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Intertidal zonation of live benthic foraminiferal assemblages from mangrove environments around south-west Penang Island, Peninsular Malaysia

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Abstract

Studies on benthic foraminifera were conducted in the mangrove forests of Teluk Tempoyak, Pulau Betong and Kuala Sungai Pinang, Penang Island, Peninsular Malaysia to examine species composition and distribution patterns in different intertidal zones. Twenty-eight live benthic foraminiferal species were successfully identified at the study locations, predominantly species with agglutinated tests. Assemblages in Pulau Betong and Teluk Tempoyak were dominated by similar species such as *Ammonia aoteana*, *Elphidium hispidulum*, *Elphidium neosimplex* and *Trochammina inflata*, while Kuala Sungai Pinang comprises a high number of *Trochammina inflata* and *Arenoparrella mexicana.* Three species, *Aubignyna perlucida*, *Elphidium neosimplex* and *Elphidium sandiegoense*, were recorded for the first time in Malaysian mangrove forests. Principal component analysis showed that sediment type and organic matter content were the dominant parameters that explained the variation of environmental gradient. Canonical correspondence analysis of these parameters with benthic foraminiferal species indicated that sand particles influenced distribution of the hyaline tests. Species with agglutinated tests were abundant in sediment with rich organic matter in combination with high silt and clay content. Species with hyaline tests dominated lower intertidal zones, while those with agglutinated tests inhabited the area from the middle to upper intertidal zones. This distribution pattern of benthic foraminiferal species mirrored patterns found at other local and global mangrove locations.

Introduction

Foraminifera are single-celled microorganisms that are one of the most important and widely distributed groups of organisms in marine environments (Gooday, 2003; Sen Gupta, 2003). They occupy all marine habitats, including marginal (i.e. lagoons, estuaries, mangroves and salt marshes), coastal and deep-sea environments (Murray, 2006). Benthic foraminifera are usually classified based on the structure of their test (shell). The calcareous type secretes calcium carbonate to form its tests, which can be divided into two groups: hyaline tests (perforated wall) and porcelaneous tests (imperforate wall) (Armstrong & Brasier, 2005). Meanwhile, agglutinated test species build their test by cementing foreign particles; usually sand grains or other small, fragmented shells (Tuckwell *et al.*, 1999). The preservation of the test depends on their surroundings, whether conductive to carbonate preservation or dissolution (Scott *et al.*, 2004). Distinct species assemblages preserved in large numbers/unit volume makes foraminifera a potential bioindicator of pollution, and several studies have shown the suitability of this benthic organism as a bioindicator (Hallock *et al.*, 2003; Le Cadre & Debenay, 2006; Frontalini & Coccioni, 2011; Debenay, 2015; Alve *et al.*, 2016). Some studies have also addressed the relationship of species assemblages to floral zone at salt marshes and used to reconstruct sea level changes (Callard *et al.*, 2011; Wright *et al.*, 2011; Horton *et al.*, 2012; Kemp *et al.*, 2013; Strachan *et al.*, 2015; Barnett *et al.*, 2016; Shaw *et al.*, 2016).

Benthic foraminifera represent a significant part of the total biomass of the meiofaunal community and play an essential role in the consumption of organic carbon in surface sediments (Mojtahid *et al.*, 2011). Some species of benthic foraminifera convert organic matter by means of kleptoplastidy where the species retain chloroplast from food sources and integrate them into their own pathway (e.g. genus *Haynesina*), while other species such as *Ammonia* rapidly ingest organic matter into cellular biomass (Pillet *et al.*, 2011; Jauffrais *et al.*, 2016; Wukovits *et al.*, 2017; Lintner *et al.*, 2020; Jesus *et al.*, 2022). The process of food uptake in foraminifera was induced by salinity in the surrounding environment. A recent laboratory experiment carried out has found that *Ammonia tepida* consumed green algae (*Dunaliella tertiolecta*) with average C of 0.8 and 1 $\mu g\, mg^{-1}$ and N of about 0.3 1 $\mu g\, mg^{-1}$ at salinity between 24 and 37 PSU, while *Haynesina germanica* recorded a lower average C of 0.3 $\mu g\, mg^{-1}$ and N of about 0.05–1 $\mu g\, mg^{-1}$(Lintner *et al.*, 2020).

Under natural conditions in nearshore marine environments, common factors contributing to the distribution and abundance of benthic foraminifera include salinity, temperature, dissolved oxygen, pH, substrate type, tidal regime and biotic influences such as competition, food supply and local disturbance (Scott *et al.*, 2004; Woodroffe *et al.*, 2005; Murray, 2006; Horton & Culver, 2008; Kemp *et al.*, 2011). Species of benthic foraminifera in marshes/mangroves environments have been identified by some authors worldwide (e.g. Scott *et al.*, 2004; Woodroffe *et al.*, 2005; Murray, 2006; Berkeley *et al.*, 2009*a*, 2009*b*; Culver *et al.*, 2012, 2013; Debenay, 2012; Gómez & Bernal, 2013; Satyanarayana *et al.*, 2014; Camacho *et al.*, 2015; Langer *et al.*, 2016). Common benthic foraminifera species that were found in mangrove ecosystems mostly consist of agglutinated taxa such as *Ammotium morenoi*, *Arenoparrella mexicana*, *Haplophragmoides wilberti*, *Miliammina fusca*, *Entzia macrescens* and *Trochammina inflata*, with some calcareous hyaline taxa (e.g. *Ammonia tepida*, *Bolivina striatula*, *Elphidium fijiense*, *Elphidium hispidulum*, *Elphidium advenum*) (Scott *et al.*, 2004; Woodroffe *et al.*, 2005; Murray, 2006; Berkeley *et al.*, 2009*a*, 2009*b*; Debenay, 2012; Culver *et al.*, 2013; Camacho *et al.*, 2015; Langer *et al.*, 2016; Abd Malek *et al.*, 2021).

Ecological baseline studies are essential to monitoring environmental changes, especially in fragile ecosystems such as mangroves. Mangrove refers to assemblages of tropical trees and shrubs that grow in the intertidal zone with adaptation to a wet, saline habitat. Mangrove is a highly productive habitat on earth and provides numerous ecosystems services for human livelihoods (Carugati *et al.*, 2018). Despite that, mangroves have been constantly cleared for aquaculture shrimp farms, industrial developments and enlargement of housing settlements (Chee *et al.*, 2017). The mangrove destruction has a profound effect on biodiversity and causes serious threats on human sustainability (Rawat & Agarwal, 2015; Carugati *et al.*, 2018). Despite that, little attention has been paid to this fragile ecosystem. Thus, recording biodiversity and monitoring ecological changes in this habitat are essential.

Environmental settings

Malaysia is divided into two parts by the South China Sea, which shares maritime borders with Singapore, Thailand, Indonesia, Brunei, Vietnam and the Philippines (Figure 1A). Located in the equatorial region, the country experiences a tropical climate with three monsoon seasons. These monsoon seasons are divided into South-west Monsoon (SWM) from early May to early October and North-east Monsoon (NEM) from early November to March. In between changing of these monsoons, the Monsoon Transitional Period (MTP) occurs from April to early May and early October to early November. Usually, a long dry period and low precipitation occurs during SWM, while NEM generates higher rainfall and tidal events (Malaysian Meteorological Department, 2017). During the sampling period, the lowest monthly precipitation occurred in June (63.8 mm) while the highest volume was recorded in September (487.8 mm).

Penang Island is situated in the Strait of Malacca, off the north-western coast of Peninsular Malaysia located between 5° 15′N–5°30′N and 100°10′–100°21′E with altitude ranging from 0–817 m above sea level, and slope degree of 0–61.598° (Khodadad & Dong-Ho, 2015) (Figure 1B). The island is a highly developed and populated area in Malaysia with a population of 752,800 and a density of 1663/km^2 on the total area of 299 km^2 (Chee *et al.*, 2017). The mangrove forests on the island cover ~6.8 km^2 and are mostly found along the west coast of Balik Pulau (Chee *et al.*, 2017) (Figure 1C). The island experiences a tropical climate with relative humidity varying from 60.9–96.8% and the annual rainfall ranges from 2670–3250 mm (Gao *et al.*, 2021). Over the past three decades, the island experienced an average sea level rise rate of 3.2 mm year^{-1} and this is expected to rise from 320–7320 mm above 2000 levels by 2100 (Gao *et al.*, 2021).

Previous foraminiferal studies in Penang Island were conducted in coastal waters and most species identified were common species found worldwide (Minhat *et al.*, 2014; Yahya *et al.*, 2014). No studies of foraminifera in the mangrove area in Penang Island have been done. The present study was conducted to determine the community structure of benthic foraminifera by analysing their assemblages and the ecological factors that contribute to their distribution at the mangrove forest. The results of this study will provide a database for monitoring ecological changes in the Penang Island mangrove forest.

Materials and methods

Sampling

For this study, three locations of mangrove forests were selected (Figure 2): Pulau Betong (PB, Figure 2.1), Kuala Sungai Pinang (KSP, Figure 2.2) and Teluk Tempoyak (TT, Figure 2.3). At each location, the mangrove areas were divided into three intertidal zones, lower: 0–0.5 m, middle: 0.5–1.0 m and upper: 1.0–1.5 m, according to the watermark label classification from Hogarth (2015). In each zone, six sampling points were laid out, with ~3–5 m between points. Sampling was performed monthly for a one-year period (from March 2017 until February 2018) during the lowest spring tide. The details of the sampling points are provided in Supplementary Table S1. Mangrove flora were identified to genus level based on Lee *et al.* (2015).

At each station, ~50 cm^3 volume (50 cm^2 surface sample by 1 cm thick) of surface sediment was collected at each point using a scoop and stored in labelled plastic bags. The samples were separated into two parts, one part was used for foraminiferal analysis and another part for organic matter (OM) and particle size analysis. *In situ* parameters were measured at each point (Table 1). A refractometer (Milwaukee model MA887) was used to measure pore-water salinity, and a pH meter (Thermo Scientific Eutech Expert) was employed to measure pore-water temperature and pH.

Samples taken for foraminiferal analysis were preserved in 80% ethanol and stained with Rose Bengal (2 g l^{-1}), following methods described by Schönfeld *et al.* (2012). About 10 cm^3 of the stained samples was washed through a 500 µm sieve and then a 63 µm sieve (Buzas-Stephens *et al.*, 2018). Only the 63 µm sieve fractions were used for the collection of benthic foraminifera (Edwards *et al.*, 2004; Hayward *et al.*, 2011; Schönfeld *et al.*, 2012; Camacho *et al.*, 2015; Debenay *et al.*, 2015). Samples smaller than this size fraction are known to contain juvenile species which are harder to identify and may cause species misidentification (Murray & Alve, 2000; Bouchet *et al.*, 2012). When possible, at least 300 specimens of benthic foraminifera were counted from each sample under a dissecting microscope (Olympus SZ51, Japan). Specimen that stained bright red colour was considered as living during the time of sampling (Schönfeld *et al.*, 2012). In ecological studies of foraminifera, it is presumed that staining with Rose Bengal is the most practical method for distinguishing living specimens because the solution will stain the organisms' protoplasm, indicating that the specimens were alive during the sample collection (Murray & Alve, 2000). The benthic foraminifera were wet picked to ensure that the stained tests would be recognizable (Edwards & Horton, 2006; Berkeley *et al.*, 2009*a*;

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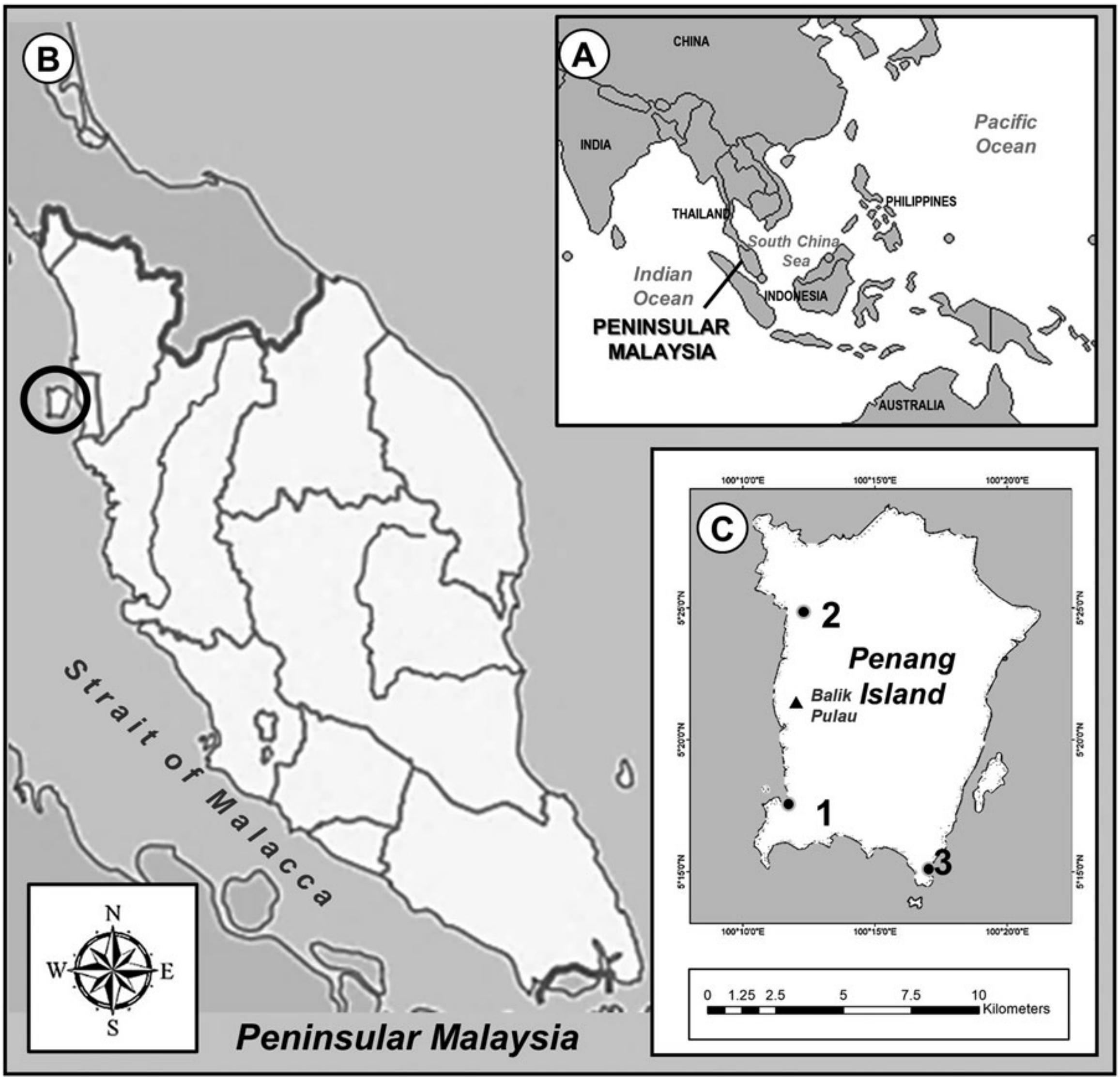

Fig. 1. (A) Location of Malaysia and bordering countries; (B) Location of Penang Island in Peninsular Malaysia; (C) Location of three mangrove forest; (1) Pulau Betong; (2) Kuala Sungai Pinang; (3) Teluk Tempoyak.

Semensatto-Jr *et al*., 2009; Shennan *et al*., 2015; Strachan *et al*., 2015; Alve *et al*., 2019). All foraminiferal specimens were stored on micropalaeontological slides and labelled accordingly. Since ecological studies are dealing with living organisms at a particular time and space, only live count data were used for statistical analysis as they provide more ecological insights (Murray, 2006). Census data for live and dead assemblages at each location were expressed as individuals/10 cm^3 and are provided in Supplementary file Tables S2 and S3.

Selected specimens of benthic foraminifera were observed using a scanning electron microscope (Carl Zeiss Leo Supra 50 VP Field Emission) at the School of Biological Sciences, Universiti Sains Malaysia (USM), Penang. A complete taxonomy list of species from this study and other mangrove locations around Malaysia was recently published (Abd Malek *et al*., 2021).

The OM content in the sediments was analysed using the loss on ignition method based on the procedures described by Dean (1974), Heiri *et al*. (2001) and Minhat *et al*. (2021). Approximately 100 g of sediments was weighed and dried overnight in an oven at 105°C. Later, 5 g of dry subsample was placed in a labelled crucible and heated in a furnace at 550°C for 4 h. The percentage of OM content was determined based on the differences between the initial and final weight. Another part of the sediment samples was analysed for particle size (sand, silt and clay) using the initial (dry) sieving method, followed by pipette analysis (Krumbein & Pettijohn, 1938).

Data analysis

At each mangrove location, the species abundance of benthic foraminifera was expressed as a percentage of relative abundance. Additionally, two-way PERMANOVA test was conducted on temporal and spatial benthic foraminifera data to test for homogeneity between the assemblages. This non-parametric test was calculated using Euclidean distance measure that was performed using Paleontological Statistics data analysis package (PAST) (Hammer *et al*., 2001).

The environmental parameters measured were analysed using principal component analysis (PCA) to reduce the dimensions of the data and to determine the parameters that best explained the environmental gradient (Hotelling, 1933; Paliy & Shankar, 2016). PCA was performed using PRIMER software version 7 (Clark *et al*., 2014). The results of the PCA were then used to investigate the relationship with the most abundant benthic foraminiferal species.

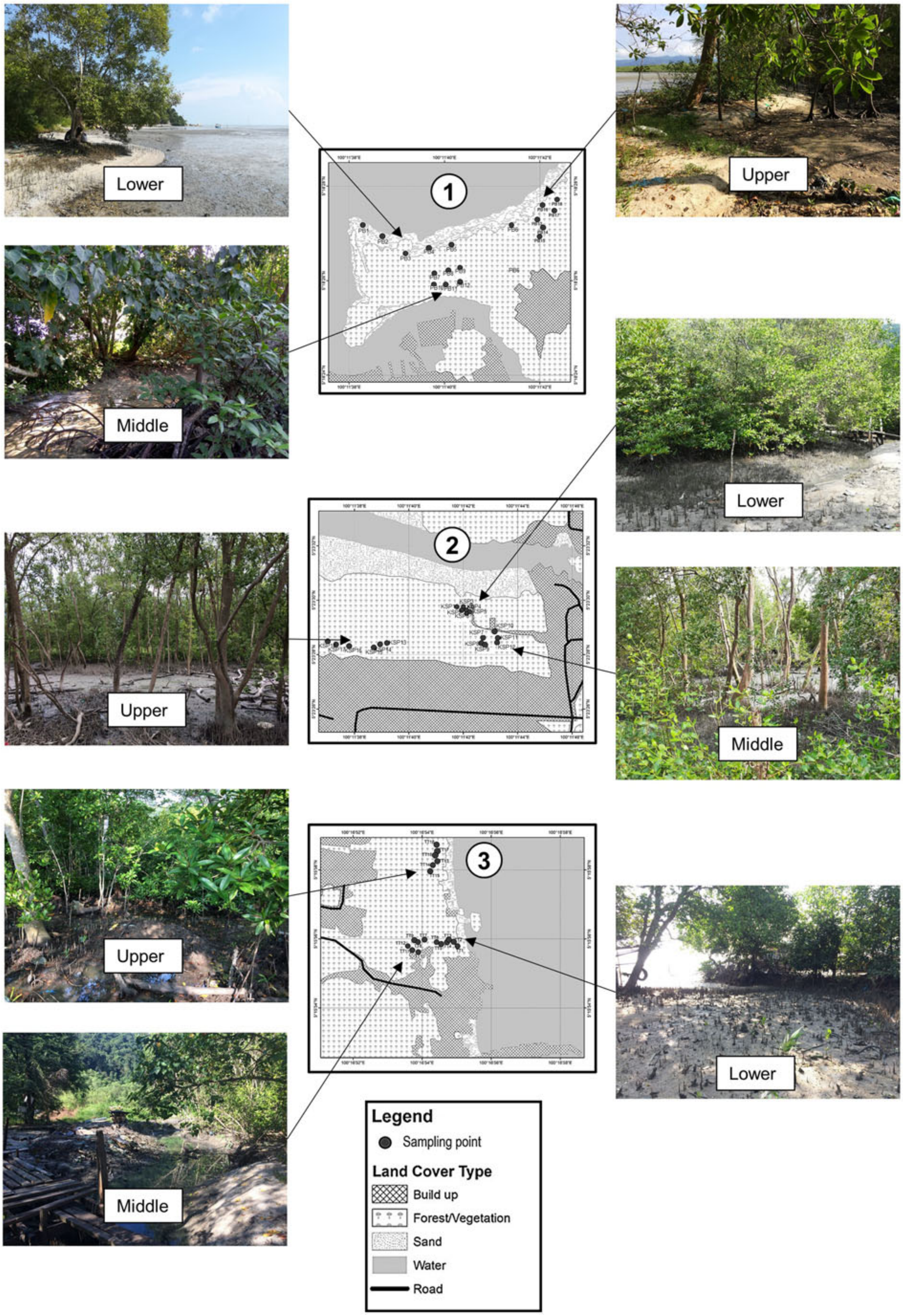

Fig. 2. Sampling points and zonation depicted at each mangrove forests: (1) Pulau Betong; (2) Kuala Sungai Pinang; (3) Teluk Tempoyak.

For this purpose, canonical correspondence analysis (CCA) was applied to the species-environmental parameters data, and was conducted in PAST software (Hammer *et al*., 2001). The data were initially screened to reduce background 'noise' that could complicate the visualization of the data pattern. Thus, for this analysis, only samples containing more than 50 specimens

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Table 1. Summary of *in situ* parameters recorded at each sampling locations

Location	Month	Pore-water pH	Pore-water temperature (°C)	Pore-water salinity (PSU)	Organic matter (%)
Pulau Betong mangrove	March 2017	7.6	30.0	28.0	6.0
	April 2017	7.5	31.0	27.0	12.0
	May 2017	7.2	29.0	31.0	6.6
	June 2017	7.4	31.0	34.0	5.5
	July 2017	7.0	30.0	29.0	7.7
	August 2017	7.1	29.0	30.0	5.6
	September 2017	7.2	29.0	29.0	7.6
	October 2017	7.4	30.0	30.0	6.2
	November 2017	7.3	28.0	24.0	8.4
	December 2017	7.0	28.0	25.0	5.8
	January 2018	7.4	28.0	28.0	7.8
	February 2018	7.0	29.0	NA	13.0
Kuala Sungai Pinang mangrove	March 2017	7.1	32.0	28.0	13.0
	April 2017	6.6	31.0	28.0	15.0
	May 2017	7.8	29.0	28.0	10.0
	June 2017	6.7	28.0	31.0	14.0
	July 2017	7.0	31.0	30.0	15.0
	August 2017	6.7	30.0	27.0	15.0
	September 2017	6.9	29.0	29.0	17.0
	October 2017	7.3	30.0	29.0	5.2
	November 2017	6.8	29.0	30.0	13.0
	December 2017	6.7	29.0	28.0	12.0
	January 2018	6.9	27.0	30.0	15.0
	February 2018	6.8	28.0	NA	14.0
Teluk Tempoyak mangrove	March 2017	7.3	28.0	28.0	14.0
	April 2017	6.4	30.0	29.0	12.0
	May 2017	7.7	30.0	29.0	9.5
	June 2017	6.8	28.0	31.0	13.0
	July 2017	7.4	30.0	29.0	11.0
	August 2017	7.1	30.0	27.0	10.0
	September 2017	7.1	30.0	27.0	7.7
	October 2017	7.3	29.0	30.0	11.0
	November 2017	6.8	29.0	29.0	9.3
	December 2017	6.5	28.0	27.0	7.4
	January 2018	7.3	27.0	30.0	11.0
	February 2018	6.7	28.0	NA	9.6

of benthic foraminifera and species with a relative abundance greater than 5% in at least one sample were used. The species abundance was logarithmically transformed into log $(1 + x)$ to reduce the influence of highly dominant species and allow a pattern of subsidiary species to appear (Frontalini *et al*., 2009; Strachan *et al*., 2015). For the environmental parameters, the data with different scale units were transformed and standardized so that those combined parameters could be analysed together (Hammer *et al*., 2001). Monte Carlo permutation tests were applied to the data to test the statistical significance of the measured environmental variables on assemblage variations based on Legendre & Birks (2012).

Results

Benthic foraminiferal abundance and environmental parameters

Based on two-way PERMANOVA results, there was a significant difference between temporal and spatial foraminifera distribution from the mangrove ($P < 0.05$) throughout the sampling period (Table 2).

Foraminiferal abundances and measured environmental parameters are shown in Figure 3 (Supplementary file Table S4). In comparison between three mangrove forests, PB mangrove recorded the highest test abundance (3814 individuals/10 cm^3)

Table 2. Results of PERMANOVA between foraminifera counts data for monthly and zones between sampling sites

Factor	SS	df	MS	*F*	*P*
Month	6937.4	11	630.7	3.7	**0.0001**
Zone	7764.6	2	3882.3	22.8	**0.0001**
Interaction	8436.6	22	383.5	2.2	**0.0001**
Residual	1.04×10^5	612	170.1		
Total	1.3×10^5	647			

df, degrees of freedom; SS, sum of squares; MS, mean squares; *F*, Fisher's statistic. Significant factors ($P < 0.05$) are shown in bold.

followed by TT (3027 individuals/10 cm^3 and KSP mangroves (780 individuals/10 cm^3). Highest assemblages at each mangrove were recorded during February (PB: 872 individuals/10 cm^3; TT: 494 individuals/10 cm^3; KSP: 209 individuals/10 cm^3).

The measured environmental parameters revealed variation throughout the year. The pore-water pH recorded was in a range of pH 6–8 at each mangrove location. The maximum pH value was recorded at TT in May (pH 7.7 ± 0.3), at PB in March (pH 7.6 ± 0.3) and at KSP in May (pH 7.8 ± 0.2). In TT mangrove, pH value >6.8 occurred during May, June, July and September with a low total number of foraminifera (<200 individuals/10 cm^3). In PB mangrove, low foraminiferal abundance occurred during May–July while KSP mangrove occurred throughout sampling period except in February. The pore-water temperature generally ranged from 27–32°C. The highest temperature was at TT in August and September (30°C ± 1.1), at PB in April (31°C ± 1.9) and at KSP in March (32°C ± 1.0). Pore-water salinity also fluctuated during certain months, with a range of 24–34 PSU. The highest PSU was recorded in June at every location: TT (31 PSU ± 3.5), PB (34 PSU ± 2.6) and KSP (31 PSU ± 1.7). Organic matter content in the mangrove sediments varied between 5–15%. The highest OM was recorded at different months at the three sites: TT: September = 17% ± 4.3; PB: February = 13% ± 8.9; KSP: June = 14% ± 12).

Sediment particle size

The sediments in the mangrove areas in all three locations were predominantly sand. The sediment particle size ranges were similar between zones in each mangrove area. The mean percentage ranged from 56–63% for sand, 11–16% for silt and 5–6% for clay (Table 3).

Benthic foraminifera species composition and zonation

Overall, 28 species of live benthic foraminifera were successfully identified from the three mangrove forests, belonging to five orders, 15 families and 22 genera (Plate A and B). The test type was predominantly agglutinated (17 species), followed by 10 hyaline and one porcelaneous. The highest number of species was found in PB mangrove (27 species), followed by TT mangrove (22 species), and the lowest was recorded in KSP mangrove (12 species).

Pulau Betong assemblages

In the lower zone, hyaline tests dominated the assemblages with species such as *A. aoteana* (max = 276 individuals/10 cm^3), *E. hispidulum* (max = 122 individuals/10 cm^3), *A. perlucida* (max = 71 individuals/10 cm^3) and *E. neosimplex* (max = 54 individuals/10 cm^3). In the middle zone, agglutinated tests recorded higher abundance with *T. inflata* (max = 60 individuals/10 cm^3) and *M. obliqua* (max = 22 individuals/10 cm^3). Towards the upper zone, *T. inflata* remained abundant in the assemblages (max = 86 individuals/10 cm^3) together with other agglutinated tests such as *M. fusca* (max = 57 individuals/10 cm^3) and *S. lobata* (max = 50 individuals/10 cm^3) (Figure 4A).

Kuala Sungai Pinang assemblages

Species abundance in KSP was very low and mostly found between lower to middle zones. The lower zone recorded low species numbers which comprised mainly *A. aoteana* (max = 15 individuals/10 cm^3). Middle zone recorded higher abundance of agglutinated tests such as *A. mexicana* (max = 96 individuals/10 cm^3), *T. inflata* (max = 69 individuals/10 cm^3) and *S. lobata* (max = 27 individuals/10 cm^3) (Figure 4B).

Teluk Tempoyak assemblages

Foraminiferal assemblages in TT were mostly similar to those at PB and KSP mangroves. The lower zone contained a high number of *A. aoteana* (max = 229 individuals/10 cm^3), *E. hispidulum* (max = 85 individuals/10 cm^3) and *A. perlucida* (max = 74 individuals/10 cm^3). In the middle zone, abundance of *A. aoteana* remained high (max = 82 individuals/10 cm^3). Other species found in the middle zone were *T. inflata* (max = 26 individuals/10 cm^3) and *A. mexicana* (max = 20 individuals/10 cm^3). In the upper zone, only *T. inflata* was recorded with high abundance (max = 67 individuals/10 cm^3) (Figure 4C).

Relationship between environmental parameters and species abundance

Environmental parameters analysed with PCA revealed that the sum of PC1 (eigenvalue = 2.3; variance = 33%) and PC2 (eigenvalue = 1.3; variance = 18%) explained half of the total environmental variation. In PC1, a higher correlation coefficient (>0.5) was contributed by OM and particle size, and in PC2, by pore-water temperature and pore-water salinity (Table 4). Based on the PCA loading scores, higher correlations were contributed by OM percentage and particle size sediments. These parameters were further analysed using CCA.

The results of CCA showing the relationship between the environmental parameters and the dominant species assemblages are presented in Figure 5. The first two axes explained 89% (axis 1 = 71.3%; axis 2 = 17.3%) of the total variation within species and the environmental parameters. The hyaline tests were significantly correlated with sand particles. Meanwhile, agglutinated tests were associated with OM content, together with silt and clay.

Discussion

Species numbers in mangrove areas

In general, foraminiferal diversity in mangrove forests is usually lower (<60 species) than that in normal marine lagoons and the deep-sea environment (>200 species) (Murray, 2006; Ortiz *et al.*, 2011; Contreras-Rosales *et al.*, 2012; Debenay, 2012; Milker & Schmiedl, 2012). The mangrove environment is often regarded as an extreme condition for benthic foraminifera owing to its high fluctuations in salinity, temperature and OM availability (Murray, 2006; Debenay, 2012). Conversely, stable environmental conditions from nearshore to deep sea have reported higher ranges of species diversity (after Murray, 2006; Debenay, 2012; Milker & Schmiedl, 2012).

Species distribution pattern according to intertidal zonation

The zonation of the benthic foraminiferal test types showed a distinct microhabitat between lower and upper zones (Figure 5). The

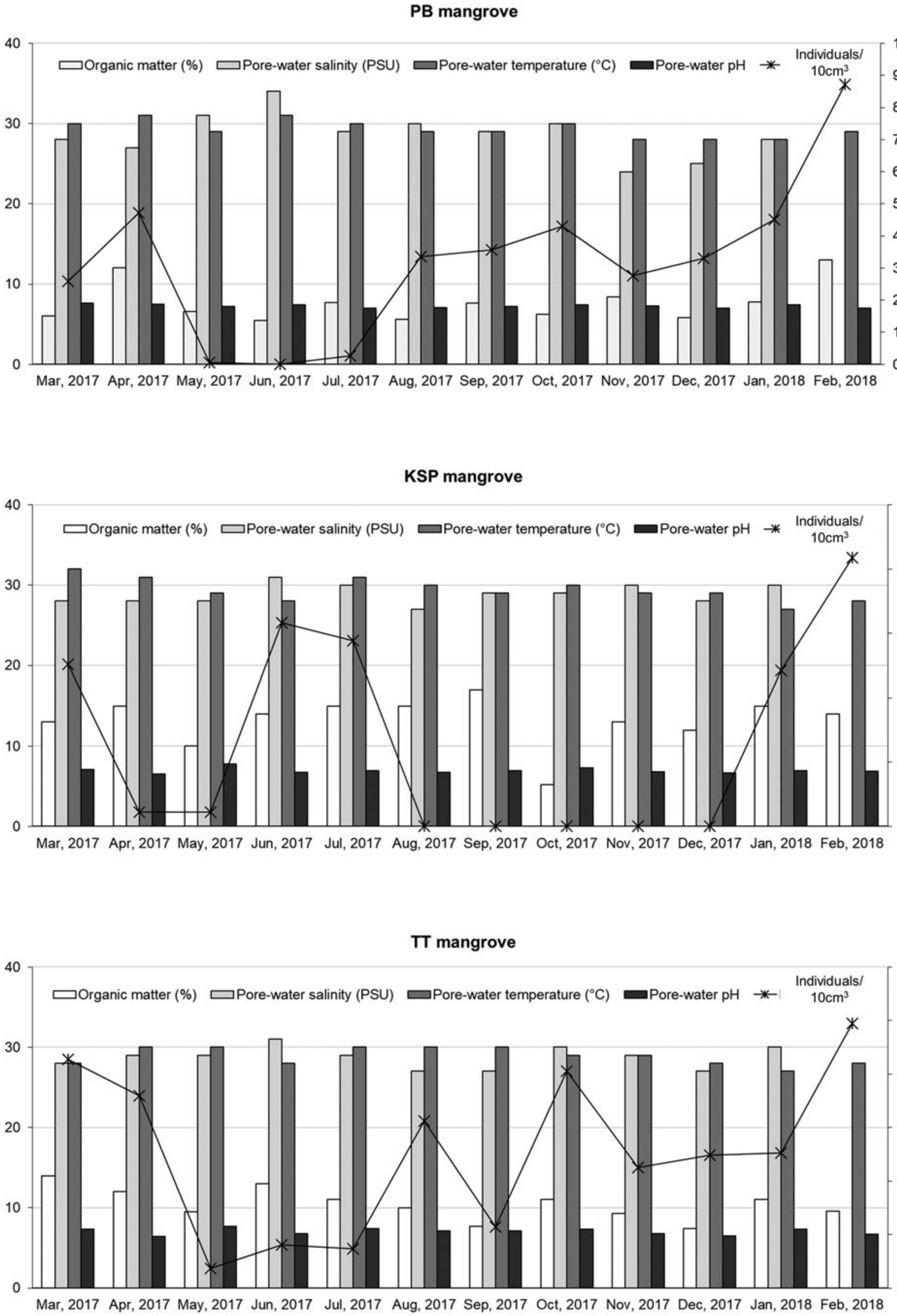

Fig. 3. Monthly foraminiferal abundance and mean environmental parameters.

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Table 3. Mean and standard deviation (SD) of particle size percentage in the mangrove sediments

		Sand (%)		Silt (%)		Clay (%)	
Location	Zone	Mean	SD	Mean	SD	Mean	SD
PB	Lower	56.3	14.0	16.0	13.5	6.3	3.7
	Middle	63.4	14.1	12.2	13.5	4.9	3.7
	Upper	56.3	14.5	16.0	13.2	6.3	3.7
KSP	Lower	56.3	13.0	16.0	14.8	6.3	6.5
	Middle	56.6	13.1	15.8	15.0	6.3	6.4
	Upper	56.3	13.7	16.0	16.0	6.3	5.8
TT	Lower	56.3	20.3	16.0	12.9	6.3	6.8
	Middle	59.3	20.8	12.0	12.7	5.8	6.8
	Upper	58.8	20.8	11.9	12.6	5.9	6.8

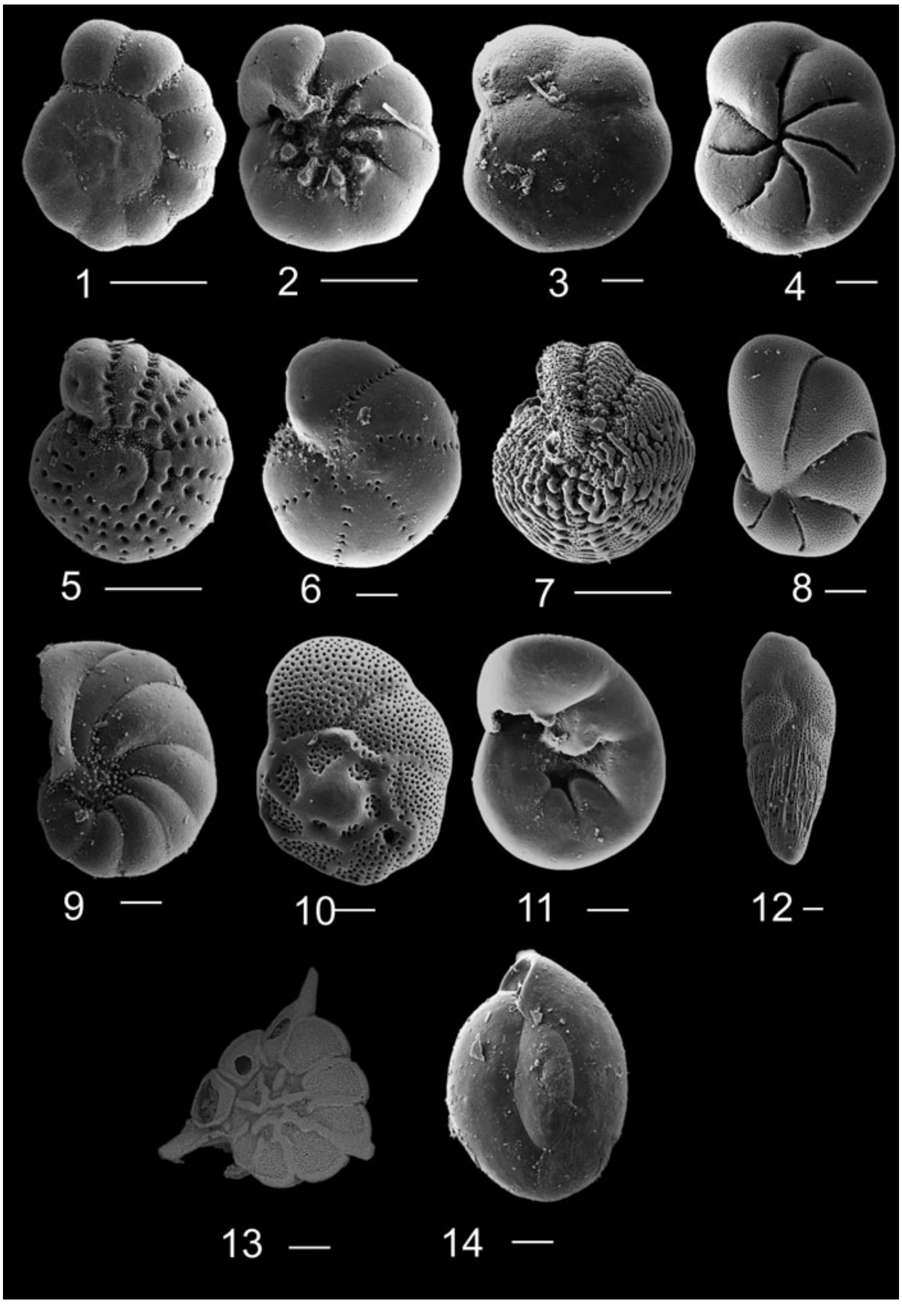

Plate A. 1. *Ammonia aoteana* spiral view, 100×, 100 µm, 2. *A. aoteana* umbilical view, 150×, 100 µm, 3. *Aubignyna perlucida* spiral view, 230×, 30 µm, 4. *A. perlucida* umbilical view, 150×, 30 µm, 5. *Elphidium fijiense* spiral view, 200×, 100 µm, 6. *Elphidium neosimplex* spiral view, 250×, 30 µm, 7. *Elphidium hispidulum* spiral view, 150×, 20 µm, 8. *Elphidium sandiegoense* spiral view, 350 × , 30 µm, 9. *Haynesina depressula* spiral view, 150×, 30 µm, 10. *Rosalina globularis* spiral view, 280× 30 µm, 11. *R. globularis* umbilical view, 280×, 30 µm, 12. *Bolivina striatula* lateral view, 350×, 20 µm, 13. *Asterorotalia pulchella* spiral view, 448 200×, 30 µm, 14. *Quinqueloculina seminula* lateral view, 350×, 30 µm. Scale bar = 100 µm.

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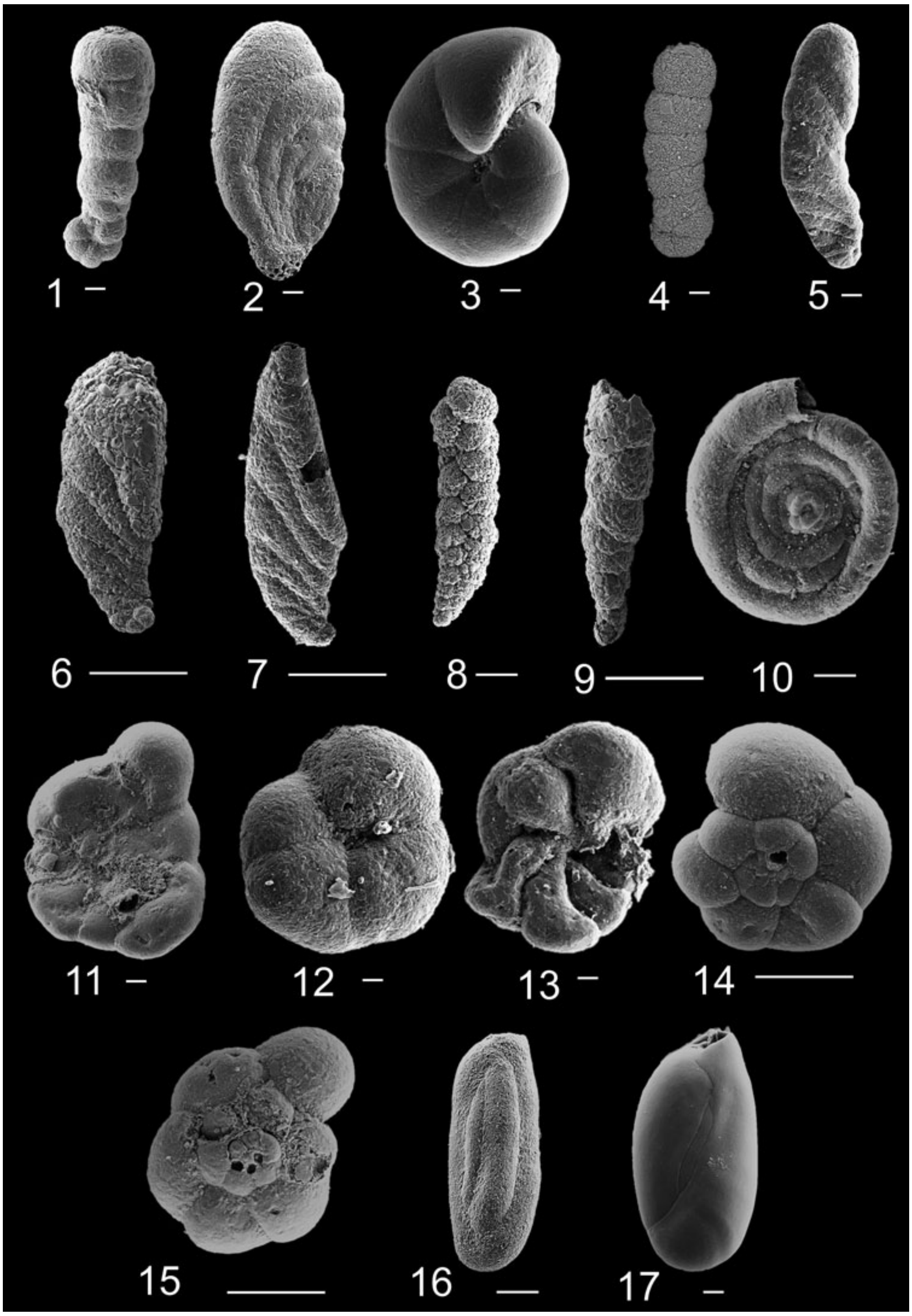

Plate B. 1. *Acupeina triperforata* dorsal view, 200×, 20 µm, 2. *Ammoastuta salsa* lateral view, 200×, 100 µm, 3. *Haplophragmoides wilberti* lateral view, 150×, 100 µm, 4. *Ammobaculites exiguus* lateral view, 300×, 300 µm, 5. *Ammotium directum* lateral view, 200×, 20 µm, 6. *Ammotium fragile* lateral view, 180×, 100 µm, 7. *Ammotium pseudocassis* lateral view, 100×, 100 µm, 8. *Caronia exilis* lateral view, 201×, 30 µm, 9. *Monotalea salsa* lateral view, 180×, 100 µm, 10. *Glomospira fijiensis* lateral view, 300×, 30 µm, 11. *Entzia macrescens* umbilical view, 200×, 20 µm, 12. *Arenoparrella mexicana* umbilical view, 150×, 20 µm, 13. *Tiphotrocha comprimata* umbilical view, 150×, 20 µm, 14. *Trochammina inflata* spiral view, 180×, 100 µm, 15. *Siphotrochammina lobata* spiral view, 180×, 100 µm, 16. *Miliammina fusca* lateral view, 250×, 30 µm, 17. *Miliammina obliqua* lateral view, 360×, 20 µm. Scale bar = 100 µm.

assemblages that contained only agglutinated tests were found mostly in PB and TT middle to upper zones, while hyaline tests dominated the lower zone. Agglutinated test species are commonly recorded in marshes, mangroves and brackish environments because this test type is able to endure low salinity and high pH conditions (Debenay & Guillou, 2002; Hayward *et al*., 2011; Shennan *et al*., 2015). At all studied locations, the upper zone was the driest area as it is periodically inundated during spring high tides. These severe conditions may not favour the establishment of benthic foraminiferal assemblages, especially the hyaline tests.

The mangrove forests in the studied locations were mostly in small patches with low floral species diversity. In this study, there was no clear relationship between benthic foraminiferal assemblages and mangrove floral zones because the mangrove forests in Penang Island are overwash type mangrove. Due to the strong impact of tidal activity, overwash mangroves often cover small areas with fewer mangrove species and no plant zonation (Sukardjo, 2006; Rodriguez *et al*., 2009). Similarly, Hadiyanto *et al*. (2018) found that in an overwash mangrove macrobenthos study, sediment type more significantly influenced the total

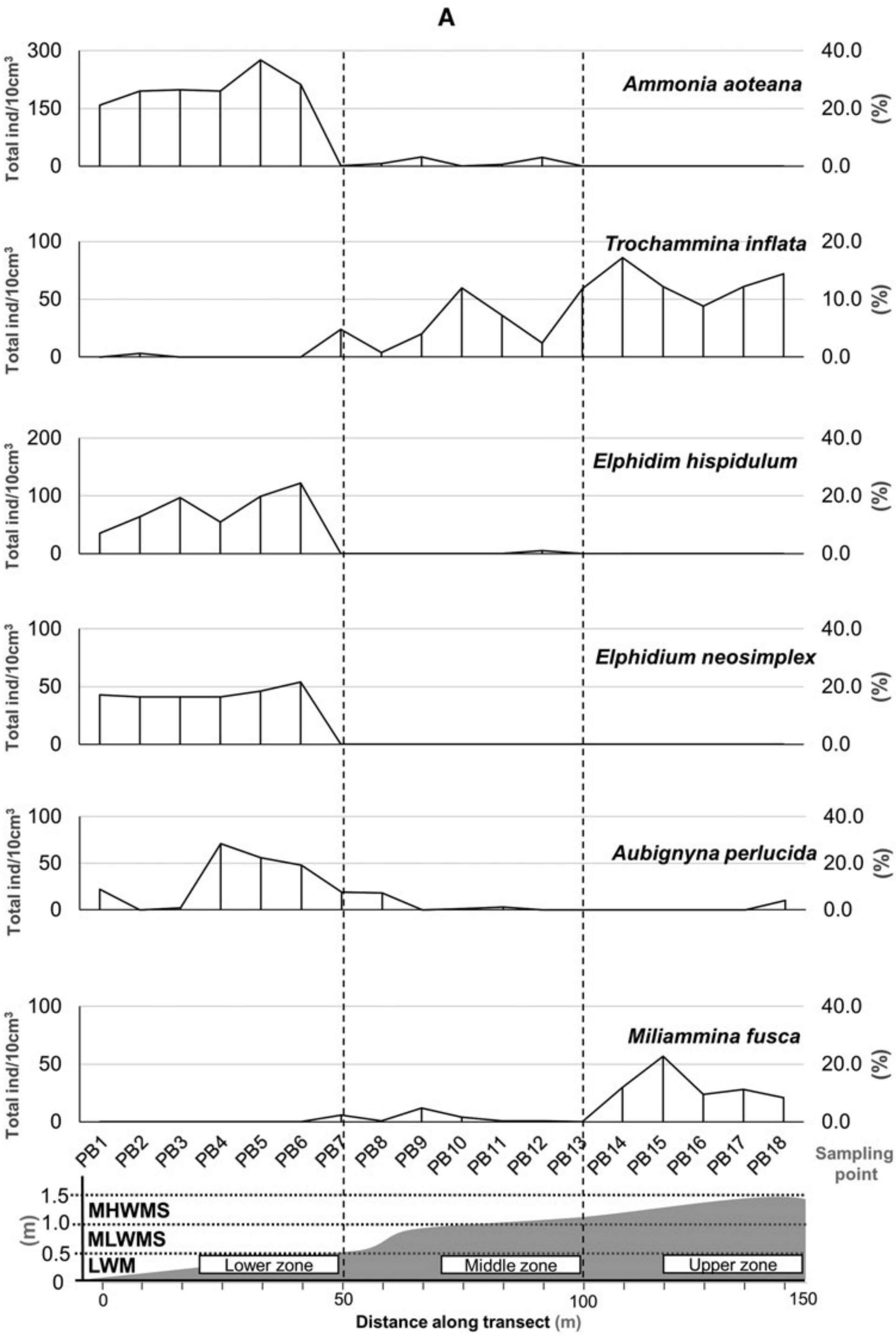

Fig. 4. Abundance of six main foraminiferal species: (A) PB mangrove; (B) KSP mangrove; and (C) TT mangrove. Water level, approximate tidal heights and sampling points are indicated.

abundance and species composition than mangrove vegetation. Also, the lower productivity in this mangrove type may differ from those in fringing and riverine mangroves which have clear mangrove plant zonations. Zonation based on mangrove plants is generally the result of local factors such as sediment transport, tidal inundation and nutrient availability (Bunt & Bunt, 1999; Woodroffe *et al*., 2005; Murray, 2006). The dominant mangrove trees in the studied location were from the genus *Avicennia* which was mostly found at the lower to the upper elevations. In TT and PB mangrove, the lower zone consists of higher abundance of *A. aoteana*. This pattern was also reported by Woodroffe *et al*. (2005) and Berkeley *et al*. (2009*b*) in fringing mangrove of Cocoa Creek, Australia, where the upper mangrove forest of *A. marina* has high abundance of *A. aoteana*. Woodroffe *et al.* (2005) suggested that *A. aoteana* is a useful species for sea-level indicators.

A lower number of agglutinated test species *M. fusca* (PB: 185 individuals/10 cm^3; TT: 130 individuals/10 cm^3; KSP: absent) and *M. obliqua* (PB: 187 individuals/10 cm^3; TT: 132 individuals/10 cm^3; KSP: 34 individuals/10 cm^3) was found in the sediment from all sampling locations. Previous studies have also reported low amounts of *M. obliqua* (64–249 individuals/10 cm^3) in mangrove sediments (Berkeley *et al*., 2009*b*; Culver *et al*., 2015). The structure of the thin-shelled test of *M. obliqua* is known to be quickly degraded after death (Hayward *et al*., 2004). Meanwhile, *M. fusca* is found in most intertidal areas, typically at the higher

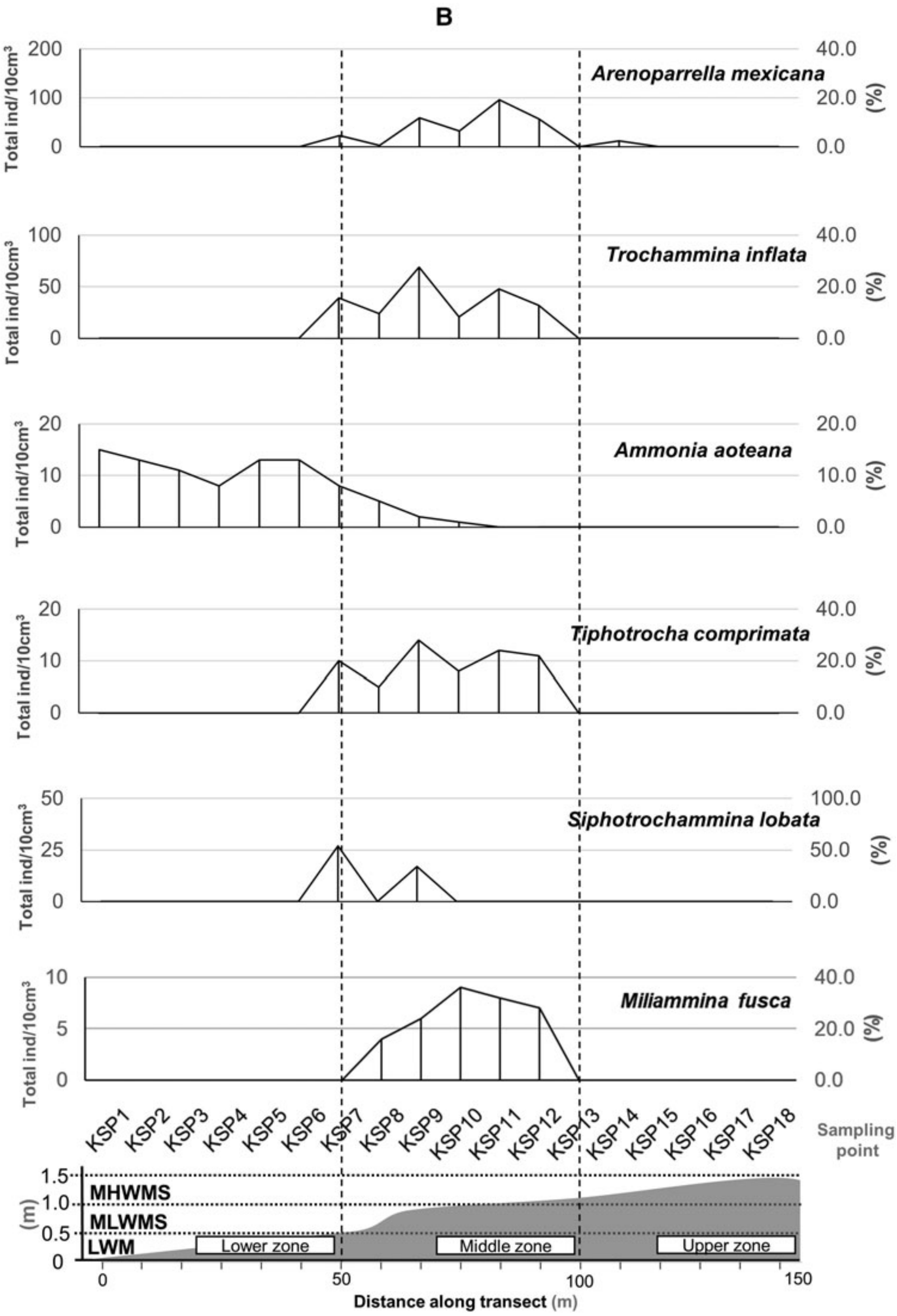

Fig. 4. Continued.

tidal elevations (Barbosa & Suguio, 1999; Horton *et al.*, 2003; Murray, 2006; Gómez & Bernal, 2013; Camacho *et al.*, 2015; Sen *et al.*, 2015).

Only one porcelaneous test (*Quinqueloculina seminula*) was found in this study. The species was found only in live assemblages of PB mangroves (13 individuals/10 cm^3), which indicated that the species was rare and might be transported from coastal waters by tidal propagation. Previously, Eichler (2019) found that porcelaneous alien species (*Quinqueloculina lamarckiana*) was transported from continental shelf to mangroves of Bertioga Channel, Brazil. The species was also rarely found in living assemblages because it might have been transported from its natural habitat (Eichler, 2019).

Our results have shown that the agglutinated tests were mainly found in the middle to upper zones. Similarly, in temperate regions where mangrove plants have been replaced with marshes, the assemblages contain dominant agglutinated with porcelaneous test (Edwards *et al.*, 2004; Scott *et al.*, 2004; Strachan *et al.*, 2015). The agglutinated tests mainly from the genera *Entzia*, *Trochammina*, *Tiphotrocha* and *Miliammina* were confined to a higher elevation area of the mean tide level (Shennan *et al.*, 2015).

The role of environmental parameters on species distribution

The factors that are commonly known to contribute to benthic foraminiferal abundance are salinity, temperature, nutrition, dissolved oxygen conditions, pH and type of substrate (Scott *et al.*, 2004; Culver & Horton, 2005; Woodroffe *et al.*, 2005; Murray, 2006; Kemp *et al.*, 2011). However, the abundance of benthic foraminifera in mangrove environments is usually controlled by the

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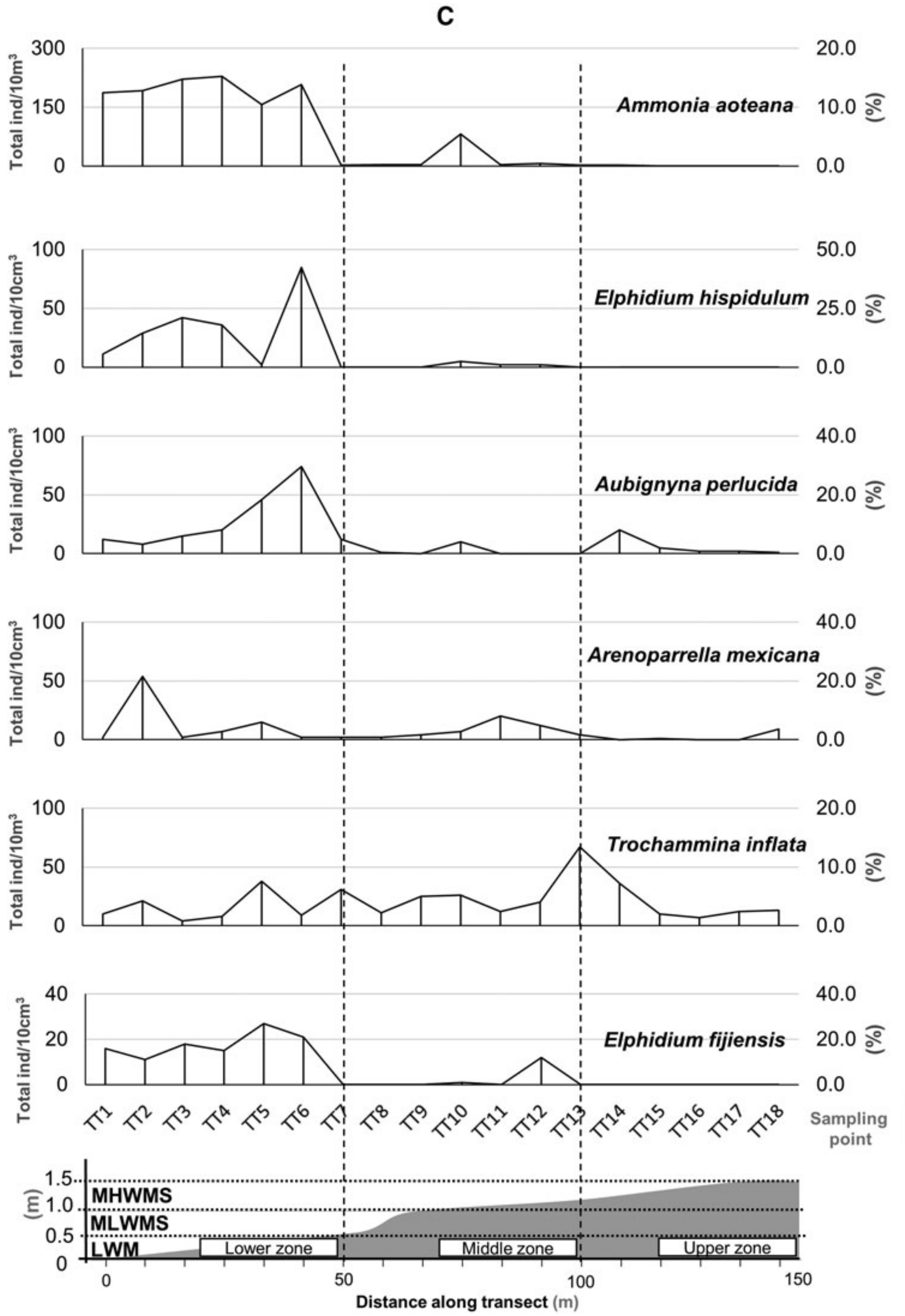

Fig. 4. Continued.

Table 4. Values of correlation coefficient from PCA

Parameters	PC 1	PC 2
Pore-water pH	0.29	0.03
Pore-water temperature	0.09	0.77
Pore-water salinity	0.17	0.77
%OM	0.76	0.01
%Sand	0.86	0.00
%Silt	0.68	0.13
%Clay	0.65	0.22

elevation of the tidal frame (Scott *et al.*, 2004; Culver *et al.*, 2013). The environments of mangrove areas, which usually have high ground temperature, high vegetation cover and high organic content, might affect the benthic foraminiferal distribution in tropical regions (Scott *et al.*, 2004; Culver & Horton, 2005; Berkeley *et al.*, 2009*a*; Culver *et al.*, 2013).

In this study, abundant hyaline test species were recovered in sediments with high sand content at the lower intertidal zone, which had higher pore-water temperature (26–32°C, mean: 29.2 ± 1.2) owing to its lower level of mangrove tree cover. However, the pore-water temperature was not at an extreme level (>32°C), therefore taphonomic loss of hyaline tests was unlikely to have occurred (Culver *et al.*, 2013). Thus, pore water

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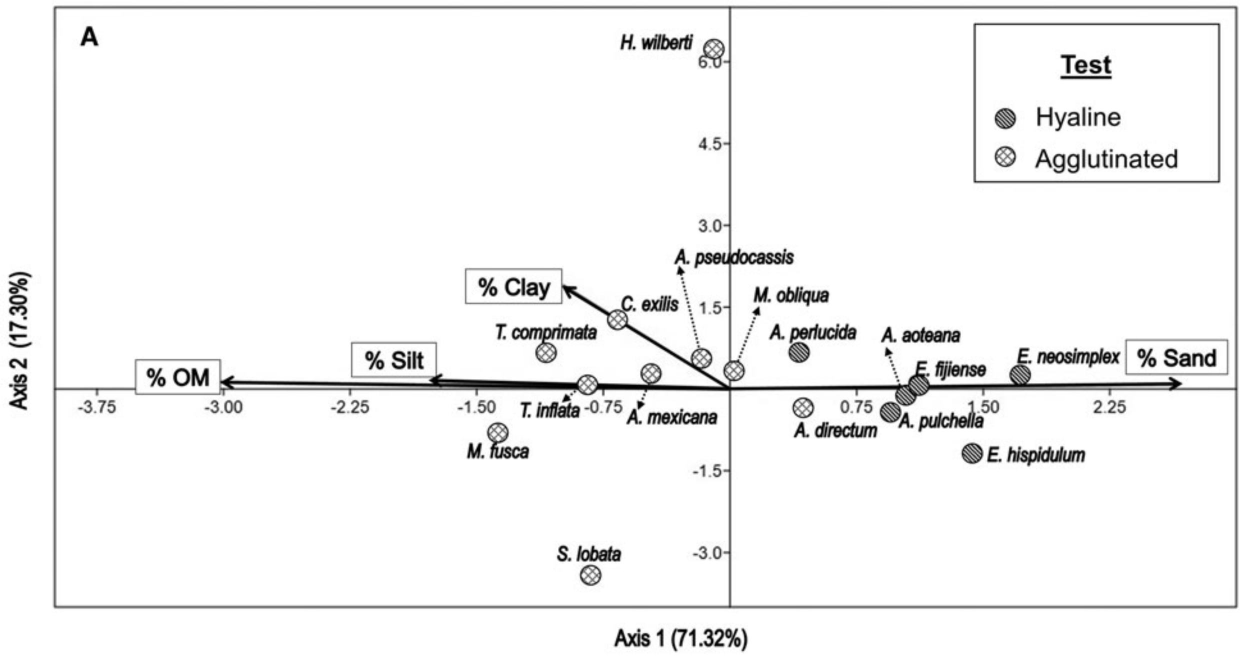

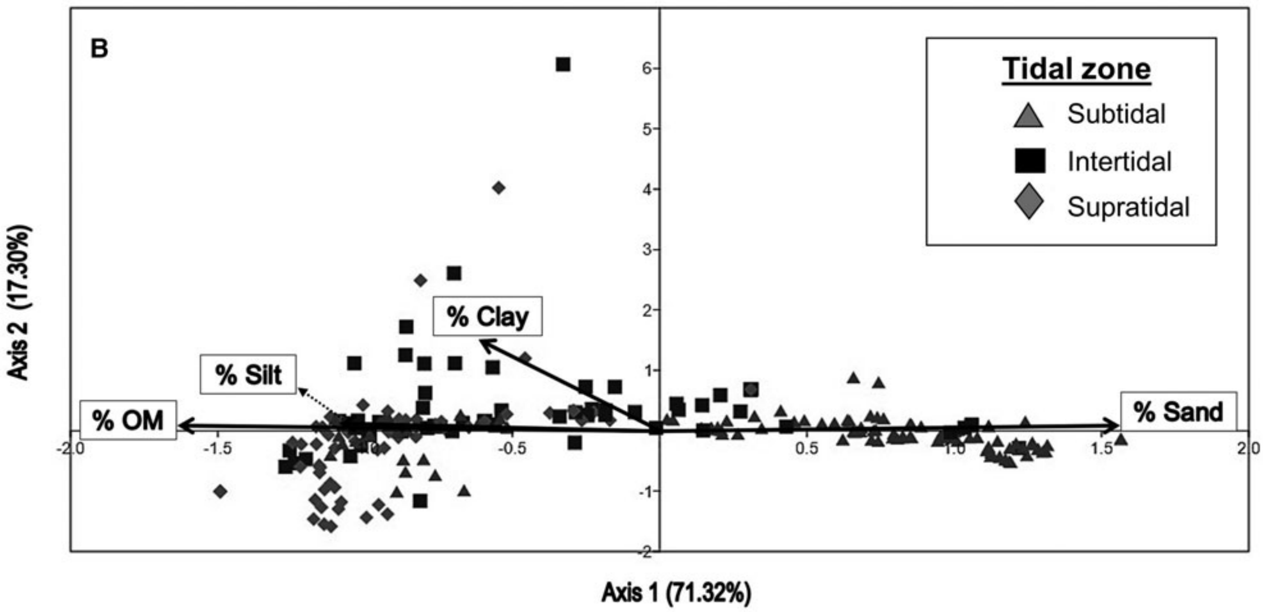

Fig. 5. CCA of the dominant species (>5% relative abundance) and the gradient of primary environmental parameters. (A) Test type as categorical factor; (B) tidal zone as categorical factor.

temperature was not regarded as a main controlling factor. Several studies have reported that increasing pore water temperatures can cause adverse effects to intertidal foraminifera (i.e. reduce locomotion, metabolism and reproduction (Buzas & Severin, 1993; Gross, 2000; Wukovits *et al*., 2017; Li *et al*., 2019; Deldicq *et al*., 2021). On a regional scale, cooler water temperatures are known to favour the preservation of agglutinated tests compared with warmer regions and tropical environments such as mangroves (Goldstein & Watkins, 1999; Debenay *et al*., 2002; Berkeley *et al*., 2009*a*).

Organic matter is also documented as a key parameter that influences the distribution of benthic foraminifera in mangrove sediments. In this study, dominant agglutinated species (*A. mexicana*, *T. inflata*, *M. obliqua*, *M. fusca*) were widely distributed in the middle to upper mangrove reaches. These species showed preferences for sediments with high OM content and silty-muddy substrate, as shown in the CCA graph. The dense aquaculture activities (i.e. shrimp ponds and fish cages) in the mangrove forests might also result in high OM in the sediments, which has been reported by some authors (Chee *et al*., 2015; Zolkhiflee *et al*., 2021). In Matang mangroves, the high presence of *A. mexicana*, together with *Haplophragmoides wilberti*, was due to the enrichment of OM by leaf litter and other bioorganic substances (Satyanarayana *et al*., 2014). These species were dominant in organic-rich sediments of shrimp ponds as reported by Debenay *et al*. (2015). *Miliammina fusca* has previously been reported as a dominant species in the lower mangrove zone (Scott *et al*., 2004; Edwards & Horton, 2006) and at the seaward edges of marsh environments with an absence of vegetation cover (Murray & Alve, 1999). Some studies have reported that foraminiferal species were sensitive to the variability and quality of organic matter on surface and in the deeper layer of sediments (e.g. Mojtahid *et al*., 2010; Papaspyrou *et al*., 2013; Barras *et al*., 2014; Cesbron *et al*., 2016). Experimental studies on organic matter degradation have shown that the process is related to the bacterial activities present in the sediment layers causing lowering of dissolved oxygen level, consequently decreasing the number of certain foraminiferal species (usually calcareous species) by making them unable to proliferate (Duffield *et al.*, 2015). Thus, further studies are required to address the variability response of species in mangrove sediments.

Other agglutinated species such as *E. macrescens* and *T. inflata* are known to have better preservation potential and ability to withstand taphonomic signatures compared with other benthic foraminiferal species (Ozarko *et al.*, 1997; Berkeley *et al.*, 2007). However, the occurrence of *E. macrescens* in this study was rare because the foraminiferal assemblages were only taken on the surface sediments. The species was thought to be an infaunal type, suggesting that it may have moved downcore (Scott *et al.*, 2004; Culver *et al.*, 2013; Strachan *et al.*, 2015). Meanwhile, *T. inflata* and *A. mexicana* thrived in areas with higher OM, especially in the dense mangroves of KSP. Similar conditions have also been reported in marshes of the USA and North Island, New Zealand (Murray, 2006).

Foraminiferal test dissolution occurs when the pH range is below optimal conditions, which range from pH 6.5–7.2 (Murray, 2006). Previous study reported that decalcification of hyaline species *Ammonia beccarii* in normal marine salinity occurred when pH decreased below pH 7.5 (Le Cadre *et al.*, 2003). In mangrove forests, pH decreases owing to the decomposition of leaf litter by bacteria in the sediments, might also explain the decrease of calcareous tests (Debenay & Guillou, 2002).

The pH recorded at the sampling sites was between 6.4–7.8 (7.1 ± 0.3). In general, pH variations within the intertidal region are higher than those in other marine environments due to freshwater input either from rainwater or river runoff (Erskian & Lipps, 1977; Debenay *et al.*, 2002, 2006; Scott *et al.*, 2004) and calcareous tests are known to be sensitive to pH fluctuations (Phleger & Bradshaw, 1966; Saraswat *et al.*, 2011; Weinmann *et al.*, 2021). Owing to pH fluctuations, several studies have applied benthic foraminifera as an indicator for ocean acidification (Haynert *et al.*, 2013; Schmidt *et al.*, 2014; Kawahata *et al.*, 2019). At lower pH values, benthic foraminifera require substantial energy to re-calcify their tests in order to survive (Woodroffe *et al.*, 2005). Similarly, abundance of agglutinated foraminifera has been reported at pH levels ranging from pH 6.2–6.6 with absence of calcareous foraminifera in vegetated mangroves at Sandy Creek, Queensland (Woodroffe *et al.*, 2005).

Comparison with other mangrove forest

Penang Island assemblages contain high numbers of agglutinated test species with 17 species. The agglutinated species in the present study were similar to those found in mangrove forests such as in Kapar, Selangor and Matang, Perak (Satyanarayana *et al.*, 2014). Meanwhile in Setiu, Terengganu, Culver *et al.* (2012, 2013) identified a high number of hyaline test species (46 species). Particularly, Setiu wetland is a fringing mangrove swamp where saltwater intrusion is higher compared with Penang Island mangroves. A higher range of salinity (>30 PSU) was known to increase the number of calcareous tests species (Hayward *et al.*, 2004; Horton & Murray, 2007; Culver *et al.*, 2012, 2015, 2019). Despite that, laboratory experiments on two calcareous species (*Ammonia tepida* and *Haynesina germanica*) have found that fluctuation in salinity had smaller impact on food uptake (Lintner *et al.*, 2020). Since the range of salinity recorded in this study was not as high as that in other studies, the number of calcareous tests recovered was low (<10 species).

Although the foraminiferal species found were mostly similar to those reported in other studies in Malaysian mangrove forests, three newly recorded species were recovered in the present study. These species were identified as *A. perlucida*, *E. neosimplex* and *E. sandiegoense*. These hyaline test species have been reported in coastal environments worldwide (Murray *et al.*, 2000; Murray, 2006; Sugawara *et al.*, 2009; Debenay, 2012). In this study, *A. perlucida* was found in all three mangrove locations, while *E. neosimplex* was only found in TT and PB mangroves. The hyaline test species, *E. sandiegoense* was only recovered in PB sediments. The rare occurrences of *A. perlucida*, *E. neosimplex* and *E. sandiegoense* in living assemblages from sampling locations were possibly due to tests being transported from their natural habitation by tidal movement and flood events (Mendes *et al.*, 2004; Debenay & Luan, 2006; Raposo *et al.*, 2018).

In general, spatial and seasonal variabilities are due to the interaction between fauna, reproduction strategy, predation and food sources (Hayward *et al.*, 2011; Scott *et al.*, 2011; Buzas *et al.*, 2015). In this study, numerous burrows found in the sediments (especially in lower to middle zones) indicated that there was intense bioturbation by macrofauna such as fiddler crabs. As a result, the fragile tests of smaller benthic foraminifera, particularly agglutinated tests were mostly destroyed (Debenay *et al.*, 2002; Debenay & Parra, 2004; Perry *et al.*, 2008). On the other hand, the rare occurrence of a calcareous hyaline test genus such as *Elphidium* indicated weak eutrophic conditions and stratification of water column (Alve, 2003).

Overall, the distribution of benthic foraminiferal tests in this study was influenced by the environmental parameters of Penang Island mangrove forests, particularly the OM content and sediment type. The distribution pattern of benthic foraminiferal tests showed microhabitat preferences at different intertidal zones, with hyaline tests dominating the lower zone assemblages and agglutinated tests in the middle to the upper zones. This zonation pattern is valuable in determining the potential consequences of habitat degradation, which is particularly prevalent in mangrove environments.

Conclusions

The distribution pattern of benthic foraminifera tests showed microhabitat preferences in which hyaline tests (*A. aoteana*, *Elphidium neosimplex* and *E. hispidulum*) were highly abundant in the lower mangrove zone, while agglutinated tests (*A. mexicana* and *Trochammina inflata*) were abundant in the middle to upper mangrove zones. The distribution pattern observed was mainly due to the influence of OM content and particle size in the sediments. The tests distribution pattern of benthic foraminifera in Penang Island showed that the number of agglutinated tests species was higher than the hyaline and porcelaneous tests, which commonly occurred in mangrove environments. The data from this study will provide a baseline for future monitoring of environmental changes in the mangrove area on Penang Island.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315422001072

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