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Local Persistence of Large Benthic Foraminifera (LBF) under Increasing Urban Development: A Case Study from Zanzibar (Unguja), East Africa

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ABSTRACT: Coastal marine management is vital for socio-ecological sustainability of developing, tropical ecosystems, which calls for diverse tools to monitor and assess water quality. The carbonate-dominated habitats off Zanzibar were chosen for study due to potential water quality degradation in a rapidly developing tourist destination heavily reliant on its coral reefs. These reefs are largely unmonitored and subject to local and global stressors. A widely used method for assessing reef health, as an early detection method of ecological changes, is the application of large benthic foraminiferal bioindicators, i.e., the FoRAM Index. We expected to find poor water quality conditions in the unmanaged reefs supported by stress-toelerant (opportunistic) foraminiferal assemblages. The dissolved inorganic nitrogen and phosphate values derived from untreated sewage effluent from Stone Town were highly variable (ranging 0.05–3.77 and 0.05–1.45 µM, respectively), moderate, and occasionally approached or exceeded critical threshold values for oligotrophic ecosystems. The analysis of total assemblages indicated an abundance of symbiont-bearing large benthic foraminifera, dominated by prolific *Amphistegina* species, comparatively low-moderate diversity, high FI values (7.6 on average), and high coral cover. A water quality gradient was reflected by subtle assemblage differences, suggesting that LBF can provide early warning signals of benthic changes, indicating the importance of long-term monitoring programs in vulnerable, rapidly developing coastal ecosystems exposed to increasing pressures.

KEY WORDS: carbonate, coral reef, bioindicator, FoRAM Index, nutrients, sewage effluent, Western Indian Ocean, coastal development, coastal marine management.

0 INTRODUCTION

Coral reefs are being affected by stress-induced ecological "phase" shifts (Done, 1992), resulting in reef degradation documented world-wide. The Western Indian Ocean (WIO) is home to approximately 16% of the world's reef species, and after the coral triangle, it hosts the second peak of global coral-reef biodiversity and productivity (Obura, 2012; Johnstone et al., 1998). The coral reefs of the Zanzibar Archipelago are an important regional asset supporting the local economy, including small-scale artisanal fisheries and tourism activities, however, they are vulnerable to increasing degradation (Rehren et al., 2022; Staehr et al., 2018; Lange and Jiddawi, 2009) from pollution (Bravo et al., 2021; Nyanda et al., 2016) and climate-related disturbances, such as the strong El Niño-driven mass coral-bleaching events (Staehr et al., 2018; McClanahan et al., 2007; Obura, 2005). Effective conservation of coral reefs here is critical to ensure that they continue to maintain their ecosystem functions and services.

A holistic understanding of Zanzibar's coral reef ecosystems is currently inadequate because of a lack of routine monitoring programs for water-quality assessments (Khamis et al., 2017; Mmochi et al., 2001). Here, as in other small tropical islands in developing states, environmental assessment and mitigation activities, such as baseline studies and monitoring, occur at limited capacities and under economic constraints (Thomas et al., 2020). Cost-effective, low-tech, and rapidly deployable tools are therefore required to provide a better under-

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standing of the general characteristics of Zanzibar's coastal ecosystems (Staehr et al., 2018; Khamis et al., 2017) as the response of its reef assemblages to environmental change is still a knowledge gap.

Foraminifera are unicellular protistan eukaryotes that form calcium carbonate or agglutinated tests. Due to their high taxonomic diversity, short turnover rates (from months to two years), and excellent preservation potential, their empty tests accumulate, often prolifically, as calcium carbonate sediments (Narayan et al., 2022; Langer, 2008). Accumulations of the total (living + dead) assemblage are time-averaged, and thus reflect monthly, annual, decadal to millennial changes. Large benthic foraminifera (LBF) are a subcategory that host eukaryotic photosymbionts (Lee and Hallock, 1987). LBF assemblages are a key to understanding shifts in benthic coral-reef assemblages, driven by water-quality changes, and the application of LBF bioindicators has seen a growth in interest (Renema, 2018). The Foraminifera in Reef Assessment and Monitoring (FoRAM) Index or FI (herein) was developed by Hallock et al. (2003), later revisited (Hallock, 2012; Reymond et al., 2012), and has since been used extensively worldwide (e.g., Prazeres et al., 2020 and references therein) as a reliable, low-cost index for assessing the status of coral reefs, over contemporary to decadal timescales.

The carbonate-rich substrates that characterize Zanzibar's diverse coastal habitats, make it an ideal location for the application of foraminiferal bioindicators for ecological quality assessments. Previously, a historical (Heron-Allen and Earland, 1915, 1914), a more recent pilot (Narayan and Westphal, 2016), and an extensive broad-scale (Thissen and Langer, 2017) studies, have assessed the occurrence, distribution, taxonomic composition and/or ecological relevance of foraminifera from Zanzibar reefs, and elsewhere in East Africa (Weinmann and Langer, 2017; Langer et al., 2013; Chasens, 1981; Pereira, 1979).

This study aims to assess the total (living + dead) foraminiferal assemblages and distribution, and their response to sewage-derived pollution in four coral reefs, located close to the historical urban center of Zanzibar, Stone Town (Fig. 1b). This study is the first detailed, combined foraminiferal and nutrient analyses for four reef sites (Chapwani, Changuu, Bawe, and Chumbe Marine Protected Area [MPA]). It complements a concurrent coral study (Herrán et al., 2017), and another larger-scale foraminiferal study (Thissen and Langer, 2017), which also examined one of the three reefs studied here (Bawe). In light of the historical and current degradation that these reefs are experiencing, our objectives are to explore the hypotheses that: (1) a strong water-quality gradient exists, from the unmanaged reefs closest to the urban center out to the MPA located furthest away; (2) differences in environmental conditions (i.e., water quality) are reflected by the foraminiferal assemblage; and (3) LBF assemblages and bioindicator indices are useful tools, as early indicators for detecting reef degradation in Zanzibar.

1 MATERIALS AND METHODS

1.1 Geographic and Environmental Setting

The Zanzibar Archipelago is located in the Western Indian Ocean (39°05′E to 39°55′E, 4°45′S to 6°30′S), along the eastern side of the Zanzibar and Pemba channels, which separate the two islands (Unguja and Pemba) from the Tanzanian mainland (Fig. 1a) by approximately 30 km (Shaghude and Wannäs, 1998). The channels are highly influenced by the northward-flowing East African Coastal Current (EACC), and the nutrient-depleted westward-flowing South Equatorial Current (SEC) (Painter, 2020; Mahongo and Shaghude, 2014; McClanahan, 1988). Tides here are semi-diurnal, mesotidal with spring and neap tidal ranges that vary between -0.2 and 4.5 m. The tropical climate is influenced by two opposing monsoon seasons: the warm (>29 °C) humid North Easterly (NE) monsoon (December to March); and the slightly cooler (>25 °C), drier, South Easterly (SE) monsoon (June to October); driven by the Inter-tropical Convergence Zone (ITCZ), which results in a long (April–May) and a short (November) rainy seasons (Fig. 1d). The former is characterized by weak, low-speed winds, and the latter by slightly stronger winds. Seasonal acceleration of the EACC likely facilitates regional flushing of the shallow sea channels (Painter, 2020; Nyandwi, 2013). There is a northward-flowing surface current through the Zanzibar Channel during the SE monsoon season, which is reversed southwards, during the NE monsoon season, due to the prevailing direction of the NE winds (Painter, 2020; Nyandwi, 2013).

As the densely (530 people per km^2) populated historical urban center, Stone Town (ST) holds approximately 25% of the total population of Zanzibar (Staehr et al., 2018), which is currently estimated at 1 671 598 with a growth rate of 3% (Ali et al., 2021). The rapid population growth and the corresponding coastal development are to a large extent associated with the tourism sector (Staehr et al., 2018). However, the management of waste effluents from ST has not kept pace with urban growth, and this has led to the deterioration of coastal water quality, with untreated domestic-sewage discharge being the main source of marine pollution (Nyanda et al., 2016; Moynihan et al., 2012).

1.2 Field Sampling

This study focused on the reef ecosystems located on the western side of Zanzibar (Fig. 1), off Stone Town (ST). Two field campaigns were undertaken. The first was conducted in late August to late October 2014 (i.e., Spring, at the end of the cool dry SE monsoon and before the short rains), and the second in April 2015 (i.e., Fall, at the end of the warm dry NE monsoon and before the long rains). Seawater was sampled along four cross-shore transects, starting from four sewage point sources along ST's shoreline, and running seawards towards the four reef islands (Table 1; Figs. 1 and 2; ESM Table S2). Sampling stations were positioned at an increasing distance from the shoreline (approximately 0–20, 50, 100, 250, 500, 1 000, and 2 000 m). Transect one (T1) ran between the major Bwawani sewage outflow of ST (to the north) and Chapwani Reef; T2 ran centrally, between Zanzibar Port, starting just off the Institute for Marine Sciences (IMS), and running seawards to the Changuu NE Reef; T3 ran between the Africa House Hotel (southern end of ST), and Bawe Reef; and T4 ran between the Kizingo outflow 3 km south of ST, with two cross-shore lines: the first running perpendicular to the shoreline and the other running (~12 km) towards the Chumbe Reef that is located in a Marine Protected Area (MPA). A stationary twelve-

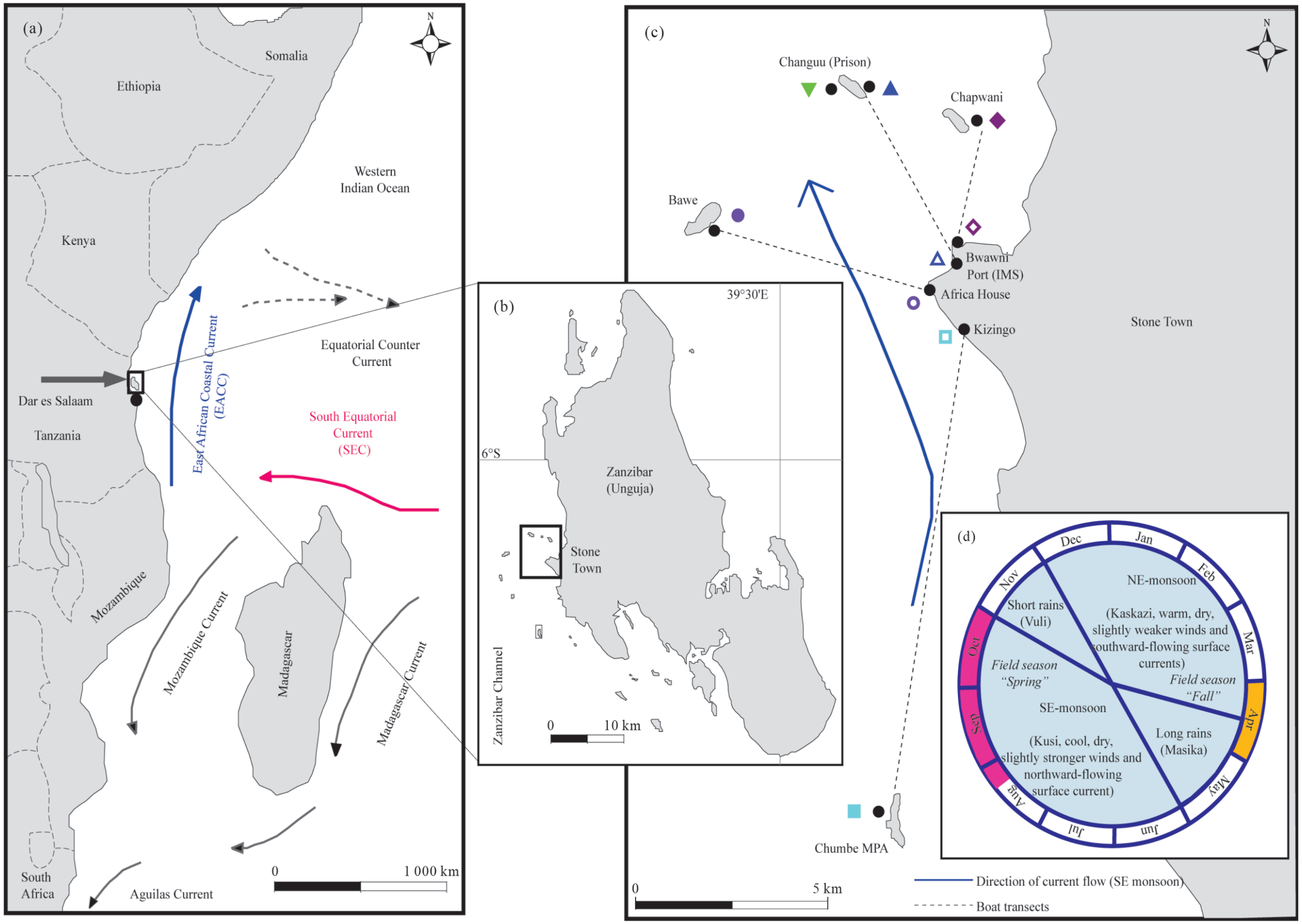

Figure 1. (a) Map of East Africa and the Western Indian Ocean region depicting the prevailing current systems, the East African Coastal Current (EACC) and the South Equatorial Current (EACC). The Zanzibar Archipelago is located off the coast of Tanzania and lies near the biodiversity center in the WIO (i.e., the northern Mozambique Channel). (b) Map of Zanzibar (Unguja) showing the location of the study area, located on the western side of Zanzibar Island, off of the historic urban center Stone Town (ST). (c) The location of the four urban shoreline sites (ST) and the four coral reef sites. Water quality and sediment samples were collected along these four long-distance, boat transects (dashed lines), originating from point sources along ST's shoreline towards fronting reefs. (d) The timing of the two opposing monsoon seasons and the two field campaigns carried out by this study.

hour sampling, starting at low tide, was carried out at the Changuu and Bawe reefs and at the IMS-Port shoreline site during the first field campaign.

The seawater samples were collected using Niskin® bottles at both the bottom and surface of the water column. The physical parameters measured included: salinity (S), temperature (T), dissolved oxygen (DO), pH and total dissolved solids (TDS), using a hand-held WTW Multiline F/Set3 multi-parameter probe. Water samples were collected in opaque 50 mL polyethylene bottles using disposable 60 mL syringes fitted with Sartorius Minisart filters (45 µm pore size), which were pre-rinsed three times with the sample water. These samples were immediately preserved with mercuric chloride solution (50 µL of a 20 gL^{-1} of $HgCl_2$ added to 100 mL sample) (campaign 1), or kept frozen (campaign 2) for transport back to the Leibniz Centre for Tropical Marine Research (ZMT) in Bremen, Germany for nutrient analysis.

A total of 104 sea floor surface-sediment samples (of approximately 50 cm^3) were collected, mostly during the first campaign. Of these, 40 samples were collected from stations along the four cross-shore boat transects, using a small Van Veen grab sampler deployed off the side of a boat. At eight stations (i.e., T1-1, T2-12, T4-5, T4-7, T4-8, T4-9, T4-10, and T4-11), the grab was not deployed, either due to Marine Protected Area (MPA) regulations, or due to unsuitable bottom substrate type. Another 62 sediment samples were hand-collected by scooping or gathering the top 1–2 cm of sediment or loose (e.g., algal) substrate while snorkeling or scuba diving (Fig. 2a). Replicate samples (3 to 5) were collected from different zones of a coral reef (backreef lagoon, reef flat, reef crest and reef slope at 5 and 10 m) along a perpendicular transect that ran from the beach of the coral island to 10 m on the reef slope.

2 LABORATORY PROCESSING AND ANALYSES

2.1 Sediment Composition

In the field, ethanol (70%) and a few drops of pre-prepared Rose Bengal dye solution (0.25 g in 100 mL) was added to some of the collected sample jars containing seawater to stain for living foraminifera. However, due to the mixed results of staining, we instead focused on obtaining the total (living + dead) assemblage as a time and cost-efficient solution and to reduce seasonal biases.

In the IMS laboratory, samples were washed with tap water through a 63 µm sieve to remove silt fractions. The retained fractions were either air or oven-dried at 40 °C, weighed and packaged for subsequent transport to Germany. At ZMT, the sediments were dry-sieved using a sieve stack and mechanical shaker and sieved into: >2 000 µm; 1 000 – 2 000 µm; 500 – 1 000 µm (medium-coarse sand); 250–500 µm (medium sand); 125 – 250 µm (fine sand); 63 – 125 µm; and <63 µm fractions (Wentworth, 1922). The weight percent (wt.%) of each individual fraction was calculated as a percentage of the total bulk (dry) sample. The carbonate content was determined from the very fine sand fraction using the Carbometer Method (Müller and Gastner, 1971) for 37 representative samples. The internal error of this procedure was less than ±1% $CaCO_3$. The carbonate content measurements are shown as the mean weight percentage (wt.% $CaCO_3$).

2.2 Water Column Nutrient Concentrations

Dissolved inorganic nutrients (nitrite: NO_2^-; nitrogen oxide: NO_x; phosphate: PO_4^{3-}; and silicate: Si), except for ammonium (NH_4^+), were analyzed using a spectrophotometer at the ZMT. Ammonium concentrations were analyzed flurometrically using the continuous-flow injection analyzing system Skalar® Alliance Flow System, Tecan® at the ZMT. The measuring procedure has a relative standard deviation <3.4% with reference to the linear regression of an equidistant 10-point calibration line from NIST standards. The nitrate (NO_3) value was calculated by the formula: $NO_x – NO_2$. Dissolved inorganic nitrogen (DIN) was determined by $NO_x + NH_4$ (i.e., NH_4^+, NO_2^-, NO_3^-), and dissolved inorganic phosphate (DIP) from PO_4^{3-}.

2.3 Analyses of Foraminiferal Assemblages

A minimum of 300 specimens per (~1 g) subsample (with two exceptions) from the ⩾0.125 mm fraction (Patterson and Fishbein, 1989) were picked from each of the (3–5) replicates and sorted. Note that the specimens were hand collected from the top 1 – 2 cm of substrate and from algal/seagrass and reef rubble debris. A taphonomic grading scheme modified from previous studies (Belanger, 2011; Berkeley et al., 2009) was used to indicate *in-situ* or autochthonous conditions (Table 2).

Taxonomic determinations were made to species level (where possible) using a Leica KL 200 LED binocular micro-

Table 1 A general description of the study sites sampled and their geographic location (latitude-longitude), given with specific reference to the four long-distance boat transects (T1 to T4) carried out; the approximate linear distance (km) of the site from the source of the sewage outfall from Stone Town (ST) is given

Site	Status	Transect (location)	Latitude (°S)	Longitude (°E)	Linear distance (km)
a. Bwawni	Main sewage outflow; unprotected	T1 (ST)	6.155 39	39.196 51	0.0
b. Chapwani	Private resort; unprotected	T1 (Reef)	6.127 86	39.196 57	3.3
c. Port/IMS	Major harbour; unprotected	T2 (ST)	6.158 09	39.191 81	0.0
d. Changuu	Private tourist resort; not managed	T2 (Reef)	6.116 49	39.167 50	5.3
f. Afr. House	Tourist area; unprotected	T3 (ST)	6.165 38	39.186 97	0.0
g. Bawe	Private tourist resort; not managed	T3 (Reef)	6.158 41	39.132 79	5.3
h. Kizingo	Southern suburb; unprotected	T4 (ST)	6.177 76	39.197 60	0.0
i. Chumbe	Chumbe Island Coral Park Ltd. and MPA; private ecotourist resort (actively managed)	T4 (Reef)	6.282 02	39.174 63	11.9

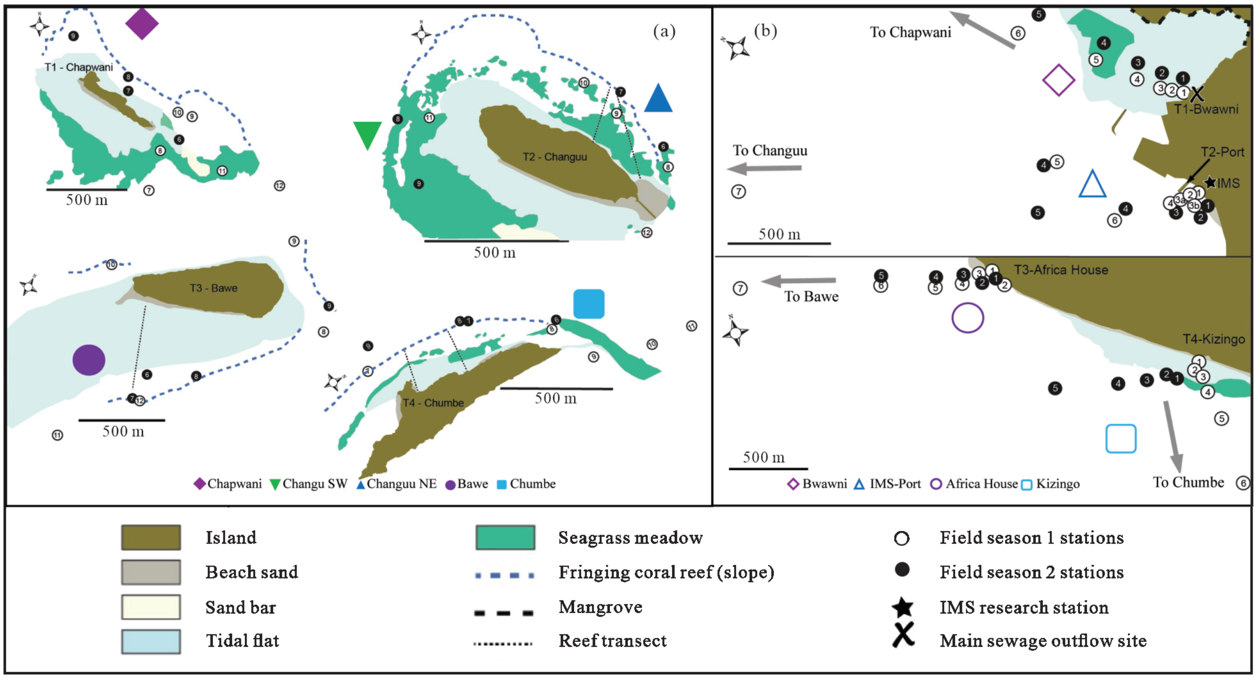

Figure 2. Map of the four (a) reef sites and (b) Stone Town shoreline sites, including sample stations. Along the ST shoreline, the first station sampled (Station 1) was located close to the sewage point source. Stations are indicated by open circles for the "Spring" and closed circles for the "Fall" field campaigns. Water quality measurements and samples were collected from the top and bottom of the water column at each station during the Spring and Fall season. Surface substrate and sediment samples were collected along the long boat transects (using a petit-grab sampler), and by snorkelling/diving (and hand collection), along reef-zone transects. Detailed information of the sites and stations can be found in Table S1.

Table 2 Taphonomic grading used in the evaluation of foraminiferal specimen

Category	Description of test state	% Preservation
T0	Test intact, fresh-looking, natural symbiont colour and/or staining, translucent, no visible surface pitting, no damage to chamber walls or aperture	100
T1	Test translucent to opaque, some pitting, limited damage to chamber walls and aperture	> 95
T2	Youngest chamber (containing aperture) may be fractured/abraded but other chambers remain mostly intact, species still identifiable	> 75
T3	Chamber walls damaged, sutures intact, evidence of boring	> 50
T4	Fractured aperture, chamber walls and sutures; encrustations and infillings	< 50
T5	Agglutinated; test encrusted by grains and minerals	--

scope, key regional taxonomic literature (Thissen and Langer, 2017; Thissen, 2014; Pereira, 1979), other plates and monographs (Debenay, 2012; Loeblich and Tappan, 1994), and online databases: World Register of Marine Species (WoRMS), and the World Foraminifera Database. To aid identification, specimens were photographed using a Tescan VEGA3 XMU Scanning Electron Microscope (SEM) and a 3D-Keyence VHX 500 digital microscope.

The FoRAM Index (FI) was applied as an indirect measure of coral-reef health, by first sorting specimens into the three functional groups as follows: o, opportunistic, stress-tolerant; h, small, heterotrophic; and s, algal symbiont-bearing, large benthic foraminifera, following Hallock et al. (2003). The proportion of individuals (P) in each functional groups was determined by the total number of individuals in each functional group (N) divided by the number of individuals in the sample (T), where $P_s = N_s/T$; $P_o = N_o/T$; and $P_h = N_h/T$. The FI was calculated as: $(10P_s) + (P_o) + (2P_h)$. Values <2 indicate water quality conditions inhospitable to symbiont-bearing organisms, and thus, reef growth values between 2 and 4 indicate marginal conditions, while values >4 indicate water-quality conditions conducive to photosymbiosis and calcification.

2.4 Statistical Analyses

To assess environmental differences along the transects between ST and the reef sites, and within and between the two sampling seasons (the first in Spring, and the second in Fall), multi one-way ANOVAs were performed on the nutrient data. Data were checked for normality (Shapiro-Wilk test) and equal variance (Brown-Forsythe test). Where significant values were recorded, pairwise comparisons using the post-hoc Tukey's test were performed to test for significant differences between individual factors. Univariate analyses were performed using SigmaPlot v. 12.5. Principal component analysis (PCA) was used to visualize environmental differences among the sites. To account for different scales and units, abiotic factors were normalized, and a Euclidean distance matrix was calculated to show similarity in two-dimensional fields and to compare data on the same scale (Clarke and Gorley, 2015; Clarke and Ainsworth, 1993).

Variability in the foraminiferal community was quantified using relative abundance (RA) or the number of individuals of a species (n) and the total number of species in a sample (T), where RA = $n100/T$. The frequency of occurrence (FO) was calculated as the ratio between the number of samples in which the species occurred (p) and the total number of samples analyzed (P), where FO = $p100/P$. Diversity was assessed using comparative indices: Margalef Richness (d), Pielou's Evenness (J′), Fisher's (α), Shannon (H'), Simpson's (D) and Hills (N1). Significant differences among the reef sites were tested using a one-way ANOVA, again using a Shapiro-Wilk test for normality and Tukey's pair-wise comparisons.

The foraminiferal relative abundance data were square-root transformed, and the Bray-Curtis (dis-) similarity distance was calculated. Differences in the foraminiferal community structure were visualized using two-dimensional, non-metric multidimensional scaling (nMDS) ordination and a similarity profile (SIMPROF) cluster analysis. A one-way analysis of similarity (ANOSIM), and pair-wise tests were used to test for differences between reef sites and habitats. Taxa contributing the most to similarity within a reef site, and to the (pairwise) dissimilarity between reef sites was determined using similarity percentage analysis (SIMPER). To assess the relationships between the foraminiferal data (biotic) and the environmental (abiotic) parameters (sediment, water and nutrients), a biotic-environmental (BIOENV-BEST) test was performed. The significance of this correlation was tested using the RELATE function (Spearman rank correlation). The above statistical analyses were performed using PRIMER v. 7 (Primer-E Ltd., UK) for Windows (Clarke and Gorley, 2015).

3 RESULTS

3.1 Sediment Composition

Grain-size distributions indicated considerable variability among the sites, with most sediment samples varying from medium (250 – 500 μm) to very coarse (1 000 – 2 000 μm). The highest (~92%) mean percent $CaCO_3$ (Table 3) was found at the reef sites with the >500 μm fraction characterized by foraminiferal tests (~70%), bivalve shells (~13%), coral fragments (~6%), gastropod shells (~5%), calcareous sponge spicules (~2%), echinoid spines (~2%) and other particles including coralline algae, serpulids, decapod fragments, balanid plates, ostracods, bryozoans and calcareous algae fragments (<2%). Detailed results on grain size and carbonate content for the ST shoreline and reef sites samples (162 in total) can be found in the ESM (Table S1; Fig. S1).

3.2 Water Column Parameters and Nutrient Concentrations

In 252 water samples, the mean values of the physicochemical parameters were within the normal range of marine conditions (Table 4). Water temperatures ranged from 25.5 to 27.1 °C during the first (Spring), and from 28.7 to 29.9 °C during the second (Fall) field campaign. A total of 731 (out of 1 079) nutrient concentration values from 252 water samples, were successfully obtained. This included 376 (from 181 samples) in the first and 355 (from 71 samples) values in the second season. Ammonium and nitrogen oxide concentrations could not be obtained for 32% of the total samples collected due to a preservation error, leaving a data gap of 181 measured NH_4, and 167 NO_x values, needed for calculating DIN values for the Spring season. The full set of nutrients (NO_2^-, NO_x, PO_4^{3-} and NH_4^+ and Si) were included in the Fall season analysis. Nutrient concentrations were highly variable, and the mean DIN (NO_x + NH_4^+) and DIP (PO_4^{3-}) concentration values were relatively moderate (0.7 ± 0.5 and 0.2 ± 0.1 μM, respectively; Table 4; Fig. S2), between the sites and across the seasons. There were significant differences in the mean nutrient concentrations between the seasons, for example, phosphate (PO_4^{3-}) and nitrite (NO_2^-) concentrations were significantly ($p < 0.05$) higher during the Spring than during the Fall in most ST and some reef sites (Table 4; Fig. S2). Overall, moderate nutrient concentrations were detectable at each reef site and did not show a strong cross-shore gradient with increasing distance from Stone Town (Figs. S2a – S2d). The (Euclidean) distance-based spatial pattern explained 30% of the variation observed in the parameters and nutrient concentration in Spring and 42% in Fall (Fig. 3).

3.3 Foraminiferal Assemblages

A total of 10 351 foraminifer specimens from the total (mixed) assemblage were analysed and 151 species from 54 genera and ~26 families were identified. Specimen conditions that were graded below T2 (with the exception of T5), comprised 10% or less of the specimen picked. The hyaline-walled rotaliid species comprised the highest (77%) relative abundance (RA), followed by the porcelaneous-miliolids (15%) and the agglutinated (8%) (Table S2). The dominantly hyaline-

Table 3 The overall mean (± SD) percent calcium carbonate (%$CaCO_3$) of the sediment samples collected from: (1)- the shoreline, (2)- channel deposits, and (3) the reefs

Sites	n	Range %$CaCO_3$	Mean % $CaCO_3$	Previous study
(1) ST	17	11–70	35 ± 21 ($p < 0.001$)*	34 ± 31
(2) Channel	6	74–83	78 ± 3 ($p < 0.001$)	69 ± 22
(3) Reefs	14	84–96	92 ± 4 ($p < 0.001$)*	89 ± 12

A Kruskal-Wallis one-way analysis of variance shows that the mean of the three samples classes were significantly different. Pairwise comparisons resulted in statistically significant (*) differences ($p < 0.050$) between the ST sites (all) versus the reef sites ($p < 0.001$) samples. A comparison is made with previous findings of Shaghude and Wannäs (2000).

Table 4 The water quality data for the four Stone Town (ST) and four reef sites (R)

Loc	Transect-Site	Season (x)	DO (mg/L)	Temp. (°C)	Salinity (PSU)	TDS (g/L)	pH	PO_4 (DIP) (μM/L)	NO_2 (μM/L)	NO_3 (μM/L)	NO_X (μM/L)	NH_4 (μM/L)	Si (μM/L)	DIN (μM/L)
ST	T1-	S_1 (12)	6.42 ± 0.30	26.58 ± 0.08	34.55 ± 0.05$^{*\#}$	52.33 ± 0.05$^{*\#}$	8.16 ± 0.02	0.35 ± 0.18^{*+}	0.16 ± 0.06$^{*+\#}$	-	-	-	-	-
	Bwawni	F_1 (10)	7.32 ± 0.21*	28.95 ± 0.07$^{\#}$	34.06 ± 0.05*	51.50 ± 0.00*	8.19 ± 0.02*	0.16 ± 0.17^{+}	0.01 ± 0.01^{+}	0.09 ± 0.06	0.10 ± 0.00*	0.77 ± 0.5*	1.42 ± 0.1$^{*\#}$	0.87 ± 0.61
	T2-	S_1 (16)	6.69 ± 0.06	25.66 ± 0.08*	35.42 ± 0.04$^{\#\$}$	53.44 ± 0.41^{*+}	8.16 ± 0.01	0.19 ± 0.03	0.47 ± 0.18	-	-	-	-	-
	Port/IMS	F_1 (10)	7.61 ± 0.11	28.92 ± 0.11*	34.05 ± 0.11^{+}	51.51 ± 0.13^{+}	8.23 ± 0.01	0.11 ± 0.04$^{*\#}$	0.03 ± 0.01$^{\#\$}$	0.26 ± 0.27	0.29 ± 0.28	0.51 ± 0.28	1.71 ± 0.26^{+}	0.80 ± 0.48
	T3-	S_1 (14)	-	26.36 ± 0.06^{+}	35.40 ± 0.00^{*+}	53.44 ± 0.05$^{\#}$	8.17 ± 0.01	0.20 ± 0.20^{+}	0.30 ± 0.10$^{*\$}$	-	-	-	-	-
	Af. House	F_1 (10)	7.66 ± 0.05*	28.95 ± 0.08^{+}	34.27 ± 0.05^{*+}	51.81 ± 0.03$^{*+\#}$	8.23 ± 0.00*	0.21 ± 0.03^{*+}	0.02 ± 0.01*	0.12 ± 0.16	0.14 ± 0.17^{+}	0.21 ± 0.1*	2.42 ± 0.20$^{\#}$	0.36 ± 0.26
	T4-	S_1 (12)	6.35 ± 0.39	26.72 ± 0.08^{*+}	34.66 ± 0.05$^{+\$}$	52.45 ± 0.08^{+}	8.15 ± 0.04	0.20 ± 0.13*	0.14 ± 0.05^{+}	-	-	-	-	-
	Kizingo	F_1 (10)	7.69 ± 0.28	29.43 ± 0.21$^{*+\#}$	34.17 ± 0.05	51.59 ± 0.03$^{\#}$	8.22 ± 0.02	0.18 ± 0.03$^{\#}$	0.04 ± 0.02^{*+}	0.30 ± 0.12	0.34 ± 0.13^{*+}	0.45 ± 0.13	2.91 ± 0.47^{*+}	0.79 ± 0.24
	Mean	S_1 (54)	6.51 ± 0.31	26.31 ± 0.42	35.04 ± 0.41	53.97 ± 0.57	8.16 ± 0.02	0.23 ± 0.14	0.29 ± 0.18	-	-	-	-	-
		F_1 (40)	7.57 ± 0.23	29.06 ± 0.25	34.14 ± 0.11	51.60 ± 0.14	8.22 ± 0.02	0.17 ± 0.09	0.03 ± 0.02	0.19 ± 0.19	0.22 ± 0.2	0.12 ± 0.05	2.12 ± 0.66	0.71 ± 0.46
	% Diff.	S_1 & F_1	16.28%	10.45%	2.57%	4.39%	0.74%	26.09%	89.66%	-	-	-	-	-
	p-value		< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.005	0.002	-	-	-	-	-
R	T1-	S_2 (12)	6.92 ± 0.09	26.63 ± 0.12$^{\#\$}$	34.55 ± 0.05$^{*+\#}$	52.33 ± 0.07$^{*+\#}$	8.19 ± 0.00	0.17 ± 0.07^{+}	0.09 ± 0.04	-	-	-	-	-
	Chapwani	F_2 (08)	7.29 ± 0.1	29.05 ± 0.18	34.1 ± 0.00	51.51 ± 0.04*	8.19 ± 0.01	0.07 ± 0.01$^{*\#}$	0.03 ± 0.01	0.24 ± 0.12	0.27 ± 0.13	0.67 ± 1.13	1.57 ± 0.16*	0.94 ± 1.15
	T2-	S_2 (10)	6.89 ± 0.11	26.12 ± 0.13$^{*\#}$	35.47 ± 0.00*	53.59 ± 0.03*	8.19 ± 0.01	0.20 ± 0.01^{*+}	0.22 ± 0.09*	-	-	-	-	-
	Changuu	F_2 (08)	8.31 ± 1.35	29.38 ± 0.33*	34.06 ± 0.05*	51.54 ± 0.05	8.26 ± 0.08	0.10 ± 0.02$^{+\$}$	0.05 ± 0.01	0.29 ± 0.09	0.34 ± 0.09	0.30 ± 0.13	1.90 ± 0.75	0.64 ± 0.19
	T3-	S_2 (10)	-	26.85 ± 0.38^{*+}	35.39 ± 0.03^{+}	53.45 ± 0.05$^{\#}$	8.18 ± 0.03	0.20 ± 0.00	0.30 ± 0.1	-	-	-	-	-
	Bawe	F_2 (08)	7.96 ± 0.22	29.15 ± 0.26	34.20 ± 0.00*	51.70 ± 0.00*	8.26 ± 0.03	0.17 ± 0.02$^{\#\$}$	0.05 ± 0.01^{+}	0.37 ± 0.19	0.41 ± 0.20	0.33 ± 0.10	2.10 ± 0.27	0.74 ± 0.30
	T4-	S_2 (20)	6.74 ± 0.09	26.24 ± 0.15$^{+\$}$	35.39 ± 0.06$^{\#}$	53.49 ± 0.06^{+}	8.18 ± 0.02	0.19 ± 0.10*	0.05 ± 0.07^{*+}	-	-	-	-	-
	Chumbe	F_2 (08)	7.65 ± 0.0	28.88 ± 0.09*	34.10 ± 0.00	51.56 ± 0.05	8.22 ± 0.01	0.20 ± 0.08^{*+}	0.04 ± 0.02	0.27 ± 0.25	0.30 ± 0.27	0.42 ± 0.10	2.36 ± 0.18*	0.73 ± 0.33
	Mean	S_2 (52)	6.84 ± 0.12	26.44 ± 0.35	35.20 ± 0.38	53.21 ± 0.52	8.18 ± 0.02	0.18 ± 0.07	0.12 ± 0.10	-	-	-	-	-
		F_2 (32)	7.80 ± 0.76	29.11 ± 0.29	34.11 ± 0.06	51.58 ± 0.08	8.23 ± 0.05	0.14 ± 0.07	0.04 ± 0.02	0.29 ± 0.17	0.33 ± 0.18	0.43 ± 0.57	1.98 ± 0.49	0.76 ± 0.60
	% Diff.	S_2 & F_2	14.04%	10.10%	3.10%	3.06%	0.61%	22.22%	66.67%	-	-	-	-	-
	p-value		<0.001	<0.001	<0.001	<0.001	<0.001	0.002	0.002	-	-	-	-	-
ST vs. R	% Diff.	S_1 & S_2	5.07%	0.49%	0.46%	0.76%	0.25%	21.74%	58.62%	-	-	-	-	-
	p-value		-	0.718	0.080	0.123	<0.001	0.028	<0.001	-	-	-	-	-
	% Diff.	F_1 & F_2	3.04%	0.17%	0.09%	0.04%	0.12%	17.65%	33.33%	52.63%	50.00%	72.09%	6.60%	7.04%
	p-value		<0.001	0.707	0.545	0.115	0.008	0.098	<0.001	0.002	0.005	0.239	0.468	0.642

The mean values (±SD) for various water quality parameters including: dissolved oxygen (DO), temperature (Temp), salinity, total dissolved solids (TDS), pH, the inorganic nutrients including: phosphate (PO_4), nitrite (NO_2), nitrate (NO_3) nitrogen oxide (NO_x) and ammonium (NH_4), silicate (Si) and dissolved inorganic nitrogen (DIN) are given in μM/L. Note that the samples collected closest to the major sewage outflow stations (i.e., Bwawani and Port/IMS) showed the highest DIP and DIN values compared to the other ST sites. The total mean value, percent difference of the means and the one-way ANOVA significance level are shown for the samples from each site collected during the spring (S; August–October) and during the second field campaign or fall (F; March–April) season. Pairwise comparisons for significant differences between sites and within each season (*) at the ST and R locations are shown. Corresponding graphs for the nutrient concentrations can be found in the ESM, Fig. S2. ***+#$.** Significantly different pairs within each field season, S vs. F.

rotaliid taxa reflected normal marine, lagoonal and reef environments (Fig. 4). The symbiont-bearing LBF(s) were the most abundant functional group (73%) in the reefs, followed by the small heterotrophic (h) (26%), and lastly the opportunistic species (o) (1%).

Among the LBF, *Amphistegina lessoni* and *A. lobifera* dominated the assemblage, and had a combined RA of 51%, and a frequency of occurrence of 100% (Tables 5 and S2). Accompanying them, *Heterostegina depressa*, *Marginopora vertebralis*, *Neorotalia calcar*, *Peneroplis pertusus*, *P. planatus*, and *Sorites orbiculus* together contributed 22%, and other LBF taxa (*Alveolinella quoyi*, *Coscinospira hemprichii*, *Amphisorus hemprichii*, *Amphistegina papillosa*, *A. radiata*, *Calcarina* sp. and *Operculina ammonioides*) comprised ~1%. Numerous rare taxa comprised <1% of the samples. The total number of species (S) within the reefs ranged between 24 and 58 and was significantly different ($p = 0.045$) between the reefs, with the highest number from the Chumbe reef slope. The diversity values were low to moderate (e.g., average Shannon $\log_2$ ranged from 2.4 ± 0.3 to 3.4 ± 0.4; Fisher-α from 6.1 ± 1.1 to 11.7 ± 3.0), as well as richness (4.0 ± 0.6 to 6.5 ± 1.7), and not significantly different between the reefs (Table S5). Among the different diversity indices calculated, there was not one that was especially more sensitive to changes in the RA than the others. Pielou's evenness values were moderate (0.5) to high (0.8) and mostly consistent across the reefs.

The nMDS plot of the foraminifera assemblages (Fig. 4) shows that the reefs closest to Stone Town, including Chapwani and Changuu NE, were well separated, with no overlap with the Chumbe Reef MPA located furthest away from ST. The Bawe Reef was the intermediate reef, showing an overlap with the Changuu NE and the Chumbe reefs. There was an overlap between the Changuu SW (backreef lagoon) seagrass meadows and Chumbe Reef. The SIMPROF analyses identi-

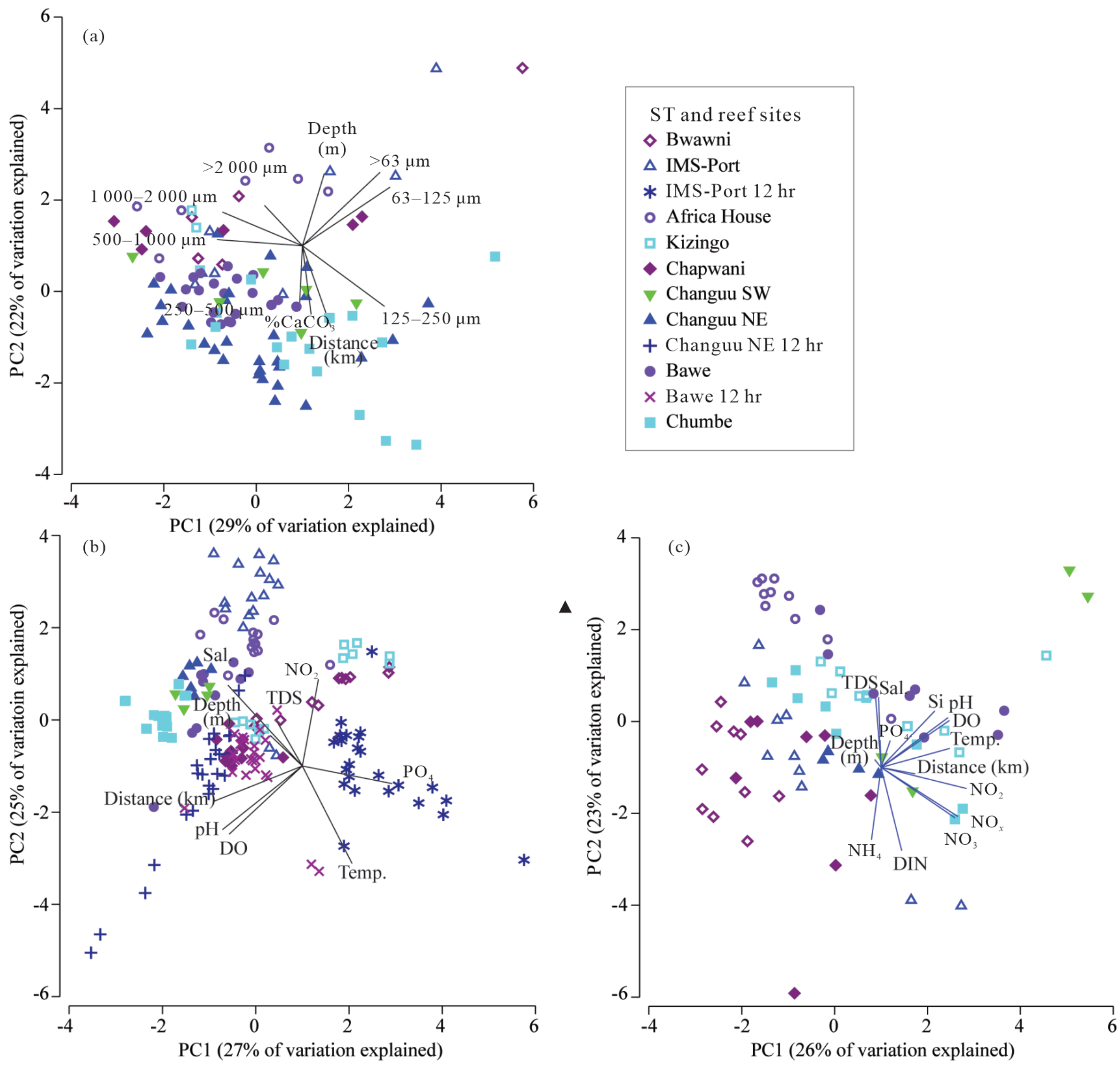

Figure 3. Principal component analysis (PCA) of the abiotic factors for (a) grain size; (b) "Spring" season parameters and nutrients; and (c) the "Fall" season parameters and nutrients. The physical parameters include temperature, salinity, total dissolved solids (TDS), pH, and dissolved oxygen (DO), nitrite (NO_2), nitrate (NO_3) nitrogen, (NO_x), ammonium (NH_4), dissolved inorganic nitrogen (DIN) and phosphate (PO_4) or dissolved inorganic phosphate (DIP). Samples that are grouped close together are more similar than samples further apart. The vector lines represent the relative contribution and importance (by length) of each variable to the observed variation among the sites. Vectors pointing in the same direction indicate a positive correlation.

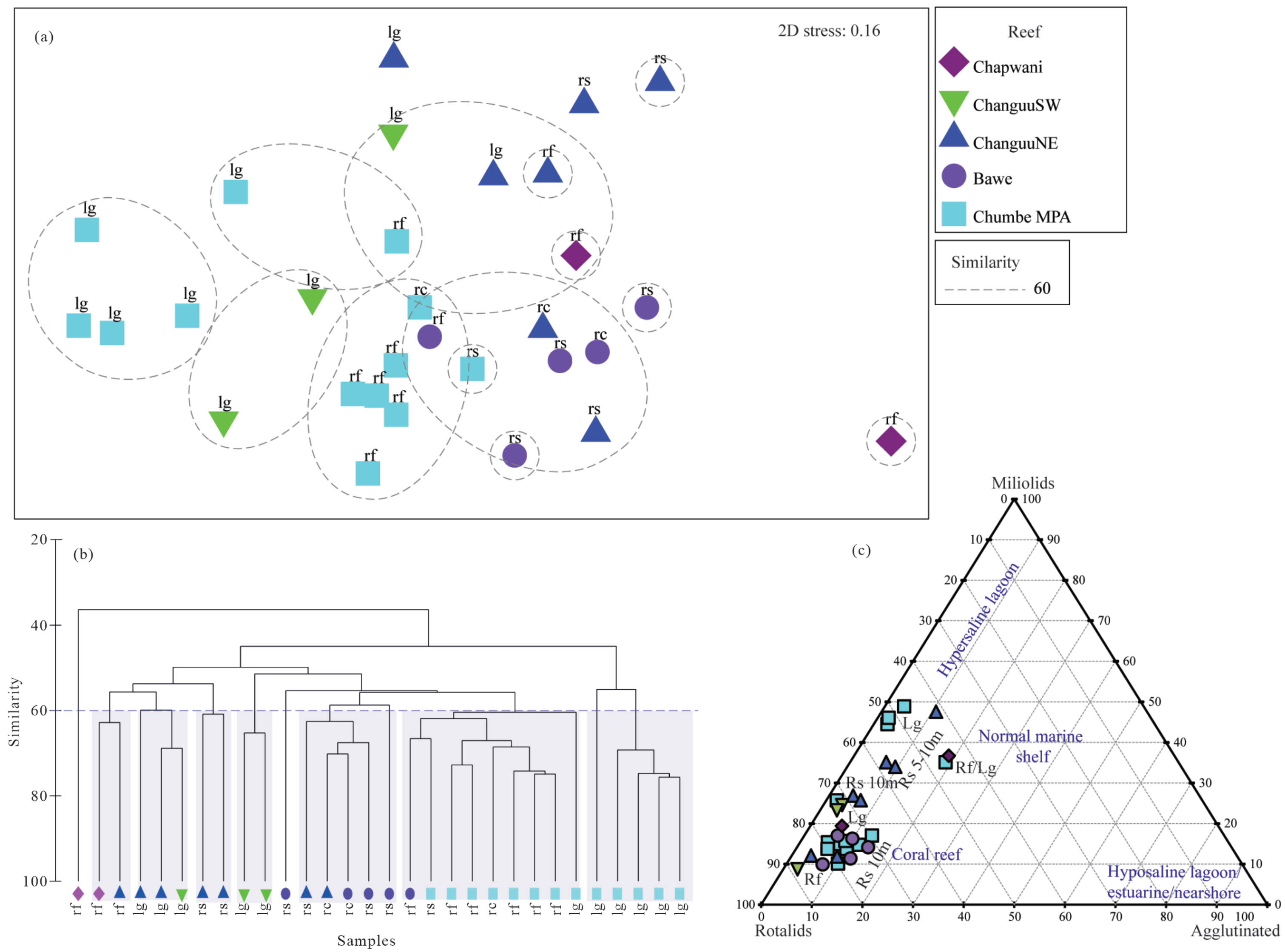

Figure 4. (a) A two-dimensional (2D), non-metric multidimensional (nMDS) plot with SIMPROF clusters, based on the Bray-Curtis similarity, showing the ordination of the foraminifera assemblages from the four reef sites and different habitats, including: lagoon (lg), reef flat (rf), crest (rc) and slope (rs). A one-way ANOSIM resulted in a Global R value of 0.51 (p = 0.001) (where R = ANOSIM test statistic, p = significance level, 999 permutations). (b) SIMPROF tests produced three main clusters (and 3 smaller one), at a similarity of 60%. (c) A ternary plot showing the distribution of the reef site samples, with respect to the proportions of the three foraminifera suborders, which reflect normal marine and coral reef environmental conditions.

Table 5 A list of the (143) benthic foraminifera taxa identified from the four reef sites, categorized into the three functional groups

Functional groups	List of taxa
Large, symbiont-bearing RA = 73%	*Alveolinella quoyi*, *Coscinopira hemprichii*, ***Peneroplis pertusus* (2)**, ***Peneroplis planatus* (2)**, *Amphisorus hemprichii*, ***Marginopora vertebralis* (1)**, ***Sorites orbiculus* (7), *Amphistegina lessoni* (28)**, ***Amphistegina lobifera* (22),** *Amphistegina papillosa*, *Amphistegina radiata*, ***Neorotalia calcar* (1)**, *Calcarina* sp. A, ***Heterostegina depressa* (7)**, *Operculina ammonoides*
Small, heterotrophic RA = 26%	*Spirotextularia sp. A*, *Spirotexutarlia floridana*?, *Gaudryina* sp. A (*G. collinsi*?), *G. quadrangularis*, *G. tenuis*?, *Martinottiella bradyana*, *Clavulina difformis*, *C. multicamerate*, *C. pacifica*, *Textularia agglutinans*, ***T. calva* (2)**, *T. candeiana*, *T. conica*, *T. cushmani*, *T. dupla*, *T. goessi*, ***T. kerimbaensis* (1)**, *T. occidentalis*, *T. pseudogramen*, *T. stricta*, *Textularia* sp. cf. *T. truncata*?, ***Textularia spp.* (2)**, *Cornuspira involvens*, *Planispirinella involute*, *Edentostomina millet*, *S. antillarum*, *S. clara*, *Spiroloculina communis*?/*angulata*?, *S. corrugata*, *S. eximia*, *S. fragilis*, *S. foveolata*, *S. subimpressa*, *Hauerina diversa*?, *Lachlanella compressiostoma*, *Lachlanella parkeri*, *Quinqueloculina agglutinans*, *Q. arenata*? ***Q. auberiana* (1)**, *Q. barnardi*, *Q. bicarinata*, *Q. bosciana*, *Q. bradyana*?/*bassensis*?, *Q. cuveriana*, *Q. disparilis*, *Q. distorqueata*, *Q. funafutiensis*, *Q. latidentella*, *Q. limbata*?, *Q. neostriatula*, *Q. oblonga*, *Q. parvaggluta*, *Q. philipinensis*, *Q. pittensis*, *Q. pseudoreticulata*, *Q. rariformis*, *Q. schlumbergeri*, *Q. seminula*, *Q. striatotrigonula*, *Q. subpolygona*, *Q. sulcata*?/*granulocostata*?, *Q. tantabiddyensis*, *Q. transversestriata*, *Q. tropicalis*, *Q. vandiemeniensis*, *Quinqueloculina* sp. A, B, C, D, E, *Miliolinella circularis*, *M. labiosa*, *M. subrotunda*, *Miliolinella* sp. cf. *M. labiosa*?, *Pseudomassilina australis*?, *P. reticulata*, *P. robusta*? *Pseudomassilina* sp. A, *Pyrgo denticulata*, *P. depressa*, *P. oblonga*, *P. striolata*, *Triloculina barnardi*, *T. bertheliniara*, *T. bicarinata*, *T. elongotricarinata*, *T. rotunda*, *T. striatotrigonula*, *T. tricarinata*, *T. trigonula*, *Triloculina* sp. cf. ***T. tricarinata* (1)**, *Sigmoilinita costata*, *Sigmamiliolinella australis*, *Sigmoilopsis elliptica*, *Schlumbergerina alveoliniformis*, *Pseudohauerina involuta*,, *Patellinella inconspicua*, *Eponides cribrorepandus*, ***E. repandus* (1)**, *Rotorbis auberi*, *Neoconcorbina* sp. A, *Rosalina bradyi*, *Ungulatelloides* sp. A, *Cibicides pseudolobatulus*, *Cibicides* sp. A, *Planorbulinella larvata*, *Cymbaloporetta bradyi*, *Cymbaloporetta squamosa*, *Cymbaloporetta tabellaeformi*, *Acervulina* sp. cf. *A. mabahethi*?, *Planogypsina acervalis*, *Epistomaroides polystomelloides*, *Anomalinella rostrata*, *Hanzawaia grossepunctata*
Opportunistic RA = 1%	*Ammonia* sp. cf. *A. tepida*, *Ammonia* sp. cf. *A. beccari*, *Elphidium advenum*, *Elphidium craticulatum*, ***Elphidium crispum* (2)**, *Elphidium fichtelianum*, *Elphidium macellum*, *Elphidium milletti*, *Elphidium* sp. cf. *E. advenum*, *Euloxostomum pseudobeyrichi*, *Parrellina hispidula*, *Reusella spinulosa*?, *Sagrinella durrandii*, *Sagrina jugosa*, *S. zanzibarica*

Fifteen species had a total RA greater than or equal to 1% (bolded), while the majority of the species were rare (<1%).

fied four main (and two minor) clusters, at a similarity of 60%. A one-way ANOSIM gave a Global R value of 0.51 (p = 0.001), indicating significant overall separation or differences among the reef assemblages (Figs. 4 and 5). An ANOSIM value of $R = 0.80$, $p = 0.001$ resulted for the combination of reef sites and habitats, indicating significant differences between the habitats. The SIMPER results show *Amphistegina lessoni* and *A. lobifera* as the top two species contributing to the observed differences between the Changuu NE, Bawe and Chumbe reefs, while *Marginopora vertebralis* contributed to the observed differences between Changuu SW and the other reefs, and *Textularia agglutinans* contributed to the observed differences between Chapwani and the other reefs (Fig. 5; Tables S3 and S4). The BIOENV-BEST and RELATE tests showed weak (R = 0.256) significant ($p < 0.01$) correlation between the biotic and abiotic variables, with fine grain sizes (125–250 and 63–125 μm), followed by nitrate (NO_2), nitrogen oxide (NO_x) and temperature accounting for the best correlation among the datasets (Fig. 3).

3.4 The FoRAM Index

The FI values ranged between 4.7 (Chapwani) and 9.3 (Changuu SW), indicating overall water quality conducive for supporting algal symbiont-bearing organisms among the reefs (Table S5). From closest to furthest from ST, they were: 6.3 ± 2.3 at Chapwani, 9.0 ± 0.3 at Changuu SW, 7.1 ± 1.2 at Changuu NE, 7.6 ± 0.7 at Bawe, 7.8 ± 0.6 at Chumbe, and 7.6 ± 1.1 overall (Table S5; Fig. 5).

4 DISCUSSION

4.1 Water Quality

Evidence of pollution from sewage effluent from western Zanzibar was first reported from Stone Town (ST) during the 1990s (Mohammed, 2002, 1990; Björk et al., 1995). In the 2000's, nutrient concentrations exceeded levels that are considered to be sustentative for healthy reef ecosystems (Nyanda et al., 2016; Moynihan et al., 2012). Locally, sewage pollution is a concern for human wellbeing, as it has been associated with local outbreaks of waterborne diseases such as cholera, diarrhea and gastroenteritis, including high levels of fecal indicator (*Enterococci*) bacteria (Nyanda et al., 2016; Moynihan et al., 2012).

This study found that nutrient concentrations near the source of sewage outflow, along the ST shoreline, were variable and at moderate levels, but generally <1.0 μM, with respect to the mean DIN and DIP concentrations, which were moderate (0.7 ± 0.5 and 0.2 ± 0.1 μM, respectively; Table 4; Fig. S2). However, point data suggest that the DIN and DIP nutrient concentration values, especially at Bwawani and the Port/IMS, occasionally approached or exceeded known threshold values of approximately 1.0 μM for DIN, and approximately 0.2 to 0.3 μM for DIP (Lapointe et al., 2004; Bell, 1992; Hallock and Schlager, 1986). For example, very high Spring PO_4 (1.5 ± 0.0 μM); and Fall NO_x (0.9 ± 0.1 μM) values were recorded at the IMS-Port; and Fall NH_4 concentration values exceeded >1.0 μM at Bwawani, closest to the main sewage outfall (1.4 ± 0.1 μM).

Similarly in the reefs, the mean DIN (0.8 ± 0.6) and DIP (0.1 ± 0.1 to 0.2 ± 0.1) concentration values reached moderate levels throughout, with mean values being occasionally as high or slightly higher, than those found along the ST shoreline. DIN was consistently elevated, whereas DIP was simultaneously low. However, point data indicate high Spring PO_4 at both Chapwani (0.4 ± 0.1 μM) and Chumbe (⩾0.4 ± 0.0 μM); and

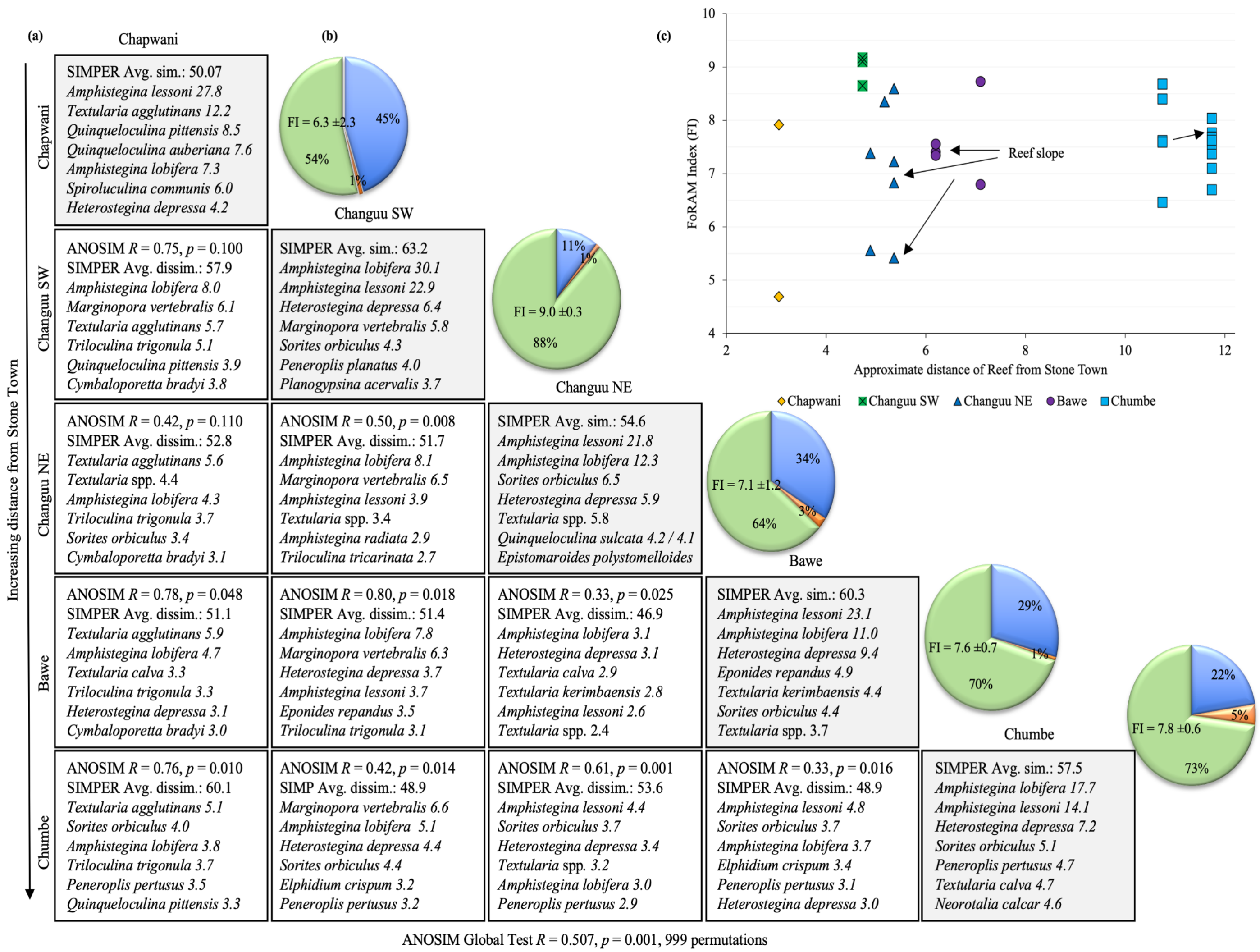

Figure 5. (a) The results of the one-way ANOSIM and SIMPER analysis, based on the Bray-Curtis similarity, of the foraminifera assemblages from the four reef sites. The ANOSIM global test (R = 0.51 p = 0.001) shows significant separation or differences among the reef sites. Pairwise test results between reefs are indicated. The SIMPER average similarity with the top species contributing to similarity (i.e., species composition and/or abundance) within each reef; and the pairwise average dissimilarity with the top species contributing to differences between the reefs is indicated (detailed SIMPER results can be found in supplementary Tables S3 and S4). (b) Pie charts showing the average percent proportion of the three functional groups: symbiont-bearing LBF (green), small, heterotrophic (blue) and stress-tolerant opportunistic (yellow) taxa. The average FoRAM Index (FI) value for each reef. (c) the FI values for the four reef (Chapwani, Changuu NE, Bawe and Chumbe) and one seagrass lagoon (Changuu SW) site. All samples resulted in FI values greater than four, indicating water quality conditions conducive for photosymbiosis, coral reef growth and carbonate production in western Zanzibar reefs.

high Fall NH_4 at Chapwani (3.4 ± 0.1 μM) and Chumbe (~0.6 ± 0.1 μM), which may reflect pulsed inundation of sewage to the reefs. Of particular interest are the DIP concentrations measured at Chumbe, which exceeded 0.2 μM. These relatively high DIP values may result from transport by tidal currents from ST, and/or exposure to the island's own wastewater from its eco-tourist resort, despite the implementation of a sewage management system (Nordlund et al., 2013). At the other coral island resort sites, septic tanks are used for transport and disposal of liquid waste off the islands (Moynihan et al., 2012). Thus, these results (somewhat) support the hypothesis of a gradient in water quality with increasing distance from Stone Town, however, they suggest that a weaker, rather than a strong gradient exists.

In naturally oligotrophic coral-reef ecosystems, inputs of excess dissolved inorganic nutrients are typically kept uniformly low due to uptake by phytoplankton, benthic algae and/or seagrass, such that the nutrient which is the most limiting in the system becomes depleted faster than the other (Laws and Redalje, 1979). Laws and Redalje (1979) documented this in their study of sewage nitrification in Kaneohe Bay, Hawaii. They found that DIP was a more sensitive indicator of sewage enrichment than DIN. Similarly, we found that the coastal waters appeared to be DIP-limited. Thus, DIN concentrations are more likely to provide a better indication of enrichment, than DIP, in western Zanzibar's reefs.

Local hydrodynamics, influenced by the monsoonal wind-driven currents, rainfall, and tidal cycles, likely exert a strong influence on water quality (Staehr et al., 2018; Nyanda et al., 2016; Moynihan et al., 2012; Lugomela et al., 2002). Our study found significantly higher nitrite (NO_2) and phosphate (PO_4) concentrations in the reefs fronting ST (Chapwani, Changuu and Bawe), and lower values in the reef located South of ST (Chumbe MPA), during the Spring campaign (August to October). These observations can partly be explained by the influence of strong SE monsoonal winds and northward-flowing currents. This pattern of current flow reverses southwards during part of the (weaker) NE monsoon (Painter, 2020; Nyandwi, 2013) and thus, this directional shift could attribute for the observed higher nutrient values found at the Chumbe MPA during the Fall campaign. The strong SE-monsoonal winds may accelerate the EACC, thereby aiding in regional flushing of the shallow channels, deepening mixed layers of the water column, and potentially entraining nutrients from depths. This could either increase or decrease nutrient redistribution and exposure in the reefs. The wind-forced NE directional currents and eddies fronting ST may not be efficient enough to flush nutrients away from ST into the deeper waters of the Zanzibar Channel (Nyandwi, 2013; Muzuka et al., 2010; Shaghude et al., 2002), thereby possibly retaining them in the water column until the SE monsoon period. Nonetheless, the role that the regional-local hydrodynamics play in nutrient redistribution and/or flushing seems to be critical to maintaining healthy reefs in western Zanzibar.

4.2 Foraminifera Response to Reef Conditions

We found that the shallow water (<15 m) fringing coral reefs and reef-associated habitats were predominantly comprised of autochthonous (as defined by the taphonomic grading) foraminiferal assemblages composed of symbiont-bearing LBF (~73%), small heterotrophic (~26%), and few stress-tolerant, opportunistic (~1%) taxa. The reefs and reef-associated habitats were associated with relatively low-moderate average species diversity and richness, and high FoRAM Index (FI) values (7.6 ± 1.1). Among the LBF, two key species, *Amphistegina lessoni* and *A. lobifera*, and a few other LBF (*Amphisorus hemprichii*, *Heterostegina depressa*, *Marginopora vertebralis*, *Neorotalia calcar*, *Peneroplis* spp. *Sorites orbiculus*), dominated the total (mixed living and death) reef assemblage. Our findings, based on the total-assemblage derived FoRAM Index, are interpreted as reflecting overall healthy coral reef conditions, conducive to photosymbiosis and reef growth.

In light of our resulting high FI values, a caveat of using the total assemblage-based FI is that the overwhelming dominance of amphisteginids in the reef sediments may lead to questioning the validity of the FI values, and whether the water quality conditions are indeed as good as the FI indicates. High amphisteginid accumulations can reflect several years of up to 1 500 years or even more of surface deposition (Carilli and Walsh, 2012; Resig, 2004), mixing of relict with recent faunas (Renema et al., 2013), and interpretations of high wave energy environments (Fajemila et al., 2015; Hallock, 2012). To reduce misinterpretation, this study used a simple taphonomic grading scheme to distinguish, to the best of our ability, specimens that were *in-situ* and most recently dead. Thus, we believe that the FI reflects conditions in the reefs, despite moderate nutrient concentrations. The accumulation rate of fairly pristine tests, relative to the rate of test alteration was not quantified here, but it may help improve future interpretations of total assemblage derived-FI values.

The number of foraminiferal species (151) that we recorded is close to the number (158) that Langer et al. (2013) reported from the Bazuto Archipelago in Mozambique, from the assessment of the ⩾0.125 mm fraction, in both studies. Thissen and Langer (2017), who studied two patch reefs off Stone Town, namely Bawe Reef and Nyange Island, in their large-scale study of the Zanzibar Archipelago, reported similar, but slightly higher, species diversity values (Shannon: 3.2 and 3.5; Fisher-alpha: 16.4 and 22, respectively), a lower range of FI values (5.4 and 4.9–5.1, respectively), and similar percent calcium carbonate (88 and 92–93, respectively) to our results. The greater number of species (i.e., 61 at Bawe and 68–75 at Nyange Island) reported from their sites may be due to collection across a wider and deeper depth range (>15–30 m), and from different types of coastal habitats than what we surveyed.

The presence of a monoculture assemblage dominated by amphisteginid LBF reported here is similar to studies from elsewhere in the Zanzibar Archipelago (Thissen and Langer, 2017) and in the Bazuto Archipelago, Mozambique (Langer et al., 2013). Diatom-bearing, low magnesium calcite (LMC), hyaline-perforate amphisteginids, are key carbonate producers, considered to be important ecosystem engineers (Langer et al., 2013) in East Africa's shallow-water reef systems. As such, their ubiquitous distribution and prominence in tropical East Africa has important implications for their role as carbonate producers under rapid environmental degradation. Further research is needed to better understand short and long-term deposition rates of these key producers in reef sediments, and the consequences of their potential decline for the carbonate budget under potentially deteriorating conditions.

In this study, the high energy, well-lit, seagrass-dominated, backreef lagoon of Changuu SW was similar to the Chumbe MPA lagoon in having the highest FI values among the reefs. However, unlike Chumbe Reef, the Changuu SW site directly fronts ST, and unlike Changuu NE Reef (on its opposite side), this area receives limited tourist visits. Nutrients here were as high, if not higher than those found along the ST shoreline (Fig. S2). Tidal currents and dense seagrass meadows likely play important roles in either flushing away or in the uptake of nutrients (Romero et al., 2006), respectively. Its seagrass meadows supported large-diameter living *Marginopora vertebralis* and exceptionally robust-looking, *A. lobifera*, which occurred in their highest (live) densities, of up to 17% and 40%, respectively (as observed during the Spring season). Among the amphisteginids, *A. lobifera* is the shallowest dweller, and has shown remarkably high tolerance to thermal stress (Stuhr et al., 2021, 2017; Schmidt et al., 2016; Engel et al., 2015). This finding may warrant further investigation into why these species, especially *M. vertebralis*, occurred in much higher abundances at Changuu SW than at the other reef/seagrass sites (i.e., Chumbe MPA), which also support similar habitats and assemblages. There could be some benefit from (episodic) exposure to higher nutrients here.

The foraminiferal assemblages at Changuu NE were similar to those found at Chapwani Reef, in having higher contributions of small-heterotrophic taxa (e. g., agglutinated *Textularia* and miliolid *Triloculina*) driving the taxonomic differences with the other reefs (Bawe and Chumbe). Changuu NE is the most frequented and accessible coral reef from ST (for tourist boats), followed by Bawe. There were visible disturbance signals observed by this and other studies, including anchor damage to corals, poor visibility due to snow-like particles in the water column, paucity of reef fish, algal overgrowth, abundance of urchins, and the crown of thorn starfish, dominant submassive corals and declining branching (*Acropora*) corals (Staehr et al., 2018; Herrán et al., 2017). There is evidence that this reef has experienced long-term changes (since the early 1990s) in its carbonate producing-communities (Staehr et al., 2018).

Elevated nutrients have been reported to have negative effects on LBF communities and growth, especially in very shallow water (Narayan et al., 2022; Prazeres et al., 2016; Reymond et al., 2013, 2011; Uthicke and Altenrath, 2010), but it is also not unusual for LBF assemblages, as for corals, to persist in “stressed” conditions found in turbid, mesotrophic ecosystems, characterized by low-light intensities and high nutrient loads (Narayan et al., 2022, 2015; Humphreys et al., 2018; Renema, 2018, 2008; Cleary et al., 2014; Narayan and Pandolfi, 2010; Uthicke and Altenrath, 2010; Renema and Trolestra, 2001). As an example, high altitude reefs (Lybolt et al., 2011; Halfar et al., 2005) and tropical upwelling regions (Humphreys et al., 2016; Reymond et al., 2016, 2014) provide examples of natural laboratories for assessing the long-term influence of seasonally variable nutrients, temperature, and carbonate chemistry on foraminiferal assemblages. In the Great Barrier Reef, millennium-scale records have shown continuous marginality associated with poor water-quality from terrestrial discharge (Narayan et al., 2015; Reymond et al., 2013). These regions are often associated with reduced reef accretion and carbonate production and provide a template for investigating reef assemblages influenced by increasing nutrification.

In summary, differences in the assemblage structure (Fig. 4) suggest a gradient in water quality with increasing distance, in the order of: Chapwani/Changuu NE to Bawe to Chumbe (with Changuu SW being an outlier). For example, Chapwani and Chumbe MPA differed in that the former supported a higher composition of heterotrophic (agglutinated and miliolid) taxa while the latter was overwhelmingly dominated by LBF. These results support the second hypothesis of differences in water quality influencing the foraminiferal assemblage. It suggests that the LBF assemblages can be useful bioindicators for monitoring the early detection of coral reef degradation in Zanzibar, in support of our third hypothesis. Renema (2018) suggested that LBF assemblages respond to stressors along a two-step threshold reflected by: (1) a change in water quality and (2) a shift in the benthic habitat. Changes in the assemblage structure can be recorded after (1) but it may not yet be apparent in (2). Our data suggest that this may be the case for Zanzibar’s reefs.

4.3 Linking Metrics for Coral Reef Health

Live coral cover, that is, the percentage of seafloor covered by living calcifying coral species, has been the most commonly used metric for determining coral reef health (Hughes, 1994). In recent years, there has been interest by reef ecologists to incorporate other complementary indices to support coral-cover data, such as fish surveys, benthic communities, crustose-coralline algae, cyanobacterial communities (Díaz-Pérez et al., 2016), carbonate reef budgets (Lange et al., 2020), and the FoRAM Index (Prazeres et al., 2020; Hallock et al., 2003). In systems such as Zanzibar that are overexploited with respect to 19 studied fisheries target groups, which include molluscan invertebrates (Rehren et al., 2022), but continue to show high live coral cover and carbonate production (Herrán et al., 2017), coral cover alone may not be sufficient to detect the nuances of reef health (Obura et al., 2019; Díaz-Pérez et al., 2016).

Foraminifera respond quickly, within a matter of days, weeks to months to nutrient influx, in comparison to corals, which typically respond slowly, over a period of a year or several years, by undergoing phase shifts (Hughes, 1994; Done, 1992). Thus, foraminiferal studies have important implications for independently interpreting the effects of live coral cover, reef species diversity and carbonate production rates in response to the increasing frequency of stressors.

The present foraminiferal study was carried out in concurrence with a coral-reef study that looked at coral cover, diversity and carbonate production along the reef slope (5 and 10 m depth) at the same four reef sites (Herrán et al., 2017). These authors found a relatively high live coral cover, high coral diversity with no significant differences between the reefs, and high average net calcium carbonate production rates (gross production-bioerosion rates) by corals, ranging up to 16 kg $CaCO_3$ $m^{-2}yr^{-1}$. The unmanaged reefs closest to ST had a live coral cover of ~52% (i.e., with the lowest values at Chapwani), whereas the protected MPA had the highest live coral cover at 67%, and the highest net carbonate production rate. In addition, submassive corals were found to dominate in the unmanaged reefs fronting ST, whereas massive as well as branching corals dominated in the Chumbe MPA. Past studies also indicate that the fast-growing, water-quality sensitive, branching *Acropora* corals have significantly declined from Changuu and Bawe reefs (Muhando, 2010), whereas they are still extensively abundant at Chumbe (Staehr et al., 2018; Herrán et al., 2017; Muhando, 2010).

These data corroborate the findings from the present study of foraminiferal assemblages. Both studies indicate the persistence of biogenic carbonate-producing functionality and photosymbiosis in western Zanzibar reefs, but each study also highlights their vulnerability to environmental stressors, namely reduced water quality from anthropogenic input. The differences in environmental conditions reflected in both studies also point to differences in reef management strategies between the unmanaged-unprotected reefs (Chapwani, Changuu and Bawe) and the MPA (Chumbe), though further research is needed. To assess whether coral reef management can maintain a healthy state will require continuous monitoring for trends with the various methods at hand (Steneck et al., 2019).

5 CONCLUSIONS

The findings of abundant LBF-dominated reef assemblages associated with moderate nutrient concentrations suggest that nutrient levels are sufficiently high to trigger a (subtle) response in the LBF species spectra but remain below the threshold levels that would induce a shift in the benthic habitat. These results may potentially indicate early stages of reef degradation. LBF and the FoRAM Index (FI) provide early warning tools and have a great potential in coral-reef monitoring and resilience management. They prove to be useful bioindicator tools for carrying out cost-effective, ecological assessments in western Zanzibar.

The combined effects of the local geographic setting (mid to outer shelf oceanic circulation), hydrodynamics (moderate tides and currents), and reef and reef-associated habit structure (i.e., extensive and dense seagrass meadows, slight turbidity), may play an important role in naturally mitigating the effects of pollution in the study area. Nonetheless, further detailed analysis of the photosymbiotic assemblages (LBF and coral) in relation to pollution-monitoring data, and with respect to the influence of the local climate and hydrodynamics, is required to determine whether Zanzibar's coral reefs are on the path to degradation or if environmental and habitat conditions can support potential resilience.

The reefs of western Zanzibar offer a unique natural laboratory for further exploration into natural, physical variability, habitat and assemblage features from which evolutionary adaptation may occur to support future carbonate-producing taxa (i.e., as a carbonate refugia). The results of this study can contribute to the existing knowledge of local marine biodiversity, support complimentary coral-reef studies (Herrán et al., 2017), support future baseline research (Staehr et al., 2018), and provide relevant information to local decision-makers in formulating appropriate and ecosystem-based management concepts for the East African and WIO regions.

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