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Benthic foraminifera as bioindicators of coral condition near mangrove environments

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ABSTRACT

Climate change stressors such as ocean warming, acidification and deoxygenation are severely threatening coral reefs and the vital ecosystem services they provide. Corals found to survive in mangrove habitats that naturally possess stressful conditions, are being increasingly studied to investigate the impact of multiple co-occurring stressors on coral growth. However, the water quality within mangrove-coral habitats and how this changes with varying distance from the mangroves remains largely unknown. We used the Foraminifera in Reef Assessment and Monitoring Index (FORAM Index) to assess the suitability of environments for coral growth across a mangrove to reef gradient. Sediment samples were collected from five sites at varying proximity to the Low Isles mangroves in the northern Great Barrier Reef. Sites were located: amongst the inner mangroves, the mangrove fringe, the adjacent leeward and windward reef margins and at Opal Reef (control) 38 km away from the mangroves. Foraminiferal community assemblages were used to determine the environmental suitability for coral growth and recovery. The poorest seawater conditions for coral occurred at the inner mangrove site with water quality improving outside the mangroves. Leeward and windward margin sites differed in their suitability for coral growth despite being a similar distance from the mangroves, indicating that water conditions were not necessarily constrained by proximity to mangroves alone. These findings have important implications for studies investigating mangrove-coral habitats as refugia and for assessing linkages between coral reefs and mangroves – two highly threatened tropical ecosystems.

1. Introduction

Coral reefs are under severe threat from climate change associated stress, with approximately 50% of coral cover estimated to have been lost in the last 40 years (Tebbett et al., 2023). Continuing emissions of anthropogenic carbon dioxide and other greenhouse gases is leading to increased levels of ocean acidification, warming and deoxygenation – three key climate stressors that compromise coral survival and by extension, the persistence of coral reefs, one of the most biodiverse ecosystems on Earth (Byrne and Fitzer, 2019; Camp et al., 2019; IPCC, 2022; Stewart et al., 2022; Klein et al., 2024).

In an effort to identify places where corals may have a greater chance of survival with ongoing environmental change, habitats where corals grow in close association with mangroves have been increasingly studied due to their potential to serve as coral refugia (Stewart et al., 2021) and potential housing of stress resilient corals (Camp et al., 2017; Tanvet et al., 2022). These coral-mangrove associations have been used to provide a natural field-based model for investigating the impact of climate change conditions on coral growth (Camp et al., 2019; Scucchia et al., 2023; Chadda-Harmer et al., 2024).

Mangrove habitats naturally possess the key stressors projected under climate change (Burt et al., 2020). They are characterised by low pH conditions due to respiration from mangrove roots as well as microbial activity and mineralisation of organic matter in sediments (Behera et al., 2014; Camp et al., 2016; Burt et al., 2020). Water temperatures surrounding mangroves are highly variable and often warmer as a result of shallow water depth and minimal flushing (Camp et al. 2017, 2019). Minimal water motion amongst mangroves and high

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activity of aerobic bacteria involved in the breakdown of organic material derived from mangroves, also contributes to low dissolved oxygen in mangrove associated waters (Nybakken and Bertness, 2005; Altieri et al., 2019; Camp et al., 2019). These stressors generally form a spatial gradient with stress conditions dissipating seaward towards the mangrove fringe and beyond due to tidal flushing and inundation (Altieri et al., 2019). Studies in mangrove-coral associated habitats have primarily relied on physiochemical data logging and analysis of discrete water samples to quantify abiotic stressors that impact corals living in association with mangroves (Camp et al. 2018, 2019). As a more time-integrated approach, bioindicators such as benthic foraminifera provide an important complementary method to determine the long term suitability of mangrove habitats for coral growth (Prazeres et al., 2020).

Foraminifera are unicellular protists which build shell-like tests that accumulate in the sediment substrate (Hohenegger, 2018; Romano et al., 2021; Abd Malek et al., 2023). Different foraminiferal taxa can characterise certain environments as they rely on specific food sources and are sensitive to differing conditions (Uthicke and Nobes, 2008). Symbiont-bearing foraminifera have similar environmental requirements as scleractinian corals as they derive their energy from photosynthetic endosymbionts and produce large calcium carbonate tests (Lee, 1996; Prazeres and Renema, 2019). Other foraminifera rely on heterotrophy and some stress-tolerant taxa can survive in extreme hypoxic, turbid, and organic matter rich conditions (Mathes et al., 2022). The Foraminifera in Reef Assessment and Monitoring (FORAM) Index developed by Hallock et al. (2003) utilises the abundance of foraminifera from three functional groups (symbiont-bearing, stress-tolerant, and other heterotrophic taxa) to predict environment suitability for coral growth (Hallock et al., 2003; Prazeres et al., 2020).

Foraminifera respond to the interactive effect of multiple factors such as temperature, light, food availability and exposure to wave action; but are not impacted by factors such as coral disease, corallivore predation, or storms. These characteristics allow foraminifera to be used to determine environment suitability for coral accretion based on water and sediment quality and not stochastic events impacting corals (Prazeres et al., 2020). The FORAM Index has been applied in many reef settings across a broad geographic distribution including the Indo-Pacific (Schueth and Frank, 2008; Uthicke and Nobes, 2008; Uthicke et al., 2010), Atlantic (Eichler and de Moura, 2020), Red Sea (El-Menhawey et al., 2020), and Mediterranean (Koukousioura et al., 2011). Healthy reefs are characterised by oligotrophic conditions and assemblages of diverse symbiont-bearing foraminifera (Uthicke and Nobes, 2008; Doo et al., 2014). Application of the FORAM Index shows that these assemblages serve as indicators of conditions that are best suited for coral growth (Hallock et al., 2003). In contrast, pure mangrove habitats tend to be inhabited by heterotrophic and stress-tolerant foraminiferal taxa and are suggested to be poorly suited for corals (Fajemila et al., 2015; Sariaslan and Langer, 2021). Mangroves and coral reefs are found as adjacent systems globally; there is however limited research on the environmental conditions at mangrove-coral associated habitats and how these conditions change across a mangrove to reef gradient, which has important implications for ecosystem connectivity (Gillis et al., 2017; Stewart et al., 2022).

In this study we investigated the impact of proximity to mangroves on the suitability for coral growth by examining foraminiferal assemblages and applying the FORAM Index to sites across a mangrove to reef gradient at Low Isles and Opal Reef in the northern Great Barrier Reef. We predicted that quantification of the three foraminiferal functional groups would reflect the contrasting mangrove to reef environmental conditions.

2. Materials and methods

2.1. Study sites

This study was conducted in the northern Great Barrier Reef at Low Isles (16° 23′ S, 145° 34′ E) and Opal Reef (16° 13′ S, 145° 53.5’ E) located 15 and 50 km respectively off the coast of Port Douglas, Australia (Fig. 1). Low Isles comprises of a 1.78 km^2 reef flat which supports a small vegetated sand cay and a mangrove swamp, called Woody Island, which is dominated by mangroves from the genera *Rhizophora* and experiences a south-easterly wave direction (Schueth and Frank, 2008; Hamylton et al., 2019). Scleractinian coral cover is greatest at the reef margin of the Low Isles complex, but small coral colonies have also been found to occur amongst the mangroves on Woody Island, growing both on the sediment substrate and directly on mangrove roots. Opal Reef is a 24.7 km^2 crescentic reef which supports extensive coral cover and serves as a control as it is considered to have no mangrove influence.

Sampling was conducted at eight stations located across five sites of varying proximity to the mangroves: (1) an inner mangrove site deep in the interior at a mangrove encapsulated lagoon (n = 5), (2) a mangrove fringe site located in a mangrove lined channel near the edge of Woody Island (n = 5), a (3) leeward margin site (n = 3) and (4) windward margin site (n = 3) located on the north-western and south-western side respectively of the Low Isles reef margin adjacent to Woody Island, and (5) an Opal Reef (control) site located 38 km from the Low Isles mangroves (n = 3) (Fig. 1, Table S1). Replicate, surficial sediment samples were collected by hand from each site between October 2022 and June 2024 at water depths less than 2.5 m using a grab sampling technique with a plastic zip lock bag (Table S1). Bags were sealed underwater to prevent loss of finer resuspended sediments. At the Inner Mangrove and Mangrove Fringe sites, samples were collected from unshaded areas at the centre of the waterway to limit the effect of photoprotection from the mangrove canopy. Salinity and depth measurements were taken at each Low Isles site using a Son Tek Castaway-CTD during the June 2024 sampling period, and at Opal Reef using a WTW multi-meter (Table S1). All samples were collected under Permit Nos. G18/40023.1 and G23/47923.1 (Great Barrier Reef Marine Park Authority).

2.2. Sediment analysis

Sediments were dried in a Binder drying chamber for 3 day at 50 °C and then individually homogenised using a riffle splitter to avoid grain size sorting. A 0.5 g subsample was taken from each sample and examined under an Olympus SZX10 stereomicroscope. Foraminiferal tests were separated from each sample and transferred to micropaleontological slides using a fine tipped brush. As tests were separated, accumulation curves were constructed for at least one sample station in each site to ensure an adequate number of specimens were collected to capture the diversity of foraminiferal genera present (Fig. S1). Based on the preliminary accumulation curves, a minimum of 80 tests were collected per sample as the plateau of the curves indicated that this sample size adequately recorded the diversity of genera at each site. Where an inadequate number of tests were present in the subsample, additional sediment was added until the minimum number of tests were collected. All tests from the subsample were collected and all size ranges were used to avoid selection bias. Abraded foraminifera were excluded from analysis as this indicates a long residence time or transportation (Fellowes et al., 2017). Foraminifera were identified to genera based on Nobes and Uthicke (2008) as well as Hayward et al. (2023) and sorted into functional groups as per Hallock et al. (2003) (Table S2). The number of foraminifera in each functional group was used to calculate the FORAM Index value for each sample using the equation:

$$FORAM\ Index = \left(10 \times \frac{N_S}{T}\right) + \left(\frac{N_O}{T}\right) + \left(2 \times \frac{N_H}{T}\right)$$

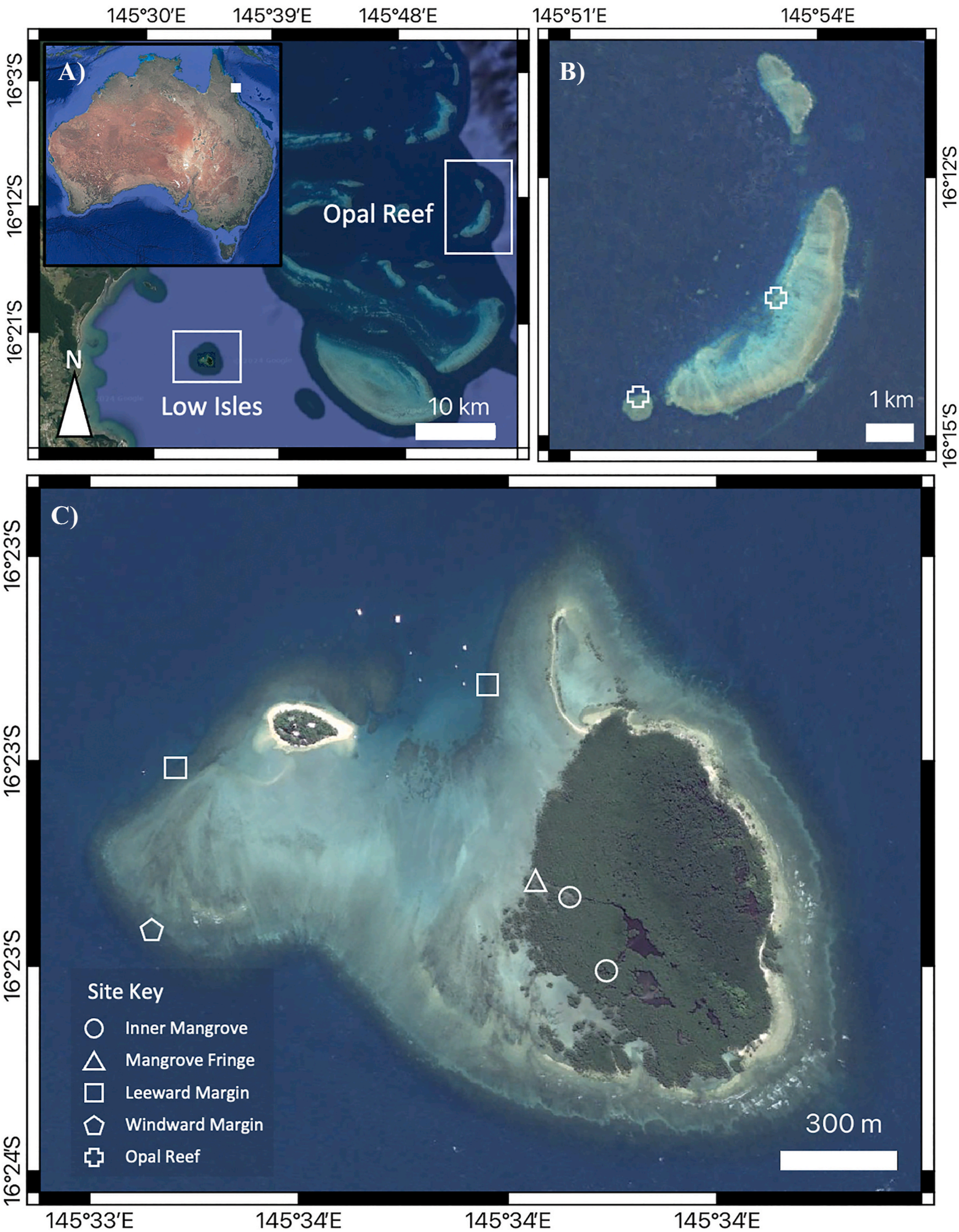

Fig. 1. Study area and sample collection sites in the northern Great Barrier Reef, Australia. **A)** Location of Low Isles and Opal Reef in relation to the Queensland coast. Inset image shows the study location (white square) in the context of Australia. **B)** Opal reef with sampling locations. **C)** Low Isles with sites. All images retain a consistent northward orientation. Satellite images sourced from GoogleEarth.

Where T is the total number of specimens analysed in the sample; N_S is the number of symbiont-bearing foraminifera; N_O is the number of stress-tolerant foraminifera; and N_H is the number of foraminifera in the other heterotrophic taxa group (Hallock et al., 2003; Prazeres et al., 2020). FORAM Index values were interpreted using the scale defined by Hallock et al. (2003), where a FORAM Index greater than 4 indicates environments favourable for coral growth; a FORAM Index between 4 and 2 indicates conditions marginally suitable for coral growth and unfavourable for coral recovery post damage; and a FORAM Index less than 2 indicates environmental conditions not suitable for coral growth. Specimens in the genera *Elphidium* were further identified to species as species-specific responses to environmental conditions have previously been observed (Renema and Troelstra, 2001; Uthicke and Nobes, 2008) (Table S3).

Sediment samples were individually dry sieved using graded sieves (63, 125, 500, 1000 and 2000 μm) to determine grain size. Sieved size fractions were weighed and weight data were input into the Grain Size Distribution and Statistic Software (Blott and Pye, 2001). The grain size composition was extracted using the Folk and Ward Method (Folk and Ward, 1957) and descriptive terminologies followed the Wentworth scale (Wentworth, 1922).

2.3. Statistical analysis

Statistical analysis was conducted using R software version 4.2.2 (R Core Team, 2022). The FORAM Index was compared across sites using a one-way analysis of variance (ANOVA) followed by a Tukey's test with statistical significance set at 0.05. The FORAM Index was the response variable and Site was the explanatory variable set as a fixed factor with five levels. FORAM Index data was logarithmically transformed, and assumptions of normality and homogeneity were tested for and met by assessment of Q-Q plots, histograms and residual plots. The FORAM Index across sites was visualised using boxplots constructed using the 'ggplot2' v.3.4.1 package (Wickham, 2016).

Differences in foraminiferal assemblages across sites were assessed by Analysis of Similarity (ANOSIM) and post hoc tests. Analysis was based on Bray-Curtis similarities and performed with 9999 permutations using the 'vegan' v.2.6–6.1 package (Oksanen et al., 2024). Patterns in foraminiferal assemblages were visualised using non-metric multidimensional scaling (nMDS) constructed with the 'ggforce' v.0.4.2 package (Pedersen, 2024). Similarity percentage (SIMPER) analysis was used to determine the foraminiferal genera contributing greatest to observed community differences between sites.

3. Results

3.1. FORAM Index

Foraminifera in Reef Assessment and Monitoring (FORAM) Index values differed across sites (ANOVA, $F_{4,14} = 29.923$, $p < 0.000$, Fig. 2). Low FORAM Index values were recorded from the Inner Mangrove (2.18 ± 0.12, mean ± standard error) and Mangrove Fringe (2.81 ± 0.26) sites. The Leeward Margin recorded values at a medium range (3.95 ± 0.12), while high FORAM Index values occurred at the Windward Margin (5.98 ± 0.77) and Opal Reef (6.27 ± 0.59) sites. A post-hoc Tukey test showed that there was no difference in FORAM Index values between the Inner Mangrove and Mangrove Fringe (mangrove) sites ($p = 0.2$). The Inner Mangrove, however, differed from the Leeward Margin, Windward Margin and Opal Reef (non-mangrove) sites ($p < 0.01$, Table S4, Fig. 2). The Mangrove Fringe differed from the Windward Margin and Opal Reef sites ($p < 0.001$), as did the Leeward Margin and Opal Reef sites ($p < 0.05$, Table S4, Fig. 2).

3.2. Foraminiferal assemblages

A total of 2061 benthic foraminifera specimens comprising 38 genera were analysed across the five sites. The average richness of foraminiferal genera was greatest at the Leeward Margin (16 ± 2.65 genera) and lowest at Opal Reef (12.33 ± 0.33 genera) (Table 1). Analysis of similarity (ANOSIM) revealed significant differences in the assemblage of foraminiferal genera between sites (Global R: 0.766, $p < 0.001$). Pairwise tests showed foraminiferal assemblages differed between mangrove and non-mangrove sites (R values between 0.897 and 1, $p < 0.05$, Table S4, Fig. 3A). Similarity percentage (SIMPER) analysis showed that *Quinqueloculina*, *Amphistegina* and *Calcarina* contributed the greatest to site differences (Table S5).

Taxa from each of the FORAM Index functional groups (symbiont-bearing, stress-tolerant, and other heterotrophic taxa) co-occurred at all sites. The greatest abundance of symbiont-bearing taxa was recorded from the Opal Reef (54.37% ± 7.44) and Windward Margin (51.33% ± 9.35) sites (Fig. 3B). *Amphistegina* was the most abundant symbiont-bearing genus, followed by *Calcarina* and *Marginopera*. The Inner Mangrove site possessed the lowest percentage of symbiont-bearing taxa (0–8.5%). Stress-tolerant taxa were most abundant at the Inner Mangrove (20.78% ± 1.68) and Mangrove Fringe (18.6% ± 1.80) sites (Fig. 3B). The most abundant stress-tolerant genera were *Elphidium*,

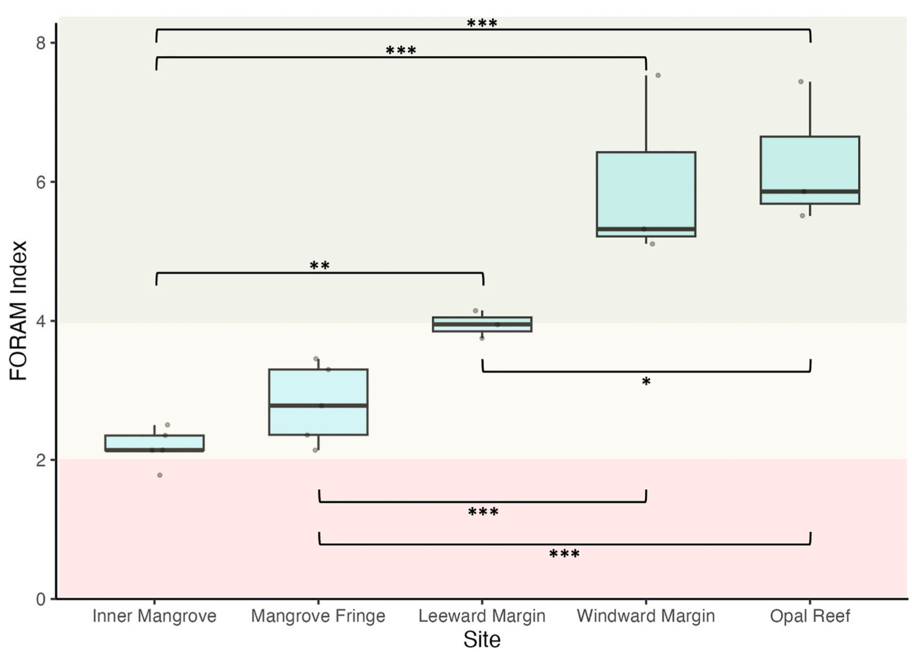

Fig. 2. Foraminifera in Reef Assessment and Monitoring (FORAM) Index results from coral sites in Low Isles, a mangrove associated coral reef ecosystem. Opal reef is considered a system with no mangrove influence. Coloured regions illustrate the interpretation of the FORAM Index in relation to water suitability for coral growth i.e., poor <2, 2 ≤ marginal ≤4, optimal >4. Box and whisker plots display the median with interquartile range, with the whiskers indicating the minimum and maximum value within 1.5 x the interquartile range. The points indicate raw values (n = 5 for the Inner Mangrove and Mangrove Fringe sites; n = 3 for all other sites). Asterisks indicate significant differences calculated using Tukey test, ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Table 1
Results of foraminiferal genera richness and sediment grain size across coral sites in Low Isles, a mangrove associated coral reef ecosystem. Opal reef is considered a system with no mangrove influence. Grain size classification and terminology follows Wentworth (1922). All results are given as mean ± standard error.

Site	Genera richness	Grain size (%)					
		Gravel (2000 μm)	Very coarse sand (1000 μm)	Coarse sand (500 μm)	Medium – fine sand (125 μm)	Very fine sand (63 μm)	Mud (<63 μm)
Inner Mangrove	14.2 ± 1.02	15.96 ± 1.32	24.91 ± 0.77	32.77 ± 1.95	23.38 ± 1.47	2.41 ± 0.47	0.58 ± 0.11
Mangrove Fringe	14.2 ± 0.97	10.66 ± 2.02	31.50 ± 10.05	30.96 ± 5.74	19.14 ± 3.30	1.16 ± 0.28	0.27 ± 0.10
Leeward Margin	16 ± 2.65	7.28 ± 2.41	15.71 ± 3.28	27.79 ± 3.40	43.76 ± 7.81	2.77 ± 0.72	0.27 ± 0.10
Windward Margin	15.33 ± 0.88	9.19 ± 1.69	20.38 ± 0.98	33.48 ± 1.67	33.52 ± 3.49	2.85 ± 0.59	0.58 ± 0.08
Opal Reef	12.33 ± 0.33	1.09 ± 1.09	7.55 ± 5.79	21.50 ± 12.57	9.40 ± 3.85	10.89 ± 5.78	0.48 ± 0.24

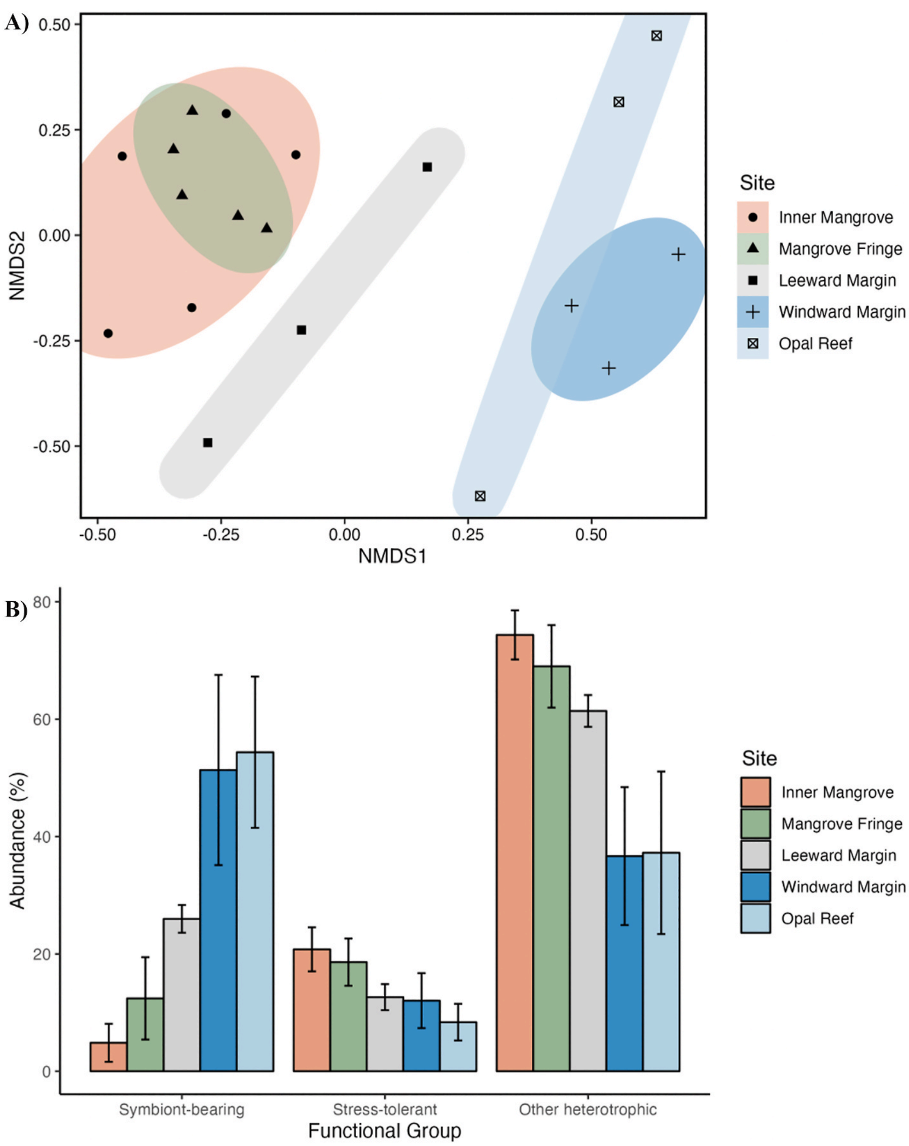

Fig. 3. Analysis of foraminifera from coral sites in Low Isles, a mangrove associated coral reef ecosystem. Opal Reef is considered a system with no mangrove influence. **A)** Non-metric multi-dimensional scaling (NMDS) plot of foraminiferal assemblages Stress: 0.15. **B)** Abundance of foraminifera from functional groups. Functional groups follow the classification from Hallock et al. (2003) and Prazeres et al. (2020). n = 5 for the Inner Mangrove and Mangrove Fringe sites; n = 3 for all other sites; standard error given as error bars.

Bolivina and *Ammonia*. *Ammonia* was not found at the Windward Margin or Opal Reef sites. Other-heterotrophic taxa were the most dominant functional group across the Inner Mangrove (74.36% ± 1.87), Mangrove fringe (69% ± 3.14) and Leeward Margin (61.4% ± 1.56) sites (Fig. 3B). *Quinqueloculina* was the most abundant genus of this functional group followed by *Cymbaloporetta* and *Rotorbis*.

3.3. Sediment characteristics

Sediments at all regions were predominantly made of sand-sized grains (Table 1). Sediments were classified as gravelly sand at Low Isles and as sand at Opal Reef. The mangrove sites contained the greatest percentage of gravel, while at all sites mud made up less than 1% of samples (Table 1). Sediments were primarily composed of biogenic carbonate material such as coral gravel, foraminiferal tests, mollusc shells, *Halimeda* plates and sea urchin spines. There was a distinct colour difference among the samples, where sediments from the mangrove regions were darker in colour. The surface texture of sediments was smooth and glossy at Opal Reef and became increasingly dull, pitted, and rough at regions closer to the mangroves.

4. Discussion

Using the Foraminifera in Reef Assessment and Monitoring (FORAM) Index, we recorded a clear gradient of environmental conditions at Low Isles in the Great Barrier Reef. The poorest seawater quality for coral growth occurred in the mangrove system interior, improving towards the adjacent reef margin. Conditions also differed between the Leeward and Windward Margin sites at Low Isles, with the Windward Margin being more favourable for coral growth and possessing conditions comparable to those observed at Opal Reef, the control site with no mangrove influence.

According to the FORAM Index, the Inner Mangrove and Mangrove Fringe sites were found to be only marginally suitable for coral growth and unsuitable for coral recovery. These sites had similar foraminiferal community assemblages that were dominated by heterotrophic and stress-tolerant taxa, such as *Bolivina* and *Ammonia*. These assemblages are typical of mangrove environments (Fajemila et al., 2015; Abd Malek et al., 2023) and indicative of high organic matter availability and low oxygen conditions (Fajemila et al., 2015; Razak et al., 2023). The FORAM Index showed that the Inner Mangrove had poorer conditions than the Mangrove Fringe, suggesting the presence of a stress gradient within the mangrove system as observed using physiochemical data at other mangroves (Altieri et al., 2019; Stewart et al., 2022). This gradient may be due to the differing location of the two sites. The Mangrove Fringe site is at the edge of the mangrove extent and therefore more exposed to tidal flow and inundation, potentially diluting the stressful conditions associated with mangrove-influenced waters (Altieri et al., 2019); whereas the Inner Mangrove site was located at the interior of the mangrove system. The differing geomorphological settings of the two sites may also contribute to the observed stress gradient, as the Mangrove Fringe is located at a channel whilst the Inner Mangrove site is located in lagoons with more confined waters and consequently a greater capacity to retain and develop conditions that would be stressful to corals (Altieri et al., 2019). Physiochemical data from a mangrove-coral habitat in Panama also showed that the interior of the mangrove system had the most stressful abiotic conditions (Stewart et al., 2022). However, unlike our findings, Stewart et al. (2022) found that abiotic conditions at the edge of the mangroves were very different to the mangrove interior. This is suggested to be because of the dense mangrove canopy shading the mangrove interior studied by Stewart et al. (2022). Shade was not an issue for our Inner Mangrove site at Low Isles, highlighting the importance of site-specific factors.

At Low Isles, mangrove-derived plant debris as well as guano from nesting birds, such as Torres Strait Pigeons, serve as potential organic matter sources (Schueth and Frank, 2008; Brothers and Bone, 2012). This facilitates aerobic bacterial activity involved in the breakdown of organic material which may contribute to reduced oxygen content (2.5–4.1 mg/L) and acidity (pH = 7.74–7.81) in mangrove influenced waters resulting in decreased coral suitability (Nybakken and Bertness, 2005; Haydon et al., 2021). Organic-rich mangrove associated sediments are generally dominated by mud-sized grains (Perry, 2007), as fine-grained sediments encourage the adsorption of organic matter (Risk and Edinger, 2011; Barrasa et al., 2014; Razak et al., 2023). Interestingly however, all sediment samples assessed in this study recorded a very low percentage of mud-sized grains (<1%) and mangrove sediments were found to contain the highest percentage of gravel, consistent with the findings of Frank and Jell (2006) at Low Isles. The near absence of mud-sized grains despite foraminiferal indication of an organic-rich setting at the mangroves, may be the result of the macrotidal regime operating at Low Isles (Hamylton et al., 2019). Suspended organic material can be utilised by organisms like foraminifera and corals but may be washed out with the tide and therefore not deposited (Jago et al., 2024). This may facilitate coral survival at the Low Isle mangroves as the deposition of fine-grained sediments and organic matter is known to smother corals and hinder coral growth (Risk and Edinger, 2011). Coloured dissolved organic material from the mangroves may also provide a photoprotective effect for corals and reduce bleaching susceptibility, further facilitating coral survival (Ayoub et al., 2008).

Outside the mangroves, conditions for coral growth improved at both reef margin sites. Samples from the Leeward Margin were classified by the FORAM Index as bordering the marginal-favourable range for coral growth whilst the Windward Margin site was indicated to possess highly favourable conditions for coral growth similar to those observed at Opal Reef. Camp et al. (2019) using physiochemical data also recorded that more favourable conditions for coral occurred outside the Low Isles mangrove. The Leeward Margin site is dominated by heterotrophic taxa, suggesting the presence of organic matter and mangrove influenced waters; this site also possesses the highest richness of foraminiferal genera on average and appears to be an intermediatory setting between the mangrove and the more pristine Windward Margin and Opal Reef environments (Fajemila et al., 2015). The Windward Margin and Opal Reef share a similar foraminiferal community dominated by symbiont-bearing taxa, similar to foraminiferal assemblages previously recorded in the outer Great Barrier Reef (Uthicke and Nobes, 2008; Uthicke et al., 2010; Doo et al., 2014). Symbiont-bearing foraminifera indicate an oligotrophic environment with warm, clear, well oxygenated water as they require similar environmental conditions to corals in order to utilise energy from photosynthesis and produce large calcareous tests (Hallock et al., 2003; Schueth and Frank, 2008; Koukousioura et al., 2011).

An unexpected distribution of the stress-tolerant genus *Elphidium* was recorded at the Windward Margin and Opal Reef despite this genus being considered an indicator for the presence of organic matter and intermittent hypoxia (El-Menhawey et al., 2020). This may be explained by the trophic plasticity of some *Elphidium* species, which can survive in high light conditions by utilising chloroplasts derived from microalgal foods but can also shift to heterotrophy and digest retained chloroplasts when needed (Lopez, 1979; Renema et al., 2001; Renema and Troelstra, 2001; Uthicke and Nobes, 2008). Of the *Elphidium* species recorded, abundance of *Elphidium craticulatum*—a species that can retain chloroplasts (Renema et al., 2001)—was greatest at the Opal Reef and Windward Margin sites, which are indicated to possess clearer, more suitable conditions for coral growth; whilst mangrove-associated sites were dominated by *Elphidium reticulosum*. These findings suggest species level identification for the *Elphidium* genera may be necessary to appropriately assign functional groups for the FORAM Index. Further work should also assess the potential for periodic hypoxia events at these reef sites, as Pezner et al. (2023) have suggested that many coral reefs already experience periods of hypoxia which again could explain these results.

Despite being a similar distance from the mangroves, better conditions for coral growth occurred at the Windward Margin compared to the Leeward Margin site, evidenced by their distinct foraminiferal assemblages with different trophic preferences. Schueth and Frank (2008) also recorded poorer conditions at the Leeward compared to Windward Margin site at Low Isles using the FORAM Index. This spatial difference is potentially due to the increased exposure of the Leeward Margin to mangrove influenced waters, as the main conduit for tidal flow and discharge of mangrove material from the reef flat is located near the Leeward Margin site (Schueth and Frank, 2008). While wave action and the arrival of non-mangrove influenced waters at the Windward Margin site may dissipate stress conditions. These findings highlight the importance of hydrodynamic forcing and geomorphological setting in influencing the persistence of stressors at and nearby mangrove environments (Schueth and Frank, 2008; Altieri et al., 2019).

5. Conclusions

This study provides the first FORAM Index assessment of the Low Isles mangrove-coral reef system across an inner mangrove to reef gradient. Our findings support the effectiveness of foraminiferal assemblages as bioindicators of environment conditions that are suitable for coral growth. Our results highlight a gradient of conditions stressful for corals from the inner mangroves to the normal conditions for coral growth at the Windward Margin approximately 940 m away. Although mangroves have previously been observed to serve as a refugia for coral growth due to reduced light stress from shading (Stewart et al., 2021), our FORAM Index analysis showed the Low Isles mangroves had limited refugia properties as background conditions were suboptimal for coral survival. The prevalence of heterotrophic foraminifera however may suggest the possibility of mangroves serving as a food source which could support more heterotrophic coral species under stressful conditions where additional food availability is advantageous. It will be important for future studies to look at feeding behaviour of corals at Low Isles to understand whether corals mirror the foraminiferal trophic patterns and rely on greater heterotrophic feeding at the mangroves and whether this changes under environmental stress scenarios such as marine heatwaves. Individual mangrove systems may provide a unique suite of services to coral but can also generate stressful conditions for coral growth, as shown by the benthic foraminiferal bioindicators at Low Isles. We recommend studies utilising mangrove-coral habitats to assess environmental conditions at each sample site as stress gradients can differ between mangrove-coral systems and are not necessarily constrained by proximity to mangroves alone.

CRediT authorship contribution statement

Dayana Chadda-Harmer: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Maria Byrne:** Writing – review & editing, Resources. **Claire E. Reymond:** Writing – review & editing, Resources. **Thomas E. Fellowes:** Writing – review & editing, Resources. **Emma F. Camp:** Writing – review & editing, Resources. **Shawna A. Foo:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107159.

Data availability

Data will be made available on request.

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