

1 **Biogeosciences**

2 **Research Paper**

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4 **Baseline for ostracod-based northwestern Pacific and Indo-Pacific shallow-**
5 **marine paleoenvironmental reconstructions: ecological modeling of species**
6 **distributions**

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28 Abstract:

29 Fossil ostracods have been widely used for Quaternary paleoenvironmental
30 reconstructions especially in marginal marine environments (e.g. for water depth,
31 temperature, salinity, oxygen levels, pollution). But our knowledge of indicator
32 species autoecology, the base of paleoenvironmental reconstructions, remains limited
33 and commonly lacks robust statistical support and comprehensive comparison with
34 environmental data. We analysed marginal marine ostracod taxa at 52 sites in Hong
35 Kong for which comprehensive environmental data are available. We applied linear
36 regression models to reveal relationships between species distribution and
37 environmental factors for 18 common taxa (mainly species, a few genera) in our
38 Hong Kong dataset, and identified indicator species of environmental parameters. For
39 example, *Sinocytheridea impressa*, widely distributed euryhaline species throughout
40 the East and South China Seas and the Indo-Pacific, indicates eutrophication and
41 bottom-water hypoxia. *Neomonoceratina delicata*, widely known species from
42 nearshore and estuarine environments in the East and South China Seas, and the Indo-
43 Pacific, indicates heavy-metal pollution and increased turbidity. The 18 taxa used for
44 this study are widely distributed geographically and divided into Widespread
45 (throughout the northwestern Pacific and Indo-Pacific regions), Temperate [South
46 China Sea to Russia (Sea of Japan coast) and Japan], Subtropical (Indo-Pacific to the
47 East China Sea), Tropical (Indo-Pacific and South China Sea), and Globally
48 Distributed Groups. With statistical support from ecological modeling and
49 comprehensive environmental data, these results provide a robust baseline for

50 ostracod-based Quaternary-Anthropocene paleoenvironmental reconstructions in the
51 tropical–extratropical northwestern Pacific and Indo-Pacific widely.

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53 Key words: Autoecology, Distribution modeling, Indicator species, Ostracoda,
54 Paleoenvironmental reconstruction, Proxy.

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56 **Key points**

57 1. We provide a robust baseline for ostracod-based (microscopic Arthropods)
58 paleoenvironmental reconstructions from Quaternary and Anthropocene marginal
59 marine sediments.

60 2. The studied species have wide distributions over the tropics and extratropics of the
61 northwestern Pacific and Indo-Pacific.

62 3. Ecological modeling established reliable indicator ostracod species for
63 paleoenvironmental reconstructions.

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67 **1. Introduction**

68 Because of their small size, high abundance and excellent fossil record, fossil
69 ostracods (microcrustaceans), have been widely used to reconstruct Quaternary
70 environmental conditions including water-depth, salinity, temperature, oxygen, and
71 pollution, especially in marginal marine sediments (Boomer & Eisenhauer, 2002;
72 Cronin, 2015; Frenzel & Boomer, 2005; Horne et al., 2012; Ruiz et al., 2005). In the
73 northwestern Pacific and Indo-Pacific there are numerous deltas (Woodroffe et al.,
74 2006) hosting accumulated Holocene marine sediments. Many studies have

75 reconstructed the depositional environments of these sediments (Alberti et al., 2013;
76 Dong et al., 2012; Irizuki et al., 2015b; Tanaka et al., 2011; Yasuhara & Seto, 2006;
77 Yasuhara et al., 2005; Zhou et al., 2015; Wang et al., 2018). Due to high
78 sedimentation rates (> 1 cm per year), fossil ostracods allow the high-resolution
79 reconstruction of human-induced environmental changes (pollution, eutrophication,
80 bottom oxygen depletion) over the past century (Irizuki et al., 2011; Irizuki et al.,
81 2015a; Irizuki et al., 2018; Yasuhara et al., 2003; Yasuhara et al., 2007).

82

83 Many have evaluated the autoecology of ostracod indicator species as the
84 basis for paleoenvironmental reconstructions (Hazel, 1988; Irizuki et al., 2003; Ozawa
85 et al., 2004; Stepanova et al., 2003; Wang et al., 1988; Yasuhara & Seto, 2006; Zhao,
86 1984; Zhao & Wang, 1988a, 1988b). Yet these studies tend to focus on only one or a
87 few targeted environmental factor(s) and lack rigorous statistical evaluation,
88 particularly statistical modeling, a common approach in contemporary ecology. This
89 is probably due to the fact that comprehensive environmental datasets are often
90 unavailable and an ecological modeling approach (especially regression modeling and
91 model selection) has not been common in this field of micropaleontology.

92

93 Hong Kong constitutes an ideal location for a marine ecological modeling
94 approach in the northwestern Pacific and Indo-Pacific regions because of extensive
95 and intensive marine environmental monitoring program and subtropical location
96 where tropical and temperate species coexist. This program provides robust datasets
97 for ecological modeling, and the subtropical location allows the investigation of
98 species with different latitudinal and geographical distributions. We employed
99 regression modeling of Hong Kong shallow-marine ostracod species to show

100 statistical relationships between species abundance, distribution and environmental
101 factors. This study allows the autoecology and statistical evaluation of common
102 tropical and extratropical species, providing a baseline for ostracod-based shallow-
103 marine paleoenvironmental reconstructions of the northwestern Pacific and Indo-
104 Pacific regions.

105

106 **2. Study area**

107 Hong Kong is situated at the southeastern corner of the Pearl River (Zhujiang) Delta,
108 and has an area of 2500 km² (Fig. 1), at 22° 12.021' to 22° 33.817' N latitude, 113°
109 53.388' to 114° 26.920' E longitude. It is an ideal location to study natural and/or
110 anthropogenic impacts on benthic communities due to its complex hydrology and
111 long history of human influence. Western Hong Kong is affected by input from the
112 Pearl River, particularly during the summer heavy rainfall (Morton & Wu, 1975),
113 when surface water salinity is strongly influenced by rainfall. Eastern Hong Kong
114 waters are mainly marine and derived from the South China Sea. As one of the most
115 urbanized coastal areas in the world, human activities including rapid industrialization,
116 sewage discharge, trawling, dredging and land reclamation have led to a deteriorated
117 marine benthic ecosystem (Blackmore, 1998; Hodgkiss & Yim, 1995; Hong et al.,
118 2017; Hu et al., 2008; Morton, 1996; Morton & Blackmore, 2001; Owen & Sandhu,
119 2000; Shin, 1977; Tanner et al., 2000).

120

121 **3. Materials and Methods**

122 **3.1. Samples and laboratory procedure**

123 In January and July of 2011 we used a Van Veen Grab to collect 100 ml of sediment
124 from the uppermost centimeter of the sea floor from 52 sites in Hong Kong marine

125 waters (Fig. 1; Supplement A), 41 of which are in open waters and 11 in typhoon
126 shelter sites. Typhoon shelters are semi-enclosed areas of water designed to protect
127 moored vessels in extreme weather (Environmental Protection Department, 2011). All
128 sites are included in the Hong Kong EPD marine water and sediment quality
129 monitoring program, which has been conducted monthly since 1986 (for water) and
130 biannually (for sediment), providing comprehensive environmental data for all
131 stations (see below).

132 Sediments were wet-sieved over a 63 μm mesh sieve and air dried or oven-
133 dried at 40 $^{\circ}\text{C}$. The residue was dry-sieved over a 150 μm mesh sieve, and ostracod
134 specimens larger than 150 μm were picked; smaller individuals are mostly early instar
135 juveniles that are often not preserved (because their shells are usually thin and
136 delicate) or difficult to identify (see Yasuhara et al., 2009 and Yasuhara et al., 2017
137 for more details). In samples containing fewer than 200 specimens, we picked all
138 individuals. If there were more than 200 specimens, we picked ostracods from a split.
139 We identified each counted specimen to species level when possible. We considered
140 both an entire carapace or a single valve as one individual for counting.

141

142 **3.2 Environmental Variables**

143 We selected parameters from the EPD monitoring program (Table 1) for our
144 regression modeling (see below), including surface productivity (Chlorophyll-a, Chl;
145 Fig. 2), water depth (D; Fig. 2), bottom water dissolved oxygen (DO; Fig. 2), bottom
146 water salinity (Sal; Fig. 2), turbidity (Tur; Fig. 2), summer bottom water temperature
147 (ST – June to September average; Fig. 2), winter bottom water temperature (WT –
148 November to February average; Fig. 2), mud content (MD; Fig. 2), and heavy metal
149 concentration (Cu, Zn, and Pb; Fig. 3). These parameters are known to control

150 ostracod faunal properties (Cronin, 2015; Cronin & Vann, 2003; Hazel, 1988; Ikeya
151 & Shiozaki, 1993; Irizuki et al., 2005; Irizuki et al., 2015a; Irizuki et al., 2018; Ruiz et
152 al., 2005; Yasuhara et al., 2007; Yasuhara et al., 2012b). We used averages over the
153 entire monitoring period (1986–2011), because the ostracods in this study were
154 mostly dead shells, thus the samples should be considered time averaged. Bottom
155 water DO is the average of the summer season (June–September), due to the likely
156 importance of summer bottom water oxygen depletion.

157

158 **4. Regression modeling**

159 Multiple linear regression modeling was used to determine the relationship between
160 common ostracod species (relative abundance of each species) and environmental
161 parameters (Supplement B). All environmental parameters were log-transformed and
162 zero centered. Salinity outliers (salinity <25: DS2 and DS3) and samples with low
163 abundance (<50 specimens: ES5, MS7, VS21, VS5 & VS6) were removed from the
164 models.

165 The best-fitting models were selected based on Akaike's Information Criterion
166 (AICc) for small sample size, in which the lower score indicates the better model
167 support considering both goodness-of-fit and model complexity (Anderson &
168 Burnham, 2002). Akaike weights were used to summarize proportional support for all
169 candidate models (Anderson et al., 2000) (Table 2). We considered parameter
170 estimates averaged over models, proportional to the support that each model received
171 (Anderson et al., 2000) (Table 3). This approach accounts for the uncertainty in model
172 selection and thus leads to appropriately broader confidence intervals than obtained
173 by relying only on the single, best-supported model. The relative importance of
174 various predictor variables was measured by the sum of Akaike weights of models

175 that included the variables in question (Brunham & Anderson, 2002).

176 We explored linear dependencies by computing variance inflation factors (VIF)
177 (Legendre & Legendre, 1998) and pairwise correlations between predictor variables
178 to assess whether multicollinearity was likely to influence regression results
179 (Yasuhara et al., 2012b). The degree of freedom is more than one for the geographic
180 region variable (see below), thus we computed generalized variance inflation factors
181 (GVIF). For continuous variables, GVIF (Table 4) is the same as VIF, but for
182 categorical variables, GVIF has degrees of freedom (Df) equal to the number of
183 coefficients associated with it (Hendrickx et al., 2004). Thus, we used $GVIF^{1/2df}$ to
184 make GVIF values comparable among those with different Df. $VIF > 20$ is usually
185 indicative of high collinearity (Legendre & Legendre, 1998). Thus we calculated an
186 equivalent threshold of 4.47 (equal to $\sqrt{20}$) for $GVIF^{1/2df}$ to assess conlinearity. Also,
187 adjusted $R^2 > 0.8$ indicates a strong correlation of variables (Hoffman, 2015). In all
188 datasets, summer temperature (ST) and copper (Cu) were highly correlated
189 ($R^2=0.8217$), and the GVIFs of ST and Cu are >20 , indicating that these correlations
190 may influence regression results. Thus, we re-ran the linear regression modeling
191 without ST and Cu. The new GVIFs of all variables were under 4.47 (Table 4).

192 We considered the degree of spatial autocorrelation in model residuals by the
193 calculation of Moran's I index for the five best models. The neighborhood size was
194 set as 2, 5, 10, 20 and 50 km. We found significant spatial autocorrelation in model
195 residuals for many cases, thus we forced the geographic region variable (R) (Water
196 Control Zones defined by EPD) to be included in all models. After this treatment,
197 spatial autocorrelation was detected only in a few models for *Propontocypris* spp.,
198 *Stigmatocythere roesmani*, and *Hemikrithe orientalis*.

199 The multiple linear regression model analyses were implemented in R

200 programming language (R Core Team, 2016). We used 'M_UM_I_N' (Bartoń, 2013) for
201 model averaging and 'SPDEP' (Bivand & Piras, 2015) to measure spatial
202 autocorrelation.

203

204 **5. Results and discussions**

205 The comprehensive ostracod dataset for the 52 sites and the environmental variables
206 enabled us to elucidate distribution patterns of common ostracod taxa and their related
207 environmental factor(s). We identified 151 species belonging to 76 genera
208 (Supplement A). Among them, 18 common taxa (mainly species, a few genera) of
209 *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l., *Nipponocythere bicarinata*,
210 *Spinileberis quadriaculeata*, *Phlyctocythere japonica*, *Loxoconcha epeterseni*,
211 *Sinocytheridea impressa*, *Neomonoceratina delicata*, *Keijella kloempritis*,
212 *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea reticulata*
213 *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*,
214 *Propontocypris* spp., *Neonesidea* spp. and *Xestoleberis* spp. (Supplement B) were
215 used for regression modelling, and their relative abundances (to the total ostracod
216 abundance in a sample) show a significant relation with environmental parameters.
217 The best three regression models are presented in Table 2 and the model-averaged
218 parameter estimates in Table 3. A small percentage of specimens of phytal genera
219 (e.g., *Xestoleberis* spp., *Neonesidea* spp.) were contained in each sample, which are
220 basically allochthonous specimens in bottom sediments transported from surrounding
221 phytal environments. The value of allochthonous species to environmental
222 interpretation is limited, however most ostracod specimens in each sample are
223 composed of benthic, muddy sediment dwellers which are considered autochthonous.

224

225 Ostracods were divided into four groups based on their geographic
226 distributions, including (a) Widespread Group; (b) Temperate Group; (c) Subtropical
227 Group; (d) Tropical Group; and (e) Globally distributed Group (Fig. 4).

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229

230 **a. Widespread Group**

231 Only one species *Pistocythereis bradyi* constitutes Widespread Group.
232 *Pistocythereis bradyi* is widely distributed throughout the marginal marine
233 environments of Japan, the East and South China Seas, and the Indo-Pacific (Fig. 4).
234 Relative abundance of *P. bradyi* was highly correlated with salinity (positive), water
235 depth (negative) and Pb (negative) (Tables 2 and 3). This indicates that the species
236 prefers relatively shallow environments with high salinity (Figs. 2 and 5). In the Pearl
237 River Delta and shallow South China Sea (Fig. 4), *P. bradyi* is dominant along the
238 inner continental shelf at water depths <100 m (mostly common between 10–50 m),
239 and at salinities from 30–40 (Li, 1985; Zhao & Wang, 1990; Zhao et al., 1986).
240 *Pistocythereis bradyi* is a typical middle muddy bay species in Japan (Irizuki et al.,
241 2006; Yasuhara & Irizuki, 2001; Yasuhara & Seto, 2006), and known from open bays
242 such as Gamagyang Bay in Korea (Abe, 1988) and Malacca Strait (Whatley & Zhao,
243 1988b). In these studies, *P. bradyi* prefers relatively high salinity and deeper water in
244 the inner continental shelf. Our data agree as to the preference for high salinity, but
245 inconsistent with the literature regarding shallower water depths (Tables 2 and 3).
246 Salinity may be more important than depth, but the restricted depth range of our sites
247 (≤ 35 m) may also be a reason for this inconsistency. Our results indicate that *P.*
248 *bradyi* is sensitive to metal pollution (Tables 2 and 3).

249

250 **b. Temperate Group**

251 Five species including *Bicornucythere bisanensis* s.l., *Nipponocythere*
252 *bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica* and *Loxoconcha*
253 *epeterseni* are distributed from Japan-Russian Coast to South China Sea.

254 *Bicornucythere bisanensis* s.l. is very common in most samples, the relative
255 abundance of which was significantly correlated with water depth (negative) (Tables
256 2 and 3) and this species prefers shallower environments (Figs. 2 and 5). In Chinese
257 and Japanese coastal areas, *B. bisanensis* s.l. is abundant in brackish water (salinity:
258 20–30) at depths less than 10 m (Ikeya & Shiozaki, 1993; Irizuki et al., 2006; Zhao et
259 al., 1986). Our results confirm this preference for shallow depths. In Japan,
260 *Bicornucythere bisanensis* is tolerant of anthropogenic impacts, especially
261 eutrophication and the resulting bottom water hypoxia (Irizuki et al., 2003; Irizuki et
262 al., 2011; Irizuki et al., 2015a; Irizuki et al., 2018; Yasuhara et al., 2003; Yasuhara et
263 al., 2007; Yasuhara et al., 2012a). We did not see a significant relation between
264 relative abundance and metal concentration, productivity, or dissolved oxygen.
265 Possibly, the more dominant presence of *S. impressa* and *N. delicata*, that are neither
266 dominant or distributed throughout most of Japan, could explain this difference.
267 These species may have a higher tolerance than *B. bisanensis* s.l.. Another
268 explanation may be that different morphotypes have different ecological preferences
269 (Abe, 1988), and only Form A is known to be tolerant to eutrophication and bottom-
270 water oxygen depletion (Irizuki et al., 2011; Irizuki et al., 2015a; Irizuki et al., 2018;
271 Yasuhara & Yamazaki, 2005; Yasuhara et al., 2007). Form A is less abundant in
272 Hong Kong, and due to the difficulty of juvenile identification, we did not divide *B.*
273 *bisanensis* into morphotypes. *Bicornucythere bisanensis* s.l. is widely distributed
274 throughout marginal marine environments around Japan, Russia (Sea of Japan coast),
275 and the East and South China Seas (Fig. 4).

276 Relative abundance of *N. bicarinata* correlated with productivity (negative)
277 (Tables 2 and 3). This is a typical middle bay species in Japan (Irizuki et al., 2006),
278 abundant on muddy substrates at water depths >10 m (Yasuhara & Seto, 2006;
279 Yasuhara et al., 2005). We found *N. bicarinata* to be sensitive to eutrophication,
280 preferring lower productivity (Figs 2 and 5). This species is known from marginal
281 marine environments around Japan and the East and South China Seas (Fig. 4).

282 Relative abundance of *S. quadriaculeata* correlated to productivity (positive),
283 and turbidity (negative) (Tables 2 and 3). This is a typical inner muddy bay species in
284 Japan (Irizuki et al., 2006), which prefers silty substrates in brackish waters, at
285 salinities from 20–30, and water depths of 2–7 m (Ikeya and Shiozaki, 1993). This
286 study shows a preference for waters with higher productivity but relatively low
287 turbidity (Tables 2 and 3), so that the species is abundant in Tolo Harbour (higher
288 productivity, lower turbidity) but not in Deep Bay (higher turbidity) (Figs. 2 and 5).
289 *Spinileberis quadriaculeata* is not tolerant to seasonal anoxia or oxygen depletion (0–
290 1 mg/L) in Uranouchi Bay, Japan (Irizuki et al., 2008), but we do not find a
291 significant correlation with dissolved oxygen content, probably due to the relatively
292 high bottom-water oxygen content (2.96–6.84 mg/L) in Hong Kong (Fig. 2;
293 Supplement B). *Spinileberis quadriaculeata* is widely distributed in marginal marine
294 environments around Japan, Russia (Sea of Japan coast), and the East and South
295 China Seas (Fig. 4).

296 Relative abundance of *P. japonica* correlated with water depth (positive)
297 (Tables 2 and 3). This species is known from relatively deeper waters (>40 m) in the
298 East China Sea (Ishizaki, 1981; Wang et al., 1988). At our sites, it has its greatest
299 abundance at the deeper southern sites (Fig. 5). *Phlyctocythere japonica* is distributed
300 around Japan (Yasuhara et al., 2002) and the East and South China Seas (Fig. 4).

301 Similarly to *P. japonica*, relative abundance of *L. epeterseni* correlated with water
302 depth (positive), and turbidity (negative) (Tables 2 and 3). It occurs in the southern
303 and eastern, deeper and less turbid regions of Hong Kong waters, but the trend is not
304 very clear (Figs 2 and 5). This species is also known from the deeper parts of Osaka
305 Bay (Yasuhara & Irizuki, 2001) and marginal marine environments around Japan
306 (Ishizaki, 1968), the East China Sea (Hou et al., 1982), and the South China Sea (Cao,
307 1998) (Fig. 4). This species is reported as *Loxoconcha modesta* in Hou & Gou (2007),
308 and also has been misidentified as *Loxoconcha viva* and *Loxoconcha sinensis* (Hou &
309 Gou, 2007). Ishizaki (1968) described *Loxoconcha laeta* and *Loxoconcha modesta*,
310 but these are the females and males of the same species (Ikeya et al., 2003). Ishizaki
311 (1981) gave the new species names *Loxoconcha epeterseni* and *Loxoconcha*
312 *tosamodesta* for *Loxoconcha laeta* and *Loxoconcha modesta*, respectively, because
313 these names were junior homonyms. Since *Loxoconcha laeta* (= *epeterseni*) appears
314 earlier than *Loxoconcha modesta* (= *tosamodesta*) in the original description (Ishizaki,
315 1968), we use the name *Loxoconcha epeterseni* for this species (e.g., see Ikeya et al.,
316 2003).

317

318

319 c. Subtropical Group

320 Six species including *Sinocytheridea impressa*, *Neomonoceratina delicata*,
321 *Keijella kloempritis*, *Neosinocythere elongata*, *Stigmatocythere roesmani* and
322 *Hemicytheridea reticulata* are reported from the East China Sea to Indo-Pacific area.

323 *Sinocytheridea impressa* [= *Sinocytheridea latiovata*; see Whatley and Zhao
324 (1988a)] is the most dominant species in this study, the relative abundance of which
325 significantly correlated with salinity (negative), dissolved oxygen (negative), mud
326 content (positive) and productivity (positive) (Tables 2 and 3). This species is

327 noticeably dominant in areas characterized by a muddy bottom including northern
328 Mirs Bay, Port Shelter and coastal Southern Waters (Fig. 5). It is also abundant in
329 Tolo Harbour, an area known for its summer hypoxia and eutrophication (Hu et al.,
330 2001; Sin & Chau, 1992). These results are consistent with previous studies indicating
331 that *S. impressa* is dominant in low salinity, nutrient-rich and turbid estuaries (Irizuki
332 et al., 2005; Tanaka et al., 2011), but we did not see a significant relation with
333 turbidity (Tables 2 and 3). *Sinocytheridea impressa* is known as a euryhaline species
334 widely distributed throughout the East and South China Seas [abundant in water
335 depths of <20 m; Whatley and Zhao (1988a)], and the Indo-Pacific (Fig. 4).

336 *Neomonoceratina delicata* (= *Neomonoceratina crispata*; see Hou & Gou,
337 2007) is very common in most of the samples, and the relative abundance
338 significantly correlates with Zn (positive), salinity (positive) and turbidity (positive)
339 (Tables 2 and 3). *Neomonoceratina delicata* is a nearshore species, abundant at depths
340 less than 30 m, at relatively high salinities (>30; Zhao and Wang, 1988). It prefers the
341 higher salinity waters in Hong Kong (Figs. 2 and 5; Tables 2 and 3) and in view of its
342 positive correlation with Zn and turbidity, is likely tolerant to human-induced
343 environmental stress such as pollution and eutrophication. This species is widely
344 known from nearshore and estuarine environments in the East and South China Seas,
345 and the Indo-Pacific (Fig. 4).

346 The relative abundance of *K. kloempritensis* correlated only with water depth
347 (positive) (Fig. 6; Tables 2 and 3). Widely known from the tropical Indo-Pacific
348 region, *K. kloempritensis* is abundant along the inner continental shelf of the South
349 and East China Seas (Fig. 4), at water depths ranging from 20–50 m and salinity close
350 to normal marine (Zhao & Wang, 1990). Our modelling results are consistent with
351 this, showing a preference for the relatively deeper waters in our study (Tables 2 and

352 3). Thus, this species is probably useful for reconstructing past sea-level changes in
353 the broad tropical and subtropical Indo-Pacific and northwestern Pacific regions as a
354 deeper water indicator.

355 Relative abundance of *N. elongata* correlated only with turbidity (positive)
356 (Tables 2 and 3). This species occurs along the entire coast of China (Fig. 4) in
357 marginal marine, especially estuarine environments shallower than 20 m (Dong et al.,
358 2012; Hou & Gou, 2007; Liu et al., 2013; Liu et al., 2017; Zhao & Whatley, 1993)
359 (Fig. 4). Known from the Indo-Pacific region, our modeling results and previous
360 studies indicate consistently that *N. elongata* prefers shallow, turbid waters like Deep
361 Bay and the Pearl River Estuary (Figs 2 and 6).

362 The relative abundance of both *S. roesmani* and *H. reticulata* correlated with
363 Pb (negative) (Tables 2 and 3), thus they are sensitive to metal pollution (but note the
364 significant autocorrelation with the modeling result of *S. roesmani*) and absent in
365 areas with high metal concentrations, e.g., Tolo and Victoria Harbours (Fig. 3, 6).
366 Relative abundance of *H. reticulata* also correlated with water depth (negative)
367 (Tables 2 and 3). This species is abundant in Tolo Harbour and the inner part of Mirs
368 Bay (Fig. 6), at shallow depths, and is also consistently found in very shallow waters
369 from the Indo-Pacific (Zhao & Whatley, 1989). Their metal-pollution sensitivity is
370 contradictory because they occur in Tolo and Victoria Harbours, both polluted regions
371 of Hong Kong, and further research is needed to better understand these results (Figs
372 2 and 6). They occur in the East and South China Seas and the Indo-Pacific region
373 (Fig. 4).

374

375 **d. Tropical Group**

376 Three species including *Loxoconcha malayensis*, *Alocopocythere goujoni* and
377 *Hemikritha orientalis* are distributed from the South China Sea to the Indo-Pacific.

378 Relative abundance of *L. malayensis* correlated with dissolved oxygen
379 (negative) and mud content (negative) (Tables 2 and 3). It is a typical tropical species
380 known from the Indo-Pacific and the South China Sea (Fig. 4). We did not find a
381 correlation with temperature, likely due to the small range of variation of bottom
382 water temperatures in Hong Kong (winter temperature: 19.10–21.49°C). This species
383 prefers coarse sediments and is resistant to low oxygen content (Table 2 and 3), as
384 seen by its abundance in Victoria Harbour (Figs. 2 and 6).

385 Relative abundance of both *A. goujoni* and *H. orientalis* correlated with
386 natural factors only. *Alocopocythere goujoni* correlated with salinity (positive)
387 (Tables 2 and 3) and occurs not only in Mirs Bay where the salinity is higher, but also
388 in Deep Bay and North Western Waters where the salinity is lower than in other areas
389 (Figs 2 and 6). The Deep Bay and North Western Waters are shallow and have
390 relatively low oxygen content. The modeling result of this species shows a marginally
391 insignificant but negative relationship to oxygen content and water depth with
392 moderately high relative importance (Table 3). We explain this inconsistency by
393 considering their preference for higher salinity and shallow water depths, and also
394 their resistance to low oxygen conditions, but further research is needed to know their
395 autoecology with better confidence. Relative abundance of *H. orientalis* correlated
396 with water depth (positive) (Tables 2 and 3; but note the significant autocorrelation
397 with the modeling result of this genus), and it is more abundant in deeper waters
398 including southern Mirs Bay (Fig. 6). It is known from depths of 20–50 m in the
399 South China Sea (Zhao & Wang, 1988a), and reported from tropical Indo-Pacific
400 marginal marine environments (Fig. 4). Our regression modeling consistently shows a

401 positive relationship between relative abundance and winter temperatures, with
402 moderately high relative importance, although the correlation is marginally
403 insignificant (Table 2 and 3).

404

405 **e. Globally Distributed Group**

406 *Propontocypris* is known as a cosmopolitan genus. The relative abundance of
407 *Propontocypris* spp. significantly correlated with productivity (negative) (Tables 2
408 and 3). This negative correlation with productivity (but note a significant
409 autocorrelation with the modeling result of this genus) indicates that the genus prefers
410 less eutrophic waters (Fig. 6). *Propontocypris* is a good swimmer (Maddocks, 1969),
411 and thus may have an advantage in obtaining food in relatively food-limited
412 environments.

413 Phytal genera including *Neonesidea* spp. and *Xestoleberis* spp. have global
414 distribution and are correlated with various environmental factors. The relative
415 abundance of *Neonesidea* spp. correlated with dissolved oxygen (positive), as
416 expected for a phytal species (Smith & Kamiya, 2002; Yamada, 2007) (Table 2 and 3;
417 Fig 7). Similarly, phytal (Irizuki et al., 2008; Sato & Kamiya, 2007; Yasuhara et al.,
418 2002) *Xestoleberis* spp. correlated with dissolved oxygen (positive), turbidity
419 (negative) and mud content (negative) (Table 2 and 3; Fig. 7). This taxon's habitat
420 preference including clear water, coarse sediment, and high oxygen content are
421 reflected in our modeling. As mentioned above, the value of allochthonous phytal
422 species to environmental interpretation is limited, but they broadly reflect adjacent
423 phytal environments.

424

425 **Summary**

426 Benthic ostracods from Hong Kong marginal marine waters studied here include
427 widespread (i.e., one species distributed throughout the northwestern Pacific–Indo-
428 Pacific region), temperate (i.e., five species distributed from the South China Sea to
429 Japan and Russia), subtropical (i.e., six species distributed from the Indo-Pacific to
430 the East China Sea), and tropical (i.e., three species distributed in the Indo-Pacific and
431 South China Sea) species and three globally distributed genera (Fig. 4). We provide a
432 robust baseline of autoecology for these common ostracod taxa based on rigorous
433 statistical modeling using comprehensive environmental data. We established reliable
434 indicator taxa for water depth, mud content, salinity, turbidity, dissolved oxygen,
435 heavy metal pollution (Pb and Zn) and eutrophication (chlorophyll-a) (Table 5). Thus
436 our results are applicable for future ostracod-based paleoenvironmental studies in a
437 wide range of localities from the tropics to the extratropics, and from the Indian
438 Ocean to the northwestern Pacific. We established pollution and eutrophication
439 indicator species in tropical environments for the first time. Anthropocene
440 paleoenvironmental and paleoecological studies in the tropics are urgently needed
441 because (1) the tropics are seriously under-studied (Wilkinson et al., 2014; Yasuhara
442 et al., 2012a), (2) tropical environments and ecosystems are vulnerable and sensitive
443 to human influences (Jackson et al., 2001; Pandolfi et al., 2003), and (3) Indo-Pacific
444 tropical environments have been seriously degraded by the human activity of rapidly
445 developing countries (Bellwood et al., 2004; Jackson, 2008; Knowlton & Jackson,
446 2008). Our results provide useful and reliable tools for tropical Anthropocene
447 research in the broad Indo-Pacific region.

448

449 **Acknowledgement**

450 We thank the Environmental Protection Department of Hong Kong, especially K.
451 Yung, for support; L. Wong, C. Law, M. Lo, and the staff of the Electronic
452 Microscope Unit of the University of Hong Kong for their technical support; B. Lin, S.
453 Wang, R. Mak and V. Wang for helping sampling; P. Frenzel, M. Warne, E. Thomas
454 and O. Friedrich for comments on an early version of the manuscript; S.W.A. Naqvi
455 for editing; T. Irizuki, T. M. Cronin, and J. Rodríguez-Lázaro for reviewing our
456 manuscript. The data used are listed in the tables and supplements. The work
457 described in this paper was partially supported by the Environment and Conservation
458 Fund of Hong Kong (project code: 19/2012), the General Research Fund of the
459 Research Grants Council of Hong Kong (project code: HKU 17303115), the Early
460 Career Scheme of the Research Grants Council of Hong Kong (project code: HKU
461 709413P), and the Seed Funding Programme for Basic Research of the University of
462 Hong Kong (project codes: 201111159140, 201611159053) (to MY).

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796 Chinese with English abstract).

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798

799 **Captions**

800

801 Fig. 1 Locality map showing the 52 sampling sites across Hong Kong, including 41
802 open water sites (blue dots) and 11 typhoon shelter sites (red open dots). From west to
803 east, DS: Deep Bay; NS: North Western waters; SS: Southern waters; VS: Victoria
804 Harbour; ES: Eastern Buffer; JS: Junk Bay; TS: Tolo Harbour; PS: Port Shelter; MS:
805 Mirs Bay.

806

807 Fig. 2 Spatial distribution of environmental parameters in Hong Kong. Mean surface-
808 water chlorophyll-a concentration; water depth; summer (June to September) bottom-
809 water dissolved oxygen content; mean bottom-water salinity; mean turbidity; mean
810 summer (June to September) bottom-water temperature; mean winter (November to
811 February) bottom-water temperature; and mean mud content. All are averaged values
812 of the data obtained during 1986–2013 (Table 1).

813

814 Fig. 3 Spatial distribution of environmental parameters in Hong Kong. Mean copper
815 (Cu) concentration, mean lead (Pb) concentration, and mean zinc (Zn) concentration
816 in surface sediments. All are averaged values of the data obtained during 1986–2013
817 (Table 1).

818

819 Fig. 4 Geographical distributions of the 18 taxa in the northwestern Pacific and Indo-
820 Pacific regions, including *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l.,
821 *Nipponocythere bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica*,
822 *Loxoconcha epeterseni*, *Sinocytheridea impressa*, *Neomonoceratina delicata*, *Keijella*
823 *kloempritensis*, *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea*
824 *reticulata* *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*,
825 *Propontocypris* spp., *Neonesidea* spp. and *Xestoleberis* spp.. The following references
826 were used mainly to determine the geographical distributions of the species: Al
827 Jumaily and Al-Sheikhly (1999); Dewi (1997); Dong et al. (2012); Fauzielly et al.
828 (2013); Gu et al. (2017); Hong et al. (2017); Hou and Gou (2007); Hussain et al.
829 (2004); Hussain et al. (2010); Hussain and Mohan (2000, 2001); Irizuki et al. (2006);
830 Irizuki et al. (2009); Iwatani et al. (2014); Jie et al. (2013); Li (1985); Mostafawi
831 (1992); Nishath et al. (2017); Noraswana et al. (2014); Pugliese et al. (2006);
832 Schornikov et al. (2014); Tanaka et al. (2009); Tanaka et al. (2011); Wang et al.
833 (1988); Wang and Zhang (1987); Wang and Zhao (1985); Zhao (1984); Zhao and
834 Wang (1988a, 1988b, 1990); Zhao and Whatley (1993); Zhou et al. (2015). Note that
835 *Sinocytheridea impressa* is know to be distributed in Japan, but their Japanese
836 distribution is very limited in certain areas of the southern part of Japan (Iwasaki,
837 1992; Tanaka et al. 2019). Thus, we did not indicate their Japanese-Russian coast
838 distribution in this figure.

839

840 Fig. 5 Spatial distribution of the relative abundance for *Pistocythereis bradyi*,
841 *Bicornucythere bisanensis* s.l., *Nipponocythere bicarinata*, *Spinileberis*
842 *quadriaculeata*, *Phlyctocythere japonica*, *Loxoconcha epeterseni*, *Sinocytheridea*

843 *impressa*, and *Neomonoceratina delicata* in Hong Kong. See Figure 1 for sampling
844 stations.

845

846 Fig. 6 Spatial distribution of the relative abundance for *Keijella kloempritis*,
847 *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea reticulata*
848 *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*, and
849 *Propontocypris* spp. in Hong Kong. See Figure 1 for sampling stations.

850

851 Fig. 7. Spatial distribution of the relative abundance for *Neonesidea* spp. and
852 *Xestoleberis* spp. in Hong Kong. See Figure 1 for sampling stations.

853

854

855 Table 1. Summary of marine water/sediment parameters. Note: 1. Summer: June,
856 July, August and September. 2. Winter: November, December, January and February.

857

858 Table 2. Best three regression models of the relative abundance of common species,
859 including *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l., *Nipponocythere*
860 *bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica*, *Loxoconcha*
861 *epeterseni*, *Sinocytheridea impressa*, *Neomonoceratina delicata*, *Keijella*
862 *kloempritis*, *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea*
863 *reticulata* *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*,
864 *Propontocypris* spp., *Neonesidea* spp. and *Xestoleberis* spp.. The table shows the
865 coefficient of each term, adjusted R^2 , the Akaike information criterion corrected for
866 small sample size (AICc), and the Akaike weight (AW). Bold denotes significance at

867 P < 0.05. Overall P is < 0.05 in all models. R: region. Other abbreviations are found in
868 Table 1.

869

870 Table 3. Model-averaged parameter estimates and CIs of the relative abundance for
871 common species including *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l.,
872 *Nipponocythere bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica*,
873 *Loxoconcha epeterseni*, *Sinocytheridea impressa*, *Neomonoceratina delicata*, *Keijella*
874 *kloempritensis*, *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea*
875 *reticulata* *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*,
876 *Propontocypris* spp., *Neonesidea* spp. and *Xestoleberis* spp.. CIs, confidence
877 intervals; RI, relative importance (the sum of the Akaike weights of models that
878 include the variable in question; see Materials and Methods); R, region. Other
879 abbreviations are found in Table 1. Bold denotes CIs that exclude zero. For R,
880 coefficient, lower CI, and upper CI values shown are averages of those for geographic
881 regions.

882

883 Table 4. GVIF value for Environmental Variables. Df, degree of freedom; R, region.
884 Other abbreviations are found in Table 1.

885

886 Table 5. Summary of autoecology for common ostracod taxa. Chl: Chlorophyll-a; D:
887 Water Depth; DO: Dissolved Oxygen; MD: Mud Content; Sal: Salinity; Tur:
888 Turbidity; WT: Winter Temperature; Pb: Lead; Zn: Zinc; R: Region. + and - marks
889 indicate significant positive and negative correlations, respectively.

890

891

892 Supplement A. Ostracod faunal list.

893

894 Supplement B. Dataset used for the regression modeling.

895