

Modern biogeography of benthic foraminifera in an urbanized tropical marine ecosystem



Briony L. Mamo^{1,2,3*}, Jonathan D. Cybulski^{4,5}, Yuanyuan Hong^{1,2,6},
Paul G. Harnik⁷, Anne Chao⁸, Akira Tsujimoto⁹, Chih-Lin Wei^{10*},
David M. Baker^{4*} and Moriaki Yasuhara^{1,2*}

¹School of Biological Sciences, Area of Ecology and Biodiversity, Swire Institute of Marine Science, Institute for Climate and Carbon Neutrality and Musketeers Foundation Institute of Data Science, The University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong SAR, China

²State Key Laboratory of Marine Pollution, City University of Hong Kong, Tat Chee Avenue, Kowloon, Hong Kong SAR, China

³School of Natural Sciences, Macquarie University, North Ryde, NSW 2109, Australia

⁴School of Biological Sciences, Area of Ecology and Biodiversity, Swire Institute of Marine Science, The University of Hong Kong, Kadoorie Biological Sciences Building, Pokfulam Road, Hong Kong SAR, China

⁵Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Republic of Panama

⁶State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China

⁷Department of Earth and Environmental Geosciences, Colgate University, Hamilton, NY, USA

⁸Institute of Statistics, National Tsing Hua University, Hsin-Chu, Taiwan

⁹Faculty of Education, Shimane University, 1060 Nishikawatsucho, Matsue, Shimane 690-8504, Japan

¹⁰Institute of Oceanography, National Taiwan University, Taipei 106, Taiwan

MY, 0000-0003-0990-1764

*Correspondence: BLM, blmamo@gmail.com; C-LW, clwei@ntu.edu.tw;

DMB, dmbaker@hku.hk; MY, moriakiyasuhara@gmail.com

Abstract: We investigated the biogeography of benthic foraminifera in a highly urbanized tropical seascape, i.e. Hong Kong, in order to assess their utility as bioindicators relative to other marine fauna. Hong Kong is one of the largest coastal cities on the planet and studies of other benthic fauna in the region are available for comparison. We found that: (1) turbid, muddy habitats host a unique foraminiferal fauna; (2) areas with intermediate levels of eutrophication have the highest foraminiferal species diversity; (3) semi-enclosed and heavily polluted environments host a distinct foraminiferal fauna, characterized by low taxonomic diversity and/or high dominance, and that is acclimated to stressful marine conditions. Biodiversity patterns of foraminifera in Hong Kong are generally consistent with those of other soft-sediment macro- and meio-fauna (e.g. polychaetes, molluscs and ostracods); however, foraminifera may be more sensitive than these other groups to eutrophication and associated changes in coastal food webs. The tolerance of some, but not other, species to eutrophic and hypoxic conditions means that foraminiferal faunas can serve as bioindicators across a wide array of environmental conditions, in contrast with corals whose sensitivity to eutrophication results in their absence from eutrophied settings. The well-known autoecology of foraminifera taxa can help to characterize environmental conditions of different habitats and regional environmental gradients. Although the use of fauna as bioindicators may be most robust when data are compared for multiple taxonomic groups, when such broad sampling is not available, benthic foraminifera are particularly well suited for environmental assessments due to their ubiquity, interspecific environmental breadth, and the well-understood environmental preference of individual taxa.

Supplementary material: Foraminiferal census data (Appendix 1) are available at <https://doi.org/10.6084/m9.figshare.c.6373203>

With one of the highest population densities globally, Hong Kong's coastal waters are a model system for assessing the effects of climate and urbanization on marine biodiversity. Urbanization has led to a variety of environmental problems, including pollution and eutrophication (Hua *et al.*

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2008). These coastal ecosystems are also strongly affected by the East Asian summer monsoon, which greatly affects precipitation and resulting freshwater discharge from the Pearl River (Morton and Morton 1983). The Pearl River watershed includes multiple megacities, such as Shenzhen, and the river is a major source of pollutants and organic matter in coastal waters in Hong Kong (Dai *et al.* 2006; Lee *et al.* 2006; Archana *et al.* 2018; Qian *et al.* 2018; Duprey *et al.* 2020; Geeraert *et al.* 2021). Urbanization and resulting environmental and ecological degradation are the future for many tropical locations (Jackson *et al.* 2001; Knowlton 2001; Hughes *et al.* 2003; Knowlton and Jackson 2008). Understanding how these processes shape biodiversity in Hong Kong can be used to understand and mitigate current and future anthropogenic and climatic impacts in the tropics more broadly (Ng *et al.* 2017).

Hong Kong's subtidal marine organisms have been relatively well studied since the pioneering work of Brian Morton in the 1980s (Morton and Morton 1983). In the twenty-first century, extensive regional-scale studies investigated the environmental factors controlling geographical variation in taxonomic diversity and faunal composition in a variety of benthic groups, including polychaetes, molluscs, corals, and ostracods (Shin and Thompson 1982; Shin 1985; Shin and Ellingsen 2004; Qiu *et al.* 2014; Duprey *et al.* 2016; Wang *et al.* 2017, 2021; Cybulski *et al.* 2020; Yeung *et al.* 2021; Hong *et al.* 2022). These studies were possible because of the wide range of environmental conditions that occur in a relatively small geographical area, and the availability of spatially well-resolved environmental data from the Environmental Protection Department (Environmental Protection Department 1986–2021). Benthic foraminifera (unicellular eukaryotes) are widely used as bioindicators due to their sensitivity to environmental conditions, including anthropogenic environmental change (Hallock *et al.* 2003; Alve *et al.* 2009; Bouchet *et al.* 2018). While many studies have investigated the factors controlling the geographical distribution, abundance, and taxonomic diversity of foraminifera in the China seas (Wang *et al.* 1980, 1988; Zhao *et al.* 1985, 1986), including areas of the South China Sea proximal to Hong Kong (Wu *et al.* 2013, 2015; Ye *et al.* 2021), few studies have examined foraminifera in Hong Kong (Yim and He 1991; Hong *et al.* 2017; Yang *et al.* 2018) and regional distributional data for Recent benthic foraminifera are unavailable (Ng *et al.* 2017).

For this study, we collected surface sediment samples spanning the major subtidal areas of Hong Kong and investigated the geographical structure of benthic foraminiferal biodiversity and compared

their biogeographical patterns with those for other organisms. We found that patterns for benthic foraminifera were largely consistent with other soft-sediment macrobenthos and ostracods, and show some similarity with corals, though corals differ markedly in their diversity patterns. Like corals, foraminifera are very sensitive to bottom-up changes in nutrient levels, but in contrast, certain foraminiferal taxa can persist in eutrophic environments whereas most corals cannot. Using benthic foraminifera as a bioindicator of environmental conditions, we were able to characterize spatial gradients in Hong Kong's coastal subtidal habitats. More eutrophic conditions characterize western habitats due to pollution from the Pearl River and other local point sources; in contrast, eastern habitats tend to be characterized by higher water quality. The highest biodiversity of benthic foraminifera was observed in habitats characterized by intermediate levels of eutrophication in the southernmost part of the study area.

Regional setting

The Hong Kong Special Administrative Region (Hong Kong) consists of over 270 islands and is located approximately 130 km south of the Tropic of Cancer. The region is characterized by a subtropical climate. Regional weather and climate are controlled by the Asian monsoon, with the wet season occurring between March and October, with the hottest and wettest months co-occurring between May and September. Geographically, Hong Kong is located at the mouth of the Pearl River, in the southeastern part of the Great Bay Area of China (Fig. 1). The Pearl River stretches for c. 2200 km with a drainage area of 453 700 km², supporting a population of over 150 million people (Duprey *et al.* 2020). The river releases 80% of its annual discharge during the wet season, forming a nutrient-rich plume of freshwater that extends eastward as far as the Taiwan Strait. During the dry season, this plume is greatly reduced and isolated to the SW of Hong Kong. This dynamic water regime results in eutrophic conditions in some coastal areas of Hong Kong. Nutrients from the Pearl River create a strong gradient of dissolved inorganic nitrogen (DIN) concentrations ranging from >80 µM in the south and west to >2 µM in the east (Archana *et al.* 2018). Sources of nutrients in this expanding urban area are diverse, and include industrial effluent, sewage, fish farm waste, DIN derived from atmospheric deposition, and oceanic DIN (Duprey *et al.* 2016; Yau *et al.* 2020). In Hong Kong, sewage effluent is the primary local source for nutrients and pollutants, which contributes to eutrophication and pollution (Geeraert *et al.* 2021).

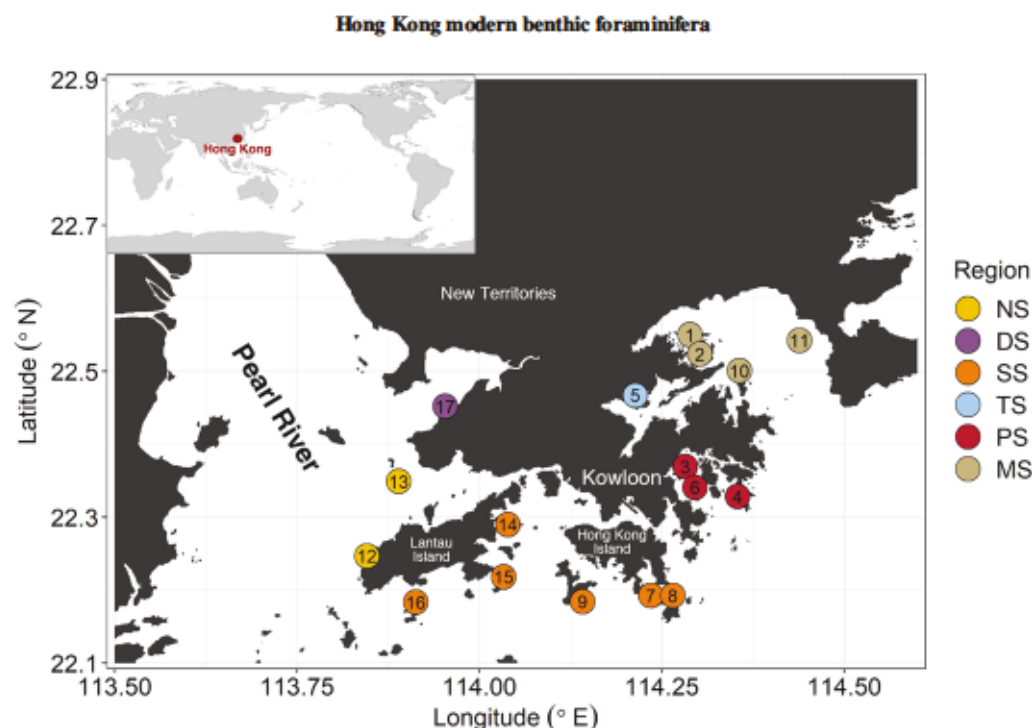


Fig. 1. Locality and index maps. NS (North Western, including Sites 12, 13), DS (Deep Bay, Site 17), SS (Southern, Sites 7–9, 14–16), TS (Tolo Harbour, Site 5), PS (Port Shelter, Sites 3, 4, 6), and MS (Mirs Bay, Sites 1–2, 10–11) are Hong Kong marine regions defined by the Environmental Protection Department (EPD: Environmental Protection Department 2011) to which each sampling site belongs. Sites 7 and 8 are in the same location, but a jitter was added to make them visible.

Materials and methods

Samples

Surface sediment samples (10 cm) were collected from 17 sites in November 2016, covering water depths ranging from 2 to 17 m, and including all major waters of Hong Kong (Fig. 1). All surface sampling sites were near-shore sandy bottom deposits except for sites 5 and 12 (Fig. 1) which were predominantly muddy estuarine deposits. Samples were hand-collected by SCUBA using a trowel and bagged on site. All samples were kept refrigerated until analysis.

Ten-centimetre-thick surface sediment samples were washed and sieved through a 63 μ m sieve and oven dried at 60°C. After drying, all samples were split using a microsplitter to avoid possible bias by sorting during picking process. Foraminiferal analysis was completed using standard picking techniques (Murray 2006). Selected specimens were imaged using a Hitachi S-3400N Variable Pressure SEM at the Electron Microscope Unit, The University of Hong Kong. Taxonomic assignments followed the World Foraminifera Database (Hayward *et al.* 2022), and are listed in Appendix 1. A total of 400

foraminiferal specimens were picked from each sample to ensure sufficient subsampling of diversity for statistical analyses (Patterson and Fishbein 1989; Buzas 1990). Both live and dead specimens were included in this total count, though the majority of specimens were dead at the time of collection and live specimens were not sufficiently abundant for effective analysis.

Quantitative analyses

We used Hill numbers (i.e. the effective number of species) parameterized by a diversity order q (Hill 1973) to estimate benthic foraminiferal diversity in each sample and Environmental Protection Department (EPD) region (Fig. 1; NS = North Western, DS = Deep Bay, SS = Southern, TS = Tolo Harbour, PS = Port Shelter, and MS = Mirs Bay; Hong Kong coastal water regions divided by EPD). Hill numbers are increasingly used by ecologists to quantify species diversity because they have mathematical properties that directly support biological reasoning about diversity, in contrast with some other biodiversity metrics (Ellison 2010; Chao *et al.* 2020). To make a fair comparison among

samples and EPD regions, the Hill numbers were rarefied or extrapolated to the same sample completeness (97%), which was the largest sample coverage possible across all samples and EPD regions (Chao *et al.* 2020). Sample completeness is measured by sample coverage (i.e. the proportion of specimens in the entire assemblage that belong to detected species), a concept developed by Alan Turing (Chao *et al.* 2020). The order q of the Hill numbers controls the sensitivity of the diversity metric to species relative abundance. When the order $q = 0$, Hill number (0D) reduces to species richness; when the order $q = 1$, Hill number (1D) measures the diversity of the abundant species; when the order $q = 2$, Hill number (2D) measures the diversity of dominant species (Chao *et al.* 2014b). The Hill numbers 1D and 2D correspond to Shannon and Simpson diversity, respectively (Chao *et al.* 2014b). Species evenness, ${}^qE_3(p) = ({}^qD - 1)/(S - 1)$, where S denotes species richness, was quantified using the continuous profiles of Hill numbers as functions of order q , following Chao and Ricotta (2019). A gradual profile suggests that the diversity of rare, abundant, and dominant species are similar, indicating a more even community, whereas a steep profile indicates an uneven community comprised of one or more dominant species. We conducted hierarchical cluster analysis to identify biofacies based on Ward's minimum variance and three Sørensen-type dissimilarity measures, including Sørensen ($q = 0$), Horn ($q = 1$), and Morisita–Horn ($q = 2$). The Ward's algorithm minimizes the error sum of squares within clusters; it tends to generate more balanced clusters and, therefore is preferred for the delineation of biofacies. The number of clusters was determined by average silhouette width, with a higher value indicating greater cohesion and separation of clusters. While classic Sørensen dissimilarity is presence-absence based, the latter two measures consider species relative abundance and quantify the compositional dissimilarities of abundant and dominant species, respectively. A non-Metric Multidimensional Scaling (nMDS; Gower 1966) was also performed to visualize and summarize spatial trends of benthic foraminiferal faunal compositions.

All analyses were implemented in RStudio (RStudio Team 2016). We used 'iNEXT' to estimate diversity (Chao *et al.* 2014a; Hsieh *et al.* 2016) and 'vegan' for our multivariate analyses (Oksanen *et al.* 2020). Figures and maps were constructed using 'ggplot2' (Wickham 2012).

Results

Foraminifera and their diversity

A total of 142 benthic foraminiferal species were found in the 6800 specimens and 17 samples that

we examined (Appendix 1; Figs 2 & 3). *Ammonia tepida* (Cushman, 1926) (Fig. 3.22–23) was the most abundant species, constituting 9.4% of all collected specimens, followed by *Triloculina barnardi* Rasheed, 1988 (in Haig 1988) (Fig. 2.7) with 7.7%, and *Amphistegina lessonii* d'Orbigny, 1832 (in Guérin-Méneville 1832) (Fig. 2.14–15) with 5.6%. All other species constituted less than 5% of the total abundance. *Ammonia tepida* was the most abundant species at three sites (Sites 3, 6 & 12), where it co-occurred with other *Ammonia* species (Fig. 3.20–25) and agglutinated species like *Ammobaculites* (Fig. 2.1). *Triloculina barnardi* was the most abundant species at Sites 1 and 2, where it co-occurred with other agglutinated species such as *Textularia* spp. and *Siphonaperta crassa* Vella, 1957 (Fig. 2.3–4), and encrusting species like *Acerulina mabahethi* (Said, 1949). *Amphistegina lessonii* was the most dominant species at Site 11 where it co-occurred with another endosymbiotic species, *Amphistegina lobifera* Larsen, 1976, as well as *Triloculina barnardi* and *Acerulina mabahethi*. Endosymbiotic species at Site 11 constituted 81% of sampled foraminiferal specimens (Table 1; Fig. 4g), indicating that there is sufficient sunlight penetration through the water column at this site to support photosynthesizing symbionts. Foraminiferal microhabitat preference (epifaunal v. infaunal) varies greatly across Hong Kong waters (Fig. 4c, d). Eleven sites exhibited approximately equal proportions of epifaunal and infaunal individuals (e.g. between 40 and 60%); however, infaunal species were dominant at Sites 1 and 2 (81 and 70% respectively) and epifaunal species were dominant at Sites 3, 5, 11 and 17 (84–95% of individuals).

The highest diversity was observed in the southern area of Hong Kong (eastern part of the SS EPD region), whereas the lowest diversity occurred in the northwestern area (DS and NS EPD regions) and Tolo Harbour (TS EPD region) (Fig. 5). These spatial diversity patterns were consistent for rare, abundant, and dominant species, as measured by Hill numbers of differing order q [i.e. diversities of rare species (0D = species richness), abundant species (1D), and dominant species (2D)] (Fig. 5). Intermediate levels of diversity were observed in the southwestern (western part of the SS EPD region) and eastern areas (PS and MS EPD regions) of the study area (Fig. 5). The diversity of rare species was higher in the eastern area than the southwestern area, but diversities of abundant and dominant species were similar between these two (Fig. 5). Gamma diversity (diversity of each EPD region) showed a similar trend (Fig. 6): gamma diversity was highest in the SS EPD region, followed by the PS, MS, and NS EPD regions, and the lowest gamma diversity was observed in the DS and TS EPD regions. The MS and PS EPD regions are

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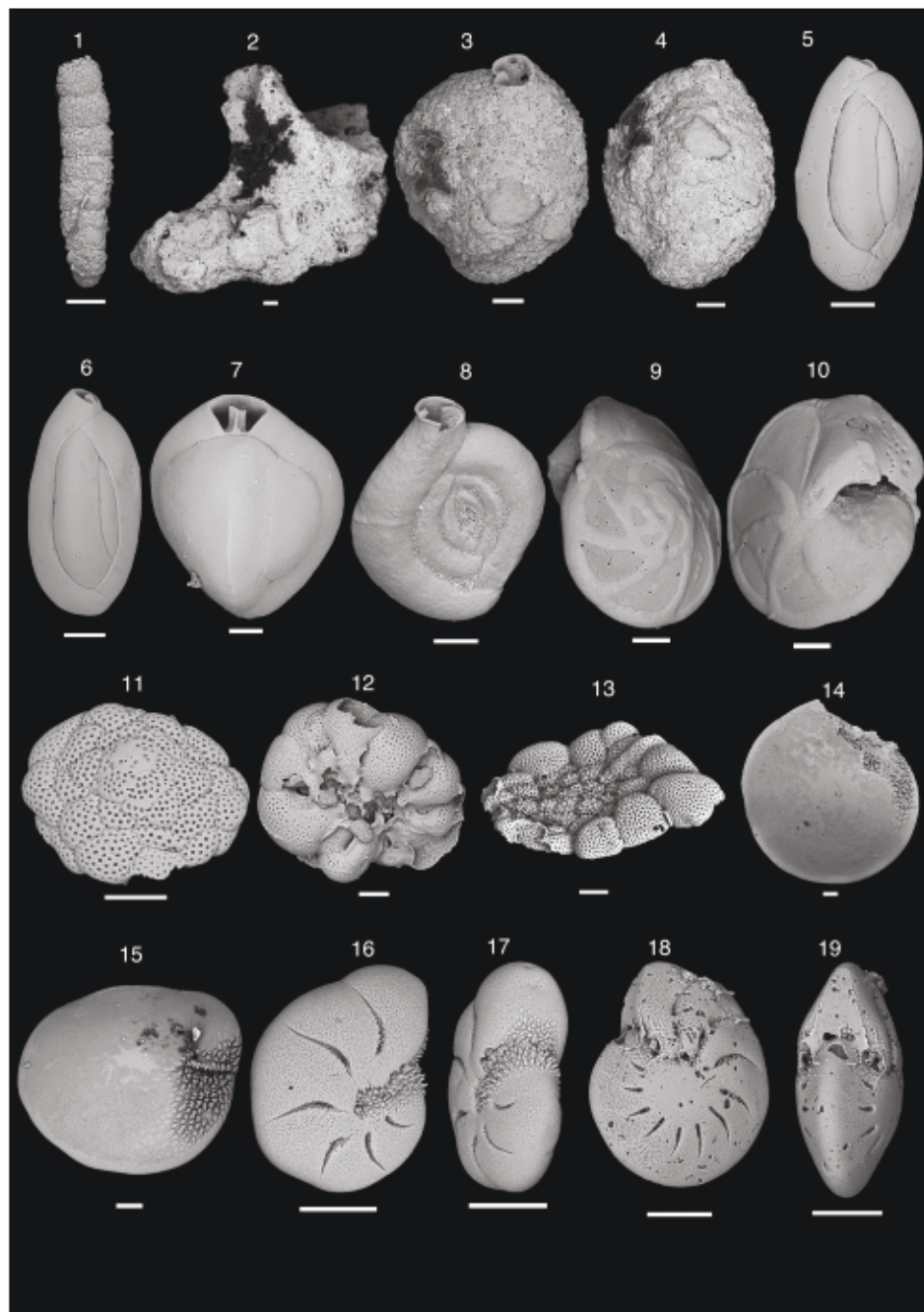


Fig. 2. Scanning electron microscopy images of selected foraminiferal species. 1, *Ammobaculites agglutinans*, lateral view. 2, *Haddonella torresiensis*, lateral view. 3, *Siphonaperta crassa*, apertural view. 4, *Siphonaperta crassa*, lateral view. 5, *Quinqueloculina* sp. 3, lateral view. 6, *Quinqueloculina* sp. 3, apertural view. 7, *Triloculina barnadi*, apertural view. 8, *Sigmoilina subtenuis*, apertural view. 9, *Eponides repandus*, spiral view. 10, *Eponides repandus*, umbilical view. 11, *Cymbaloporella bradyi*, spiral view. 12, *Cymbaloporella bradyi*, umbilical view. 13, *Acervulina mahabathi*, spiral view. 14, *Amphistegina lessonii*, spiral view. 15, *Amphistegina lessonii*, umbilical view. 16, *Haynesina* sp. 1, lateral view. 17, *Haynesina* sp. 1, peripheral view. 18, *Haynesina* sp. 2, lateral view. 19, *Haynesina* sp. 2, peripheral view. Scale bar = 100 μ m.

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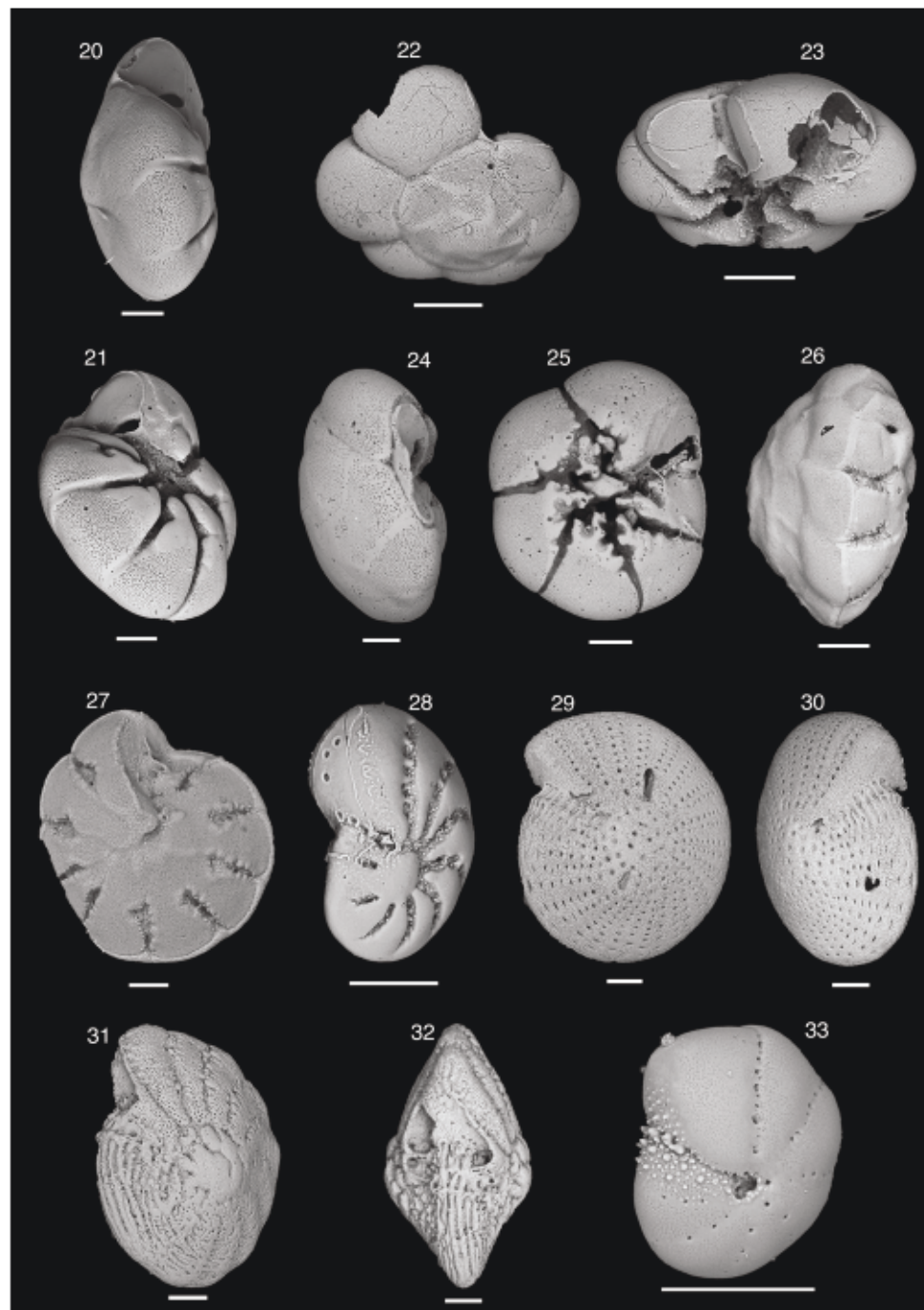


Fig. 3. Scanning electron microscopy images of selected foraminiferal species. 20, *Ammonia confertitesta*, peripheral view. 21, *Ammonia confertitesta*, umbilical view. 22, *Ammonia tepida*, spiral view. 23, *Ammonia tepida*, umbilical view. 24, *Ammonia* sp. 1, peripheral view. 25, *Ammonia* sp. 1, umbilical view. 26, *Rotalidium annectens*, peripheral view. 27, *Rotalidium annectens*, umbilical view. 28, *Elphidium advenum*, lateral view. 29, *Elphidium biperforatum*, lateral view. 30, *Elphidium biperforatum*, peripheral view. 31, *Elphidium hispidulum*, lateral view. 32, *Elphidium hispidulum*, peripheral view. 33, *Elphidium* sp. 6, lateral view. Scale bar = 100 μ m.

Hong Kong modern benthic foraminifera

Table 1. List of miliolid (M), agglutinated (A), endosymbiotic (E), and encrusting (Ec) species in this study

Species name	Miliolids	Agglutinated	Endosymbiotic	Encrusting
<i>Acervulina mabahethi</i>				Ec
<i>Adelosina carinatastriata</i>	M			
<i>Ammobaculites agglutinans</i>		A		
<i>Ammobaculites</i> sp. 1		A		
<i>Ammobaculites</i> sp. 2		A		
<i>Ammobaculites</i> sp. 3		A		
<i>Amphistegina lessonii</i>			E	
<i>Amphistegina lobifera</i>			E	
<i>Amphistegina radiata</i>			E	
<i>Amphistegina</i> sp. 1			E	
<i>Haddonina torresiensis</i>		A		Ec
<i>Haplophragmoides canariensis</i>		A		
<i>Hauerina fragilissima</i>	M			
<i>Hauerina</i> sp. 1	M			
<i>Miliolinella</i> sp. 1	M			
<i>Miliolinella</i> sp. 2	M			
<i>Miliolinella</i> sp. 3	M			
<i>Miliolinella</i> sp. 4	M			
<i>Operculina</i> sp. 1			E	
<i>Peneroplis pertusus</i>	M		E	
<i>Peneroplis planatus</i>	M		E	
<i>Pyrgo</i> sp. 1	M			
<i>Pyrgo</i> sp. 2	M			
<i>Quinqueloculina bosciana</i>	M			
<i>Quinqueloculina distorta</i>	M			
<i>Quinqueloculina lamarckiana</i>	M			
<i>Quinqueloculina neostriata</i>	M			
<i>Quinqueloculina parkeri</i>	M			
<i>Quinqueloculina philippinensis</i>	M			
<i>Quinqueloculina</i> cf. <i>philippinensis</i>	M			
<i>Quinqueloculina pseudoreticulata</i>	M			
<i>Quinqueloculina seminulum</i>	M			
<i>Quinqueloculina subpolygona</i>	M			
<i>Quinqueloculina</i> sp. 1	M			
<i>Quinqueloculina</i> sp. 2	M			
<i>Quinqueloculina</i> sp. 3	M			
<i>Quinqueloculina</i> sp. 4	M			
<i>Quinqueloculina</i> sp. 5	M			
<i>Quinqueloculina</i> sp. 6	M			
<i>Quinqueloculina</i> sp. 7	M			
<i>Quinqueloculina</i> sp. 8	M			
<i>Quinqueloculina</i> sp. 9	M			
<i>Quinqueloculina</i> sp. 10	M			
<i>Quinqueloculina</i> sp. 11	M			
<i>Quinqueloculina</i> sp. 12	M			
<i>Quinqueloculina</i> sp. 13	M			
<i>Reophax</i> sp. 1		A		
<i>Reophax</i> sp. 2		A		
<i>Sahulina conica</i>		A		
<i>Sigmoilina subtenuis</i>	M			
<i>Siphonaperta crassa</i>	M	A		
<i>Siphonaperta</i> sp. 1	M	A		
<i>Sorites orbicularis</i>	M		E	
<i>Spiroloculina angulata</i>	M			
<i>Spiroloculina corrugata</i>	M			
<i>Spiroloculina</i> sp. 1	M			
<i>Spiroloculina</i> sp. 2	M			
<i>Spiroloculina</i> sp. 3	M			

(Continued)

Table 1. Continued.

Species name	Miliolids	Agglutinated	Endosymbiotic	Encrusting
<i>Spiroloculina</i> sp. 4	M			
<i>Spiroloculina</i> sp. 5	M			
<i>Textularia compacta</i>		A		
<i>Textularia foliacea</i>		A		
<i>Textularia jparkeri</i>		A		
<i>Textularia lateralis</i>		A		
<i>Textularia</i> sp. 1		A		
<i>Textularia</i> sp. 2		A		
<i>Textularia</i> sp. 3		A		
<i>Textularia</i> sp. 4		A		
<i>Textularia</i> sp. 5		A		
<i>Textularia</i> sp. 6		A		
<i>Textularia</i> sp. 7		A		
<i>Textularia</i> sp. 8		A		
<i>Triloculina barnardi</i>	M			
<i>Triloculina</i> sp. 1	M			
<i>Triloculina</i> sp. 2	M			
<i>Trochammina</i> sp. 1		A		

We used the following references for the assignment: Kaminski (2014) (for agglutinated species); Hallock (1999) and Hallock *et al.* (2003) (for endosymbiotic species); Hayward *et al.* (2022) (for miliolid and encrusting species).

characterized by high species richness (0D) and comparatively low diversities of abundant (1D) and dominant species (2D). In contrast, evenness was highest in the DS EPD region, followed by the SS EPD region and then the NS EPD region, and lowest in the TS and MS EPD regions (Fig. 6).

Multivariate analysis

The nMDS results showed clear separation of four biofacies, which were also generally recognized by cluster analyses based on Sørensen, Horn, and Morisita–Horn dissimilarities (Fig. 7; Table 2). The three dissimilarity measures consider faunal composition based on different levels of species information from occurrence to relative abundance. Cluster analyses based on Sørensen and Horn dissimilarities indicate that dividing sites into four clusters resulted in the greatest average silhouette width; the analysis based on Morisita–Horn, however, indicates that seven clusters may be a better choice for this dissimilarity measure. For consistency and comparability, four clusters were used to determine the biofacies. The Hong Kong foraminiferal fauna was characterized by a southern–eastern fauna that is broadly distributed from the southern part to the eastern part of Hong Kong in the nMDS and cluster results based on species presence/absence (i.e. Sørensen dissimilarity) (Biofacies 1; Sites 1–2, 4, 6–9, 16; Fig. 7a, b) and on abundant species (Horn dissimilarity) (Biofacies 1; Sites 1–2, 4, 7–11; Fig. 7c, d). In the cluster analysis results based on Morisita–Horn dissimilarity, southern water (Biofacies 4; Sites 7–

9; Fig. 7e, f) and eastern water faunas (Biofacies 1; Sites 1–2, 4, 10–11; Fig. 7e, f) were further separated, but these biofacies are still proximal to each other in the nMDS plot (Fig. 7f). Biofacies 2 was distributed around southwestern Hong Kong around Lantau Island in all nMDS and cluster analysis results (Sørensen: Sites 3, 12–15; Horn and Morisita–Horn: Sites 13–16). Depending on the dissimilarity measure that was used, Biofacies 3 was found in Tolo Harbour (Site 5), Port Shelter (Site 3, 4), Deep Bay (Site 17), and/or southwestern end of Hong Kong (=southeastern Pearl River delta on the west of Lantau Island; Site 12) (Fig. 7). The eastern part of Mirs Bay constituted a distinct biofacies (Biofacies 4; Sites 10–11) only in the Sørensen-based analysis (Fig. 7a). The sites assigned to Biofacies 4 vary strongly depending on the dissimilarity measure used, and thus this biofacies does not have the same ecological meaning among cluster analyses with different dissimilarity measures. However, the sites assigned to other clusters (Biofacies 1–3) are mostly stable regardless of the dissimilarity measure used, suggesting that each of these biofacies has similar ecological meaning among different cluster analyses.

Discussion

The strongest biogeographical patterns for benthic foraminifera in Hong Kong include the widely-distributed southern–eastern water Biofacies 1 in the Sørensen (i.e. rare species-based) and Horn (i.e.

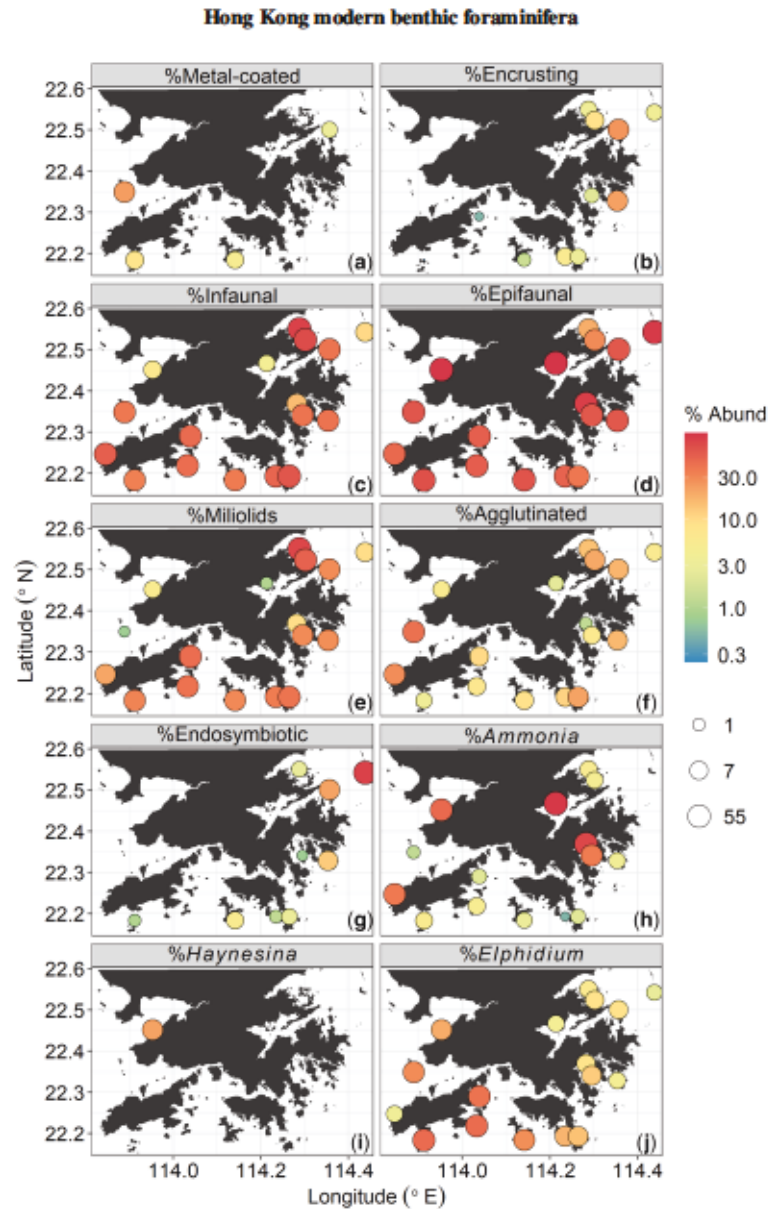


Fig. 4. Distribution and relative abundance (% Abund; represented by colour and dot size, as in the legends) of key foraminiferal groups: (a) metal-coated/infilled specimens; (b) encrusting taxa; (c) infaunal taxa; (d) epifaunal taxa; (e) miliolids; (f) agglutinated taxa; (g) endosymbiotic taxa; (h) genus *Ammonia*; (i) genus *Haynesina*; and (j) genus *Elphidium*. Table 2 shows the list of miliolid, agglutinated, endosymbiotic, and encrusting taxa. Appendix 1 shows the list of infaunal and epifaunal taxa. See Figure 1 for site details.

abundant-species-based) cluster analyses and the two biofacies (1 + 4) in the Morisita–Horn (i.e. dominant species-based) analysis, which distinguish the western part of the SS EPD region and parts of the PS and MS EPD regions (Figs 1 & 7). The dominance of *Triloculina* at two of the sites in Biofacies 1 (Sites 1 & 2), along with the high proportion of

infaunal species (Fig. 4), indicates depleted oxygen levels at the sediment–water interface (Burke 1981). However, the dominance of epifaunal, rotaline species such as *Elphidium* spp. (Fig. 3.28–33), *Ammonia* spp. (Fig. 2.14–15), *Ammonia* spp. (Fig. 2.13), and *Eponides repandus* (Fichtel and Moll, 1798) (Fig. 2.9–10) at the remaining

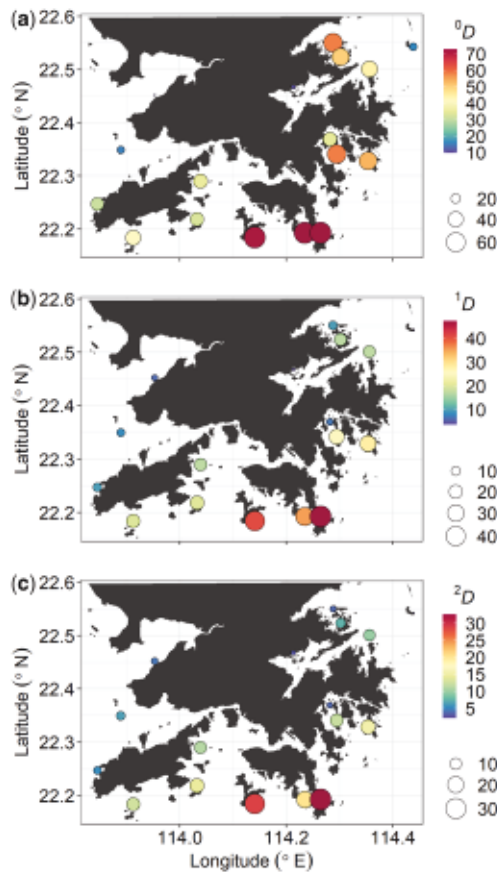
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Fig. 5. Alpha diversity (i.e. diversity of individual sites) heat maps of Hong Kong benthic foraminiferans. Distributions of Hill numbers 0D (a: $q = 0$, species richness), 1D (b: $q = 1$, exponential Shannon), and 2D (c: $q = 2$, inversed Simpson). We used 97% sample coverage to standardize the Hill number estimates. Diversities are represented by colour and dot size as in the legends. Sites 7 and 8 are in the same location, but a jitter was added to make them visible.

sites in Biofacies 1 (Fig. 4) indicates environmental conditions that are sufficiently oxygenated to support attached or free-living taxa on the sea floor. This faunal variation presumably reflects varying environmental and ecological conditions within this area. This may account for the dominance of *Ammonia* spp. (Fig. 3.20–25) in this biofacies, that are capable of best resisting this variation, particularly in oxygenation (Hayward *et al.* 2021). This vast southern–eastern water fauna is generally consistent with previous studies of other benthic organisms, macrobenthos (total soft-sediment macrobenthos in grab samples, which is dominated by polychaetes and then molluscs) and ostracods, which have found a unique suite of species in this area that are tolerant

of muddy and turbid conditions. In these other groups, the southern water fauna has an even wider distribution in the west, covering not only the southern and southeastern waters but also the southwestern waters of Hong Kong (Shin and Ellingsen 2004; Hong *et al.* 2022) (Fig. 8). For foraminifera, this expansive southern–eastern biofacies is further subdivided when dissimilarity is based on dominant species (i.e. Morisita–Horn dissimilarity, Biofacies 1 and 4; Fig. 7e, f); the southern water fauna as described above and an eastern water fauna characterized by higher abundance of endosymbiotic species (particularly amphistegnids) (Fig. 4). This eastern water foraminiferal biofacies occurs where coral diversity is also greatest (Qiu *et al.* 2014; Duprey *et al.* 2016, 2020; Cybulski *et al.* 2020). This is because endosymbiotic foraminifera, and scleractinian corals, both require less turbid, more oligotrophic water for efficient photosynthesis. Due to inputs from the Pearl River, these conditions are only found in the eastern waters of Hong Kong. Indeed, turbidity is lowest along the eastern side of Hong Kong (Fig. 9). Similar geographical subdivisions of the southern fauna were documented in a recent macrofaunal study (Wang *et al.* 2021), and these may also be related to water quality.

Interestingly, the highest foraminiferal diversity is found in the highly turbid southern waters (eastern part of the SS EPD region) (Fig. 5). This high diversity in the southern region is generally consistent with previous studies of ostracods and macrobenthos that documented elevated diversity in the central region of Hong Kong, although their diversity maxima were located somewhat further north, on the north side of Hong Kong Island (Wang *et al.* 2017; Hong *et al.* 2022). In contrast, corals show a clear west to east increase in diversity with their highest species diversity in eastern waters (Yeung *et al.* 2021). The greatest abundance of coral that are more susceptible to environmental stressors (Cybulski *et al.* 2020) is also found in eastern waters. This biogeographical difference between foraminifera and corals is perhaps because endosymbiotic species compose a limited part of the foraminiferal fauna (Fig. 4). Moderate levels of eutrophication (Fig. 9) may be beneficial for some soft-sediment benthos, as discussed in Hong *et al.* (2022), and our results suggest that this may also be true for benthic foraminifera.

Biofacies 2 (Fig. 7), particularly in the eastern part, is characterized by the dominance of *Ammonia* spp. and agglutinated taxa (Fig. 4) including *Ammonia* spp. (Fig. 2.1), which are most commonly found in marsh-like environmental settings and able to endure harsh environmental conditions (Alve 1995; Sen Gupta *et al.* 1996; Murray 2006). *Ammonia tepida*, in particular, is able to tolerate episodic oxygen-deficient conditions in areas with enriched organic carbon (Li *et al.* 2013; Hayward *et al.*

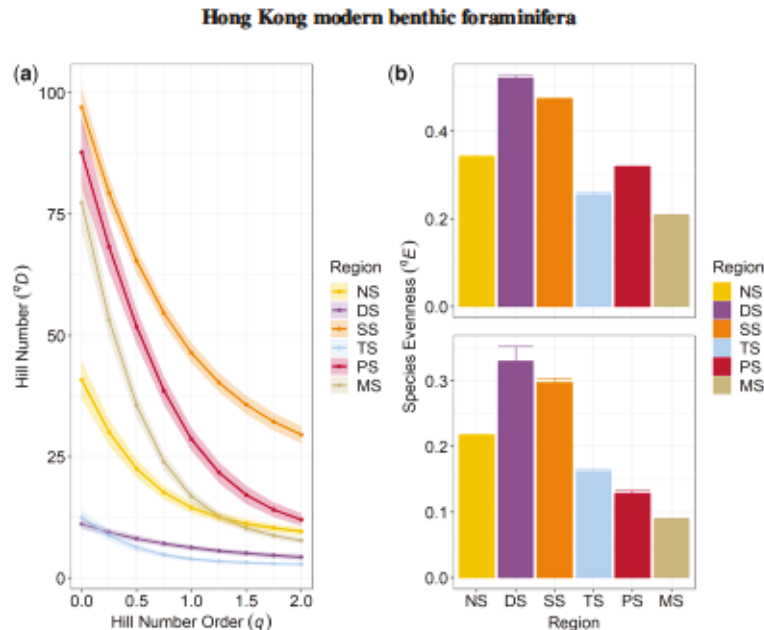


Fig. 6. Gamma diversity results of Hong Kong benthic foraminifera. (a) Hill number profile of each EPD region. The shaded areas show 95% confidence interval of the profiles. Overall elevation of the profiles indicates the diversity based on Hill numbers across different order q between 0 and 2. Levelness of the lines indicates evenness. (b) Evenness based on normalized slope of Hill number profile for order $q = 1$ (top) and order $q = 2$ (bottom). All based on 97% sample coverage. NS, North Western; DS, Deep Bay; SS, Southerm; TS, Tolo Harbour; PS, Port Shelter; MS, Mirs Bay.

2021), and also dominates in areas proximal to the discharge of heavy metals, sewage, chemical effluents, and fertilizers (Seiglie 1971, 1975; Setty 1976; Setty and Nigam 1984; Yanko *et al.* 1992). Other dominant taxa in this biofacies include *Elphidium* spp. (Fig. 3.28–33) and *Rotalidium annectens* (Parker and Jones, 1865) (Fig. 3.26–27). *Elphidium advenum* (Cushman, 1922) (Fig. 3.28) and *Elphidium excavatum* (Terquem, 1875) are known to be pollution-tolerant and opportunistic species that occur in harbours and estuarine settings polluted with trace metals (Alve 1995; Li *et al.* 2013), and *Rotalidium annectens* is a shallow-water species that was found by Li *et al.* (2013) to commonly occur in the most highly polluted areas of the Pearl River Estuary. Biofacies 2 also contained one site where foraminiferal specimens were found infilled with heavy-minerals (Site 13) and the abundance of these specific species in this site was several times higher than those of the other sites where metal-coated/infilled specimens were collected (Sites 9–10, 16). Specimens of *Ammonia* spp., *Rotalidium* spp. and *Elphidium* spp. were found coated, or had their chambers in-filled with heavy-minerals (Fig. 10). While geochemical analysis of these metals was beyond the scope of the current study, previous studies have found this phenomenon in carbonate facies with reductive conditions at the

sediment surface (Maiklem 1967), and have shown that *Ammonia tepida* is a bioindicator of trace metal pollutants such as Cr, Cu, Ni, Pb and Zn, particularly Cu and Zn as these two metals are more easily absorbed than other elements (Samir and El-Din 2001; Li *et al.* 2013). Along with the mineral-infused specimens collected in this biofacies, the occurrence of low diversity fauna typically associated with marsh habitats at sites not characterized by these environmental conditions, indicate that stressful environmental conditions affect this region of Hong Kong waters. It is likely that the Pearl River is the source of nutrients and pollutants affecting this fauna, though available environmental data are not sufficiently well resolved to confirm this (Fig. 9).

Heading west, the switch between Biofacies 1 and 2 (in the Sørensen and Horn results) is reflected by the loss of endosymbiotic species and the increased abundance of *Elphidium* spp (Figs 4 & 7; Table 2). Whilst the rarity and lack of endosymbiotic foraminifera in Biofacies 2 reflect turbid water preventing photosynthesis, the higher abundance of *Elphidium* around Sites 14 and 15 indicates that the eutrophic conditions are not too severe. *Elphidium* are comparatively more vulnerable to eutrophication than more low-oxygen-tolerant *Ammonia* (Sen Gupta and Platon 2006; Tsujimoto *et al.* 2008; Yasuhara *et al.* 2012) that are comparatively rare in Biofacies 2

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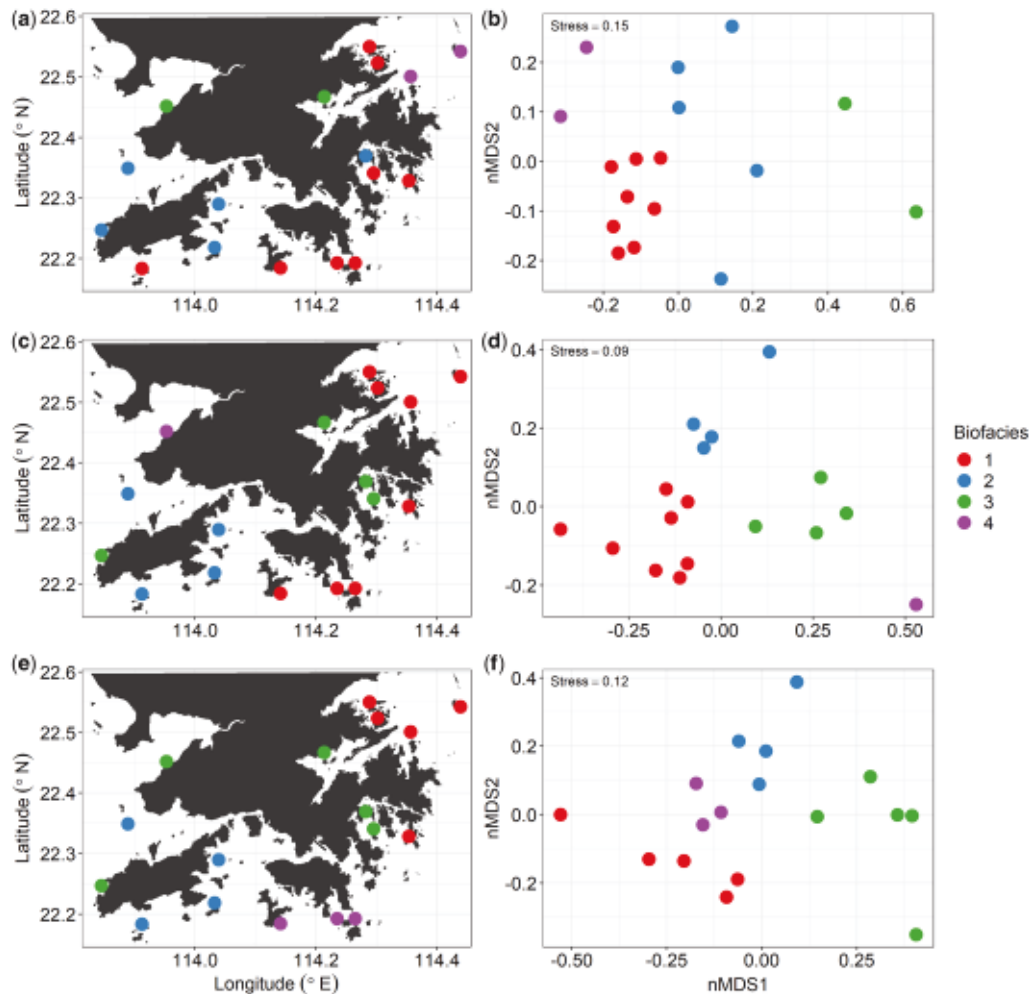


Fig. 7. Hong Kong benthic foraminiferal faunal distributions. Maps (left panels) and nMDS ordinations (right panels) showing biofacies based on (a and b) Sørensen, (c and d) Horn, and (e and f) Morisita–Horn dissimilarities and Ward’s minimum variance cluster analysis. Note that the colour schemes are independent among top, middle and bottom panels; thus, the biofacies based on different dissimilarities are not necessarily related. See Figure 1 for site details.

(Fig. 4). Indeed, chlorophyll-*a* concentration is intermediate in this region (Fig. 9), supporting our interpretation. Distribution data for other benthic groups in southwestern Hong Kong are rather limited (Wang *et al.* 2017, 2021; Hong *et al.* 2021, 2022; Yeung *et al.* 2021) (Fig. 8) and this region should be the focus of future benthic surveys.

Biofacies 3 incorporates the sites at Deep Bay, Tolo Harbour and/or Port Shelter (Sites 3, 5–6, 17) depending on the dissimilarity used. This biofacies consists almost entirely of epifaunal taxa (93–95%), and is dominated by rotaline *Ammonia* spp., *Elphidium* spp. and *Haynesina* spp. (Fig. 2.16–19) (Figs

4 & 7; Table 2). Similar to the other dominant taxa of this biofacies, *Haynesina* are known to be pollution-tolerant taxa within estuarine settings with concentrations of heavy metals (Alve 1995; Li *et al.* 2013). Biofacies 3 results are consistent with earlier foraminiferal studies (Yim and He 1988) and also ostracod and macrobenthic results showing the faunal similarity at least between Tolo Harbour and Port Shelter (Wang *et al.* 2021; Hong *et al.* 2022). Hong *et al.* (2022) attributed the faunal characteristic of Tolo Harbour and Port Shelter to Pb pollution. However, while Pb concentration is indeed high in Tolo Harbour, it is not elevated in Port Shelter (Fig. 9).

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Table 2. List of the top 10 species with the highest % mean occurrence (for Sørensen dissimilarity) or % mean relative abundance (for Horn and Morisita–Horn dissimilarity) for Biofacies 1–4

Sørensen		Horn		Morisita–Horn	
Biofacies 1					
<i>Triloculina barnardi</i>	0.1290	<i>Triloculina barnardi</i>	0.1499	<i>Triloculina barnardi</i>	0.2194
<i>Elphidium advenum</i>	0.0591	<i>Amphistegina lessonii</i>	0.1188	<i>Amphistegina lessonii</i>	0.1787
<i>Acervulina mabahethi</i>	0.0533	<i>Acervulina mabahethi</i>	0.0776	<i>Acervulina mabahethi</i>	0.1047
<i>Ammonia tepida</i>	0.0441	<i>Elphidium advenum</i>	0.0460	<i>Siphonaperta crassa</i>	0.0547
<i>Elphidium craticulatum</i>	0.0388	<i>Siphonaperta crassa</i>	0.0398	<i>Amphistegina lobifera</i>	0.0503
<i>Siphonaperta crassa</i>	0.0348	<i>Amphistegina lobifera</i>	0.0342	<i>Elphidium craticulatum</i>	0.0296
<i>Elphidium hispidulum</i>	0.0338	<i>Elphidium craticulatum</i>	0.0338	<i>Haddonina torresiensis</i>	0.0266
<i>Eponides repandus</i>	0.0307	<i>Eponides repandus</i>	0.0291	<i>Textularia foliacea</i>	0.0241
<i>Cymbaloporella bradyi</i>	0.0235	<i>Cymbaloporella bradyi</i>	0.0241	<i>Neonorbina clara</i>	0.0182
<i>Ammonia confertitesta</i>	0.0216	<i>Textularia foliacea</i>	0.0216	<i>Ammonia tepida</i>	0.0171
Biofacies 2					
<i>Ammonia tepida</i>	0.1705	<i>Elphidium hispidulum</i>	0.1575	<i>Elphidium hispidulum</i>	0.1575
<i>Elphidium hispidulum</i>	0.0890	<i>Rotalidium annectens</i>	0.1125	<i>Rotalidium annectens</i>	0.1125
<i>Rotalidium annectens</i>	0.0710	<i>Elphidium craticulatum</i>	0.0863	<i>Elphidium craticulatum</i>	0.0863
<i>Ammobaculites agglutinans</i>	0.0705	<i>Elphidium biperforatum</i>	0.0850	<i>Elphidium biperforatum</i>	0.0850
<i>Ammonia confertitesta</i>	0.0670	<i>Sigmoilina subtenuis</i>	0.0506	<i>Sigmoilina subtenuis</i>	0.0506
<i>Elphidium craticulatum</i>	0.0550	<i>Siphonaperta crassa</i>	0.0363	<i>Siphonaperta crassa</i>	0.0363
<i>Elphidium biperforatum</i>	0.0440	<i>Ammobaculites</i> sp. 3	0.0356	<i>Ammobaculites</i> sp. 3	0.0356
<i>Quinqueloculina</i> sp. 3	0.0400	<i>Ammonia tepida</i>	0.0350	<i>Ammonia tepida</i>	0.0350
<i>Ammobaculites</i> sp. 3	0.0325	<i>Ammobaculites agglutinans</i>	0.0344	<i>Ammobaculites agglutinans</i>	0.0344
<i>Sigmoilina subtenuis</i>	0.0300	<i>Elphidium advenum</i>	0.0306	<i>Elphidium advenum</i>	0.0306
Biofacies 3					
<i>Ammonia confertitesta</i>	0.2350	<i>Ammonia tepida</i>	0.3388	<i>Ammonia tepida</i>	0.2735
<i>Ammonia</i> sp. 1	0.2188	<i>Ammonia confertitesta</i>	0.2306	<i>Ammonia confertitesta</i>	0.1895
<i>Ammonia tepida</i>	0.1963	<i>Ammobaculites agglutinans</i>	0.0600	<i>Ammonia</i> sp. 1	0.0890
<i>Haynesina</i> sp. 1	0.0675	<i>Quinqueloculina</i> sp. 3	0.0381	<i>Ammobaculites agglutinans</i>	0.0480
<i>Elphidium</i> sp. 6	0.0588	<i>Elphidium advenum</i>	0.0306	<i>Quinqueloculina</i> sp. 3	0.0415
<i>Haynesina</i> sp. 2	0.0438	<i>Trochammina</i> sp. 1	0.0194	<i>Elphidium</i> sp. 6	0.0320
<i>Elphidium</i> sp. 7	0.0400	<i>Ammonia convexa</i>	0.0188	<i>Haynesina</i> sp. 1	0.0270
<i>Ammonia convexa</i>	0.0388	<i>Quinqueloculina seminulum</i>	0.0163	<i>Elphidium advenum</i>	0.0245
<i>Quinqueloculina</i> sp. 3	0.0325	<i>Nonionoides</i> sp. 1	0.0156	<i>Elphidium</i> sp. 7	0.0185
<i>Haplophragmoides canariensis</i>	0.0225	<i>Miliolinella</i> sp. 1	0.0144	<i>Trochammina</i> sp. 1	0.0175
Biofacies 4					
<i>Amphistegina lessonii</i>	0.4200	<i>Ammonia</i> sp. 1	0.4175	<i>Elphidium advenum</i>	0.1017
<i>Acervulina mabahethi</i>	0.1088	<i>Haynesina</i> sp. 1	0.1350	<i>Eponides repandus</i>	0.0725
<i>Triloculina barnardi</i>	0.1013	<i>Elphidium</i> sp. 6	0.1175	<i>Elphidium craticulatum</i>	0.0408
<i>Amphistegina lobifera</i>	0.0850	<i>Haynesina</i> sp. 2	0.0875	<i>Cymbaloporella bradyi</i>	0.0367
<i>Haddonina torresiensis</i>	0.0413	<i>Elphidium</i> sp. 7	0.0800	<i>Quinqueloculina</i> sp. 3	0.0350
<i>Siphonaperta crassa</i>	0.0288	<i>Quinqueloculina</i> sp. 3	0.0550	<i>Triloculina barnardi</i>	0.0342
<i>Elphidium crispum</i>	0.0175	<i>Haplophragmoides canariensis</i>	0.0450	<i>Acervulina mabahethi</i>	0.0325
<i>Elphidium craticulatum</i>	0.0163	<i>Ammonia confertitesta</i>	0.0250	<i>Elphidium crispum</i>	0.0300
<i>Textularia lateralis</i>	0.0150	<i>Ammonia tepida</i>	0.0125	<i>Quinqueloculina</i> sp. 10	0.0267
<i>Elphidium advenum</i>	0.0138	<i>Trochammina</i> sp. 1	0.0100	<i>Quinqueloculina</i> sp. 8	0.0250

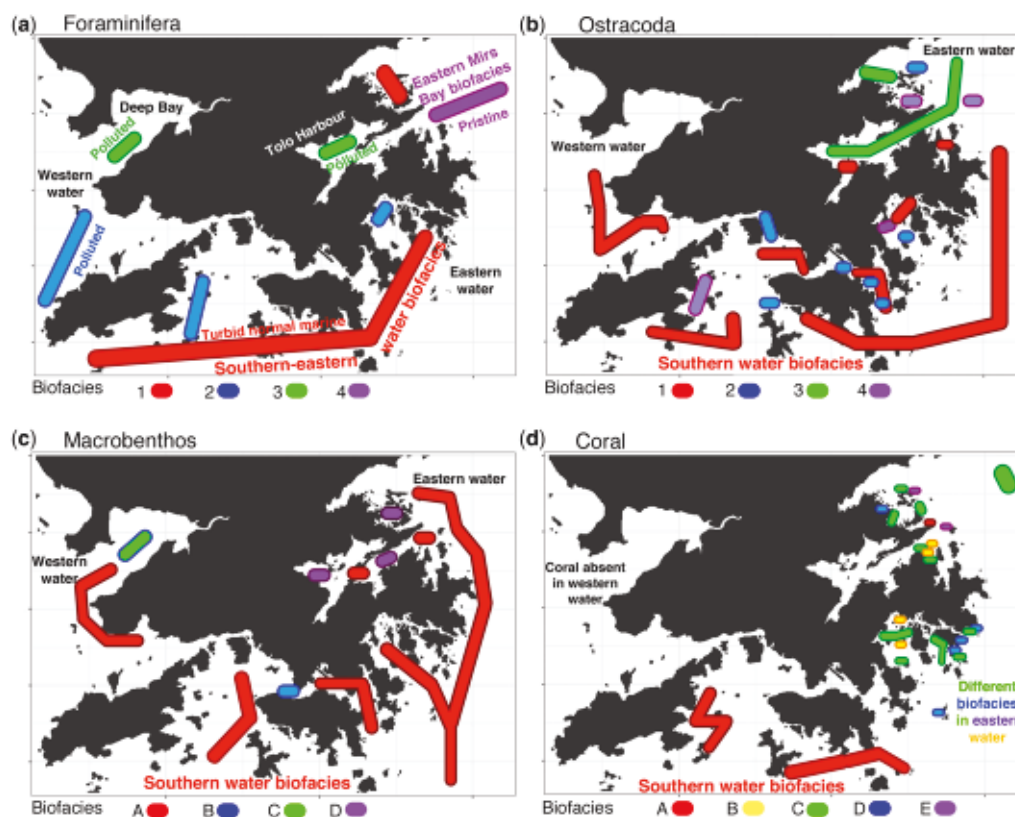
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Fig. 8. Comparison of biofacies distributions in (a) benthic foraminifera, (b) ostracods, (c) macrobenthos, and (d) corals. Simplified after this study (benthic foraminifera), Hong *et al.* (2022) (ostracods), Wang *et al.* (2017) (macrobenthos), and Yeung *et al.* (2021) (corals). Names of biofacies, geographical location, and their characteristics discussed in the main text are indicated on the figure. Foraminiferal and ostracod studies are based on surface sediments including both living and dead specimens (this study; Hong *et al.* 2022). Coral and macrobenthic studies are on living ones (Wang *et al.* 2017; Yeung *et al.* 2021). Note that the colour schemes are independent among panels, and clustering methods to recognize biofacies are not consistent among studies.

Generally speaking, Pb pollution in Hong Kong's marine sediments is not high with respect to the United States Environmental Protection Agency sediment guidelines (Hong *et al.* 2022). As previously discussed in Biofacies 2, *Ammonia*, particularly *Ammonia tepida*, is a well-known pollution-, eutrophication-, and hypoxia-tolerant, opportunistic foraminiferal taxon (Tsujimoto *et al.* 2008; Ye *et al.* 2021). This pattern is consistent with a recent study showing low diversity and high abundance of stress-tolerant ostracod species *Sinocytheridea impressa* in Tolo Harbour and Port Shelter, though this study did not include ostracod faunas in Deep Bay and the southeastern region of Hong Kong (Hong *et al.* 2022) (Fig. 8). Foraminiferal indicator taxa show much clearer distributional trends regarding this human-impact regime, indicating that benthic foraminifera are strong environmental indicators,

particularly for organic matter input and resulting eutrophication and deoxygenation (Sen Gupta and Platon 2006; Rabalais *et al.* 2007; Tsujimoto *et al.* 2008; Yasuhara *et al.* 2019). We interpret these results to suggest that similarly stressful benthic environments and habitats can be distributed across many isolated or separated locations within a region, especially semi-enclosed areas with localized eutrophication and pollution sources (Archana *et al.* 2016; Cybulski *et al.* 2020; Duprey *et al.* 2020; Geeraert *et al.* 2021). Yet the responsible environmental factor or pollutant is uncertain from available environmental data (Fig. 9), partly because of incomplete spatial coverage of water quality monitoring. Sites 5 and 12 of Biofacies 3 were the only areas in the study that were not sand-dominated substrates, but instead were silt/clay dominated from surrounding mangroves (Site 5) or Pearl River sedimentation (Site 12). It is

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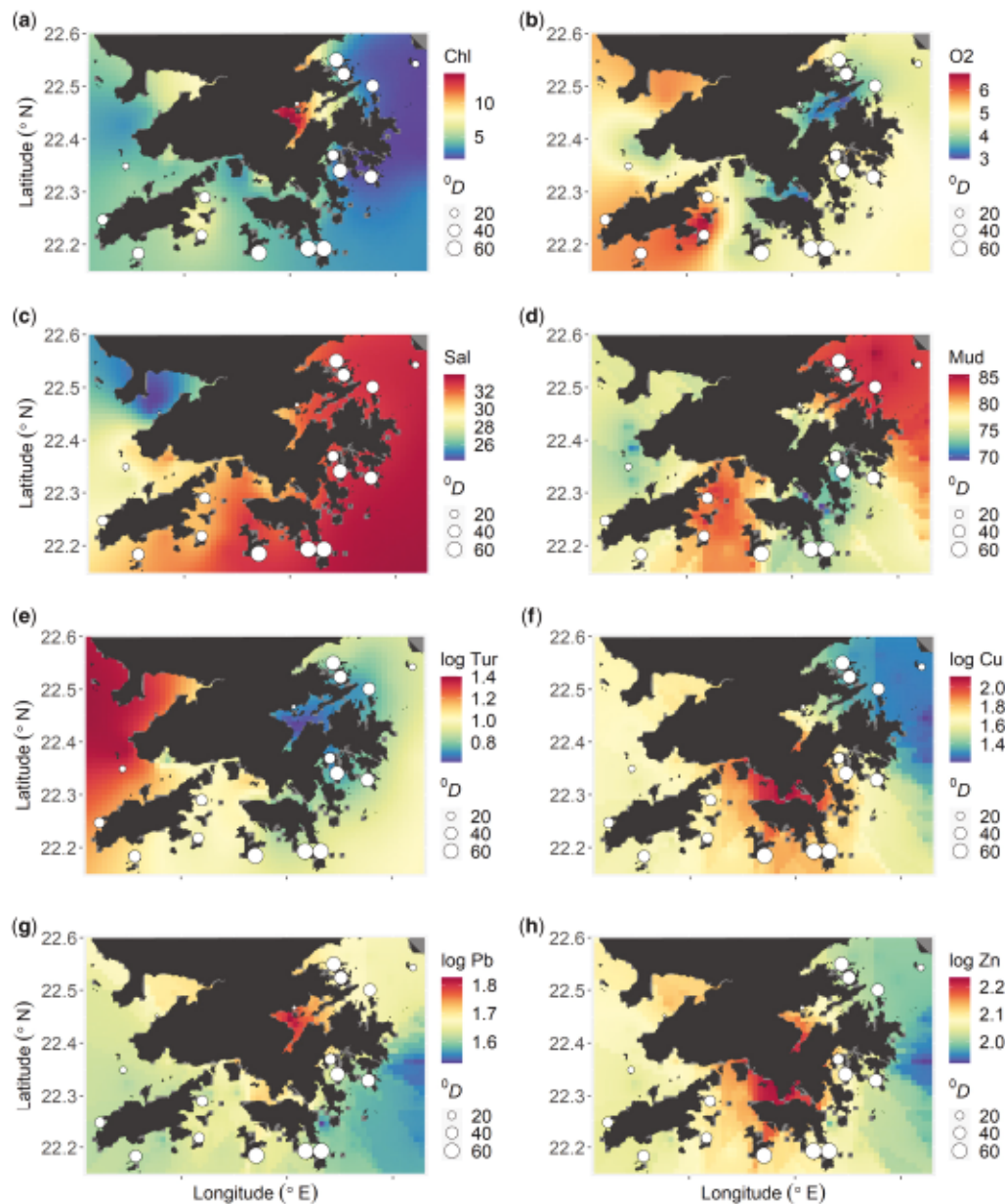


Fig. 9. Distributions (heat maps) of selected environmental factors, including (a) chlorophyll-*a* ($\mu\text{g l}^{-1}$), (b) dissolved oxygen (mg l^{-1}), (c) salinity (psu), (d) mud content [$\%\text{w/w}$ ($<63\ \mu\text{m}$)], (e) turbidity (NTU), (f) copper concentration (mg kg^{-1}), (g) lead concentration (mg kg^{-1}), and (h) zinc concentration (mg kg^{-1}). Distributions of Hill numbers 0D ($q = 0$, species richness) overlaid. Source: from Hong *et al.* (2021), based on the EPD monitoring programme data (Environmental Protection Department 2011). Note that these EPD sites do not necessarily correspond to the sites of this study.

possible that this substrate difference caused some of the biodiversity changes that we see. However, it is interesting to note that, regardless of the substrate, Biofacies 3 sites all group together in the nMDS

plot, indicating that there are other controlling factors. Thus, we highlight the need for benthic and environmental surveys with higher spatial resolution and more complete coverage of all Hong Kong waters.

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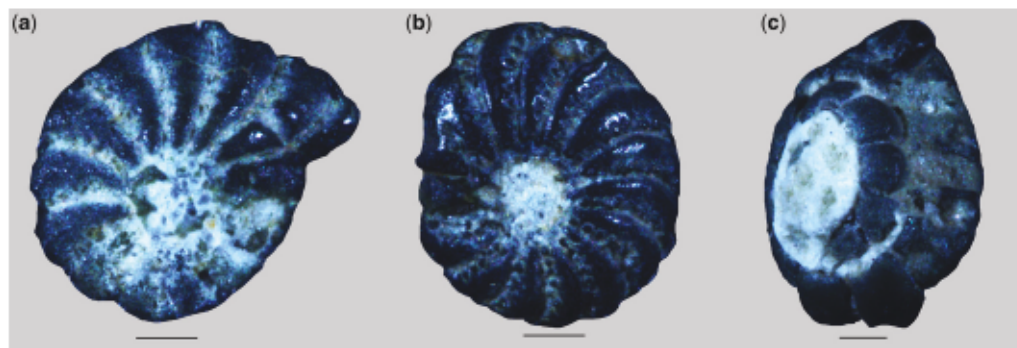


Fig. 10. Examples of heavy mineral-coated/infilled specimens indicated by the black and dark brown discoloration: (a and b) *Elphidium* spp.; (c) *Rotalidium* sp. Scale bar = 100 μ m.

Biofacies 4 constitutes a distinct fauna in eastern Mirs Bay in the Sørensen result (Fig. 7). Interestingly Biofacies 4 is comprised of taxa frequently found in carbonate reef settings. It is overwhelmingly dominated by endosymbiotic fauna (Site 11, 81%; Fig. 4), particularly *Amphistegina lessonii* (Fig. 2.14–15), and encrusting species (Site 10) such as *Acervulina mabahethi* (Fig. 2.13) and *Haddonina torresiensis* (Chapman, 1898) (Fig. 2.2). *Amphistegina lessonii* is a tropical species able to tolerate lower temperatures (12–20°C) (Murray 2006), greater water depths (to 150 m), and higher energy levels (more intensive wave action generates thicker test walls) (Mamo 2016) compared to most tropical species. The abundance of encrusting *Haddonina torresiensis* and *Acervulina mabahethi* which have all chambers attached to a seafloor substrate, may also be indicative of a higher energy marine setting. Similar abundance of *Amphistegina* was found previously in this area, just south of Mirs Bay, off High Island, by Yim and He (1991). Biofacies 4 falls within the least eutrophicated area in Hong Kong (according to the chlorophyll-*a* data; Fig. 9), which merits further investigation, since this region is seldom covered by Hong-Kong-wide benthic surveys (Wang *et al.* 2017), except for corals (Yeung *et al.* 2021). In corals, faunal composition is quite variable, and multiple biofacies are observed in Mirs Bay (Qiu *et al.* 2014), consistent with this biogeographical separation of benthic foraminifera in Mirs Bay (Fig. 8).

Conclusions

In this study we have shown the heightened sensitivity of benthic foraminifera to oligotrophic/eutrophic states, the presence of pollutants and heavy metals, and variation in water quality (e.g. turbidity) in Hong Kong waters. We identified four biofacies

including turbid, normal marine (Biofacies 1), polluted (Biofacies 2 and 3), and ‘pristine’ (i.e. least impacted) (Biofacies 4 in the Sørensen result) marine ecosystems (Fig. 8). Benthic ostracods may better represent faunal characteristics of soft-sediment benthos in general, since their biofacies distribution is similar to that of soft-sediment macrobenthos (Fig. 8) (Hong *et al.* 2022), but benthic foraminifera are more sensitive to changes in trophic conditions and also occur across a wider range of environmental condition than corals (Fig. 8). Corals are also sensitive to eutrophication, but cannot tolerate highly eutrophic environments and are often rare or absent where such conditions occur (Fig. 8). Thus, benthic foraminifera can be a good bioindicator that is applicable across the complete oligotrophic/eutrophic spectrum. Benthic foraminifera and ostracods are both shelled microscopic-sized organisms (called microfossils) that are abundant enough for quantitative faunal and diversity analyses using a small amount (e.g. 100 cm³, 50 cm³ or less) of sediment, and their shells are amenable to long-term storage of raw sediment samples without any fixation (especially if dried, refrigerated, or frozen). In addition, both groups have excellent fossil records (Yasuhara *et al.* 2017, 2020; Yasuhara 2019). Our foraminiferal results and their comparison with previous studies show that combined foraminiferal and ostracod analyses are an efficient way for holistically characterizing marine benthic environments and ecosystems in the past and present.

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Author contributions **BLM:** conceptualization (equal), data curation (equal), formal analysis (equal), investigation (equal), methodology (equal), project administration (equal), validation (equal), visualization (equal), writing – original draft (equal), writing – review & editing (supporting); **JDC:** conceptualization (supporting), data curation (supporting), formal analysis (supporting), investigation (equal), project administration (supporting), visualization (supporting), writing – original draft (supporting), writing – review & editing (supporting); **YH:** conceptualization (supporting), formal analysis (supporting), investigation (supporting), methodology (supporting), visualization (equal), writing – original draft (supporting), writing – review & editing (equal); **PGH:** conceptualization (supporting), investigation (supporting), writing – original draft (supporting), writing – review & editing (supporting); **AC:** conceptualization (supporting), methodology (equal), software (equal), visualization (supporting), writing – original draft (supporting), writing – review & editing (supporting); **AT:** data curation (supporting), formal analysis (supporting), investigation (supporting), methodology (supporting), validation (supporting), visualization (supporting), writing – original draft (supporting), writing – review & editing (supporting); **C-LW:** data curation (equal), formal analysis (lead), methodology (lead), software (equal), validation (supporting), visualization (lead), writing – original draft (supporting), writing – review & editing (supporting); **DMB:** conceptualization (supporting), funding acquisition (supporting), investigation (supporting), supervision (supporting), writing – original draft (supporting), writing – review & editing (supporting); **MY:** conceptualization (equal), data curation (supporting), formal analysis (equal), funding acquisition (lead), investigation (supporting), methodology (equal), project administration (equal), resources (equal), supervision (lead), validation (equal), visualization (supporting), writing – original draft (lead), writing – review & editing (lead).

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Data availability All data generated or analysed during this study are included in this published article (and its supplementary information files).

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