1 Reefal ostracod assemblages from the Zanzibar Archipelago (Tanzania)

2 Skye Yunshu Tian[1], Martin Langer[1], Moriaki Yasuhara[2,3], Chih-Lin Wei[4]

4 [1] Bonn Institute for Organismic Biologie, Paläontologie, Universität Bonn, Bonn,
5 Germany
6 [2] School of Biological Sciences, Area of Ecology and Biodiversity, Swire Institute of
7 Marine Science, The University of Hong Kong, Hong Kong SAR, China
8 [3] State Key Laboratory of Marine Pollution, City University of Hong Kong, Hong Kong
9 SAR, China
10 [4] Institute of Oceanography, National Taiwan University, Taipei 106, Taiwan
11 Correspondence to: Skye Yunshu Tian skyeystian@gmail.com
12 Martin Langer martin.langer@uni-bonn.de

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-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-affined and algae-affined taxa
28 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 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. Does ostracod exhibit higher

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

51 the characteristic ostracod taxa occupying different niches on coral reefs? Answers to

52 these questions are important for a holistic understanding of the reef ecosystem and

53 may hint at the underlying mechanisms that support such extraordinary reef diversity.

54 With intensifying anthropogenic disturbances at local to global scales, the need to

55 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,

69 the focus of previous studies mainly revolved around taxonomy, and biogeography to

70 a lesser degree, while quantitative assessments of biodiversity are largely lacking

71 (Tabuki, 1987, 1990; Mostafawi et al., 2005). The highest species richness (S=74) was

72 reported for a reef slope environment in Pulau Seribu, Java (Whatley and Watson, 1988)

73 in contrast to much lower values at lagoons (S=27-42) (Babinot and Degaugue-

74 Michalski, 1996; Weissleader et al., 1989) and reef flat (S=34) (Mostafawi et al., 2005).

75

76 Reefal ostracods are even less known in other tropical regions outside of the central

77 Indo-Pacific. Along the eastern coast of Africa, where the reef ecosystem is productive

78 and biodiverse, the only studies on ostracod assemblages are perhaps Hartmann (1974)

79 and Jellinek (1993) that document more than 200 species inhabiting the algae facies

80 and reefal facies across the littoral zone in Kenya. Here we present the first large-scale

81 study on reefal ostracods from the Zanzibar Archipelago, Tanzania, a biodiversity

82 hotspot of great conservation interests and vulnerability to increasing anthropogenic

83 impacts (Grimsditch et al., 2009). We investigated the geographical structure of

84 ostracod diversity and composition in relation to environmental habitats among three

85 major islands of Pemba, Zanzibar, and Mafia. We compared the patterns with those of

86 benthic foraminifera (Thissen and Langer, 2017) to explore complex environmental

87 controls on the two groups of meio-benthos. This study is a major step towards better

88 understanding of tropical shallow-marine ostracods in eastern Africa and provides

89 valuable insight into the ostracod-reef association in general.

90

91 **2 Regional setting**

92 The Zanzibar Archipelago is located along the eastern coast of Tanzania in the Western

93 Indian Ocean (Fig. 1) (Thissen and Langer, 2017). It belongs to the eastern African

94 biogeographic province that stretches from Somalia to the northeastern coast of South

95 Africa (Costello et al., 2017; Obura, 2012). The archipelago is strongly influenced by

96 the warm, westward-flowing South Equatorial Current and the northward-flowing East

97 African Coastal Current (Narayan et al., 2022). The western coastlines are more

98 protected, with generally higher coral coverage, whereas the eastern coastlines are

99 exposed to large physical disturbances and strong wave energy (Thissen and Langer,

100 2017). Tides there are semi-diurnal, with a maximum range of 4.5 m and a neap tidal

101 range of 0.9 m (Thissen and Langer, 2017; Narayan et al., 2022). The islands possess a

102 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

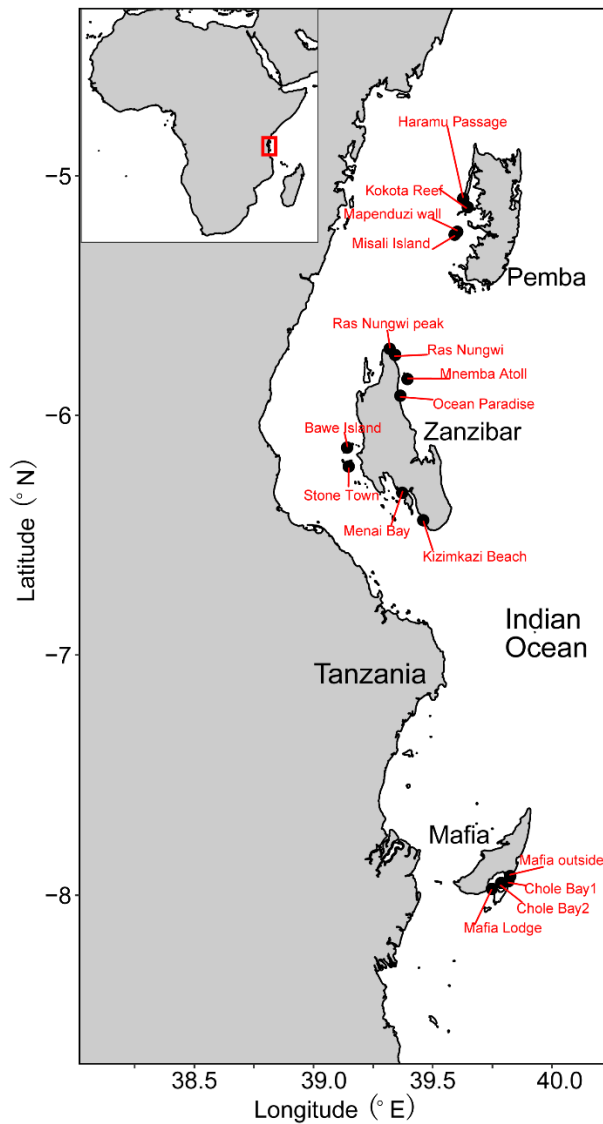
113   the Pemba reefs are likely in pristine conditions with the highest coverage of live hard

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.

119

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

121 sample sites.

122

123 **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 table 1). Depositional depths of all samples range from 0 to 42 m across

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

129 benthic habitats, including a nearshore mangrove, coastal sand flats, and fringing-, fore-,

130 and back-reefs (Table 1). Note that the mangrove habitat may be underrepresented in

131 current study as we have only one such site, however. Samples were collected by

132 SCUBA diving to scrape along the seabed and fill plastic containers with surface

133   sediments from the top 2 cm, in order to avoid the loss of finer particles due to

134   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   Large volume samples were split into aliquot fractions using a microsplitter. The

142   sample materials were primarily death assemblages though a very small number of

143   specimens were preserved with soft parts (less than 1% among all observed individuals),

144   indicating they were alive at the time of collection. Both live and dead specimens were

145   included in the total count to represent time-averaged assemblages, which method

146   effectively defines reef habitats and provides general environmental and diversity data

147   useful in paleoecology (Glenn-Sullivan and Evans, 2001; Langer and Lipps, 2003). A

148   single valve or a carapace was considered as one individual, which is a standard

149   counting method in ostracod research (Yasuhara et al., 2017). Selected specimens were

150   imaged using a Scanning Electron Microscope (SEM).

151

152

153

154

155

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	back 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 (^0D) reduces to species richness; when

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

172 the order $q=2$, Hill number (^2D) 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 ^1D and ^2D 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, $^qE_3(p) = (^qD − 1)/(S − 1)$, where ^qD

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).

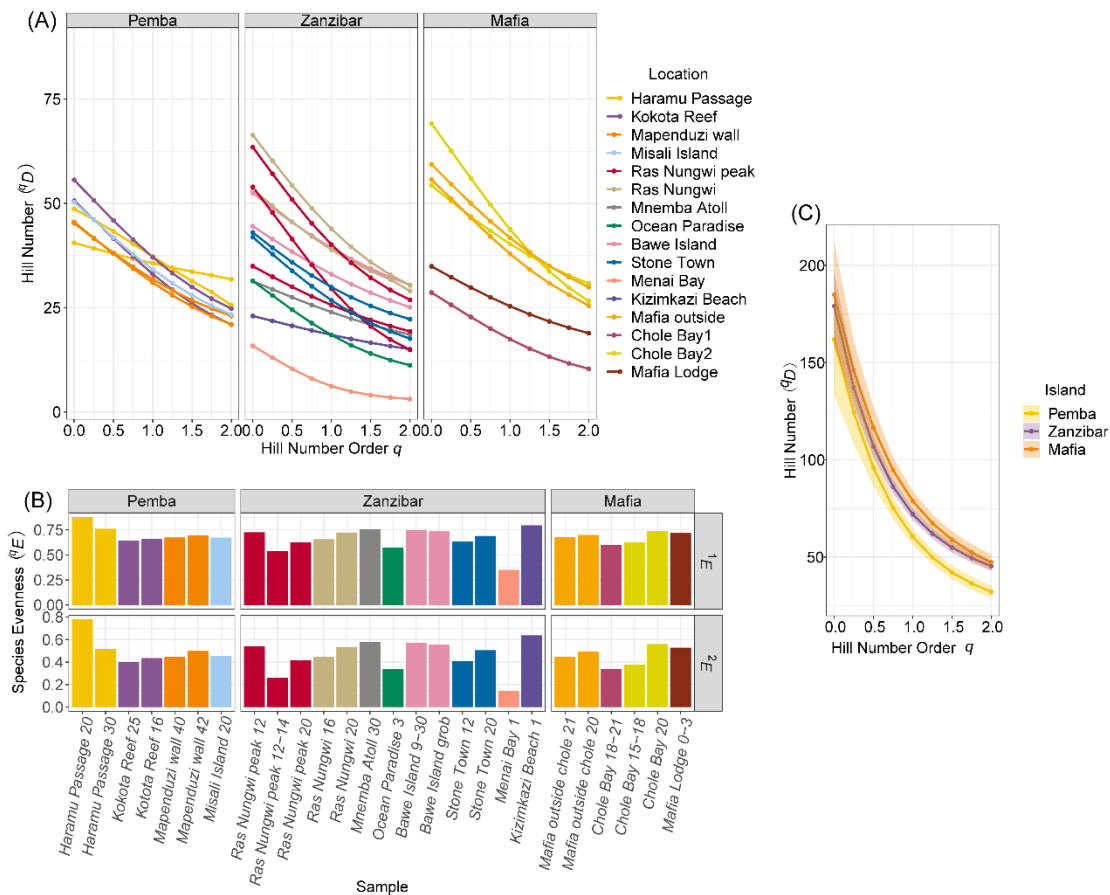
4 Results

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, ^0D) and abundant (^1D) 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-B). 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 (^2D) 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, S1). With respect to the gamma diversity of each island, Mafia and Zanzibar were almost equally

 diverse across all order *q,* while Pemba had significantly lower diversity for abundant

238   and dominant species (Figs. 2C, S2).

239

240

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.

250

251

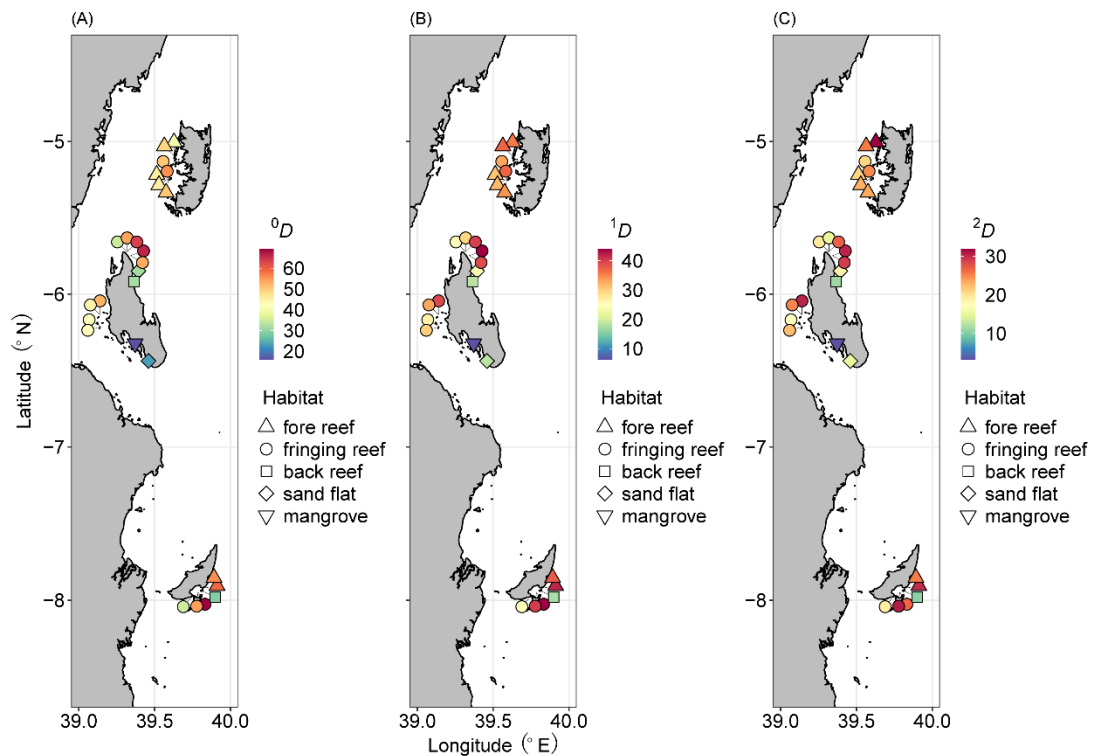



Fig. 3. Diversity maps of the Zanzibar archipelago ostracod. Distributions of Hill
numbers ^{0}D (A: $q = 0$, species richness), ^{1}D (B: $q = 1$, exponential Shannon), and ^{2}D
(C: $q = 2$, inversed Simpson). We used 82.5% sample coverage to standardize the Hill
number estimates. Diversity and habitat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

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
optimum number of clusters to be four (Fig. S3). The NMDS results showed a clear
separation of four biofacies based on Horn and Morisita-Horn dissimilarities, but not
Sørensen dissimilarity, which was calculated with a relatively high stress value (0.26)
(Fig. S4). Ostracod faunas in Pemba Island constituted a distinct group across all levels

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

272 4). Ras Nungwi, Ras Nungwi peak, and nearby Menemba Atoll were congregated with

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

274 Chole Bay 2 in Sørensen, Mafia outside, Chole Bay 1 and Chole Bay 2 in Horn, Ocean

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

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

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

278 cluster analyses (Fig. 4). Specifically, they scattered around the entire Zanzibar Island

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

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

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

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

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

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

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

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

287 on Horn dissimilarity most reasonably captured the underlying ecological significance

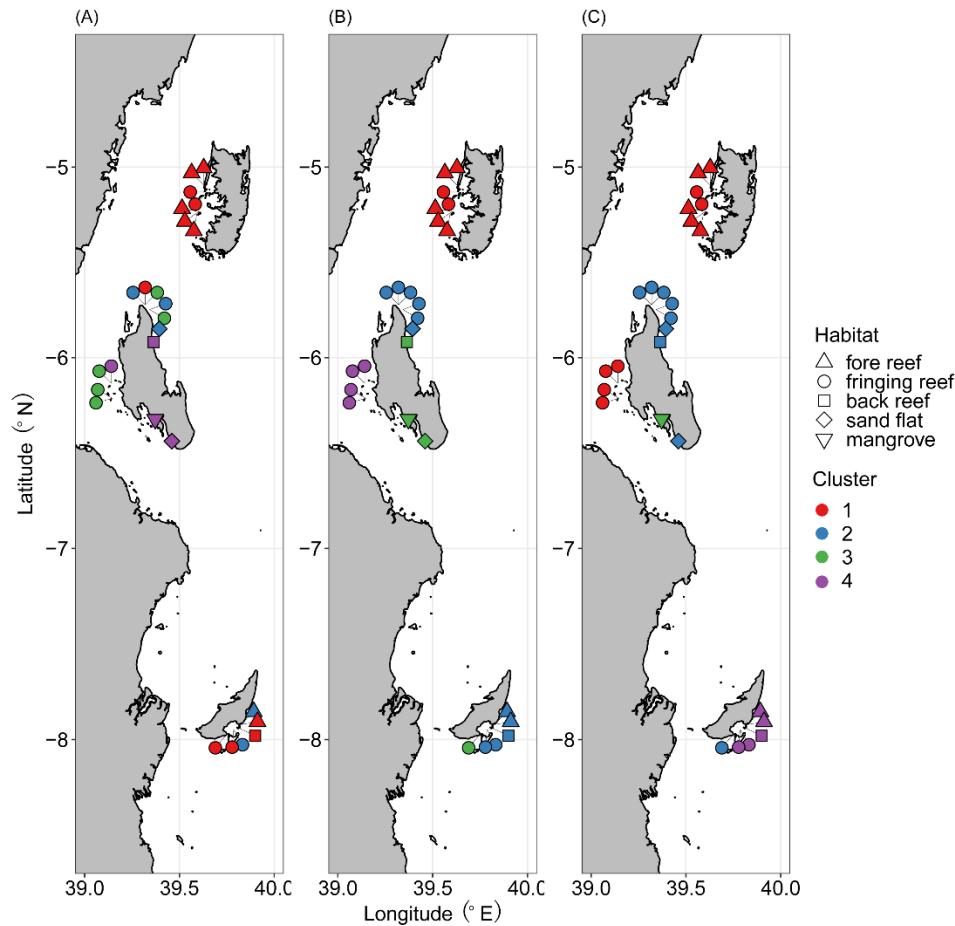
288 of reefal versus non-reefal facies as determined by benthic community, depth, and

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

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

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

292

293

294

295 Fig. 4. Distribution of ostracod Biofacies 1-4 based on (A) Søensen, (B) Horn, and (C)

296 Morisita-Horn dissimilarities and Ward's minimum variance cluster analysis. Note that

297 the color schemes are independent among panels; thus, the biofacies based on different

298 dissimilarities are unrelated. Cluster and habitat are represented by color and shape as

299 in the legends, respectively.

300

301 Each biofacies based on Horn dissimilarity index was demonstrated with the top 10

302 species of highest mean relative abundance as shown in Table 2 and Figure 5.

303 Noticeably, the Pemba fauna in Biofacies 1 was dominated by genus *Neonesidea* (*N.*

304 cf. *crepidula* and *N. schulzi*) and *Bosasella* (*B. profunda* and *B. elongate*), together with

305 *Paracytheridea tschoppi* (Fig. 6; Table 2). Biofacies 2 included the most diverse sites

306 in Zanzibar and Mafia, which all shared similar faunal structures with a high abundance

307 of *Loxocorniculum* sp. 2, *Xestoleberis rotunda, Paracytheridea albatros* and

308 *Loxoconcha* sp. 3. Biofacies 3 composed of low-diversity sites in Zanzibar and Mafia

309 was distinguished by highly abundant *Perissocytheridea estuaria*, *Xestoleberis hanaii*,

310 as well as three *Loxoconcha* species (*L.* sp. 3, *L. ghardaqensis* and *L. lilljeborgii*).

311   Finally, the faunal structure of Biofacies 4 in western Zanzibar showed some

312   similarities to that of Biofacies 1 in Pemba with many common species, however, they

313   clearly differed by the dominance of *Xestoleberis hanaii* and *Patrizia nucleuspersici* in

314   Biofacies 4.

315

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

317   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	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

318

319

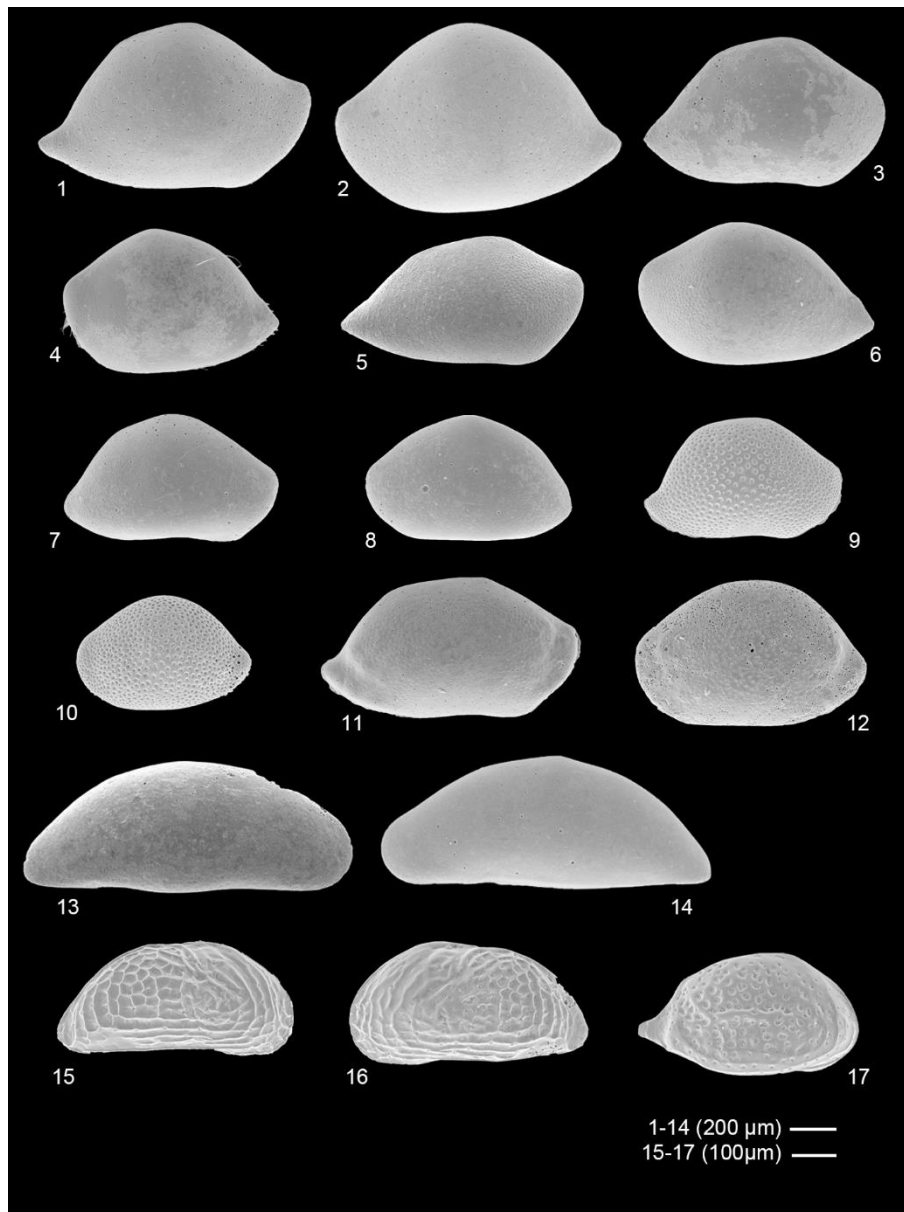



Fig. 5. Scanning electron microscopy images of the top 10 ostracod species of highest %
mean relative abundance for Biofacies 1-4 based on Horn dissimilarity. **1**, *Neonesidea*
cf. *crepidula*, RV, Kokota reef25; **2**, *Neonesidea* cf. *crepidula*, LV, Haramu Passage30;
3, *Neonesidea paiki*, RV, 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*, RV,

330 Menai bay1; **16**, *Perissocytheridea estuaria*, LV, Menai bay1; **17**, *Perissocytheridea*?

331 sp. 2, RV, Bawe island grob. All adults and lateral views.

332

333

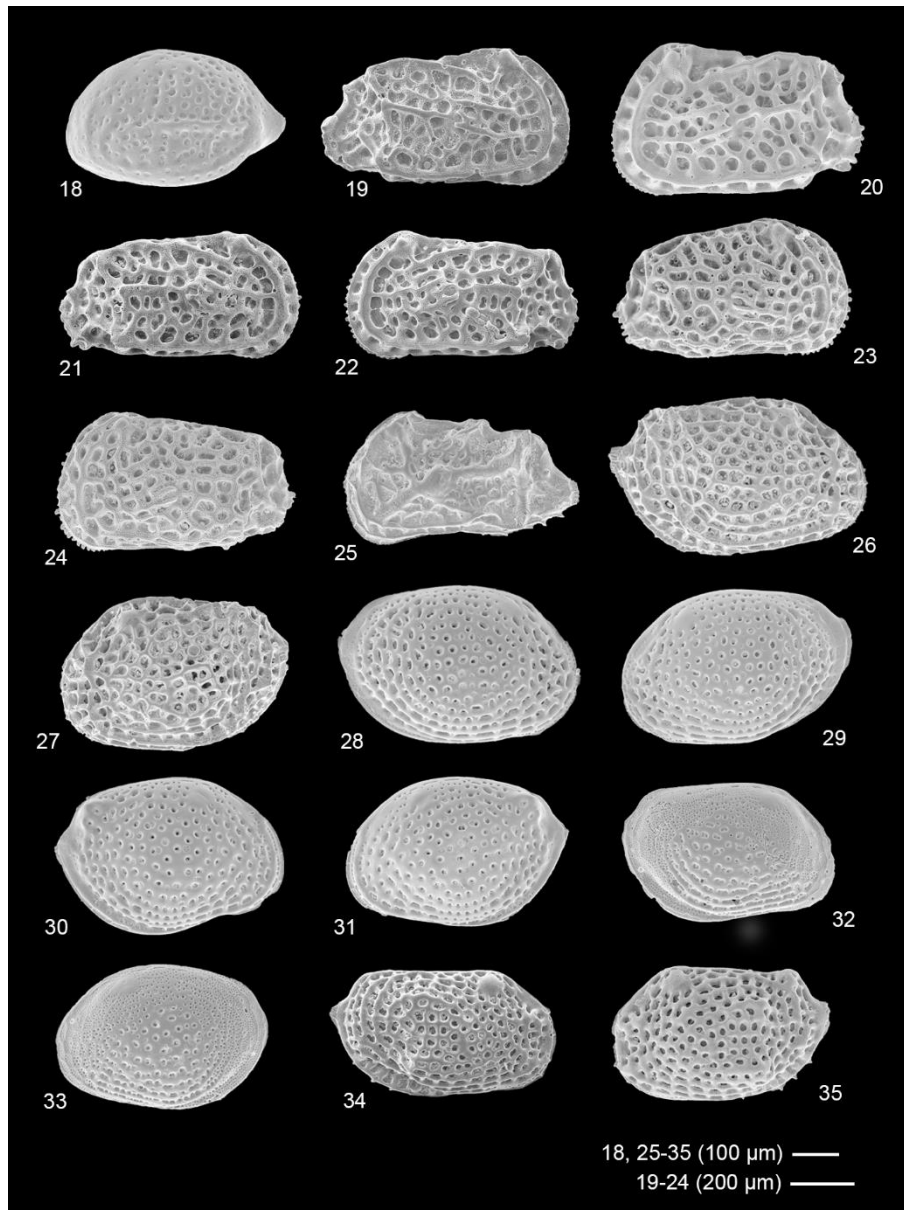



Fig. 5. Continued. **18**, *Perissocytheridea*? sp. 2, LV, Bawe island9-30; **19**, *Bosasella elongate*, RV, Haramu Passage30; **20**, *Bosasella elongate*, LV, Mapenduzi wall42; **21**, *Bosasella profunda*, RV, Haramu Passage20; **22**, *Bosasella profunda*, LV, Mapenduzi wall42; **23**, *Bosasella* sp. 1, RV, Kokota reef25; **24**, *Bosasella* sp. 1, LV, Kotota reef16; **25**, *Caudites exmouthensis*, LV, RusNungwi16; **26**, *Loxoconcha ghardaqensis*, RV, Mnemba atoll30; **27**, *Loxoconcha ghardaqensis*, LV, Ras Nungwi peak12; **28**, *Loxoconcha* cf. *gisellae*, RV, Bawe island9-30; **29**, *Loxoconcha* cf. *gisellae*, LV, Bawe island9-30; **30**, *Loxoconcha lilljeborgii*, RV, Bawe island9-30; **31**, *Loxoconcha*

lilljeborgii, LV, Bawe island grob; **32**, *Loxoconcha* sp. 3, RV, Stone town20; **33**, *Loxoconcha* sp. 3, LV, Stone town20; **34**, *Loxocorniculum* sp. 2, RV, Haramu Passage30; **35**, *Loxocorniculum* sp. 2, LV, Kotota reef16. All adults and lateral views.

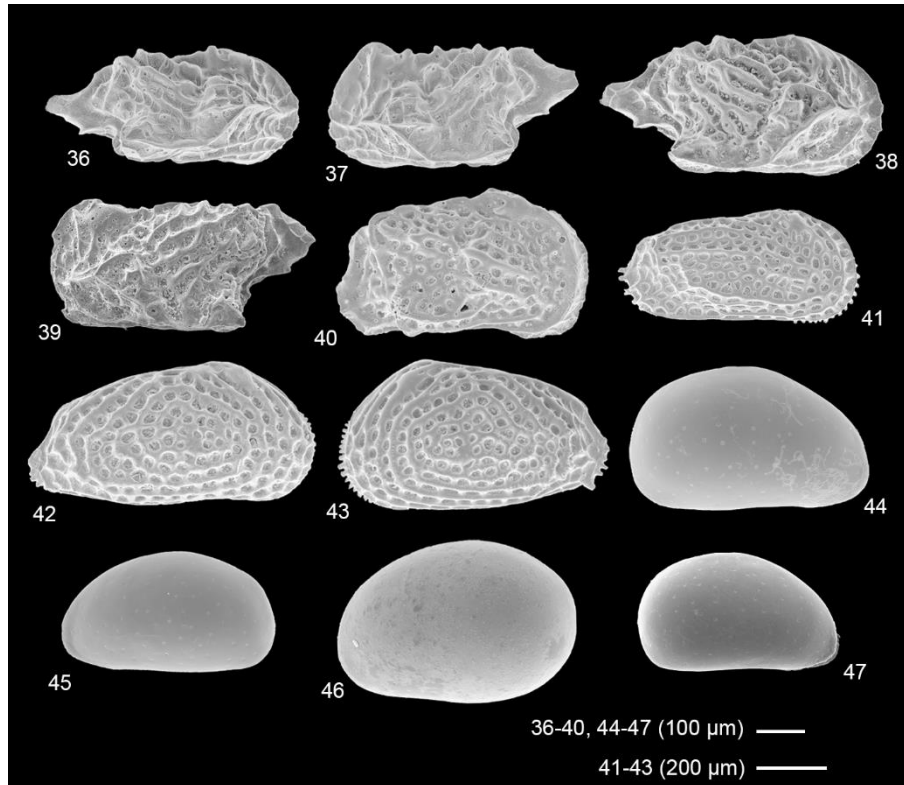
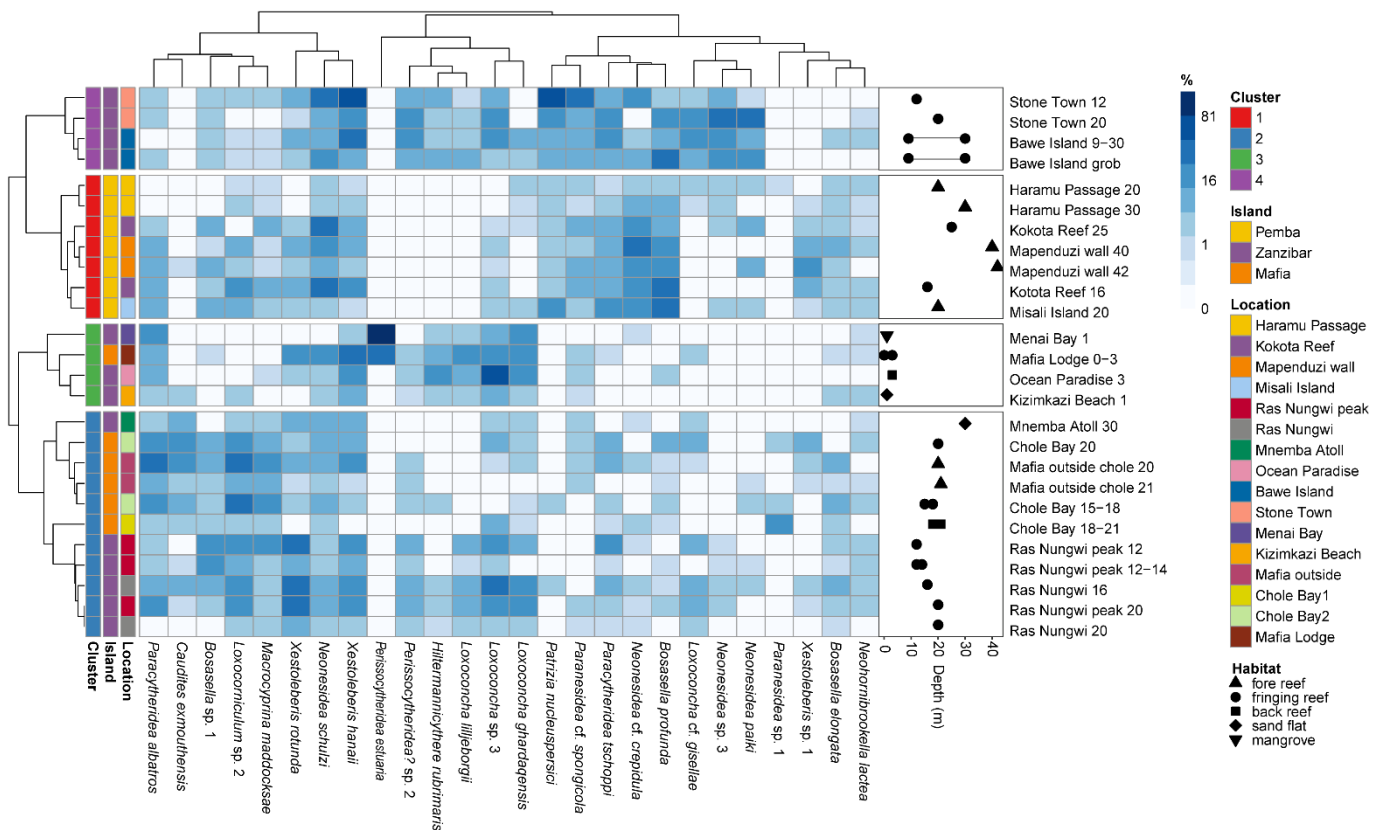



Fig. 5. Continued. **36**, *Paracytheridea albatross*, RV, Kokota reef25; **37**, *Paracytheridea albatross*, LV, Kotota reef16; **38**, *Paracytheridea tschoppi*, RV, Kokota reef25; **39**, *Paracytheridea tschoppi*, LV, Mapenduzi wall42; **40**, *Neohornibrookella lactea*, RV, Misali island20; **41**, *Hiltermannicythere rubrimaris*, RV, Stone town20; **42**, *Patrizia nucleuspersici*, RV, Stone town20; **43**, *Patrizia nucleuspersici*, LV, Stone town12; **44**, *Xestoleberis hanaii*, RV, Bawe island9-30; **45**, *Xestoleberis hanaii*, LV, Kokota reef25; **46**, *Xestoleberis rotunda*, LV, Ras Nungwi peak12; **47**, *Xestoleberis* sp. 1, RV, Mapenduzi wall42. All adults and lateral views.

356

357 Fig. 6. Dendrograms based on Horn dissimilarity between samples and Hellenger

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

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

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

361 samples are shown by their corresponding depth ranges).

362

363 **5 Discussion**

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

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

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

367 indicating inconsistent faunal structures across different levels of species information

368 from occurrence to relative abundance (Fig. 4). In terms of the presence/absence of

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

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

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

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

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

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

be ubiquitous across the entire neritic zone despite showing certain ecological preferences, and the redeposition processes may further facilitate the mixing of death assemblages to blur the spatial signal at a local scale (Frenzel and Boomer, 2005). Consequently, species presence in all available habitats may translate to considerable faunal similarities among biofacies as measured by Sørensen index. When considering the composition of abundant species (Horn dissimilarity) (Fig. 4B), the identification of four biofacies instead reflected significant changes in ostracod assemblages along two important environmental gradients, which are benthic community type and water depth. Specifically, Biofacies 1 and 2 characterize typical fore reefs in deep subtidal (sampling depth 16-42 m) and fringing reefs in shallow subtidal (12-30 m), respectively (Fig. 6). Biofacies 3 indicates intertidal habitats with plant cover (0-3 m), and finally Biofacies 4 features degraded fringing reefs in shallow subtidal (9-30 m) (see discussion below).

We summarized the ecological preferences of dominant genera in each biofacies based on Horn dissimilarity (Table 3 and Fig. 6) and investigated how key environmental factors (benthic community type, water depth, and anthropogenic disturbance) may control the distribution and diversity of reefal ostracod assemblages. First of all, *Neonesidea* and *Paranesidea* (family Bairdiidae) are typical reefal genera that reach their maximum diversity and incidence on reefs and reef-associated habitats in tropical shallow-marine environments (Whatley and Watson, 1988; Maddocks, 2013; Titterton and Whatley, 1988). Their dominance in Biofacies 1 is consistent with our background understanding that the Pemba reefs were pristine and healthy (Ussi et al., 2019; Grimsditch et al., 2009). However, it should be noted that individual species of these genera likely have different environmental tolerance. For example, *N.* cf. *crepidula* were restricted to Biofacies 1 while *N. schulzi* were widespread among four biofacies inhabiting both reef and algae habitats (Fig. 6) (Mostafawi et al., 2005). *Bosasella* as another prominent component of Biofacies 1 is also known to occur on coral reefs in the western Indian Ocean (Munef et al., 2012; Jellinek, 1993). *Paracytheridea* and *Caudites* on the other hand are loosely categorized as reefal genera, as their dominance on coral reefs was reported but not studied in detail (Whatley and Watson, 1988; Keyser and Mohammed, 2021). In this study, they were common on fore- and fringing-reefs in Biofacies 1 and 2 (Fig. 6). *Loxoconcha* and *Loxocorniculum* (family Loxoconchidae) 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. 6).
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 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. 7).

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	Nogueira and Ramos (2016); Keyser (1977)

431

432

433

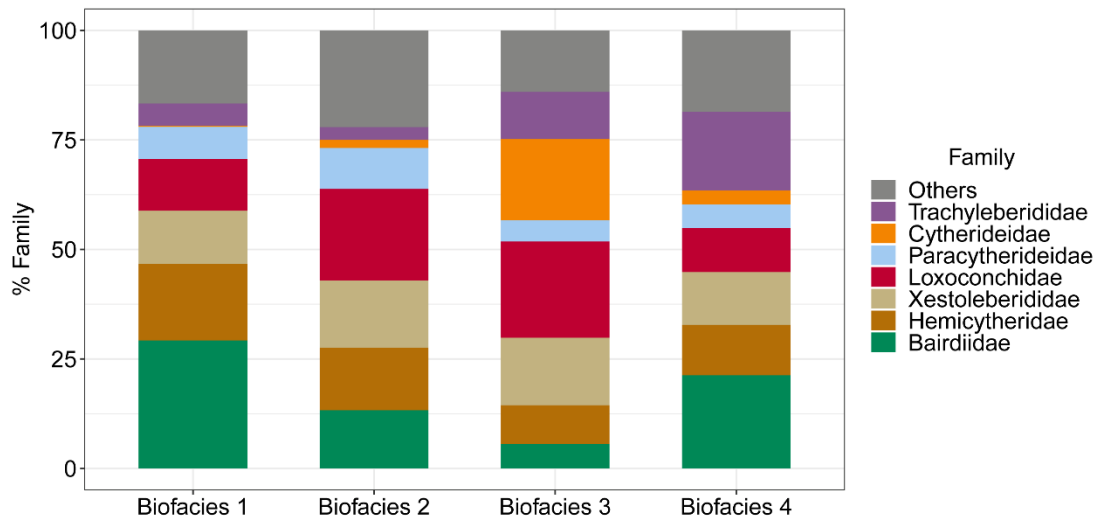



Fig. 7. Family composition of Biofacies 1-4 based on Horn dissimilarity. The top 5 families of the highest % relative abundance in each biofacies are shown.

436

Thus, our study indicates that the distribution of shallow-marine ostracods in 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. 6-7). Moderately high levels of diversity in terms of rare, abundant, and dominant species were observed for these ostracod assemblages (Fig. 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

450   *Bosasella profunda*, *Paracytheridea tschoppi*, and *Paranesidea* cf. *spongicola* in both

451   facies (Fig. 6). Indeed, they were grouped together based on the composition of

452   dominant species (Morisita-Horn analysis) (Fig. 4C). Faunal similarities between

453   Pemba and Stone Town make sense as they are in comparable baseline conditions of

454   water depths and hydrology along the protected western coast of the Zanzibar

455   Archipelago, in contrast to Ras Nungwi and Chole Bay that are exposed to oceanic

456   disturbances from the east (Fig. 1). However, Biofacies 4 was differentiated from

457   Biofacies 1 by the dominance of *Patrizia* in conjunction with the absence of *Neonesidea*

458   cf. *crepidula*. It also had the highest relative abundance of Trachyleberididae genera

459   among all facies (Fig. 7), for example, *Adencythere*, *Strobilocythere, Bradyon,* and

460   *Actinocythereis*, but their ecologies are not well understood. Stressful environmental

461   conditions in terms of overexploitation, tourism and coastal pollution offer the most

462   possible explanation for such a unique faunal composition and comparatively low

463   diversity of Biofacies 4 (Fig. 3) (Bravo et al., 2021; Larsen et al., 2023). Consistently,

464   foraminifera and coral surveys indicated early stages of reef degradation there (Narayan

465   et al., 2022; Bravo et al., 2021; Thissen and Langer, 2017) It is possible that ongoing

466   anthropogenic disturbances near the Stone Town will eventually exceed the critical

467   threshold levels to cause more pronounced changes in ostracod faunal structures in

468   terms of dominant species through a shift in benthic habitat (Narayan et al., 2022; Hong

469   et al., 2022). Other than Biofacies 1 and 4, Biofacies 2 mostly represented a different

470   type of relatively shallow (12-20 m) fringing-back reef habitats of Ras Nungwi, Chole

471   Bay, and Mafia outside, in addition to a deeper (30 m) sand flat of Mnemba Atoll (Fig.

472   6). Algal taxa (Loxoconchidae and Xestoleberididae) and reefal taxa (Bairdiidae,

473   *Bosasella*, *Paracytheridea*, and *Caudites*) reached equally high levels of relative

474   abundance there (Figs. 6-7). Microhabitats on the reef platforms of Biofacies 2 are

475   believed to be diverse and heterogenous with interlaced live and dead corals, algae and

476   seagrass, calcareous sands, as well as bare substrate rock (Ussi et al., 2019; Larsen et

477   al., 2023), which facilitated the coexistence of reefal and algal ostracods and

478   consequently the highest diversity of local assemblages (Fig. 3). The remaining

479   Biofacies 3 corresponded to the shallowest intertidal habitats with various benthic

480   communities, including a marginal back reef, a marginal fringing reef, a sand flat, and

481   a mangrove (Fig. 6). Typical reefal taxa (Bairdiidae and *Bosasella*) dropped to their

482   lowest relative abundance in this facies, replaced by large numbers of Loxoconchidae,

483   *Perissocytheridea,* and *Hiltermannicythere* that well adapted to shallow euryhaline

484   conditions (Figs. 6-7). Not surprisingly, the diversity of Biofacies 3 was much lower

485   than that of open-ocean reefal facies, as drastic changes in temperature, salinity,

486   dissolved oxygen, and wave energy in the intertidal zone may be too challenging for

487   many marine taxa (Fig. 3) (Morley and Hayward, 2007; Frenzel and Boomer, 2005).

488   The mangrove habitat at Menai Bay was unique concerning the absolute dominance of

489   *Perissocytheridea* in line with its lowest diversity and evenness (Figs. 2B, 3). It indeed

490   constituted an independent biofacies based on Morisita-Horn analysis (Fig. 4C).

491

492   The division scheme of four biofacies based on Horn dissimilarity explicitly revealed

493   spatial patterns of ostracod distribution in aspect of diversity and composition, as

494   discussed above. Our results are generally concordant with a previous study on benthic

495   foraminifera, which separated six clusters of Pemba, Stone Town, Mafia Bay, Ras

496   Nungwi, Mnemba Atoll, and Menai Bay, respectively (Fig. 8B) (Thissen and Langer,

497   2017). Each of these foraminifera clusters corresponded to major habitat types, as

498   argued by the authors (Thissen and Langer, 2017), and we accordingly pointed out the

499   consistent role of habitat factors in shaping the biogeography of both ostracod and

500   foraminifera biotas. However, the diversity patterns of these two groups were

501   apparently different among reefal habitats (Figs. 3, 8A). High, moderate, and low levels

502   of diversity were recorded on fore reefs (Pemba), fringing reefs (Mafia and Zanzibar),

503   and intertidal (Zanzibar) for foraminifera, in contrast to fringing reefs (Mafia and

504   Zanzibar), fore reefs (Pemba), and intertidal (Zanzibar) for ostracods, respectively.

505   Such discrepancies may imply a tight association of foraminifera with reef ecosystem

506   and their ultra-sensitivity to reef health, since their diversity generally decreased from

507   pristine, mature reefs to degraded, marginal reefs. Ostracods, on the other hand, may

508   be less confined or specific to reef habitats. The occupation of coral and algae substrate

509   by distinct faunal groups allows them to thrive in the transitional zone between marginal

510   and true reefs. Another important factor accounting for the different distributional

511   patterns between ostracods and foraminifera is likely their tolerance to eutrophication

512   and pollution. Previous studies indicate that an intermediate level of eutrophication is

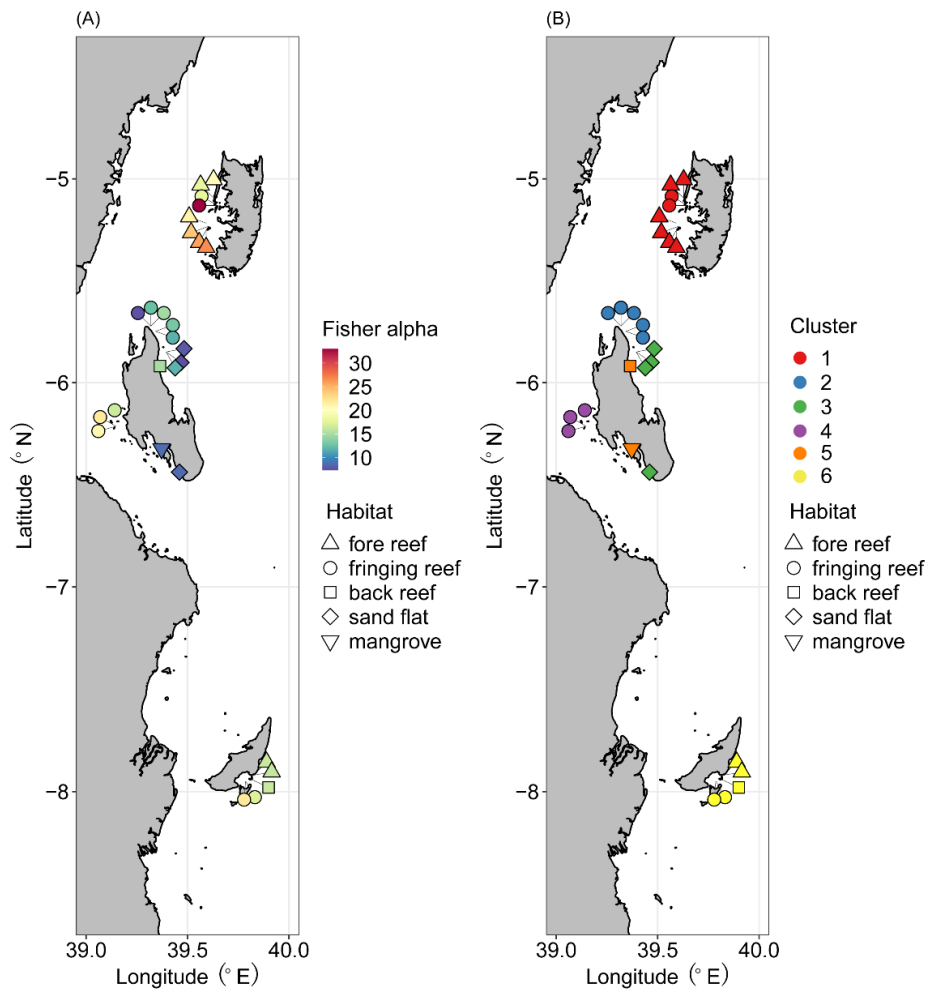
513   beneficial to ostracods and many other soft sediment benthos, which are also resistant

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

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

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

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

518 (Mamo et al., 2023). In our case, it makes sense that the highest diversity of
519 foraminifera was found in pristine and oligotrophic Pemba waters.

520

521 Fig. 8. Distributions of benthic foraminifera (A) diversity measured as Fisher alpha
522 index; (B) cluster groups based on Q-mode cluster analysis. Modified from Thissen and
523 Langer (2017). Diversity/cluster and habitat are represented by color and shape as in
524 the legends, respectively.

525

526 Most importantly, this study established a clear benthic community axis along which
527 the composition and diversity of ostracod assemblage vary, i.e., from coral reefs to
528 algae turfs. We identified typical reefal association (Bairdiidae-*Bosasella*) versus algal
529 association (Loxoconchidae-Xestoleberididae) (Fig. 7), and their relative dominance
530 may be used as a direct indication of benthic community type. As there is a growing
531 interest to monitor the degradation of reef ecosystems from the coral-dominated phase
532 to the algae-dominated phase (Roth et al., 2018; Knowlton and Jackson, 2008;
533 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 local to global scales, and many reefal species are at risk of extinction. It is of great importance that we inspect and understand the immense biodiversity of meiobenthos on coral reefs as an indispensable part of the ecosystem.

Data availability

Ostracod census data is available in the online supplementary materials.

Author contributions

Each named author has participated sufficiently in the work to take public responsibility for the content. SYT and ML developed the concept. ML collected the samples. SYT performed the research and collected the data. SYT and CLW analysed the data. SYT drafted the manuscript. ML, MY, and CLW reviewed and edited the manuscript.

Competing interests

The authors declare that they have no competing interests.

Acknowledgements

We thank Stephanie Pietsch, Jens Thissen, Anna Weinmann, and Michael Kunert for their help with fieldwork; Jingfang He for her help in the lab. The work described in this paper was supported by Humboldt Research Fellowship (to SYT), a grant from the German Science Foundation (DFG, LA 884/10-1) (to ML), grants from the Research Grants Council of the Hong Kong Special Administrative Region, China (project codes: HKU 17306023, G-HKU709/21) (to MY), and grants from the National Science and Technology Council, Taiwan (project codes: NSTC 112-2611-M-002-011) (to CW).

References

Babinot, J.-F. and Degaugue-Michalski, F.: Lagoonal to reefal ostracod assemblages from Holocene and Recent deposits, Chesterfield Islands and northern New Caledonia (southwestern Pacific), Micropaleontology, 351-362, https://doi.org/10.2307/1485957, 1996.

Bravo, H., Cannicci, S., Huyghe, F., Leermakers, M., Sheikh, M. A., and Kochzius, M.: Ecological health of coral reefs in Zanzibar, Reg. Stud. Mar. Sci., 48, 102014, https://doi.org/10.1016/j.rsma.2021.102014, 2021.

Carvalho, S., Cunha, M. R., Pereira, F., Pousão-Ferreira, P., Santos, M., and Gaspar, M.: The effect of depth and sediment type on the spatial distribution of shallow soft-bottom amphipods along the southern Portuguese coast, Helgol. Mar. Res., 66, 489-501, https://doi.org/10.1007/s10152-011-0285-9, 2012.

Chao, A. and Ricotta, C.: Quantifying evenness and linking it to diversity, beta diversity, and similarity, Ecology, 100, e02852, https://doi.org/10.1002/ecy.2852, 2019.

Chao, A., Chiu, C.-H., and Jost, L.: Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers, Annu. Rev. Ecol. Evol. Syst., 45, 297-324, https://doi.org/10.1146/annurev-ecolsys-120213-091540, 2014a.

Chao, A., Gotelli, N. J., Hsieh, T., Sander, E. L., Ma, K., Colwell, R. K., and Ellison, A. M.: Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies, Ecol. Monogr., 84, 45-67, https://doi.org/10.1890/13-0133.1, 2014b.

Chao, A., Kubota, Y., Zelený, D., Chiu, C. H., Li, C. F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C. L., and Costello, M. J.: Quantifying sample completeness and comparing diversities among assemblages, Ecol. Res., 35, 292-314, https://doi.org/10.1111/1440-1703.12102, 2020.

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., and Chaudhary, C.: Marine biogeographic realms and species endemicity, Nat. Commun., 8, 1-10, https://doi.org/10.1038/s41467-017-01121-2, 2017.

Fox, R. and Bellwood, D.: Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs, Coral Reefs, 32, 13-23, https://doi.org/10.1007/s00338-012-0945-5, 2013.

Frenzel, P. and Boomer, I.: The use of ostracods from marginal marine, brackish waters as bioindicators of modern and Quaternary environmental change, Palaeogeogr., Palaeoclimatol., Palaeoecol., 225, 68-92, https://doi.org/10.1016/j.palaeo.2004.02.051, 2005.

Gavrilets, S. and Losos, J. B.: Adaptive radiation: contrasting theory with data, Science, 323, 732-737, https://doi.org/10.1126/science.1157966, 2009.

Glenn-Sullivan, E. C. and Evans, I.: The effects of time-averaging and taphonomy on the identification of reefal sub-environments using larger foraminifera: Apo Reef, Mindoro, Philippines, Palaios, 16, 399-408, https://doi.org/10.1669/0883-1351(2001)016%3C0399:TEOTAA%3E2.0.CO;2, 2001.

Grimsditch, G. D., Tamelander, J., Mwaura, J., Zavagli, M., Takata, Y., and Gomez, T.: Coral reef resilience assessment of the Pemba channel conservation area, Tanzania, IUCN2009.

Hartmann, G.: Zur Kenntnis des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostküste von Südafrika und Mocambique unter besonderer Berücksichtigung der Polychaeten und Ostracoden, Mitteil. Hamburg. Zoolog. Mus. Inst., 69, 229-521, 1974.

Hill, M. O.: Diversity and evenness: a unifying notation and its consequences, Ecology, 54, 427-432, https://doi.org/10.2307/1934352, 1973.

Hong, Y., Yasuhara, M., Iwatani, H., Harnik, P. G., Chao, A., Cybulski, J. D., Liu, Y., Ruan, Y., Li, X., and Wei, C.-L.: Benthic ostracod diversity and biogeography in an urbanized seascape, Mar. Micropaleontol., 174, 102067, https://doi.org/10.1016/j.marmicro.2021.102067, 2022.

Hsieh, T., Ma, K., and Chao, A.: iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers), Methods Ecol. Evol., 7, 1451-1456, https://doi.org/10.1111/2041-210X.12613, 2016.

Jellinek, T.: Zur Ökologie und Systematik rezenter Ostracoden aus dem Bereich des kenianischen Barriere-riffs, Senckenb. Lethaea, 73, 83-335, 1993.

Kamiya, T.: Morphological and ethological adaptations of Ostracoda to microhabitats in Zostera beds, Dev. Palaeontol. Stratigr., 11, 303-318, https://doi.org/10.1016/S0920-5446(08)70191-2, 1988.

Keyser, D.: Ecology and zoogeography of recent brackish-water ostracoda (Crustacea) from south-west Florida, in: Aspects of ecology and zoogeography of recent and fossil Ostracoda, 207-222, 1977.

Keyser, D. and Mohammed, M.: Taxonomy of recent shallow marine Ostracods from Al-Hudeida City-Yemen, Mar. Micropaleontol., 164, 101974, https://doi.org/10.1016/j.marmicro.2021.101974, 2021.

Knowlton, N.: Iconic coral reef degraded despite substantial protection, Proc. Natl. Acad. Sci. USA., 109, 17734-17735, https://doi.org/10.1073/pnas.1215836109, 2012.

Knowlton, N. and Jackson, J. B. C.: Shifting baselines, local impacts, and global change on coral reefs, PLoS Biol., 6, e54, https://doi.org/10.1371/journal.pbio.0060054, 2008.

Kohn, A. J., Ormond, R., Gage, J., and Angel, M.: Why are coral reef communities so diverse, in: Marine biodiversity: Patterns and processes, Cambridge University Press, 201-215, 1997.

Kruskal, J. B.: Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis, Psychometrika, 29, 1-27, https://doi.org/10.1007/BF02289565, 1964.

Langer, M. and Lipps, J.: Foraminiferal distribution and diversity, Madang reef and lagoon, Papua New Guinea, Coral Reefs, 22, 143-154, https://doi.org/10.1007/s00338-003-0298-1, 2003.

Larsen, J., Maar, M., Rasmussen, M. L., Hansen, L. B., Hamad, I. Y., and Stæhr, P. A. U.: High-

resolution hydrodynamics of coral reefs and tracing of pollutants from hotel areas along the west coast of Unguja Island, Zanzibar, Mar. Pollut. Bull., 191, 114968, https://doi.org/10.1016/j.marpolbul.2023.114968, 2023.

Leray, M. and Knowlton, N.: DNA barcoding and metabarcoding of standardized samples reveal patterns of marine benthic diversity, Proc. Natl. Acad. Sci. USA., 112, 2076-2081, https://doi.org/10.1073/pnas.1424997112, 2015.

Maddocks, R. F.: Revision of Recent Bairdiidae (Ostracoda), in: Bulletin of the United States National Museum, 1969.

Maddocks, R. F.: New and poorly known species of Neonesidea (Bairdiidae, Ostracoda, Crustacea) from French Frigate Shoals, the Hawaiian Islands, Zootaxa, 3608, 457–510-457–510, https://doi.org/10.11646/zootaxa.3608.6.3, 2013.

Mamo, B. L., Cybulski, J. D., Hong, Y., Harnik, P. G., Chao, A., Tsujimoto, A., Wei, C.-L., Baker, D. M., and Yasuhara, M.: Modern biogeography of benthic foraminifera in an urbanized tropical marine ecosystem, Geological Society, London, Special Publications, 529, SP529-2022-2175, https://doi.org/10.1144/SP529-2022-175, 2023.

Morley, M. S. and Hayward, B. W.: Intertidal and shallow-water ostracoda of the Waitemata Harbour, New Zealand, Records of the Auckland Museum, 17-32, https://www.jstor.org/stable/42905892, 2007.

Mostafawi, N., Colin, J.-P., and Babinot, J.-F.: An account on the taxonomy of ostracodes from recent reefal flat deposits in Bali, Indonesia, Revue de micropaleontologie, 48, 123-140, https://doi.org/10.1016/j.revmic.2004.12.001, 2005.

Munef, M. A., Al-Wosabi, M. A., Keyser, D., and Al-Kadasi, W. M.: Distribution and taxonomy of shallow marine Ostracods from northern Socotra Island (Indian Ocean)-Yemen, Revue de micropaléontologie, 55, 149-170, https://doi.org/10.1016/j.revmic.2012.06.004, 2012.

Narayan, G. R., Herrán, N., Reymond, C. E., Shaghude, Y. W., and Westphal, H.: Local Persistence of Large Benthic Foraminifera (LBF) under Increasing Urban Development: A Case Study from Zanzibar (Unguja), East Africa, J. Earth Sci., 33, 1434-1450, https://doi.org/10.1007/s12583-022-1702-5, 2022.

Nogueira, A. A. E. and Ramos, M. I. F.: The genus Perissocytheridea Stephenson, 1938 (Crustacea: Ostracoda) and evidence of brackish water facies along the Oligo-Miocene, Pirabas Formation, eastern Amazonia, Brazil, J. South Am. Earth Sci., 65, 101-121, https://doi.org/10.1016/j.jsames.2015.11.007, 2016.

Obura, D.: The diversity and biogeography of Western Indian Ocean reef-building corals, PLOS ONE, e45013, https://doi.org/10.1371/journal.pone.0045013, 2012.

Oksanen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R., Simpson, G., and Solymos, P.: Vegan community ecology package version 2.5-7 November 2020, R Project for Statistical Computing: Vienna, Austria, 2020.

Plaisance, L., Caley, M. J., Brainard, R. E., and Knowlton, N.: The diversity of coral reefs: what are we missing?, PloS one, 6, e25026, https://doi.org/10.1371/journal.pone.0025026, 2011.

Roth, F., Saalmann, F., Thomson, T., Coker, D. J., Villalobos, R., Jones, B., Wild, C., and Carvalho, S.: Coral reef degradation affects the potential for reef recovery after disturbance, Mar. Environ. Res., 142, 48-58, https://doi.org/10.1016/j.marenvres.2018.09.022, 2018.

Souza, M. C. S., Massei, K., Vianna, P. C. G., Santos, C. A. G., Mishra, M., and da Silva, R. M.: Assessment of macrobenthos diversity and a zoning proposal for Seixas coral reefs (northeastern Brazil), Mar. Pollut. Bull., 195, 115443, https://doi.org/10.1016/j.marpolbul.2023.115443, 2023.

Tabuki, R.: Preliminary report on ostracode fauna from Sekisei-sho area, Yaeyama Islands, Bulletin of College of Education, 31, pls. 1-2, 1987.

Tabuki, R.: The Ostracoda of the Sekisei-sho area, Ryukyu Islands, Japan: a preliminary report on the ostracods from coral reefs in the Ryukyu Islands, Ostracoda and global events, 365, pls. 1-2, 1990.

Thissen, J. and Langer, M.: Spatial Patterns and Structural Composition of Foraminiferal Assemblages from the Zanzibar Archipelago (Tanzania), Palaeontographica Abteilung A, 308, 1-67, https://doi.org/10.1127/pala/308/2017/1, 2017.

Tian, S. Y., Yasuhara, M., Robinson, M. M., and Huang, H.-H. M.: Ostracod eye size: A

719 taxonomy-free indicator of the Paleocene-Eocene Thermal Maximum sea level, Mar.
720 Micropaleontol., 174, 101994, https://doi.org/10.1016/j.marmicro.2021.101994, 2022.

721 Titterton, R. and Whatley, R.: Recent Bairdiinae (Crustacea, Ostracoda) from the Solomon
722 Islands, J. Micropalaeontol., 7, 111-142, https://doi.org/10.1144/jm.7.2.111, 1988.

723 Ussi, A., Mohammed, M., Muhando, C., and Yahya, S.: Ecological impact of thermal stress in
724 reefs of Zanzibar following the 2016 elevated higher sea surface temperatures, in: Climate
725 Change and Coastal Resources in Tanzania, Springer Climate, 93-115, 2019.

726 Weissleader, L. S., Gilinsky, N. L., Ross, R. M., and Cronin, T. M.: Biogeography of marine
727 podocopid ostracodes in Micronesia, J. Biogeogr., 16, 103-114,
728 https://doi.org/10.2307/2845084, 1989.

729 Whatley, R. C. and Watson, K.: A preliminary account of the distribution of Ostracoda in recent
730 reef and reef associated environments in the Pulau Seribu or Thousand Island Group, Java Sea,
731 Dev. Palaeontol. Stratigr., 11, 399-411, https://doi.org/10.1016/S0920-5446(08)70197-3, 1988.

732 Wickham, H.: reshape2: flexibly reshape data: a reboot of the reshape package, R package
733 version, 1, 2020.

734 Yasuhara, M., Tittensor, D. P., Hillebrand, H., and Worm, B.: Combining marine macroecology
735 and palaeoecology in understanding biodiversity: microfossils as a model, Biol. Rev., 92, 199-
736 215, https://doi.org/10.1111/brv.12223, 2017.

737