu$ m fraction for a research project, the additional study of a smaller number of samples in the >63  $\mu$ m fraction enables estimation of whether reliance on the larger fraction has introduced a size bias and provides an indication of the information loss (Sen Gupta et al. 1987).

Due to the small average grain size through the OTR core the exclusion of the >63  $\mu$ m fraction in this study risked loss of information regarding species present in the OTR lagoon and therefore in recognising changes over time. The three layers examined to assess this risk, however, did not have a higher number of taxa or a higher diversity than the >125  $\mu$ m fraction. Mamo (2016) used the >63  $\mu$ m fraction for analysing surface samples from the Capricorn Group. Genus richness of Mamo's surface samples from the lagoon was significantly lower than found in the core, suggesting that excluding the < 125  $\mu$ m from the core samples is not excluding taxa (Chi-squared = 11.34, p = 0.0008). Through the core only one specimen of one genus (*Asanonella*) appeared solely in the 63 - 125  $\mu$ m fraction. For this core, the >125  $\mu$ m fraction is adequate for tracking changes in foraminifera assemblages.

#### Assemblages through the core

All layers in First Lagoon are dominated by SBF, predominately small miliolids, on average  $57 \pm 17\%$  (Mean  $\pm$  SD) of all taxa across all layers of the core. LBF represent less than 5% of all individual Foraminifera identified through the core. Species of *Quinqueloculina* represent between 34% and 53% of specimens with mean relative abundance (RA) of  $44 \pm 6\%$  (Mean  $\pm$  SD). Some of the *Quinqueloculina* and small miliolids have been classified into different genera of small miliolids by the World Foraminifera Database (Hayward et al. 2019) since Mamo (2016). All analyses were rerun changing the allocation of taxa between these genera with little impact to diversity indices, clustering or foraminiferal specific indices and no change in the overall result of no significant change among the time intervals through the core. The most recent taxonomic allocations are detailed in the data sheet attached with Appendix 1. Davies (1976) reported that the lower energy areas of the OTR

lagoon were dominated by miliolids and that the reef crest was dominated by the LBF *Baculogysina*. *Baculogysina* was not recovered in the core samples and in low numbers (n < 2) in Mamo (2016) surface samples (excluding site 54, n = 4), indicating that foraminifer tests from the reef crest are not transported to this part of the lagoon. In the nine surface samples analysed from Mamo (2016), small miliolid represent  $69 \pm 11\%$  (Mean  $\pm$  SD), with *Quinqueloculina* representing between 29% and 47% of the foraminifer assemblages. *Adelosina* was more abundant in the surface samples, reaching 20% while it reached a maximum 5% in the 1726 AD core layer.

Small miliolids like *Quinqueloculina, Triloculina* and *Spiroloculina* are common in reef lagoons where they live an epiphytic lifestyle and are abundant on dead coral and macroalgae substrate (Vénec-Peyré 1991; Bicchi et al. 2002; Murray 2006). SBF abundance in lagoonal and estuarine environments are not indicators of poor water quality (Murray 2006). Analysis of atoll lagoons in the Maldives and Barbuda (Caribbean) reported high diversity and abundance of small porcelaneous taxa, representing in excess of 50% of fauna with high numbers of *Quinqueloculina* and *Triloculina* (Brasier 1975; Parker and Gischler 2011). Porcelaneous taxa are common around patch reefs in New Caledonia (Debenay 2012). Sixty five percent of the taxa identified in 32 lagoonal patch reefs in Belize were also Miliolidae (Wallace and Schafersman 1977).

Agglutinated foraminifer are rare in the core, not reaching 1% in any layer and only represented by 3 genera, *Textularia* (n = 10), *Reophax* Montfort, 1808 (n = 2) and *Olgita* Mikhalevich, 2017 (n = 2). In Mamo's surface samples, one specimen of *Reophax* was reported, but none in OTR lagoon (Mamo 2016). *Textularia* was recovered from surface samples in the OTR lagoon in low numbers (n < 10) but only found in larger numbers (n = 47) from the channel between Wistari and Heron reefs (35 m depth) (Mamo 2016). High number of agglutinated foraminifer have been reported in deeper lagoonal bodies of water in New Caledonia (Debenay 2012). The OTR lagoon is a shallow lagoon (Maxwell 1968). Given the shallowness of the core collection site (4 m) high numbers of agglutinated taxa were not expected.

The sessile, encrusting or bio-eroding genera found in the sediment core included: *Lobatula* Fleming 1828; *Spirillina* Ehrenberg 1843; *Cornuspira* Schultze 1854; *Cibicidoides* Thalmann 1939; *Neoconorbina* Hofker 1951; *Rosalina* d'Orbigny 1826; *Acervulina* Schultze 1854; *Millettiana* Banner, Pereira and Desai 1985; *Cymbaloporella* Cushman 1927 and *Cymbaloporetta* Cushman 1928 (Vénec-Peyré 1996; Richardson-White and Walker 2011). These often small, cryptic taxa can remain attached to rocky surfaces after death and therefore may be understated in sampling (Bicchi et al. 2002). The combined RA of encrusting taxa averaged  $11 \pm 2$  % (Mean  $\pm$  SD). Their presence in the

core layers is indicative of hard surfaces, such as dead coral although some are known to also encrust algae (Brasier 1975). Experiments on the taphonomy of GBR corals found that encrusting taxa on dead coral were more abundant in high energy shallow waters (Pandolfi and Greenstein 1997). Mamo found *Millettiana milletti* to be the most abundant live-collected foraminifer from the Capricorn Group (Mamo 2016).

Twelve genera of LBF that have been identified as abundant in various areas of the GBR including *Marginopora, Baculogysina, Calcarina, Amphistegina, Peneroplis, Amphisorus* Ehrenberg, 1839, *Heterostegina, Sorites, Neorotalia, Operculina, Alveolinella* and *Cycloclypeus* (Scoffin and Tudhope 1985; Uthicke and Fabricius 2012; Mamo 2016; Doo et al. 2017). All except *Amphisorus* and *Cycloclypeus* were identified in OTR surface samples (Mamo 2016). Most of the LBF were absent from the OTR core. A number of LBF species are associated with algal cover and it is on the reef crests that LBFs are found in high numbers (Doo et al. 2017). On Lizard Island algal cover was reported as the primary substrate for living foraminifera (Baccaert 1987).

The most abundant LBF found through the core was *Sorites*, which houses dinoflagellate symbionts and are epiphytes, commonly associated with sea grass and coral rubble (Nobes et al. 2008; Reymond et al. 2013). The presence of *Sorites* is usually associated with seagrass meadows and macroalgal beds, however the OTR lagoon has no seagrass meadow (Linley and Koop 1986). The two main genera of LBF found through the core, *Sorites* and *Peneropolis*, house dinoflagellate and rhodophytic photosymbionts, respectively, which are able to utilise light at greater depths than the diatoms housed by corals and the calcarinids that are common on the reef flats (Uthicke and Nobes 2008; Renema 2018).

There were 50 (77%) rare genera with a mean abundance of  $22 \pm 5$  (mean  $\pm$  SD) through the core (where rare is defined as a taxon with less than 1% of total count). Surface sampling by Mamo (2016) reported 36 rare genera in the OTR lagoon (70%) and a high proportion of rare species (74%) was also reported on Heron Island, from sampling across the reef flat and lagoon (Strotz et al. 2016). Of the rare taxa found in the core, 13 were not recorded in Mamo (2016) (Appendix 3, Plate 5). One genus that was rare in the surface samples, *Abditodentrix*, was not rare in the core samples reaching 5% of the count in 1855 AD and 1726 AD, possibly reflecting spatial heterogeneity. There was no significant change in the number, or diversity of rare taxa among core layers or time intervals (Table 3). Based on the number of rare taxa in the core that were not found in the surface samples, the slope of the rarefaction curves and the Chao1 estimates, it is likely that there are additional taxa, not yet sampled within the OTR lagoon (Fig. 6 and Fig. 7). These data suggest more sampling is required to

determine the SBF diversity in the southern region of the GBR with an estimated ~ 7  $\pm$  5 (mean  $\pm$  SE) genera yet to be found.

While foraminifer assemblages vary among layers, there was no significant difference over the three time intervals (ANOSIM, R = 0.03, p = 0.36 and MVABUND, LRT = 190.2, p = 0.118), nor did layers in the same interval cluster together either under Q-mode analysis, NMDS or using polar coordinates (Figs 10 - 12). Variation between layers could be the result of spatial heterogeneity. While the NMDS appears to show a temporal gradient with the pre-colonial dates, there was no significant trend by years or over the three time intervals. In 1991 AD and 1855 AD *Quinqueloculina* has the lowest RA (n = 35% and n = 33%), resulting in an assemblage composition influenced by *Bolivina* and *Abditodentrix* as shown in the NMDS and clustering together in both the Q-mode and Polar clusters. This has the effect of an increase in the proportion of infaunal taxa in these two layers (Fig. 9).

Foraminiferal assemblages in the lagoon are predominantly composed of epifaunal taxa (including encrusting forms), with infaunal foraminifera morphotypes only exceeding 30% in 1991 AD (Fig. 9). Some taxa, such as species of *Uvigerina* d'Orbigny, 1826 and *Bolivina*, are able to tolerate reduced oxygen conditions and are believed to be capable of living deeply infaunal, up to 10 cm below the top of the sediment surface (Loubere and Gary 1990). They are often in high abundance in anoxic conditions, but there is no evidence for significant change in these taxa among time intervals (chi-squared = 0.62, df = 2, p-value = 0.73). There is no core layer where infaunal taxa dominate.

#### **Diversity measures**

Genus richness through the core is significantly higher than in the surface samples (Chi-squared = 11.34, p = 0.0008). This is to be expected since both surface and core samples represent time averaged assemblages although time averaging through the core is greater, with accumulation of surface layers representing 2.5 years per 1 cm layer.

Peak richness of 43 genera occurs in 1927 AD, which is the year with highest rare taxa (n = 28), and the highest count after removing unidentified taxa (n = 517) (Table 5). Highest diversity indicated by Shannon's H (2.77) and Fisher's alpha (13.34) is in 1855 AD, which also has the highest Simpson value (0.86) (Fig. 8). The high Shannon's H accompanies low dominance of *Quinqueloculina* (n = 128, 148 ± 42, mean ± SD) and *Elphidium* (n = 27, 39 ± 10, mean ± SD) and high genera richness. The lowest Fisher's alpha of 7.83 is in 1914 AD, which is also the year with the lowest number of taxa per sample. These three layers all sit within the colonial time interval, exhibiting high variation

within this interval. The assemblage indices such as richness, Shannon (H), Fisher's alpha and Simpson's (D) do not show significant changes among the three time intervals, although there is notable variability among layers (Table 5, Fig. 8).

#### Foraminifera specific indices (FSI & FI)

Low numbers of LBF in the core result in low FIs. The FI averaged  $2.37 \pm 0.15$  (mean  $\pm$  sd) (Fig. 8). There is no significant difference among the three time intervals (Chi-squared = 5.6, p = 0.06). The FI of the surface samples from Mamo 2016, yield similar FI values, with the exception of one site (site 54) located close to the reef flat (Table 6). Including site 54, the FI is  $2.66 \pm 0.88$  (mean  $\pm$  SD), however removing site 54 the mean FI is  $2.37 \pm 0.23$  (mean  $\pm$  SD) the same FI as the core. FI values from both the core and the surface sample are typically interpreted as an environment that is not conducive to coral growth (Hallock et al. 2003).

Several researchers, including the FI designer, have highlighted that the FI needs to be adapted to function as a relevant index to reflect local conditions (Renema 2006; Uthicke and Nobes 2008; Hallock 2012; Uthicke and Fabricius 2012; Renema 2018). More data about the functioning of individual species of Foraminifera reveals different weightings should be attached to different taxa (especially epiphytic forms) based on their known response to natural and anthropogenic environmental variables.

The presence of high numbers of SBF within lagoonal environments is not necessarily an indication of poor water quality (Dimiza et al. 2016). An alternative to the FI, the Foram Stress Index (FSI), was proposed for Mediterranean ecosystems and designed to address environments such as lagoons where SBF are often dominant taxa (Dimiza et al. 2016). This index is suitable for areas where LBF may be in lower numbers such as fine-grained soft bottom environments including lagoons, coastal lakes and basins. This index classifies taxa *Ammonia, Bolivina, Melonis* and *Textularia* as stress tolerant (Dimiza et al. 2016).

The FSI, like other the indices, showed no significant difference among the three time intervals (Chisquared = 1.69, p = 0.4), but was significantly lower than Mamo's surface samples (Chi-squared = 9.32, df = 1, p = 0.002) which while possibly indicating that modern samples may be more stressed requires further investigation (Fig. 9). The counts of *Bolivina* and *Bulimina* were much higher through the core, n = 130 compared to n = 36 in surface samples (Mamo 2016). Lower *Bolivina* numbers in surface samples (Mamo 2016) may indicate difference in grain size at the point of collection or reflect the fact that this taxon is infaunal and therefore collected in lower numbers from the surface. There is no significant difference through the core among the three time intervals for the abundance of *Bolivina* (Chi-squared = 1.28, df = 1, p = 0.53).

The presence of a high numbers of *Bolivina* in the OTR core reflects the lagoonal environment and associated fine sediment grain size (Haig 1993). Haig (1993) classified over 60 species as "buliminid" within the Papuan Lagoon of New Guinea. Taxa included OTR genera: *Bolivina; Loxostomina* Saidova, 1975; *Abditodentrix; Sagrinella* Saidova, 1975; *Rugobolivinella elegans* Parr, 1932; *Sigmavirgulina* Loeblich and Tappan 1957; *Bulimina; Buliminoides* Cushmann, 1911; *Siphogenerina* Schlumberger, 1882; *Fijiella* Loeblich and Tappan, 1962; *Trifarina* Cushman, 1923. Taxa since revised and classified into the families Bolivinitidae, Buliminoide Buliminoididae, Siphogenerinoididae, Reussellidae and Uvigerinidae, that show a wide ecological range in relation to geography and both water depth and grain size/mud content (Hayward and Brazier 1980). *R. elegans* is a common species in tropical lagoons enclosed by coral reefs, between 3-35 m depth in association with *Hauerina* d'Orbigny, 1839, *Quinqueloculina, Triloculina* LBF and *Elphidium* (Hayward and Brazier 1980). Combining taxa into a "Buliminid" grouping as per Haig (1993) represents  $11 \pm 4 \%$  (mean  $\pm$  SD) of the taxa in the OTR lagoon core, with no significant change between pre-colonial, colonial and modern time intervals (chi-squared = 2.76, df = 2, p-value = 0.25).

As the FSI is being applied to fossilised groups, it may be influenced by time averaging. Interestingly, the layer with the lowest FSI is at 75 mm (1991  $\pm$  7 AD), the year that flood plumes were reported to have reached Heron Island resulting in a 28% reduction in salinity (Devlin et al. 2001). There is a distinct decline in RA = 53% of *Quinqueloculina* in 1978 AD to 35% at this level and a corresponding increase in the RA of *Bolivina* to peak abundance (n = 52) and a domination of infaunal taxa (Fig. 9), but this shift is not evident before or after this sample. This shift in relative abundance drives a decline in both epifaunal morphotypes and the FSI, which according to the index author (Dimiza et al. 2016) can be indicative of a decline in water quality. To ascertain whether this shift is anything more than a spatial variation require further investigation of the layers around this depth.

#### **Taphonomic signals**

A difference can occur between living or surface faunal assemblages and those that are found down through the core due to the taphonomic effects. Taphonomic factors can include predation, dissolution and abrasion and the influence of each will differ in different environments (Glenn-Sullivan and Evans 2001). There has been little research into the taphonomy of Foraminifera specifically in carbonate sediment environments (Walker and Goldstein 1999). Test structure is important in determining the likelihood of preservation with thinner and more perforate tests being less likely to

withstand dissolution (Walker and Goldstein 1999). There is no significant change in the percentage of milioline tests through the core indicating no shift in dominant test structure (chi-squared = 1.87, df = 2, p-value = 0.39) Foraminifera may, however, have higher preservation in carbonate settings than in siliclastic or terrigenous sediment due to the buffering of pore waters, which may limit dissolution (Kotler et al. 1992; Martin 1999; Glenn-Sullivan and Evans 2001).

Given the abundance of very fine sediment the main taphonomic influence within the OTR lagoon are likely to be from bioerosion, predation and wave energy (Glenn-Sullivan and Evans 2001). Wave energy at the core site is minimal due to the lack of fetch, and abrasion is generally not considered to be an important factor in these carbonate settings (Lobegeier 2002). This leaves pre-burial bioerosion and predation as the principal factors likely to cause post-mortem changes to the foraminifer assemblage. Little is known about selective predation on foraminifer (Walker and Goldstein 1999). If pre-burial processes are the main taphononomic factor impacting the core assemblage, it could lead to the preferential preservation of infaunal taxa, such as *Bolivina*, which would become enriched in comparison to epifaunal taxa through the core (Goldstein and Harben 1993). There is no down core trend of increasing infaunal taxa consistent with such a taphonomic hypothesis (Fig. 9).

Bioerosion in quiet reef waters is common and combined with sediment reworking by callianassid shrimp can result in test fragmentation (Lobegeier 2002). In a study of foraminifera from ten atoll lagoons, test preservation was reported as very good with only superficial bioerosion reported in miliolid tests from the shallowest lagoons (Bicchi et al. 2002). There were low levels of bioturbation reported in the area at the time of core collection, however a callianassid shrimp was found at the 110 mm depth in the core (Kosnik et al. 2015), fauna which were reported by other researchers to be active in First Lagoon, along with rays and holothurians (Frith 1983). Evidence suggests mixing in the top 150 mm of the core, but below this level sediment is preserved in chronological order (Kosnik et al. 2015).

High rates of sedimentation, low bioturbation and low energy environments can enhance preservation potential (Brett and Baird 1986). While the fragile tests of some species will be more prone to damage over time than more robust tests, the OTR lagoon may have high foraminifera preservation potential (Kotler et al. 1992; Martin 1999; Glenn-Sullivan and Evans 2001). There is no significant difference in the number of test per mg of sediment through the three time intervals (chi-squared = 2, df = 2, p = 0.37), nor is there a significant difference in the taxonomic composition of the intervals. Further, the number of unidentifiable specimens did not change significantly among the three time intervals (Fig. 5). There is no evidence to suggest that taphonomic factors are responsible for the lack of change in foraminifer assemblages through the core.

#### Natural stressors – Extreme Weather

Frith (1983) estimated that for the period from 1909 to 1980 cyclonic activity within 160 km of OTR occurred biennially and that this may impact the Lagoon. In 2009, OTR was hit by Cyclone Hamish a category 4 storm, which resulted in damage to coral cover in some areas of the reef. However, the storm did not impact benthic cover within the lagoon, which appeared to be predominantly impacted by increased levels of broken coral transported from the reef crest (Woolsey et al. 2012).

Tropical cyclones in 1949 and 1959 caused heavy damage and flooding in Gladstone and Rockhampton. Current ripples in the sediment of the NW part of First lagoon on OTR at 3 m depth were reported after cyclone David in 1980, but not in the SE corner (Frith 1983). From 1960 to 1990 significant coral damage was reported in five separate years (1967, 1972, 1976, 1980) as a result of cyclones on the northern edge of Heron Island (Connell et al. 1997). In 1991, Cyclone Joy caused flooding in the Burdekin and Fitzroy rivers that resulted in plumes that caused reduced salinity (to 27 from ~ 35 PSU) and coral damage was reported in the Capricorn-Bunker reefs (Devlin et al. 2001). Floodwaters were reported to cover the SE Heron reef flat, however the plume is not reported to have reached OTR (Devlin et al. 2001). A study on Heron reef Foraminifera assemblages before and after Cyclone Hamish in 2009 reported subtle, but significant, differences in pre and post event diversity and assemblage composition (Strotz et al. 2016). Immediately following the event a homogenising of assemblages across sampling sites was reported along with significant variations in the pre and post-cyclonic abundance of *Cymbaloporetta bradyi* (Cushman, 1915) and *Rudigaudryina minor* (Chapman 1902).

The sedimentation rate for the core was estimated at 2.5 yrs per cm and age uncertainties range between five and 26 yrs. As such it is unlikely that events such as cyclones, which are regular in this area, would be detected in the core. Strotz et al. (2016) analysed pre and post-cylonic impact at Heron reef and pointed to variations in diversity and indicator taxa as a means of identifying cyclones within the sedimentary record. While there were variations in the abundance of indicator taxa *C. bradyi*, through the core the overall number of specimens was still low. In 1927 AD the occurrence of *C. bradyi* rose to seven specimens from a background level of an average of one per layer. There was no evidence of change in the foraminifera assemblage associated with extreme events within the core.

#### **One Tree Reef and Lagoon**

Reefs structures are diverse; the internal structure of OTR with reticulate reefs contrasts markedly with the more open Heron reef lagoon (Maxwell 1968). Inner shelf reefs have greater terrigenous input than outer shelf reefs (Maxwell 1968). OTR lagoon and Heron reef lagoon are reasonably small,

enclosed and shallow in comparison to many reefs where work has been conducted on large, open coastal or atoll lagoons (Brasier 1975; Bicchi et al. 2002; Makled and Langer 2011; Parker and Gischler 2011; Debenay 2012; Chen and Lin 2017).

To better understand current foraminiferal assemblages and decipher any fluctuations over time at OTR, further cores should be obtained from other sections of the lagoon and reef flat/margin. Davies (1976) noted reticulate and patch reef systems create numerous microhabitats and there are shift in depth and coverage across the lagoon floor (Fig. 13). Sections of the lagoon cannot be crossed at low tide due to the extensive reticulate reef system and coral microatolls (Mamo 2016).

The lagoon on OTR is not a homogenous environment. Bathymetry through the lagoon and the structures around the edge of the lagoon vary significantly (Fig. 13). Depth through the lagoons ranges up to 10-12 m along the coral algal rim in the north and as evidenced by the sample from Mamo (2016) site 54, the assemblage of foraminifera are likely to vary within the lagoon (Davies 1976) (Appendix 5). Factors such as variation in algal cover directly impact the composition of foraminiferal assemblages.

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**Fig. 13.** One Tree Reef and Bathymetric map. Bottom inset shows the bathymetry along the transect through the lagoon from A to A<sub>1</sub> (Davies 1976).

Coral reef lagoons often act as a reservoir for particulate matter and organic detritus (Frith and Mason 1986). Under normal wind conditions OTR First Lagoon acts as sink for suspended particles such as

fine sediment and plant matter from the island and reef crest (Frith 1983; Koop and Larkum 1987). Due to the separation of the lagoon from the open ocean each day during low tide, OTR is estimated to have a higher deposition rate than some other GBR lagoons; up to ten times higher than the Davies reef lagoon on the central GBR (Hansen et al. 1992). This higher level of enrichment with organic matter along with the reduced presence of macroalgae for epiphytic larger foraminifer may account for the lack of LBFs in the lagoon sediment and higher numbers of SBF. Lagoons on Heron reef and OTR have influence from vegetated cays, and as such may differ from those reefs without sand cays. Further surface samples of the foraminifer from across a variety of lagoon types would improve knowledge of the modern diversity and assemblage composition of lagoon foraminifers within GBR.

It has been proposed that since the establishment of the research station in 1971 the OTR lagoon has become significantly enriched with dissolved inorganic nitrogen (Bell et al. 2007). While OTR is a restricted access zone the research station can accommodate up to 26 people and has three composting toilets and composts organic waste (Archibald et al. 2019). Other sources of nutrients may come from the presence of bird rookeries on the island (Archibald et al. 2019). Peak generic richness (S = 43) occurs in the 1927 AD layer and declines 33% by 1978 AD (S = 29) but diversity increases again by 1991 AD (S = 40). However, 1978 AD has one of the highest FSI values though the core, recording low levels of opportunistic taxa that are commonly associated with increased nutrient levels. Foraminifera assemblages from the core do not provide evidence indicating a decline in the condition of the OTR lagoon.

In a study of ten French Polynesian lagoons (Bicchi et al. 2002), species richness was proposed to be positively correlated with the surface area of the lagoon and the degree of openness between the lagoon and the ocean. However, richness assessment of other lagoons in the GBR have not been made outside of the Capricorn Group, making it impossible to compare genus richness in the OTR lagoon with other areas. Makled and Langer (2011) collected 3000 specimens from the Chukk Lagoon Atoll System, a much larger, deeper and more open lagoon than on OTR, and reported 104 species from 63 genera. This area is near the hot spot of modern, tropical marine diversity, so could be considered a reasonable representation of high diversity (Makled and Langer 2011). The ability to accurately monitor changes over time in the OTR lagoon using Foraminifera preserved in sediment cores would increase with replicate cores (Bouchet et al. 2018).

Most work on Foraminifera within the GBR region has focussed on LBF. This is the result of several factors, not least being the applicability of the FI to assess water quality and changes in water quality in reef systems. The ease with which LBF can be identified and their recognised role in the

sedimentary budget has also encouraged interest in this group of Foraminifera. Their ecological (photosymbiont) similarity to hermatypic corals and role as a model organism or early warning system for corals has further added to the body of study (Spezzaferri et al. 2018). LBF on OTR have been investigated in depth across the algal flat (Doo et al. 2017). However, there needs to be further work in understanding the diversity and ecology of SBF in this region, which were the dominant taxa within the lagoon. Foraminifera play an important role in ecosystem functioning and SBF are relatively understudied, particularly within the GBR. Indices such as the FSI may be more suitable for non-reef zones in the GBR, and effectiveness will be improved with better understanding of the ecology of GBR SBF.

The comparison of Mamo (2016) surface samples and the core highlight the benefits of using both methods. Core samples have greater time-averaged samples and appear to enable the collection of deeper infaunal taxa than surface collection. Consideration must be given to the impact of taphonomic processes when assessing changes through a core. Surface collection can provide a better understanding of the spatial distribution of Foraminifera within the study area.

Examination of changes in Foraminiferal assemblages through the sediment core from OTR First Lagoon show fluctuations over time, but no significant change across time intervals corresponding with the colonisation and industrialisation of Australia. Further work within the OTR lagoon examining changes in sediment cores from different areas of the lagoon, combined with sampling and research in other GBR lagoons would enhance understanding of the changes in these understudied areas. The study of GBR SBF ecology and diversity, currently understudied in comparison with LBF, would be improved by examining areas beyond the reef crests and reef flats.

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# Appendix 1 Link to R Script and Data Files

http://marinescience.mq.edu.au/postgrad/bauder/appendix1.zip The linked zip file contains the following R scripts and data files:

## Data sediment:

Sediment and Weight data Core400\_weight\_data.csv LayerSplitWeight.csv oti-lead.txt

## Data Foraminifera:

## Foraminifera count data

Total Count and genus allocations - OTRB\_Species\_Genera\_Family\_Morpho.csv

 $Total\ Count\ and\ genus\ allocations\ with\ Functional\ Type\ amended\ to\ calculate\ the\ FSI\ -OTRB\_Species\_Genera\_Family\_Morpho.csv$ 

Mamo Data Data\_Mamo\_Lagoon1.csv Mamo\_Appendix\_A\_Lagoons.csv Result\_MamoANDCore.csv

## Scripts:

Sediment and weight scripts 1ResultsFig4-CRSvCICAgeagreement.R 1ResultsFig5-sedimentYB.R

Data import scripts DataImportManipulation2019b.R DataImportManipulation2019eco.R plotPreferences.R Figures and analyses scripts 1Results\_Raretaxa\_sigtests\_all\_Fractions.R 1Results\_ForamIndices.R 1ResultsFig4-CRSvCICAgeagreement.R 1ResultsFig5-sedimentYB.R 1ResultsFig6-SeptCombinedRarefaction\_Curve.R 1ResultsFig7-ChaoThreePanelYB.R 1ResultsFig8-RA\_Abundance\_Div\_panels.R 1ResultsFig9-Morphogroups.R 1ResultsFig10\_Fig11\_Cluster\_NMDS.R 1Results\_Fig\_12\_Diversity\_UsingECOINDR .R

# Appendix 2 Relative Abundance (%)

2004				
2004	Quinqueloculina	44	2.3	9.1
	Elphidium	13		
	Bolivina	5		
1991	Quinqueloculina	35	2.1	8.6
	Bolivina	12		
	Elphidium	10		
	Cibicioides	7		
1978	Quinqueloculina	53	2	97
1770	Flnhidium	15	2	5.1
	Lipnatum	15		
1927	Quinqueloculina	44	2.3	9.2
	$\widetilde{E}lphidium$	9		
	Bolivina	7		
1914	Quinqueloculing	46	23	9.6
1714	Flnhidium	14	2.5	5.0
	Cibicioides	5		
		C C		
1855	Quinqueloculina	34	2.2	9.2
	Elphidium	10		
	Bolivina	5		
	Abditodentrix	5		
1726	Quinqueloculina	43	25	93
1720	Elnhidium	9	2.5	2.5
	Abditodentrix	5		
	Sorites	5		
1649	Quinqueloculina	46	2.4	9.5
	Elphidium	17		
	Sorites	5		
1623	Quinqueloculina	52	2.5	9.8
	$\widetilde{E}lphidium$	14		
	Sorites	6		

Most common genera and relative abundance of taxa representing 5% and above of total specimen count (> 125  $\mu$ m ) for the layer and the corresponding Foram Index and Foram Stress Index.

## Appendix 3 Plates containing SEM images of Foraminifera

## Plate 1. Quinqueloculina

- 1. *Quinqueloculina* sp. 1, MPAL0596, scale bar =  $100 \mu m$
- 2. *Quinqueloculina* sp. 1, MPAL0597, scale bar =  $100 \mu m$
- 3. *Quinqueloculina* sp. 1, MPAL0598, scale bar =  $100 \,\mu m$
- 4. *Quinqueloculina cf. Q. multimarginata* Said, 1949, MPAL0599, scale bar = 20 μm
- 5. *Quinqueloculina transversestriata* (Brady, 1881), MPAL0600, scale bar = 100 µm
- 6. *Quinqueloculina subpolygona* Parr, 1945, MPAL0601, scale bar =  $100 \mu m$
- 7. *Quinqueloculina neostriatula* Thalmann, 1950, MPAL0602, scale bar =  $50 \mu m$
- 8. *Quinqueloculina neostriatula* Thalmann, 1950, MPAL0603, scale bar =  $20 \,\mu m$
- 9.  $\tilde{Q}$ uinqueloculina baccaerti, Mamo, 2016, MPAL0604, scale bar = 50 µm
- 10. *Quinqueloculina baccaerti*, Mamo, 2016, MPAL0605, scale bar = 100 μm
- 11.  $\tilde{Q}uinqueloculina$  sp. 2 Mamo 2016, MPAL0606, scale bar = 100  $\mu$ m
- 12.  $\widetilde{Q}$ uinqueloculina sp. 2 Mamo 2016, MPAL0607, scale bar = 100 µm
- 13.  $\tilde{Q}uinqueloculina seminula$ , (Linneaus, 1758), MPAL0608, scale bar = 50  $\mu$ m
- 14.  $\tilde{Q}uinqueloculina \ seminula$ , (Linneaus, 1758), MPAL0609, scale bar = 50  $\mu$ m
- 15. Quinqueloculina c.f. Q. patagonica d'Orbigny, 1839, MPAL0610, scale bar = 50 μm
- 16. Quinqueloculina c.f. Q. patagonica d'Orbigny, 1839, MPAL0611, scale bar = 50 μm
- 17. *Quinqueloculina c.f. Q. patagonica* d'Orbigny, 1839, MPAL0612, scale bar = 50 μm
- 18. *Quinqueloculina bosciana* d'Orbigny, 1839, MPAL0613, scale bar = 100 μm
- 19. *Quinqueloculina bosciana* d'Orbigny, 1839, MPAL0614, scale bar = 50 µm
- 20. Quinqueloculina bosciana d'Orbigny, 1839, MPAL0615, scale bar = 100 μm
- 21. *Quinqueloculina* sp. 2, MPAL0616, scale bar =  $100 \mu m$
- 22. *Quinqueloculina* sp. 3, MPAL0617, scale bar =  $50 \mu m$
- 23.  $\tilde{Q}uinqueloculina$  sp. 3, MPAL0618, scale bar = 50  $\mu$ m
- 24.  $\widetilde{Q}$ uinqueloculina sp. 6 Mamo 2016, MPAL0619, scale bar = 100 µm
- 25. *Quinqueloculina* sp. 6 Mamo 2016, MPAL0620, scale bar = 100 μm

## Plate 2.

#### Bolivinitidae, Reussellidae and Buliminidae

- 1. Bolivina variabilis (Williamson, 1858), MPAL0621, scale bar = 50 μm
- 2. Bolivina variabilis (Williamson, 1858), MPAL0622, scale bar = 50 µm
- 3. Bolivina variabilis (Williamson, 1858), MPAL0623, scale bar = 50 μm
- 4. Bolivina variabilis (Williamson, 1858), MPAL0624, scale bar = 50 μm
- 5. *Bolivina striatula* Cushman, 1922, MPAL0625, scale bar = 50 μm
- 6. *Bolivina striatula* Cushman, 1922, MPAL0626, scale bar =  $50 \mu m$
- 7. Loxostomina limbata (Brady, 1881), MPAL0627, scale bar = 50 μm
- 8. Loxostomina limbata (Brady, 1881), MPAL0628, scale bar =  $50 \,\mu m$
- 9. Loxostomina limbata (Brady, 1881), MPAL0629, scale bar =  $50 \ \mu m$
- 10. Loxostomina limbata (Brady, 1881), MPAL0630, scale bar =  $50 \ \mu m$
- 11. Sigmavirgulina tortuosa (Brady, 1881), MPAL0631, scale bar =  $50 \mu m$
- 12. Sigmavirgulina Loeblich and Tappan, 1957, MPAL0632, scale bar =  $50 \ \mu m$
- 13. Sigmavirgulina Loeblich and Tappan, 1957, MPAL0633, scale bar =  $50 \ \mu m$
- 14. Abditodentrix rhomboidalis (Millett, 1899), MPAL0634, scale bar =  $20 \ \mu m$
- 15. Abditodentrix rhomboidalis (Millett, 1899), MPAL0635, scale bar =  $50 \ \mu m$
- 16. Abditodentrix rhomboidalis (Millett, 1899), MPAL0636, scale bar =  $100 \,\mu m$
- 17. Buliminoides williamsoniana (Brady, 1881), MPAL0637, scale bar =  $50 \ \mu m$
- 18. Buliminoides williamsoniana (Brady, 1881), MPAL0638, scale bar =  $50 \ \mu m$
- 19. Sagrinella jugosa (Brady, 1884), MPAL0639, scale bar = 50 μm

20. Fijiella simplex (Cushman, 1929), MPAL0640, scale bar = 50 µm

## Plate 3. Other Miliolids

- 1. Sorites orbiculus (Forsskål in Niebuhr, 1775), MPAL0641, scale bar = 50 μm
- 2. Sorites orbiculus (Forsskål in Niebuhr, 1775), MPAL0642, scale bar = 50 µm
- 3. Hauerina pacifica Cushman, 1917, MPAL0643, scale bar = 50 μm
- 4. Hauerina earlandi Rasheed, 1971, MPAL0644, scale bar =  $50 \,\mu m$
- 5. Hauerina earlandi Rasheed, 1971, MPAL0645, scale bar = 50 µm
- 6. Spiroloculina angulata Cushman, 1917, MPAL0646, scale bar = 100 μm
- 7. *Spiroloculina angulata* Cushman, 1917, MPAL0647, scale bar = 50 μm
- 8. Spiroloculina corrugata Cushman and Todd, 1944, MPAL0648, scale bar =  $100 \mu m$
- 9. Spiroloculina corrugata Cushman and Todd, 1944, MPAL0649, scale bar = 100 µm
- 10. Spiroloculina foveolata Egger, 1893, MPAL0650, scale bar = 50 μm
- 11. *Pyrgo*? sp.1, MPAL051, scale bar = 50  $\mu$ m
- 12. Pseudhauerina involuta (Cushman, 1946), MPAL0652, scale bar = 100 µm
- 13. Pseudhauerina involuta (Cushman, 1946), MPAL0653, scale bar = 50 μm
- 14. Pseudomassilina macilenta (Brady, 1884), MPAL0655, scale bar = 50 µm
- 15. *Triloculina*? sp. 1, MPAL0656, scale bar =  $50 \mu m$
- 16. *Triloculina barnadi* Haig, 1988, MPAL0657, scale bar = 50 μm
- 17. Triloculina barnadi Haig, 1988, MPAL0658, scale bar = 100 μm
- 18. Siphonaperta crassa Vella, 1957, MPAL0659, scale bar = 100 μm
- 19. Siphonaperta crassa Vella, 1957, MPAL0660, scale bar = 20 μm
- 20. Adelosina carinatastriata Wiesner, 1923, MPAL0661, scale bar = 100 µm
- 21. Adelosina carinatastriata Wiesner, 1923, MPAL0662, scale bar = 50 µm
- 22. Adelosina carinatastriata Wiesner, 1923, MPAL0663, scale bar = 50 µm
- 23. Adelosina cf. A. pulchella (d'Orbigny, 1826), MPAL0664, scale bar = 100 μm

## Plate 4. Other Taxa

- 1. *Elphidium maorium* Hayward, 1997, MPAL0665, scale bar =  $100 \mu m$
- 2. Elphidium maorium Hayward, 1997, MPAL0666, scale bar = 100 µm
- 3. *Elphidium maorium* Hayward, 1997, MPAL0667, scale bar =  $100 \mu m$
- 4. *Elphidium fichtelianum* (d'Orbigny, 1846), MPAL0668, scale bar = 50 μm
- 5. *Elphidium oceanicum* Cushman, 1933, MPAL0669, scale bar =  $50 \mu m$
- 6. *Elphidium macellum* (Fichtel & Moll, 1798), MPAL0670, scale bar = 50 μm
- 7. *Elphidium advenum* (Cushman, 1922), MPAL0671, scale bar = 50 μm
- 8. *Cibicidoides cf. C. basilanensis* McCulloch, 1977, MPAL0672, scale bar = 50 µm
- 9. Cibicidoides cf. C. basilanensis McCulloch, 1977, MPAL0673, scale bar = 50 µm
- 10. Cibicidoides cf. C. basilanensis McCulloch, 1977, MPAL0674, scale bar = 100 µm
- 11. Pileolina? minogasaformis (Ujiié, 1992), MPAL0675, scale bar = 50 μm
- 12. Pileolina? minogasaformis (Ujiié, 1992), MPAL0676, scale bar = 50 µm
- 13. *Pileolina* sp 3 Debenay 2012, MPAL0677, scale bar = 50 μm
- 14. Haynesina depressula (Walker & Jacob, 1798), MPAL0678, scale bar = 50 μm
- 15. *Glabratella*? sp. 1, MPAL0679, scale bar = 50  $\mu$ m
- 16. *Glabratella*? sp. 1, MPAL0680, scale bar =  $20 \mu m$
- 17. *Glabratella*? sp. 1, MPAL0681, scale bar =  $50 \,\mu m$
- 18. *Cymbaloporetta bradyi* (Cushman, 1915), MPAL0682, scale bar = 50 μm
- 19. *Cymbaloporetta bradyi* (Cushman, 1915), MPAL0683, scale bar = 50 µm
- 20. Millettiana milletti (Heron-Allen & Earland, 1915), MPAL0684, scale bar = 50 μm
- 21. Millettiana milletti (Heron-Allen & Earland, 1915), MPAL0685, scale bar = 50 µm
- 22. Millettiana milletti (Heron-Allen & Earland, 1915), MPAL0686, scale bar = 50 µm

## Plate 5

## Rare Taxa

- 1. Cornuspira planorbis Schultze, 1853, MPAL0687, scale bar = 50 μm
- 2. Spirillina grosseperforata Zeng 1979, MPAL0688, scale bar = 50 μm
- 3. *Patellina formosa* Heron-Allen and Earland, 1932 MPAL0689, scale bar =  $50 \mu m$
- 4. Patellina formosa Heron-Allen and Earland, 1932 MPAL0690, scale bar = 50 μm
- 5. *Planispirillina* sp.1, MPAL0691, scale bar =  $50 \mu m$
- 6. *Planispirillina* sp.1, MPAL0692, scale bar =  $50 \mu m$
- 7. Uvigerina cf. U. porrecta Brady, 1879, MPAL0693, scale bar = 50 μm
- 8. *Procerolagena*? sp. 1, MPAL094, scale bar =  $50 \mu m$
- 9. Lobatula mayori (Cushman, 1924), MPAL0695, scale bar = 100 µm
- 10. Trifarina angulosa (Williamson, 1858), MPAL0696, scale bar = 100 μm
- 11. Neoconorbina? sp. 1, Mamo 2016, MPAL0697, scale bar =  $50 \mu m$
- 12. Acervulina mabahethi (Said, 1949), MPAL0698, scale bar = 100 μm
- 13. Peneroplis pertusus (Forsskål in Niebuhr, 1775), MPAL0699, scale bar = 20 μm
- 14. *Krebsina*? sp. 1 MPAL0700, scale bar =  $50 \mu m$
- 15. *Asanonella tubilifera* (Heron-Allen and Earland, 1915), MPAL0701, scale bar = 20 μm
- 16. Textularia lateralis Lalicker, 1935. MPAL0702, scale bar = 50 μm
- 17. Textularia lateralis Lalicker, 1935. MPAL0703, scale bar = 50 μm
- 18. Textularia lateralis Lalicker, 1935. MPAL0704, scale bar = 50 μm
- 19. *Textularia* sp. 1, MPAL0705, scale bar =  $100 \mu m$
- 20. Reophax? sp. 1, MPAL0706, scale bar =  $50 \,\mu m$

Appendix 3Plate 1Quinqueloculina







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## Plate 4 Other Common Taxa







## Appendix 4 – Details of the DER indices

A pdf describing this package and the calculation of all indices is attached at:

https://cran.r-project.org/web/packages/EcoIndR/EcoIndR.pdf

The majority are standard diversity indices, with the exception of a the EcoIndR Rarity index.

For this index:

S = number of species (species richness)

s = number of samples

rij = number of records of the species i in the sample j

R = total number of records considering all the species in all samples

r = chosen rarity cut off point (as a percentage of occurrence)

$$R = 1 - \frac{\sum_{i=1}^{S} \sum_{j=1}^{s} \frac{r_{ij}}{R}}{S}$$



Appendix 5 – Map of One Tree Reef collection sites from Mamo (2016)

Appendix 5. Figure depicting the surface sampling sites from Mamo (2016) for One Tree Reef Lagoon and the substrate type within the lagoon. Image adapted from Figure 2 (e), Mamo (2016).