1 Reefal ostracod assemblages from the Zanzibar Archipelago (Tanzania)

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14 **Abstract**

15 Tropical reefs encompass tremendous biodiversity yet are imperiled by increasing
16 natural and anthropogenic disturbances worldwide. Meiobenthic biotas on coral reefs,
17 for example, ostracods, may experience substantial diversity loss and compositional
18 changes even before being examined. In this study, we investigated the reefal ostracod
19 assemblages from the highly diverse and productive ecosystem in the Zanzibar
20 Archipelago (Pemba, Zanzibar, and Mafia islands), Tanzania, to understand how their
21 diversity and faunal structure vary in response to water depth, benthic community type,
22 and human impacts. We characterized four distinct ostracod faunas associated with
23 different benthic habitats, which were deep fore reefs, shallow fringing reefs, degraded
24 fringing reefs, and algae-al covered intertidal flats. We identified typical ostracod
25 associations, i.e., Bairdiidae versus Loxoconchidae-Xestoleberididae, that showed
26 affinities to hard corals or algae on the reef platforms, respectively. Highest diversity
27 was found on shallow fringing reefs where coral-affinedreefal and algae-affinedalgal
28 taxa exhibited maximum overlap of their distributional ranges, while the sand flats,
29 mangrove, and marginal reefs within the intertidal zone had much lower diversity with
30 high dominance of euryhaline taxa. Along the western coast of Zanzibar Island, coastal
31 development likely resulted in a unique faunal composition and comparatively low
32 diversity of ostracod assemblages among those in reefal habitats, in conjunction with
33 overall reef ecosystem degradation. This study represents the first large-scale
34 assessment of shallow-marine ostracods in the Zanzibar Archipelago. It lays a solid

35 foundation for future research into the ecological significance of ostracods on coral

36 reefs.

37

38 **1 Introduction**

39 Coral reefs as the most diverse ecosystem in the marine realm hold great ecological and

40 economic values, yet our knowledge of its enormous biodiversity is far from complete.

41 Compared with well-studied, conspicuous macrofauna (Souza et al., 2023), meiofauna

42 on coral reefs are highly under-represented in current research despite being

43 ecologically essential components and contributing significantly to total biodiversity

44 (Leray and Knowlton, 2015; Plaisance et al., 2011). Ostracoda (Crustacea) among all

45 meio-benthos has a tight association with reef environments tracing back to the lower

46 Paleozoic (Whatley and Watson, 1988). It is considered As a useful model organism in

47 modern and paleo biodiversity research because of its high fossilization potential, high

48 abundance, and ubiquity in almost all marine ecosystems (Yasuhara et al., 2017).

49 However, ostracods on coral reefs are poorly understood. , Ddoes ostracod exhibit

50 higher diversity in reefal habitats compared with other soft sediment environments?

51 What are the characteristic ostracod taxa occupying different niches on coral reefs?

52 Answers to these questions are important for a holistic understanding of the reef

53 ecosystem and may hint at the underlying mechanisms that support such extraordinary

54 reef diversity. With intensifying anthropogenic disturbances at local to global scales,

55 the need to examine reefal ostracods before they perish is pressing.

56

57 Studies targeting tropical shallow-marine ostracods on coral reefs are surprisingly

58 deficient. Across the circumtropical belt, the central Indo-Pacific receives the most

59 attention for its diverse reefal ostracods, with pioneering studies identifying distinct

60 faunas associated with depth habitats from the shallow intertidal to deep reefal zones

61 (Whatley and Watson, 1988; Babinot and Degaugue-Michalski, 1996). Apart from

62 bathymetry, the distribution of reefal ostracods seems also related to benthic

63 community type (coral reefs versus seagrass/algal beds), sediment type (i.e., sandy

64 versus muddy deposits), in addition to local hydrology (i.e., exposure to wave energy)

65 (Weissleader et al., 1989; Whatley and Watson, 1988; Babinot and Degaugue-

66 Michalski, 1996; Tabuki, 1990, 1987). However, most of these works are confined to

67 small geographic areas and based on limited (sub)fossil materials. An extensive

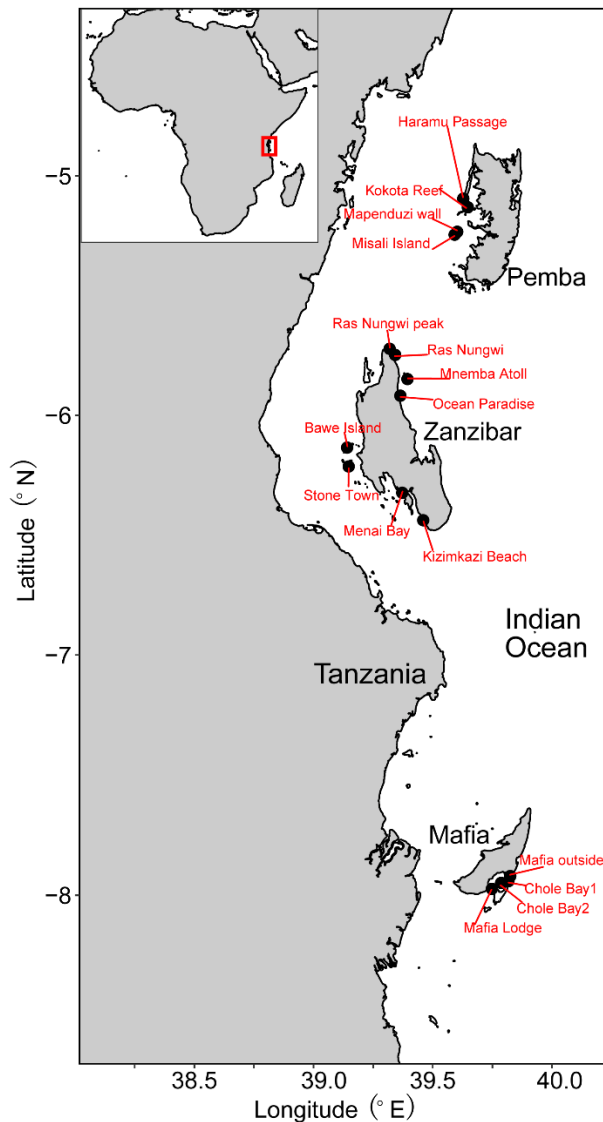
68 regional-scale survey of reefal ostracods has never been conducted. More importantly,

the focus of previous studies mainly revolved around taxonomy, and biogeography to a lesser degree, while quantitative assessments of biodiversity are largely lacking (Tabuki, 1987, 1990; Mostafawi et al., 2005). The highest species richness (S=74) was reported for a reef slope environment in Pulau Seribu, Java (Whatley and Watson, 1988) in contrast to much lower values at lagoons (S=27-42) (Babinot and Degaugue-Michalski, 1996; Weissleader et al., 1989) and reef flat (S=34) (Mostafawi et al., 2005).

Reefal ostracods are even less known in other tropical regions outside of the central Indo-Pacific. Along the eastern coast of Africa, where the reef ecosystem is productive and biodiverse, the only studies on ostracod assemblages are perhaps Hartmann (1974) and Jellinek (1993) that document more than 200 species inhabiting the algae facies and reefal facies across the littoral zone in Kenya. Here we present the first large-scale study on reefal ostracods from the Zanzibar Archipelago, Tanzania, a biodiversity hotspot of great conservation interests and vulnerability to increasing anthropogenic impacts (Grimsditch et al., 2009). We investigated the geographical structure of ostracod diversity and composition in relation to environmental habitats among three major islands of Pemba, Zanzibar, and Mafia. We compared the patterns with those of benthic foraminifera (Thissen and Langer, 2017) to explore complex environmental controls on the two groups of meio-benthos. This study is a major step towards better understanding of tropical shallow-marine ostracods in eastern Africa and provides valuable insight into the ostracod-reef association in general.

2 Regional setting

The Zanzibar Archipelago is located along the eastern coast of Tanzania in the Western Indian Ocean (Fig. 1) (Thissen and Langer, 2017). It belongs to the eastern African biogeographic province that stretches from Somalia to the northeastern coast of South Africa (Costello et al., 2017; Obura, 2012). The archipelago is strongly influenced by the warm, westward-flowing South Equatorial Current and the northward-flowing East African Coastal Current (Narayan et al., 2022). The western coastlines are more protected, with generally higher coral coverage, whereas the eastern coastlines are exposed to large physical disturbances and strong wave energy (Thissen and Langer, 2017). Tides there are semi-diurnal, with a maximum range of 4.5 m and a neap tidal range of 0.9 m (Thissen and Langer, 2017; Narayan et al., 2022). The islands possess a great variety of benthic habitats from the littoral to open-water zone, with mangroves,

103 vegetated sand flats, and reef complexes. Reefs are mainly fringing reefs that are
104 situated on the narrow continental shelf (Mafia, Zanzibar) or are separated from the
105 African mainland by the deep Pemba channel (Pemba) (Thissen and Langer, 2017).
106 Noticeably, the major islands are subject to very different degrees of human exploration,
107 as Zanzibar is densely populated and highly urbanized while Mafia and Pemba are
108 largely uninhabited (Narayan et al., 2022). Stone Town and Bawe, in particular, are
109 faced with a direct discharge of untreated domestic sewage along the western coast of
110 Zanzibar Island, where moderate levels of reef deterioration have been found with
111 diversity decrease and coral cover loss (Bravo et al., 2021; Larsen et al., 2023).
112 Although extensive long-term monitoring is still lacking, previous studies indicate that
113 the Pemba reefs are likely in pristine conditions with the highest coverage of live hard
114 corals, while the Zanzibar reefs are often dominated by dead corals intermingled with
115 algae and seagrass habitats (Ussi et al., 2019; Larsen et al., 2023; Grimsditch et al.,
116 2009). No quantitative assessment of reef health has been conducted in Mafia Island,
117 unfortunately, but our field observations suggested moderate to good conditions at our
118 sampling sites.

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120   Fig. 1. Locality map showing three major islands of the Zanzibar Archipelago with

121   sample sites.

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3 Materials and methods

124   3.1 Samples

125   26 surface sediment samples were collected from 16 sites during two field campaigns

126   in 2005 at the islands of Zanzibar and Pemba, and in 2012 at Mafia Island

127   (supplementary tTable 1). Depositional depths of all samples range from 0 to 42 m

128   across the intertidal and subtidal zones. The selected sampling sites cover all major

129   types of benthic habitats, including a nearshore mangroves, coastal sand flats, and

130   fringing-, fore-, and back-reefs (Table 1). Note that the mangrove habitat may be

131   underrepresented in current study as we have only one such site, however. Samples

132   were collected by SCUBA diving to scrape along the seabed and fill plastic containers

133 ~~bags~~ with surface sediments from the top 2 cm, in order to avoid the loss of finer

134 particles due to suspension.

135

136 Most sampling sites were fine to medium-grained carbonate-rich, bioclastic sands and

137 deposits with some reef rubble. Sediments were washed through a 63 μm sieve and

138 oven dried at 50 ℃. The residue was dry sieved over a 150 μm mesh sieve and ostracods

139 were picked from the >150 μm size fraction, because smaller individuals are usually

140 early juveniles that are not preserved and/or difficult to identify (Yasuhara et al., 2017).

141 ~~Sediment rich~~ Large volume samples were split into aliquot fractions using a

142 microsplitter. The sample materials were primarily death assemblages though a very

143 small number of specimens were preserved with soft parts (less than 1% among all

144 observed individuals), indicating they were alive at the time of collection. Both live and

145 dead specimens were included in the total count to represent time-averaged

146 assemblages, which method effectively defines reef habitats and provides general

147 environmental and diversity data useful in paleoecology (Glenn-Sullivan and Evans,

148 2001; Langer and Lipps, 2003). A single valve or a carapace was considered as one

149 individual, which is a standard counting method in ostracod research (Yasuhara et al.,

150 2017). Selected specimens were imaged using a Scanning Electron Microscope (SEM).

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156 Table 1. Ostracod assemblage information including raw species richness, number of

157 counted individuals, and abundance per gram sediment, in addition to a characterization

158 of benthic habitat in terms of sediment type and algae coverage in each location.

Sample	Species richness	No. individuals	Abundance (per g)	Habitat	Sediment type	Algae coverage
Haramu Passage20	37	69	1.645	fore reef	bioclastic sand	Low
Haramu Passage30	35	60	4.212	fore reef	bioclastic sand	Low
Kokota Reef25	64	235	4.176	fringing reef	bioclastic sand	Low
Kokota Reef16	78	364	50.845	fringing reef	bioclastic sand	Low
Mapenduzi wall40	60	235	37.337	fore reef	bioclastic sand	Low

Mapenduzi wall42	55	188	22.212	fore reef	bioclastic sand	Low
Misali Island20	65	254	29.480	fore reef	bioclastic sand	Low
Ras Nungwi peak12	56	296	14.775	fringing reef	bioclastic sand	Medium
Ras Nungwi peak12-14	46	116	7.635	fringing reef	bioclastic sand	Medium
Ras Nungwi peak20	81	311	67.845	fringing reef	bioclastic sand	Low
Ras Nungwi16	92	408	40.674	fringing reef	bioclastic sand	Medium
Ras Nungwi20	37	76	16.497	fringing reef	bioclastic sand	Low
Mnemba Atoll30	33	87	45.218	sand flat	bioclastic sand	Medium
Ocean Paradise3	46	231	57.750	back reef	bioclastic sand	High
Bawe Island9-30	80	410	102.015	fringing reef	bioclastic sand	High
Bawe Island grob	64	308	13.077	fringing reef	bioclastic sand	High
Stone Town12	77	519	176.291	fringing reef	bioclastic sand	High
Stone Town20	66	361	158.542	fringing reef	bioclastic sand	High
Menai Bay1	36	241	21.294	mangrove	fine-grained sand	High
Kizimkazi Beach1	24	59	27.949	sand flat	fine-grained sand	High
Mafia outside21	44	94	20.764	fore reef	bioclastic sand	Medium
Mafia outside20	82	347	96.657	fore reef	bioclastic sand	Medium
Chole Bay 1 (18-21)	27	74	3.664	bBack reef	bioclastic sand	Medium
Chole Bay 2 (15-18)	77	241	55.658	fringing reef	bioclastic sand	Medium
Chole Bay 2 (20)	72	281	69.383	fringing reef	bioclastic sand	Medium
Mafia Lodge (0-3)	62	397	65.576	fringing reef	fine-grained sand	High

159

160 3.2 Quantitative analysis

161 We used Hill numbers (i.e., the effective number of equally abundant species)

162 parameterized by a diversity order *q* to estimate ostracod diversity in each sample and

163 island (Hill, 1973). Hill numbers have several major advantages over other diversity

164 indices and are increasingly adopted by ecologists (Chao et al., 2020). For example, the

165 Hill numbers will double when combining two identically distributed but distinct

166 communities, so they obey the "doubling property" and behave like species richness

167 (Chao et al., 2014b). In other words, the unit of Hill numbers is also "species" and thus

168 is more ecologically meaningful than other traditional diversity indices. Also, the order

169   q of the Hill numbers controls the sensitivity of the diversity metric to species relative

170   abundance. When the order $q=0$, Hill number (^{0}D) reduces to species richness; when

171   the order $q=1$, Hill number (^{1}D) measures the diversity of the abundant species; when

172   the order $q=2$, Hill number (^{2}D) measures the diversity of dominant species (Chao et

173   al., 2014b). Therefore, besides species richness, the Hill numbers also estimate the

174   effective (or hypothetical) numbers of abundant and dominant species. Coincidentally,

175   the Hill numbers ^{1}D and ^{2}D are equivalent to the exponential of Shannon entropy and

176   Simpson index (hereafter referred to as Shannon and Simpson diversity), respectively

177   (Chao et al., 2014b), making them conceptually easy to understand by ecologists. To

178   make a fair comparison among multiple assemblages, we standardized the Hill numbers

179   with rarefaction or extrapolation to the largest sample completeness possible across

180   samples (82.5%) and across islands (98.6%) (Chao et al., 2020). The standard error and

181   95% confidence intervals of the Hill numbers were estimated by bootstrap resampling,

182   which was repeated 1000 times. Species evenness, $^{q}E_{3}(p) = (^{q}D - 1)/(S - 1)$, where ^{q}D

183   denotes Hill numbers of order q, and S denotes species richness, was quantified using

184   the continuous profiles of Hill numbers as functions of order q (Chao and Ricotta, 2019).

185   A gradual profile suggests a more even community in which the species richness and

186   number of abundant and dominant species are similar. In contrast, a steep profile

187   indicates an uneven community comprised of one or a few dominant species (Mamo et

188   al., 2023).

189

190   To distinguish biofacies associated with different benthic habitats, we conducted

191   hierarchical cluster analysis based on Ward's minimum variance and three Hill number-

192   based dissimilarity indices, including Sørensen ($q=0$), Horn ($q=1$), and Morisita-Horn

193   ($q=2$), to estimate the effective proportion of un-shared species in the ostracod

194   assemblages (Chao et al., 2014a). Similarly, the order q controls the sensitivity of the

195   Hill number-based dissimilarities to species relative abundance. While the classic

196   Sørensen dissimilarity is presence-absence based, the latter two indices are designed to

197   quantify the compositional dissimilarities of abundant and dominant species,

198   respectively. The Ward's algorithm is preferred for delineating biofacies because it

199   minimizes the error sum of squares within clusters and generates more balanced clusters.

200   The number of clusters was determined by considering both the structure of the

201   dendrograms and the average silhouette width, with a higher value indicating greater

202   cohesion and separation of clusters. We also performed a non-Metric Multidimensional

Scaling (nMDS) to visualize and summarize faunal similarities among ostracod assemblages in two-dimensional space. Stress values were calculated to quantitatively weigh the 'goodness of fit' between the original input data matrix and the ultrametric matrix of the resultant nMDS scatter plots (Hong et al., 2022; Kruskal, 1964). We used a compositional heat map to illustrate the relationships between samples by Horn dissimilarities and between species by Hellenger distances.

All analyses were implemented in RStudio. We used the package '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, 2020).

4 Results

4. 1 Diversity

A total of 6262 ostracods were recovered from 26 samples at 16 locations around the Zanzibar Archipelago. They represent remarkably diverse ostracod assemblages comprised of 235 species under 77 genera. Exceedingly high abundance was found at Stone Town, while sites at Bawe Island and Mafia outside were also abundant, in contrast to the lowest abundance at Haramu Passage and Chole Bay 1 (Table 1). Considering the alpha diversity of individual sample as measured by Hill number of different order q, the spatial diversity patterns were relatively consistent for rare (i.e., species richness, ^{0}D) and abundant (^{1}D) species. The highest values were recorded for fringing reefs at Chole Bay 2 and Ras Nungwi, followed by fringing reefs at Mafia outside and Ras Nungwi peak (Figs. 2A, 3A-B2A, 3, S1-S2). Moderately high levels of diversity were observed at fore reef sites in Pemba Island and fringing reefs at Bawe, Stone Town, and Mafia Lodge. In terms of the diversity of dominant (^{2}D) species, there was a more homogenous distribution with similarly high values found at various fringing and fore reefs, including Chole Bay 2, Mafia outside, Haramu Passage, Bawe Island, Ras Nungwi and Ras Nungwi peak (Figs. 2A, 3C). All remaining localities (Chole Bay 1, Mnemba Atoll, Ocean Paradise and Kizimkazi Beach) characterized by sand flat and back reef habitats had consistently low diversity across all order q, especially Menai Bay that was lined with mangrove stands (Figs. 2A, 3). Evenness was highest at Haramu Passage and lowest at Menai Bay for both orders $q=1$ and $q=2$ (Figs. 2B, S13). With respect to the gamma diversity of each island, Mafia and Zanzibar were

237 almost equally diverse across all order *q,* while Pemba had significantly lower diversity

238 for abundant and dominant species (Figs. 2C, S24).

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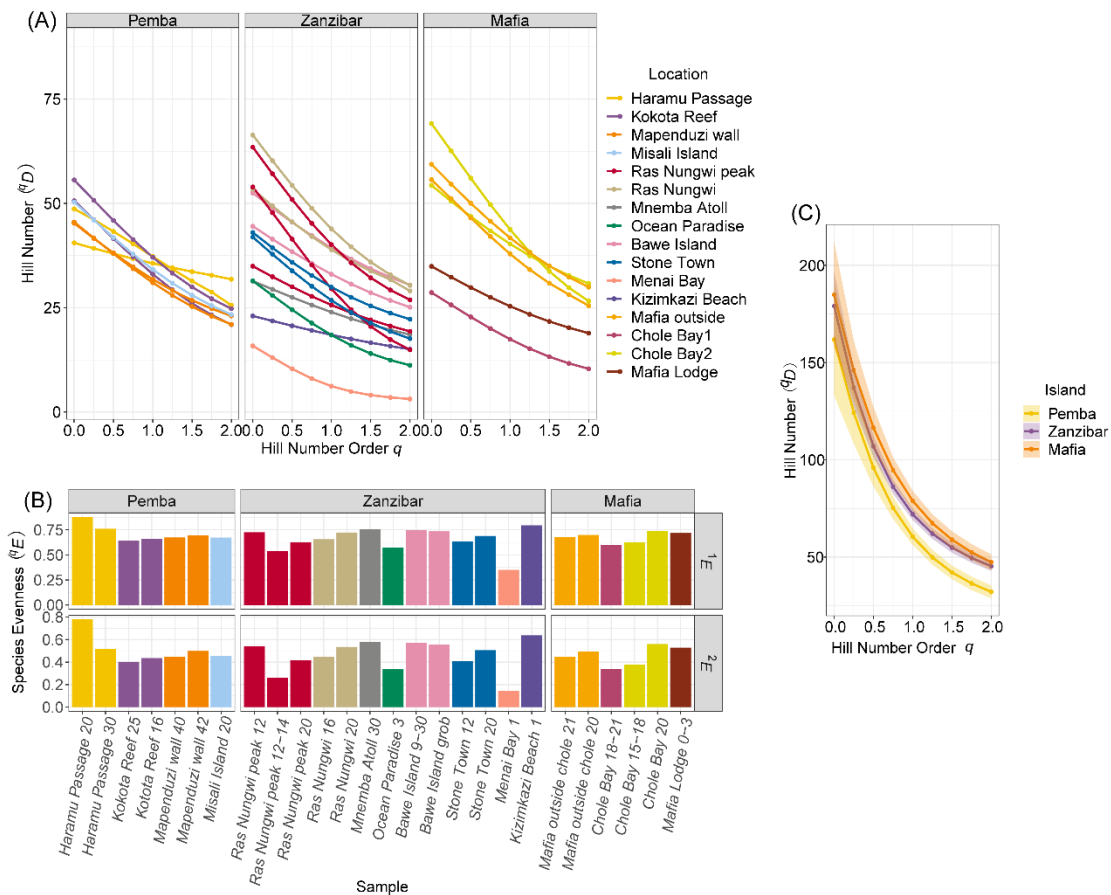
241 Fig. 2. Diversity results of the Zanzibar Archipelago ostracods. (A) Alpha diversity of

242 each sample shown by Hill number profile based on 82.5% sample coverage. The

243 overall elevation of the profile indicates the diversity based on hill number across

244 different order *q.* The levelness of the line indicates species evenness of the assemblage,

245 because a complete leveled diversity profile would suggest that the numbers of total,

246 common and dominant species are all the same. (B) Evenness of each sample as the

247 normalized slope of Hill number profile for order *q*=1 and *q*=2 based on 82.5% sample

248 coverage. (C) Gamma diversity of each island shown by Hill number profile based on

249 98.6% sample coverage. The shade area shows 95% confidence interval of the profile.

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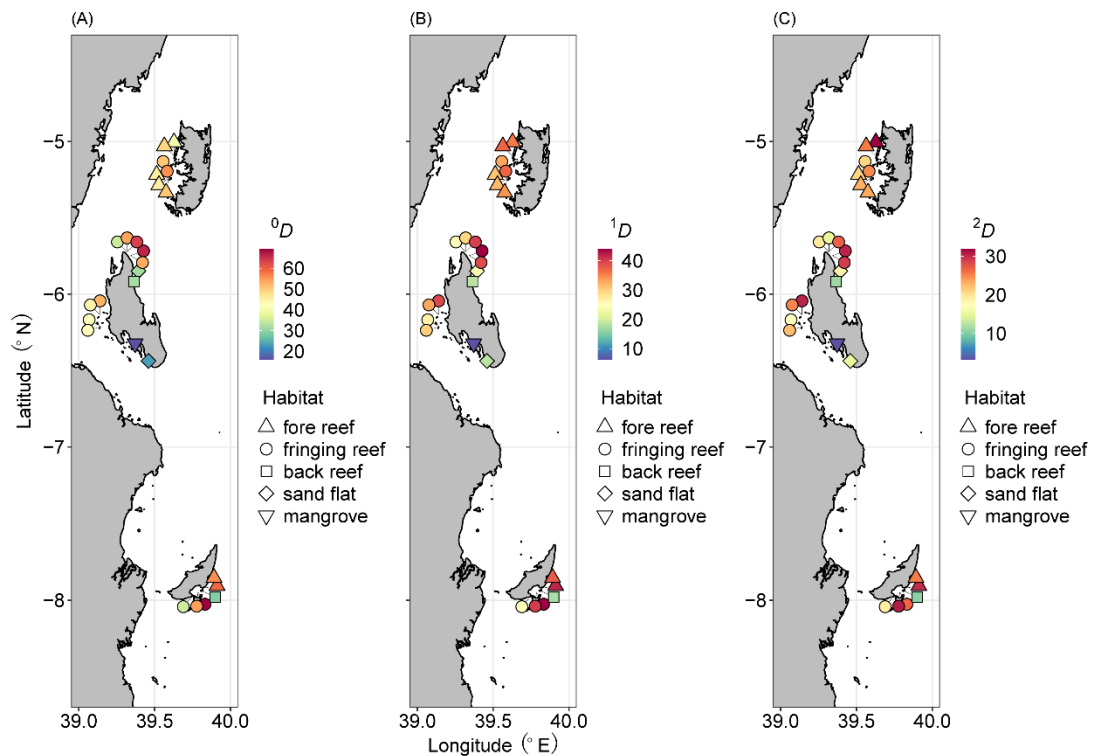
Fig. 3. Diversity maps of the Zanzibar archipelago ostracod. Distributions of Hill numbers ^{0}D (A: $q = 0$, species richness), ^{1}D (B: $q = 1$, exponential Shannon), and ^{2}D (C: $q = 2$, inversed Simpson). We used 82.5% sample coverage to standardize the Hill number estimates. Diversity and habitat are represented by color and shape as in the legends, respectively. ~~Diversity maps of Zanzibar archipelago ostracod. Distributions of Hill numbers ^{0}D (A: $q = 0$, species richness), ^{1}D (B: $q = 1$, exponential Shannon), and ^{2}D (C: $q = 2$, inversed Simpson). We used 82.5% sample coverage to standardize the Hill number estimates. Diversity and habitat are represented by color and shape as in the legends, respectively.~~

4.2 Multivariate analysis

First, cluster analyses based on Sørensen, Horn, and Morisita-Horn dissimilarities delineated biofacies considering faunal composition in terms of species occurrence, relative abundance of abundant species, and relative abundance of dominant species, respectively. The greatest average silhouette width suggested the division of samples into ten clusters for all three dissimilarity measures; however, it is beyond interpretable to have too many clusters, given the size of our dataset. We, therefore, referred to the structure of the dendrograms based on three dissimilarity measures to determine the

271   optimum number of clusters to be four (Fig. S3̲5̶). The NMDS results showed a clear

272   separation of four biofacies based on Horn and Morisita-Horn dissimilarities, but not

273   Sørensen dissimilarity, which was calculated with a relatively high stress value (0.26)

274   (Fig. S4̲4̶). Ostracod faunas in Pemba Island constituted a distinct group across all levels

275   of faunal composition from presence/absence to relative abundance (Biofacies 1; Fig.̲

276   4̲.̲ 5̶). Ras Nungwi, Ras Nungwi peak, and nearby Menemba Atoll were congregated

277   with different sites around Zanzibar and Mafia in Biofacies 2, including Mafia outside

278   and Chole Bay 2 in Sørensen, Mafia outside, Chole Bay 1 and Chole Bay 2 in Horn,

279   Ocean Paradise, Kizimkazi Beach and Mafia Lodge in Morisita-Horn analysis (Fig. 4̲5̶).

280   Samples assigned to Biofacies 3 and 4 strongly varied depending on the dissimilarity

281   matrix used, indicating these biofacies have different ecological meaning among three

282   cluster analyses ̲(̲F̲i̲g̲.̲ ̲4̲)̲. Specifically, they scattered around the entire Zanzibar Island

283   based on Sørensen dissimilarity. Biofacies 4 was distributed along the western coast of

284   Zanzibar, including Stone Town and Bawe, and Biofacies 3 covered the remaining

285   Zanzibar locations (Menai Bay, Ocean Paradise and Kizimkazi Beach) in addition to

286   Mafia Lodge based on Horn dissimilarity. On the other hand, when Morisita-Horn

287   dissimilarity was applied, Menai Bay was different from all other sites as a distinctive

288   Biofacies 3 while most Mafia sites (Mafia outside, Chole Bay 1, and Chole Bay 2)

289   aggregated in Biofacies 4. Considering the performance of multivariate analyses to

290   reflect and interpret biological patterns, we think that cluster and NMDS results based

291   on Horn dissimilarity most reasonably captured the underlying ecological significance

292   of reefal versus non-reefal facies as determined by benthic community, depth, and

293   possibly anthropogenic disturbances (see the Discussion section). We therefore focus

294   on the four biofacies as divided by Horn-based analysis to scrutinize their diversity and

295   compositional structure in relation to a set of environmental variables.

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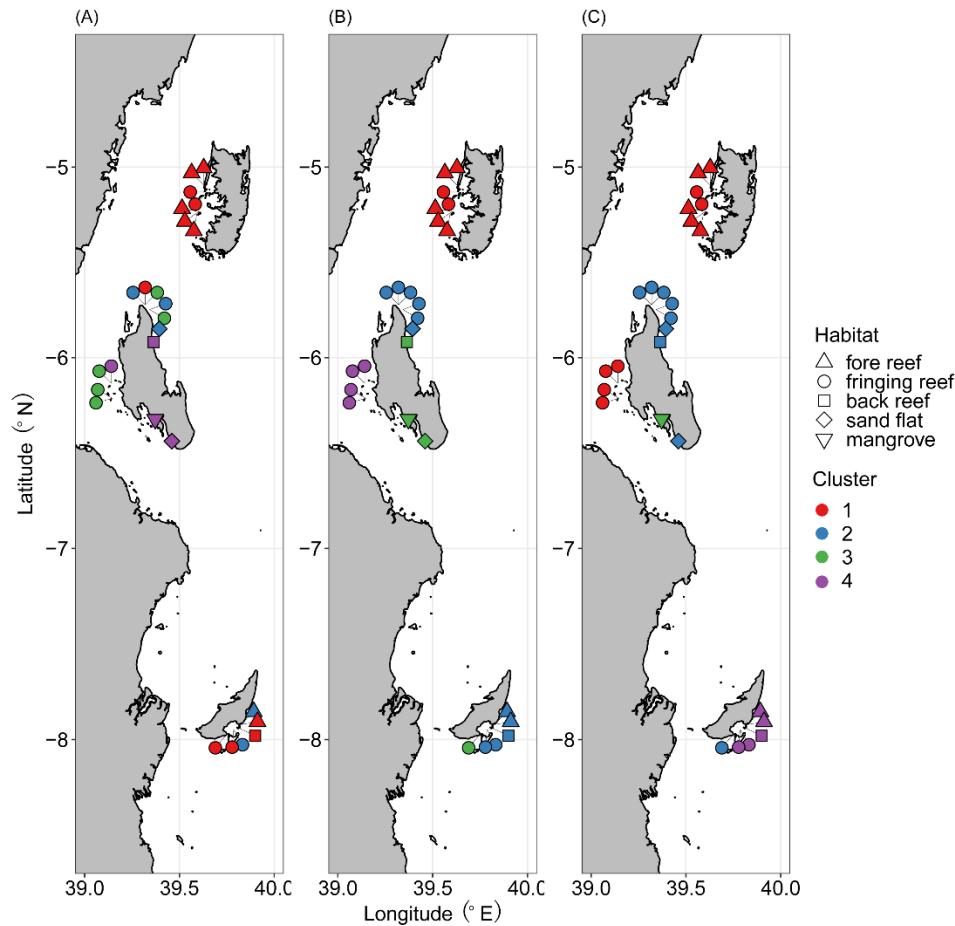
Fig. 45. Distribution of ostracod Biofacies 1-4 based on (A) Søensen, (B) Horn, and (C) Morisita-Horn dissimilarities and Ward's minimum variance cluster analysis. Note that the color schemes are independent among panels; thus, the biofacies based on different dissimilarities are unrelated. Cluster and habitat are represented by color and shape as in the legends, respectively.

Each biofacies based on Horn dissimilarity index was demonstrated with the top 10 species of highest mean relative abundance as shown in Table 2 and Figure 5s 6 8. Noticeably, the Pemba fauna in Biofacies 1 was dominated by genus *Neonesidea* (*N.* cf. *crepidula* and *N. schulzi*) and *Bosasella* (*B. profunda* and *B. elongate*), together with *Paracytheridea tschoppi* (Fig. 69; Table 2). Biofacies 2 included the most diverse sites in Zanzibar and Mafia, which all shared similar faunal structures with a high abundance of *Loxocorniculum* sp. 2, *Xestoleberis rotunda, Paracytheridea albatros* and *Loxoconcha* sp. 3. Biofacies 3 composed of low-diversity sites in Zanzibar and Mafia was distinguished by highly abundant *Perissocytheridea estuaria* sp.1, *Xestoleberis hanaii*, as well as three *Loxoconcha* species (*L.* sp. 3, *L. ghardaqensis* and *L.*

315 *lilljeborgii*). Finally, the faunal structure of Biofacies 4 in western Zanzibar showed

316 some similarities to that of Biofacies 1 in Pemba with many common species, however,

317 they clearly differed by the dominance of *Xestoleberis hanaii* and *Patrizia*

318 *nucleuspersici* in Biofacies 4.

319

320 Table 2. List of top 10 species of highest % mean relative abundance for Biofacies 1-4

321 based on Horn dissimilarity.

Species	Biofacies1	Biofacies2	Biofacies3	Biofacies4
Neonesidea cf. *crepidula*	0.085857	NA	NA	NA
Bosasella profunda	0.079436	NA	NA	0.040846
Neonesidea schulzi	0.075285	0.032551	0.024322	0.041291
Paracytheridea tschoppi	0.035779	NA	NA	0.028826
Loxocorniculum sp. 2	0.030562	0.063399	NA	NA
Xestoleberis hanaii	0.028593	0.039954	0.084378	0.071834
Patrizia nucleuspersici	0.02842	NA	NA	0.057965
Paranesidea cf. *spongicola*	0.026203	NA	NA	0.029754
Xestoleberis sp. 1	0.023801	NA	NA	NA
Bosasella elongata	0.023369	NA	0.017579	NA
Xestoleberis rotunda	NA	0.061861	NA	NA
Paracytheridea albatros	NA	0.045056	0.037464	NA
Loxoconcha sp. 3	NA	0.041327	0.110386	NA
Bosasella sp. 1	NA	0.040122	NA	NA
Macrocyprina maddocksae	NA	0.039264	NA	NA
Caudites exmouthensis	NA	0.027832	NA	NA
Paranesidea sp. 1	NA	0.025497	NA	NA
Perissocytheridea *estuaria* ~~sp.1~~	NA	NA	0.157932	NA
Loxoconcha ghardaqensis	NA	NA	0.073153	NA
Hiltermannicythere rubrimaris	NA	NA	0.04805	NA
Loxoconcha lilljeborgii	NA	NA	0.033061	NA
Neohornibrookella lactea	NA	NA	0.018616	NA
Neonesidea sp. 3	NA	NA	NA	0.048331
Neonesidea paiki	NA	NA	NA	0.042016
Loxoconcha cf. *gisellae*	NA	NA	NA	0.035319
Perissocytheridea? sp. 2	NA	NA	NA	0.029391

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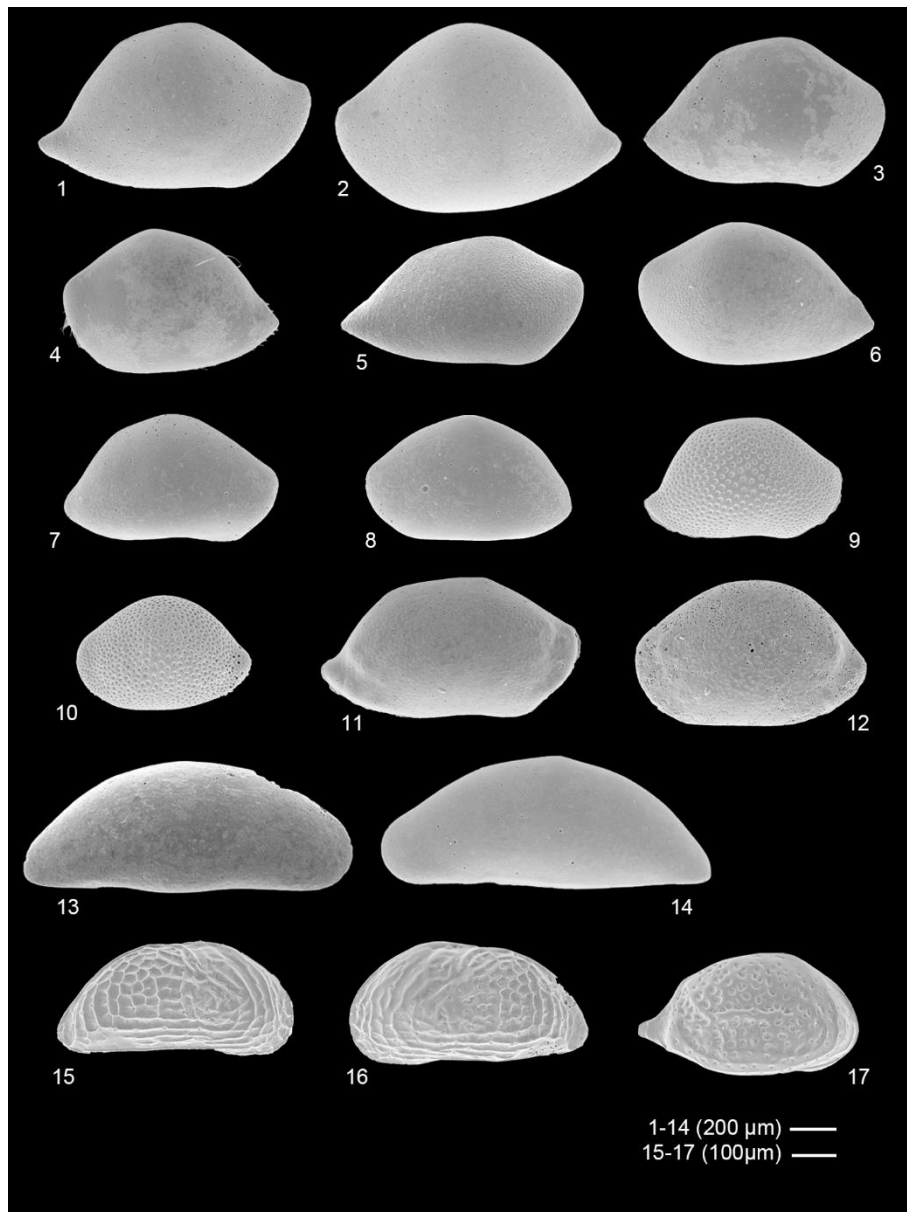


Fig. 56. Scanning electron microscopy images of the top 10 ostracod species of highest % mean relative abundance for Biofacies 1-4 based on Horn dissimilarity. **1**, *Neonesidea* cf. *crepidula*, RV, Kokota reef25; **2**, *Neonesidea* cf. *crepidula*, LV, Haramu Passage30; **3**, *Neonesidea paiki*, RV, Bawe island9-30; **4**, *Neonesidea paiki*, LV, Kokota reef25; **5**, *Neonesidea schulzi*, RV, Mapenduzi wall42; **6**, *Neonesidea schulzi*, LV, Kokota reef25; **7**, *Neonesidea* sp. 3, RV, Bawe island9-30; **8**, *Neonesidea* sp. 3, LV, Bawe island9-30; **9**, *Paranesidea* cf. *spongicola*, RV, Bawe island9-30; **10**, *Paranesidea* cf. *spongicola*, LV, Kokota reef25; **11**, *Paranesidea* sp. 1, RV, Chole bay18-21; **12**, *Paranesidea* sp. 1, LV, Chole bay18-21; **13**, *Macrocyprina maddocksae*, RV, Haramu Passage20; **14**, *Macrocyprina maddocksae*, LV, Kotota reef16; **15**, *Perissocytheridea estuaria*sp.1, RV, Menai bay1; **16**, *Perissocytheridea estuaria*sp.1,

LV, Menai bay1; **17**, *Perissocytheridea*? sp. 2, RV, Bawe island grob. All adults and
lateral views.

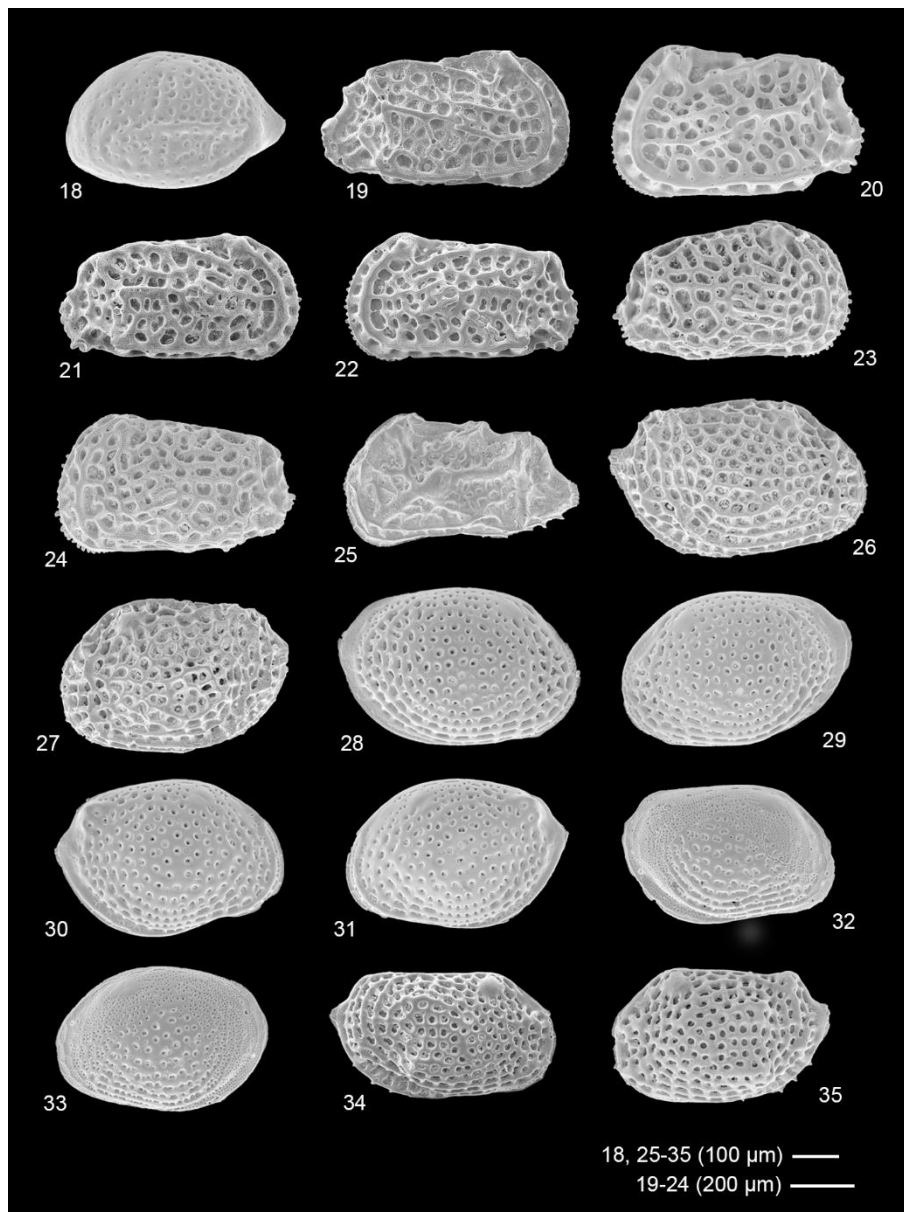



Fig. 57. Continued. ~~Scanning electron microscopy images of the top 10 ostracod species of highest % mean relative abundance for Biofacies 1-4 based on Horn dissimilarity.~~ **18**, *Perissocytheridea*? sp. 2, LV, Bawe island9-30; **192**, *Bosasella elongate*, RV, Haramu Passage30; **203**, *Bosasella elongate*, LV, Mapenduzi wall42; **214**, *Bosasella profunda*, RV, Haramu Passage20; **225**, *Bosasella profunda*, LV, Mapenduzi wall42; **236**, *Bosasella* sp. 1, RV, Kokota reef25; **247**, *Bosasella* sp. 1, LV, Kotota reef16; **258**, *Caudites exmouthensis*, LV, RusNungwi16; **269**, *Loxoconcha ghardaqensis*, RV, Mnemba atoll30; **2710**, *Loxoconcha ghardaqensis*, LV, Ras

Nungwi peak12; **28**11, *Loxoconcha* cf. *gisellae*, RV, Bawe island9-30; **29**12, *Loxoconcha* cf. *gisellae*, LV, Bawe island9-30; **30**13, *Loxoconcha lilljeborgii*, RV, Bawe island9-30; **31**14, *Loxoconcha lilljeborgii*, LV, Bawe island grob; **32**15, *Loxoconcha* sp. 3, RV, Stone town20; **33**16, *Loxoconcha* sp. 3, LV, Stone town20; **34**17, *Loxocorniculum* sp. 2, RV, Haramu Passage30; **35**18, *Loxocorniculum* sp. 2, LV, Kotota reef16. All adults and lateral views.

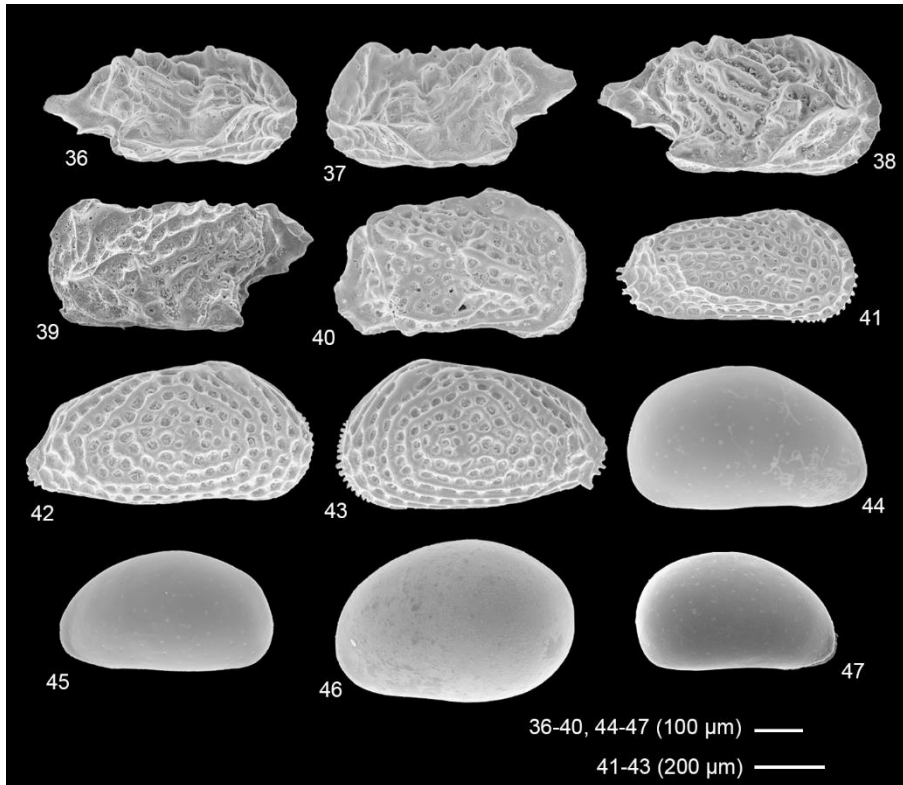
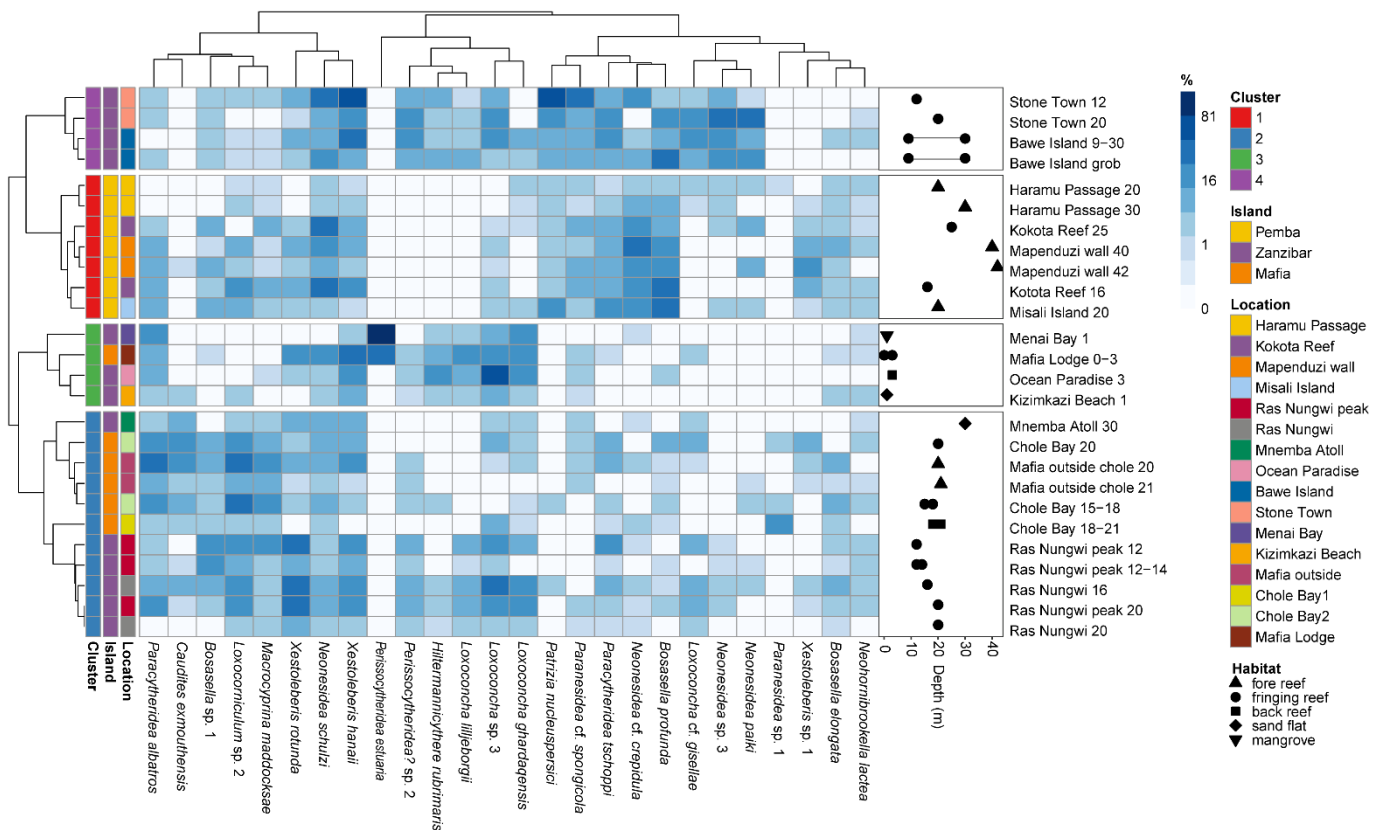



Fig. 58. Continued. ~~Scanning electron microscopy images of the top 10 ostracod species of highest % mean relative abundance for Biofacies 1-4 based on Horn dissimilarity.~~ **36**1, *Paracytheridea albatross*, RV, Kokota reef25; **37**2, *Paracytheridea albatross*, LV, Kotota reef16; **38**, *Paracytheridea tschoppi*, RV, Kokota reef25; **39**4, *Paracytheridea tschoppi*, LV, Mapenduzi wall42; **40**5, *Neohornibrookella lactea*, RV, Misali island20; **41**6, *Hiltermannicythere rubrimaris*, RV, Stone town20; **42**7, *Patrizia nucleuspersici*, RV, Stone town20; **43**8, *Patrizia nucleuspersici*, LV, Stone town12; **44**9, *Xestoleberis hanaii*, RV, Bawe island9-30; **45**10, *Xestoleberis hanaii*, LV, Kokota reef25; **46**11, *Xestoleberis rotunda*, LV, Ras Nungwi peak12; **47**12, *Xestoleberis* sp. 1, RV, Mapenduzi wall42. All adults and lateral views.

366

367 Fig. 69. Dendrograms based on Horn dissimilarity between samples and Hellenger

368 distances between top 10 species of highest mean relative abundance in each cluster.

369 The blue heatmap indicates the relative (%) abundance of each species in each sample.

370 The side panel shows water depth and habitat type of each sample (note that several

371 samples are shown by their corresponding depth ranges).

372

373 **5 Discussion**

374 Through Hill number profile and multivariate analyses, we quantified a highly diverse

375 ostracod fauna in the Zanzibar Archipelago composed of four distinct biofacies. The

376 delineation of biofacies varied considerably depending on the dissimilarity matrix used,

377 indicating inconsistent faunal structures across different levels of species information

378 from occurrence to relative abundance (Fig. 45). In terms of the presence/absence of

379 species (Sørensen dissimilarity), all Pemba sites united in Biofacies 1 but the

380 assignment of Zanzibar and Mafia sites into Biofacies 1-4 seemingly conformed to a

381 noisy pattern (Fig. 4A). Accordingly, four biofacies intersected with each other in

382 nMDS space with relatively high stress value (Fig. S4A). A possible explanation is that

383 the occurrence of individual species may be homogenous among sites in similar

384 environmental conditions within a finite geographic region. Many species are likely to

385   be ubiquitous across the entire neritic zone despite showing certain ecological

386   preferences, and the redeposition processes may further facilitate the mixing of death

387   assemblages to blur the spatial signal at a local scale (Frenzel and Boomer, 2005).

388   Consequently, species presence in all available habitats may translate to considerable

389   faunal similarities among biofacies as measured by Sørensen index. When considering

390   the composition of abundant species (Horn dissimilarity) (Figs. 4B ~~and 5B~~), the

391   identification of four biofacies instead reflected significant changes in ostracod

392   assemblages along two important environmental gradients, which are benthic

393   community type and water depth. Specifically, Biofacies 1 and 2 characterize typical

394   fore reefs in deep subtidal (sampling depth 16-42 m) and fringing reefs in shallow

395   subtidal (12-30 m), respectively (Fig. 6~~9~~). Biofacies 3 indicates intertidal habitats with

396   plant cover (0-3~~0~~ m), and finally Biofacies 4 features degraded fringing reefs in shallow

397   subtidal (9-30 m) (see discussion below).

398

399   We summarized the ecological preferences of dominant genera in each biofacies based

400   on Horn dissimilarity (Table 3 and Fig. 6~~9~~) and investigated how key environmental

401   factors (benthic community type, water depth, and anthropogenic disturbance) may

402   control the distribution and diversity of reefal ostracod assemblages. First of all,

403   *Neonesidea* and *Paranesidea* (family Bairdiidae) are typical reefal genera that reach

404   their maximum diversity and incidence on reefs and reef-associated habitats in tropical

405   shallow-marine environments (Whatley and Watson, 1988; Maddocks, 2013; Titterton

406   and Whatley, 1988). Their dominance in Biofacies 1 is consistent with our background

407   understanding that the Pemba reefs were pristine and healthy (Ussi et al., 2019;

408   Grimsditch et al., 2009). However, it should be noted that individual species of these

409   genera likely have different environmental tolerance. For example, *N.* cf. *crepidula*

410   were restricted to Biofacies 1 while *N. schulzi* were widespread among four biofacies

411   inhabiting both reef and algae habitats (Fig. 6~~9~~) (Mostafawi et al., 2005). *Bosasella* as

412   another prominent component of Biofacies 1 is also known to occur on coral reefs in

413   the western Indian Ocean (Munef et al., 2012; Jellinek, 1993). *Paracytheridea* and

414   *Caudites* on the other hand are loosely categorized as reefal genera, as their dominance

415   on coral reefs was reported but not studied in detail (Whatley and Watson, 1988; Keyser

416   and Mohammed, 2021). In this study, they were common on fore- and fringing-reefs in

417   Biofacies 1 and 2 (Fig. 6~~9~~). *Loxoconcha* and *Loxocorniculum* (family Loxoconchidae)

418   as two phylogenetically related and ecologically similar genera exhibited ubiquitous

distribution around the Zanzibar Archipelago with highest relative abundance in Biofacies 3 followed by Biofacies 2. As generalists, they thrive on a wide variety of benthic habitats across the neritic zone and show affinities to plant substrates (algae and seagrass beds) in particular (Munef et al., 2012; Keyser and Mohammed, 2021; Kamiya, 1988). The ecology of *Xestoleberis* is very similar to that of Loxoconchidae, living both on coral reefs and algal flats (Keyser and Mohammed, 2021; Munef et al., 2012; Whatley and Watson, 1988; Kamiya, 1988). This genus was almost equally weighted in all biofacies, although individual species clearly preferred different environments, as *X. hanaii* prevailed in Biofacies 3 and 4 while *X. rotunda* only in Biofacies 2 (Fig. 69). *Patrizia* is documented as a reefal genus in lower littoral zone along the eastern coast of tropical Africa (Jellinek, 1993). It dominated the relatively deep fringing-reef faunas of Biofacies 4, which were subject to sewage-derived nutrient and trace metal pollution from the Zanzibar Town (Narayan et al., 2022; Bravo et al., 2021). Different from all the above-discussed genera, *Hiltermannicythere* and *Perissocytheridea* are restricted to shallow intertidal environments as phytal and sediment-dwelling taxa, respectively (Jellinek, 1993), which explains their abundance in our Biofacies 3. *Perissocytheridea* is especially considered a bioindicator of brackish water facies, adapting to euryhaline conditions (Nogueira and Ramos, 2016; Keyser, 1977). Furthermore, we revealed a more generalized pattern of the compositional differences among biofacies with the top 5 families of highest mean relative abundance in each biofacies (Fig. 710).

Table 3. Autoecology summary of important ostracod genera.

Genus	Predominant habitats	References
Neonesidea	Coral reef	Whatley and Watson (1988); Maddocks (2013); Titterton and Whatley (1988); Maddocks (1969)
Paranesidea	Coral reef	Titterton and Whatley (1988); Whatley and Watson (1988); Maddocks (1969)
Bosasella	Coral reef	Munef et al. (2012)
Loxoconcha	Algal mat and reef	Keyser and Mohammed (2021); Whatley and Watson (1988); Munef et al. (2012); Kamiya (1988)
Loxocorniculum	Algal mat and reef	Munef et al. (2012); Kamiya (1988)
Xestoleberis	Algal mat and reef	Keyser and Mohammed (2021); Whatley and Watson (1988); Munef et al. (2012); Kamiya (1988)
Patrizia	Coral reef	Jellinek (1993)

Hiltermannicythere	Intertidal algal mat	Jellinek (1993); Keyser and Mohammed (2021)
Paracytheridea	Coral reef	Whatley and Watson (1988)
Caudites	Coral reef	Whatley and Watson (1988); Keyser and Mohammed (2021)
Perissocytheridea	Intertidal sand flat, euryhaline~~brackish water~~	Nogueira and Ramos (2016); Keyser (1977)

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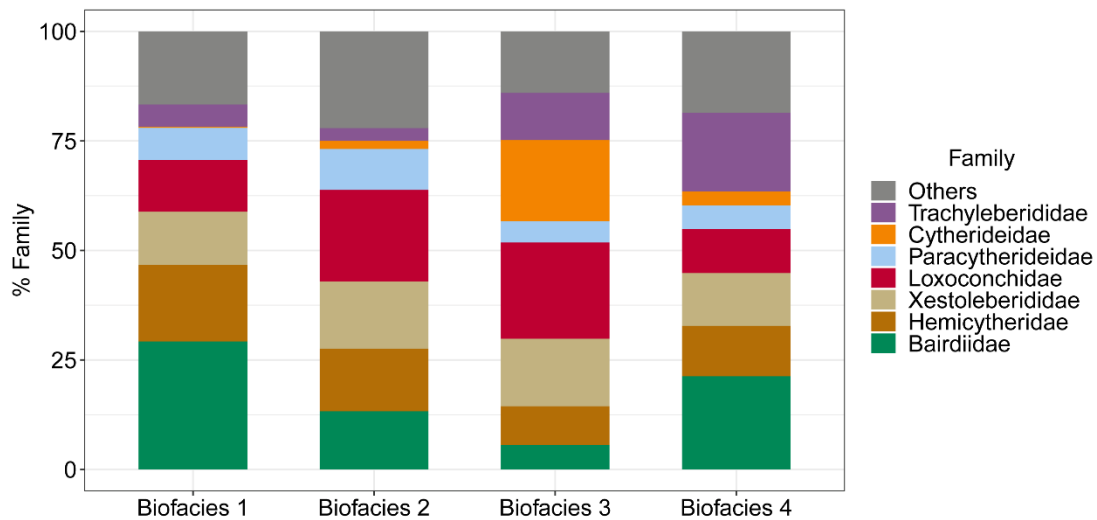


Fig. 7~~10~~. Family composition of Biofacies 1-4 based on Horn dissimilarity. The top 5 families of the highest % relative abundance in each biofacies are shown.

446

Thus, our study indicates that the distribution of shallow-marine ostracods in the ~~the~~ Zanzibar Archipelago is characterized by three reefal facies and one intertidal facies. Yet slight differences in bathymetry, benthic community type, and anthropogenic impacts likely contributed to subtle faunal changes among the reefal Biofacies 1, 2, and 4. The fore reefs in Pemba (Biofacies 1) were deepest with high incidence and diversity of live hard corals (Gavrilets and Losos, 2009; Ussi et al., 2019), which accounted for the definite dominance of ostracod reefal taxa (Bairdiidae and *Bosasella*) over algal taxa (Loxoconchidae and Xestoleberididae) (Figs. 6~~9~~-7~~10~~). Moderately high levels of diversity in terms of rare, abundant, and dominant species were observed for these ostracod assemblages (Fig.~~s. 2~~ 3). The Pemba reefs are thereby considered the most mature and authentic reef ecosystem, serving as a natural reference for comparing with other sites. The fringing-reef fauna of western Zanzibar (Stone Town and Bawe, Biofacies 4) exhibited certain similarities with the Pemba fauna as indicated by the

prevalence of *Bosasella profunda*, *Paracytheridea tschoppi*, and *Paranesidea* cf. *spongicola* in both facies (Fig. 6~~9~~). Indeed, they were grouped together based on the composition of dominant species (Morisita-Horn analysis) (Fig. 4~~5~~C). Faunal similarities between Pemba and Stone Town make sense as they are in comparable baseline conditions of water depths and hydrology along the protected western coast of the Zanzibar Archipelago, in contrast to Ras Nungwi and Chole Bay that are exposed to oceanic disturbances from the east (Fig. 1). However, Biofacies 4 was differentiated from Biofacies 1 by the dominance of *Patrizia* in conjunction with the absence of *Neonesidea* cf. *crepidula*. It also had the highest relative abundance of Trachyleberididae genera among all facies (Fig. 7~~10~~), for example, *Adencythere*, *Strobilocythere, Bradyon,* and *Actinocythereis*, but their ecologies are not well understood. Stressful environmental conditions in terms of overexploitation, tourism and coastal pollution offer the most possible explanation for such a unique faunal composition and comparatively low diversity of Biofacies 4 (Fig. s. 3 ~~2 3~~) (Bravo et al., 2021; Larsen et al., 2023). Consistently, foraminifera and coral surveys indicated early stages of reef degradation there (Narayan et al., 2022; Bravo et al., 2021; Thissen and Langer, 2017) It is possible that ongoing anthropogenic disturbances near the Stone Town will eventually exceed the critical threshold levels to cause more pronounced changes in ostracod faunal structures in terms of dominant species through a shift in benthic habitat (Narayan et al., 2022; Hong et al., 2022). Other than Biofacies 1 and 4, Biofacies 2 mostly represented a different type of relatively shallow (12-20 m) fringing-back reef ~~reefal~~ habitats of Ras Nungwi, Chole Bay, and Mafia outside, in addition to a deeper (30 m) sand flat of Mnemba Atoll ~~, and Mnemba Atoll~~ (Fig. 6~~5B~~). Algal taxa (Loxoconchidae and Xestoleberididae) and reefal taxa (Bairdiidae, *Bosasella*, *Paracytheridea*, and *Caudites*) reached equally high levels of relative abundance there (Figs. 6~~9~~-7~~10~~). ~~Most sites in Biofacies 2 were relatively shallow (12-21 m) except for Mnemba Atoll (30 m), and they covered the transitional zone from intertidal sandy bottom to subtidal true reefs.~~ Microhabitats on the reef platforms of Biofacies 2 are believed to be diverse and heterogenous with interlaced live and dead corals, algae and seagrass, calcareous sands, as well as bare substrate rock (Ussi et al., 2019; Larsen et al., 2023), which facilitated the coexistence of reefal and algal ostracods and consequently the highest diversity of local assemblages (Fig. s. 3~~2 3~~). The remaining Biofacies 3 corresponded to the shallowest intertidal habitats with various benthic communities, including a marginal back reef, a marginal fringing reef, a sand flat, and

494 a mangrove (Fig. 65B). Typical reefal taxa (Bairdiidae and *Bosasella*) dropped to their
495 lowest relative abundance in this facies, replaced by large numbers of Loxoconchidae,
496 *Perissocytheridea,* and *Hiltermannicythere* that well adapted to shallow euryhaline
497 conditions (Figs. 69-710). Not surprisingly, the diversity of Biofacies 3 was much lower
498 than that of open-ocean reefal facies, as drastic changes in temperature, salinity,
499 dissolved oxygen, and wave energy in the intertidal zone may be too challenging for
500 many marine taxa (Fig. s. 32 3) (Morley and Hayward, 2007; Frenzel and Boomer,
501 2005). The mangrove habitat at Menai Bay was unique concerning the absolute
502 dominance of *Perissocytheridea* in line with its lowest diversity and evenness (Figs.
503 2B, 3 2 3). It indeed constituted an independent biofacies based on Morisita-Horn
504 analysis (Fig. 45C).

505

506 The division scheme of four biofacies based on Horn dissimilarity explicitly revealed
507 spatial patterns of ostracod distribution in aspect of diversity and composition, as
508 discussed above. Our results are generally concordant with a previous study on benthic
509 foraminifera, which separated six clusters of Pemba, Stone Town, Mafia Bay, Ras
510 Nungwi, Mnemba Atoll, and Menai Bay, respectively (Fig. 811B) (Thissen and Langer,
511 2017). Each of these foraminifera clusters corresponded to major habitat types, as
512 argued by the authors (Thissen and Langer, 2017), and we accordingly pointed out the
513 consistent role of habitat factors in shaping the biogeography of both ostracod and
514 foraminifera biotas. However, the diversity patterns of these two groups were
515 apparently different among reefal habitats (Figs. 3, 811A). High, moderate, and low
516 levels of diversity were recorded on fore reefs (Pemba), fringing reefs (Mafia and
517 Zanzibar), and intertidal (Zanzibar) for foraminifera, in contrast to fringing reefs (Mafia
518 and Zanzibar), fore reefs (Pemba), and intertidal (Zanzibar) for ostracods, respectively.
519 Such discrepancies may imply a tight association of foraminifera with reef ecosystem
520 and their ultra-sensitivity to reef health, since their diversity generally decreased from
521 pristine, mature reefs to degraded, marginal reefs. Ostracods, on the other hand, may
522 be less confined or specific to reef habitats. The occupation of coral and algae substrate
523 by distinct faunal groups allows them to thrive in the transitional zone between marginal
524 and true reefs. Another important factor accounting for the different distributional
525 patterns between ostracods and foraminifera is likely their tolerance to eutrophication
526 and pollution. Previous studies indicate that an intermediate level of eutrophication is
527 beneficial to ostracods and many other soft sediment benthos, which are also resistant

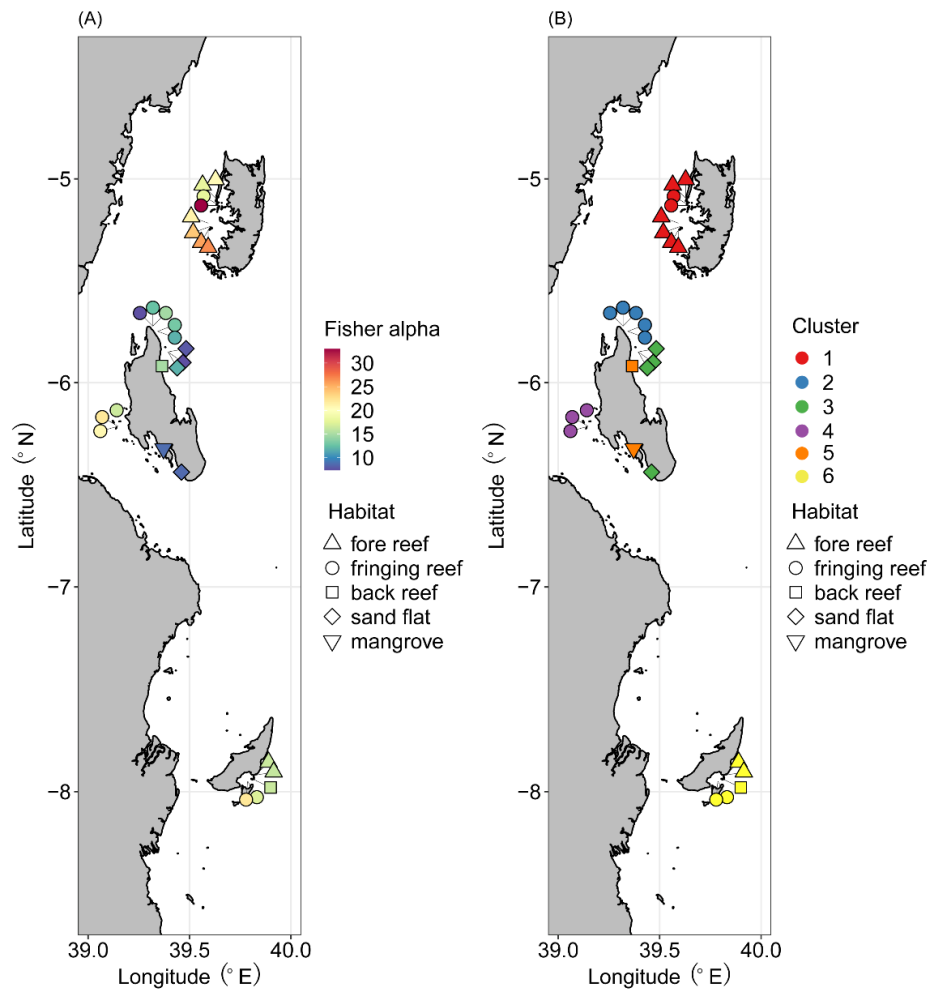
528 to heavy metal pollution in highly urbanized areas (Hong et al., 2022). Consistently,

529 our sampling sites at Stone Town reported the highest abundance of ostracods (Table

530 1). Foraminifera on the other hand are susceptible to environmental stressors, as shown

531 by low taxonomic richness and high dominance of the faunas in eutrophic conditions

532 (Mamo et al., 2023). In our case, it makes sense that the highest diversity of

533 foraminifera was found in pristine and oligotrophic Pemba waters.

534

535 Fig. 811. Distributions of benthic foraminifera (A) diversity measured as Fisher alpha

536 index; (B) cluster groups based on Q-mode cluster analysis. Modified from Thissen and

537 Langer (2017). Diversity/cluster and habitat are represented by color and shape as in

538 the legends, respectively.

539

540 Most importantly, this study established a clear benthic community axis along which

541 the composition and diversity of ostracod assemblage vary, i.e., from coral reefs to

542 algae turfs. We identified typical reefal association (Bairdiidae-*Bosasella*) versus algal

543 association (Loxoconchidae-Xestoleberididae) (Fig. 710), and their relative dominance

may be used as a direct indication of benthic community type. As there is a growing interest to monitor the degradation of reef ecosystems from the coral-dominated phase to the algae-dominated phase (Roth et al., 2018; Knowlton and Jackson, 2008; Knowlton, 2012), our finding is of potential conservation value. Ostracod species diversity was higher on shallow fringing reefs than on deep fore reefs, as the former ecosystem harbored evenly weighted reefal and algal taxa within a dynamic mosaic of microhabitats. Our results thus strongly indicate the importance of coral reefs in harboring conspicuously high levels of meiobenthic biodiversity, likely through finer niche partitioning (Kohn et al., 1997; Fox and Bellwood, 2013). Along with the benthic community factor, we quantified prominent changes in faunal structure and diversity along a depth gradient, as the intertidal euryhaline assemblages transited to subtidal fully marine assemblages. It is widely recognized that shallow-marine biotas are especially susceptible to depth associated changes, such as temperature, salinity, wave action, and light penetration (Carvalho et al., 2012; Tian et al., 2022). This study showed that a narrow depth zone across the intertidal and subtidal (~40 m) was further divided and occupied by distinct biofacies. Such a finely tuned vertical gradient of diversity and faunal composition added to an exceedingly large regional species pool (235 species) in this tropical shallow-marine setting. Last but not least, it should be aware that the effects of depth and benthic community type are often intertwined with each other in determining ostracod assemblages, as the habitat-building corals and algae essentially exhibit depth distributions. At a regional scale like the Zanzibar Archipelago, the combined effects of water depth and benthic community characteristics should be considered in studying the spatial patterns of benthic organisms.

6 Conclusion

In conclusion, this study showed that the diversity and faunal composition of reefal ostracod assemblages vary along benthic community and bathymetric gradients, which may also be altered by local anthropogenic disturbances. Ostracod faunas on shallow fringing reefs were especially diverse, which may be explained by high levels of habitat complexity and heterogeneity. The relative dominance of reefal taxa (Bairdiidae) versus algal taxa (Loxoconchidae-Xestoleberididae) is likely determined by the proportion of coral versus algae cover on the reef platforms, though more extensive studies beyond this region are needed to confirm the universality of this pattern. Coral reefs worldwide are vulnerable to ongoing climate changes and other human impacts at

578 local to global scales, and many reefal species are at risk of extinction. It is of great

579 importance that we inspect and understand the immense biodiversity of meiobenthos

580 on coral reefs as an indispensable part of the ecosystem.

581

582 **Data availability**

583 Ostracod census data is available in the online supplementary materials. will be

584 deposited into The Paleobiology Database. DOI will be added later.

585

586 **Author contributions**

587 Each named author has participated sufficiently in the work to take public responsibility

588 for the content. SYT and ML developed the concept. ML collected the samples. SYT

589 performed the research carried out the experiments and collected the data. SYT and

590 CLW analysed the data performed the data analyses. SYT drafted the manuscript. ML,

591 MY, and CLW reviewed and edited the manuscript.

592

593 **Competing interests**

594 The authors declare that they have no competing interests.

595

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604

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