



# Baseline for ostracod-based northwestern Pacific and Indo-Pacific shallow-marine paleoenvironmental reconstructions: ecological modeling of species distributions

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**Abstract.** Fossil ostracods have been widely used for Quaternary paleoenvironmental reconstructions, especially in marginal marine environments (e.g., for water depth, temperature, salinity, oxygen levels, pollution). But our knowledge of indicator species autoecology, the base of paleoenvironmental reconstructions, remains limited and commonly lacks robust statistical support and comprehensive comparison with environmental data. We analyzed marginal marine ostracod taxa at 52 sites in Hong Kong for which comprehensive environmental data are available. We applied linear regression models to reveal relationships between species distribution and environmental factors for 18 common taxa (mainly species, a few genera) in our Hong Kong dataset and identified indicator species of environmental parameters. For example, *Sinocytheridea impressa*, a widely distributed euryhaline species throughout the East and South China Sea and the Indo-Pacific, indicates eutrophication and bottom-water hypoxia. *Neomonoceratina delicata*, a widely known species from nearshore and estuarine environments in the East and South China Sea and the Indo-Pacific, indicates heavy metal pollution and increased turbidity. The 18 taxa used for this study are widely distributed geographically and divided into the following groups: widespread (throughout the northwestern Pacific and Indo-Pacific regions), temperate (South China Sea to Russia (Sea of Japan coast) and Japan), subtropical (Indo-Pacific to the East China Sea), tropical (Indo-Pacific and South China Sea), and globally distributed. With statistical support from ecological modeling and comprehensive environmental data, these results provide a robust baseline for ostracod-based Quaternary–Anthropocene paleoenvironmental reconstruc-

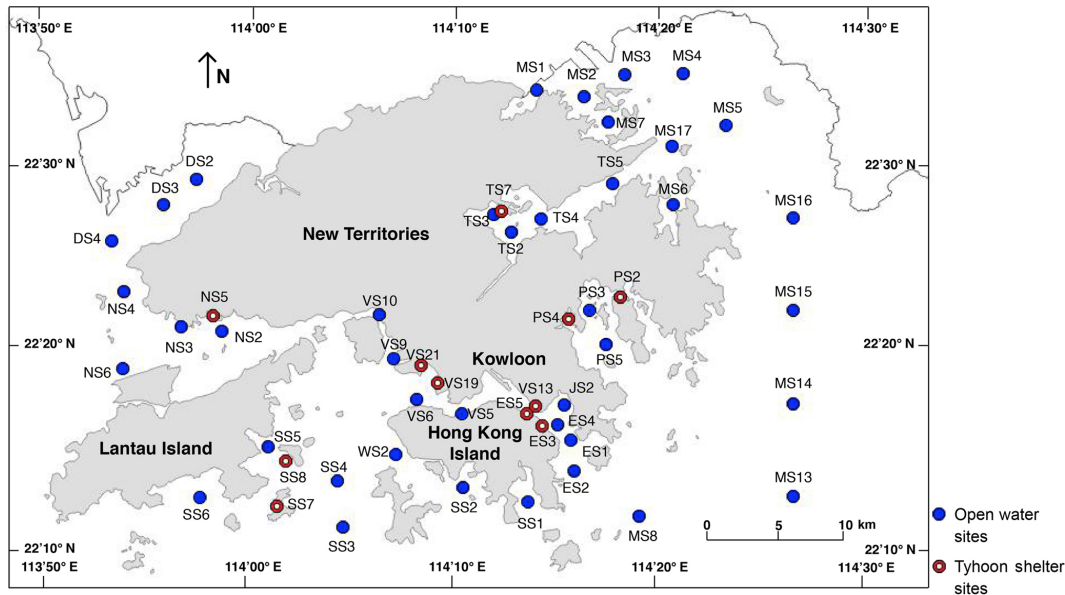
tions in the tropical–extratropical northwestern Pacific and Indo-Pacific.

## Highlights.

1. We provide a robust baseline for ostracod-based (microscopic Arthropods) paleoenvironmental reconstructions from Quaternary and Anthropocene marginal marine sediments.
2. The studied species have wide distributions over the tropics and extratropics of the northwestern Pacific and Indo-Pacific.
3. Ecological modeling has established ostracod species as reliable indicators for paleoenvironmental reconstructions.

## 1 Introduction

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



**Figure 1.** Locality map showing the 52 sampling sites across Hong Kong, including 41 open water sites (blue dots) and 11 typhoon shelter sites (red open dots). From west to east, DS: Deep Bay; NS: northwestern waters; SS: southern waters; VS: Victoria Harbour; ES: eastern buffer; JS: Junk Bay; TS: Tolo Harbour; PS: Port Shelter; MS: Mirs Bay.

(Alberti et al., 2013; Dong et al., 2012; Irizuki et al., 2015b; Tanaka et al., 2011; Yasuhara and Seto, 2006; Yasuhara et al., 2005; Zhou et al., 2015; Wang et al., 2018). Due to high sedimentation rates ( $> 1 \text{ cm year}^{-1}$ ), fossil ostracods from these sediments allow for the high-resolution reconstruction of human-induced environmental changes (pollution, eutrophication, bottom oxygen depletion) over the past century (Irizuki et al., 2011, 2015a, 2018; Yasuhara et al., 2003, 2007).

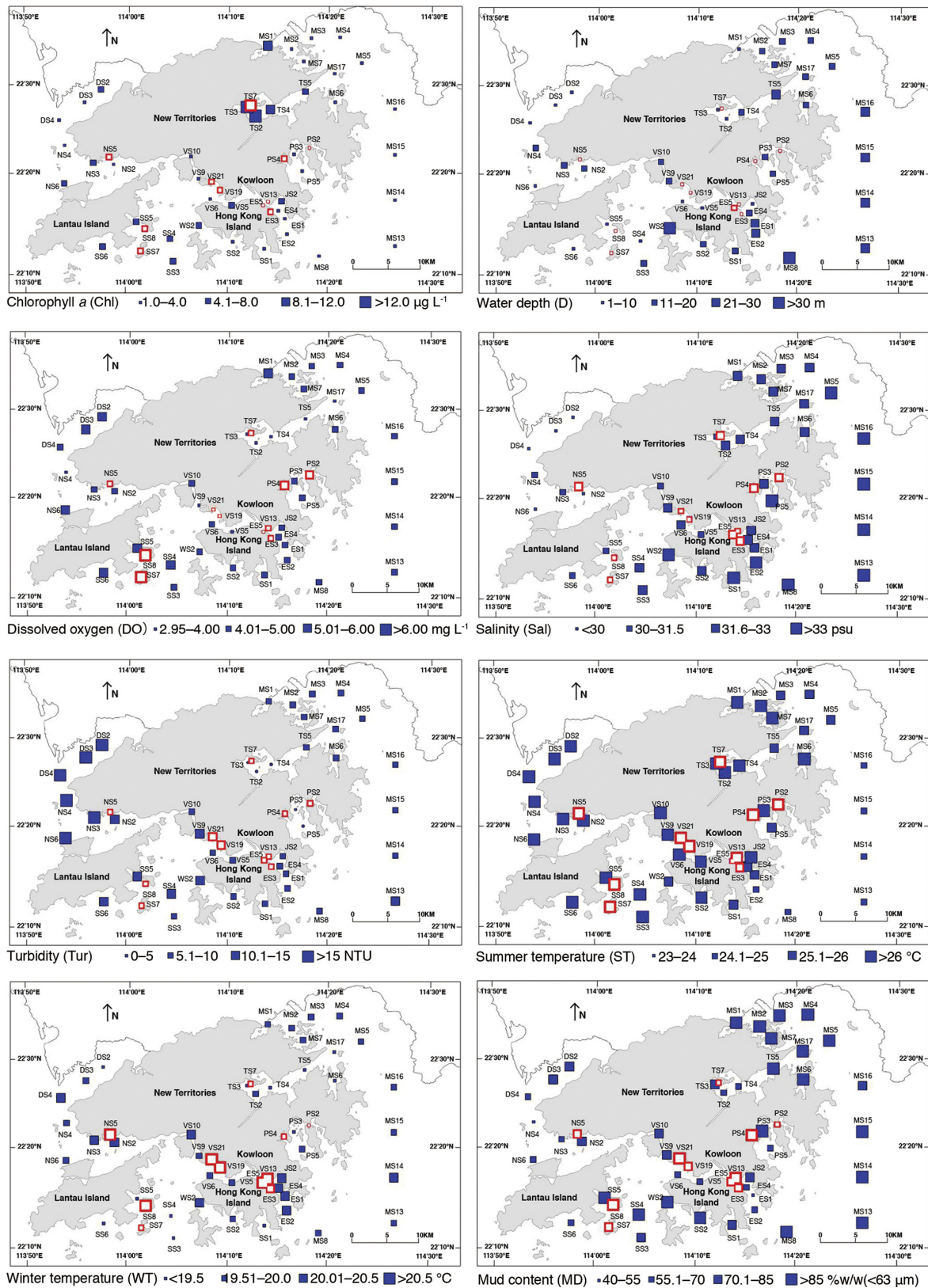
Many have evaluated the autoecology of ostracod indicator species as the basis for paleoenvironmental reconstructions (Hazel, 1988; Irizuki et al., 2003; Ozawa et al., 2004; Stepanova et al., 2003; Wang et al., 1988; Yasuhara and Seto, 2006; Zhao, 1984; Zhao and Wang, 1988a, b). Yet these studies tend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

Hong Kong constitutes an ideal location for a marine ecological modeling approach in the northwestern Pacific and Indo-Pacific regions because of an extensive and intensive marine environmental monitoring program and a subtropical location where tropical and temperate species coexist. This program provides robust datasets for ecological modeling, and the subtropical location allows for the investigation of species with different latitudinal and geographi-

cal distributions. We employed regression modeling of Hong Kong shallow-marine ostracod species to show statistical relationships between species abundance, distribution, and environmental factors. This study allows for the autoecology and statistical evaluation of common tropical and extratropical species, providing a baseline for ostracod-based shallow-marine paleoenvironmental reconstructions of the northwestern Pacific and Indo-Pacific regions.

## 2 Study area

Hong Kong is situated at the southeastern corner of the Pearl River (Zhujiang) Delta and has an area of  $2500 \text{ km}^2$  (Fig. 1) at  $22^{\circ}12.021'$  to  $22^{\circ}33.817'$  N latitude,  $113^{\circ}53.388'$  to  $114^{\circ}26.920'$  E longitude. It is an ideal location to study natural and/or anthropogenic impacts on benthic communities due to its complex hydrology and long history of human influence. Western Hong Kong is affected by input from the Pearl River, particularly during the summer heavy rainfall (Morton and Wu, 1975) when surface water salinity is strongly influenced by rainfall. Eastern Hong Kong waters are mainly marine and derived from the South China Sea. As one of the most urbanized coastal areas in the world, human activities including rapid industrialization, sewage discharge, trawling, dredging, and land reclamation have led to a deteriorated marine benthic ecosystem (Blackmore, 1998; Hodgkiss and Yim, 1995; Hong et al., 2017; Hu et al., 2008; Morton, 1996; Morton and Blackmore, 2001; Owen and Sandhu, 2000; Shin, 2011; Tanner et al., 2000).



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

**Table 1.** Summary of marine water–sediment parameters.

Parameter (abbreviation)	Unit	Sampling depth–material	Season
Chlorophyll <i>a</i> (Chl)	$\mu\text{g L}^{-1}$	Surface water	All year
Water depth (D)	m		All year
Dissolved oxygen (DO)	$\text{mg L}^{-1}$	Bottom water	Summer <sup>1</sup>
Mud content (MD)	% w/w (< 63 $\mu\text{m}$ )	Bottom sediment	All year
Salinity (Sal)		Bottom water	All year
Turbidity (Tur)	NTU	Bottom water	All year
Summer temperature (ST)	$^{\circ}\text{C}$	Bottom water	Summer <sup>1</sup>
Winter temperature (WT)	$^{\circ}\text{C}$	Bottom water	Winter <sup>2</sup>
Copper (Cu)	$\text{mg kg}^{-1}$	Bottom sediment	All year
Lead (Pb)	$\text{mg kg}^{-1}$	Bottom sediment	All year
Zinc (Zn)	$\text{mg kg}^{-1}$	Bottom sediment	All year

<sup>1</sup> Summer: June, July, August, and September. <sup>2</sup> Winter: November, December, January, and February.

### 3 Materials and methods

#### 3.1 Samples and laboratory procedure

In January and July 2011 we used a Van Veen Grab to collect 100 mL of sediment from the uppermost centimeter of the seafloor from 52 sites in Hong Kong marine waters (Fig. 1; Supplement S1), 41 of which are in open waters and 11 in typhoon shelter sites. Typhoon shelters are semi-enclosed areas of water designed to protect moored vessels in extreme weather (Environmental Protection Department of Hong Kong, 2011). All sites are included in the Hong Kong EPD marine water and sediment quality monitoring program, which has been conducted monthly (for water) and biannually since 1986 (for sediment), providing comprehensive environmental data for all stations (see below).

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

#### 3.2 Environmental variables

We selected parameters from the EPD monitoring program (Table 1) for our regression modeling (see below), including surface productivity (chlorophyll *a*, Chl; Fig. 2), water depth (D; Fig. 2), bottom-water dissolved oxygen (DO; Fig. 2), bottom-water salinity (Sal; Fig. 2), turbidity (Tur; Fig. 2), summer bottom-water temperature (ST – June to

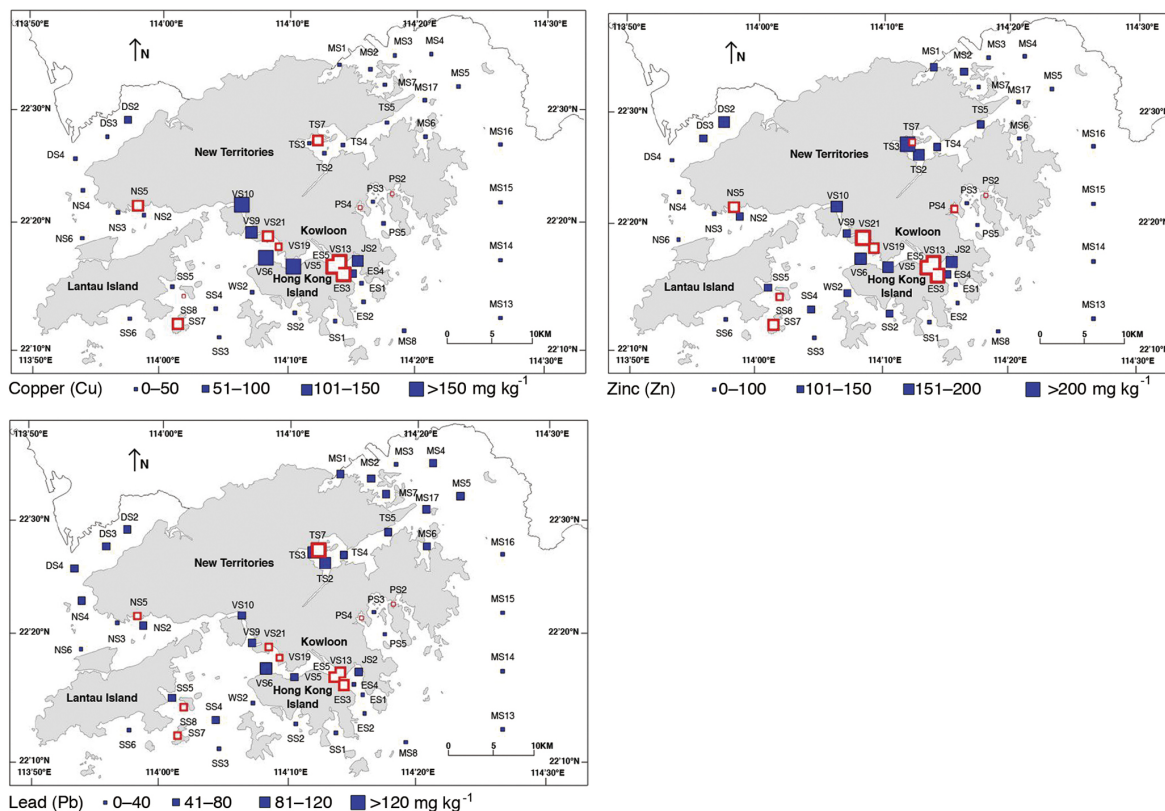
September average; Fig. 2), winter bottom-water temperature (WT – November to February average; Fig. 2), mud content (MD; Fig. 2), and heavy metal concentration (Cu, Zn, and Pb; Fig. 3). These parameters are known to control ostracod faunal properties (Cronin, 2015; Cronin and Vann, 2003; Hazel, 1988; Ikeya and Shiozaki, 1993; Irizuki et al., 2005, 2015a, 2018; Ruiz et al., 2005; Yasuhara et al., 2007, 2012b). We used averages over the entire monitoring period (1986–2011) because the ostracods in this study were mostly dead shells, and thus the samples should be considered time averaged. Bottom-water DO is the average of the summer season (June–September) due to the likely importance of summer bottom-water oxygen depletion.

### 4 Regression modeling

Multiple linear regression modeling was used to determine the relationship between common ostracod species (relative abundance of each species) and environmental parameters (Supplement S2). All environmental parameters were log-transformed and zero centered. Salinity outliers (salinity < 25: DS2 and DS3) and samples with low abundance (< 50 specimens: ES5, MS7, VS21, VS5, and VS6) were removed from the models.

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





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

measured by the sum of the Akaike weights of models that included the variables in question (Burnham and Anderson, 2002).

We explored linear dependencies by computing variance inflation factors (VIFs) (Legendre and Legendre, 1998) and pairwise correlations between predictor variables to assess whether multicollinearity was likely to influence regression results (Yasuhara et al., 2012b). The degree of freedom is more than one for the geographic region variable (see below), and thus we computed generalized variance inflation factors (GVIFs). For continuous variables, GVIF (Table 4) is the same as VIF, but for categorical variables, GVIF has degrees of freedom (DoF) equal to the number of coefficients associated with it (Hendrickx et al., 2004). Thus, we used  $\text{GVIF}^{1/2\text{DoF}}$  to make GVIF values comparable among those with different DoF.  $\text{VIF} > 20$  is usually indicative of high collinearity (Legendre and Legendre, 1998). Thus we calculated an equivalent threshold of 4.47 (equal to  $\sqrt{20}$ ) for  $\text{GVIF}^{1/2\text{DoF}}$  to assess conlinearity. Also, adjusted  $R^2 > 0.8$  indicates a strong correlation of variables (Hoffman, 2015). In all datasets, summer temperature (ST) and copper (Cu) were highly correlated ( $R^2 = 0.8217$ ), and the GVIFs of ST and Cu are  $> 20$ , indicating that these correlations may influence regression results. Thus, we re-ran the linear regression

modeling without ST and Cu. The new GVIFs of all variables were under 4.47 (Table 4).

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

The multiple linear regression model analyses were implemented in R programming language (R Core Team, 2016). We used “ $M_{UMIN}$ ” (Bartoń, 2013) for model averaging and “SPDEP” (Bivand and Piras, 2015) to measure spatial autocorrelation.

## 5 Results and discussion

The comprehensive ostracod dataset for the 52 sites and the environmental variables enabled us to elucidate distribution patterns of common ostracod taxa and their related environmental factor(s). We identified 151 species belong-

**Table 2.** Best three regression models of the relative abundance of common species, including *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l., *Nipponocythere bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica*, *Loxoconcha epeterseni*, *Sinocytheridea impressa*, *Neomonoceratina delicata*, *Keijella kloempritisensis*, *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea reticulata*, *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*, *Propontocypris* spp., *Neonesidea* spp., and *Xestoleberis* spp. The table shows the coefficient of each term, adjusted  $R^2$ , the Akaike information criterion corrected for small sample size (AIC), and the Akaike weight (AW). Bold denotes significance at  $P < 0.05$ . Overall,  $P$  is  $< 0.05$  in all models. R: region. Other abbreviations are found in Table 1.

Model	Chl	D	DO	MD	Sal	Tur	WT	Pb	Zn	R	$R^2$	AIC	AW
<i>Pistocythereis bradyi</i>													
1		<b>-0.12</b>			<b>2.67</b>			<b>-0.21</b>		<b>-0.06</b>	0.61	-163.64	0.52
2		<b>-0.13</b>			<b>2.87</b>	0.04		<b>-0.20</b>		<b>-0.05</b>	0.61	-159.79	0.08
3		<b>-0.12</b>	0.07		<b>2.83</b>			<b>-0.21</b>		<b>-0.07</b>	0.60	-159.42	0.06
<i>Bicornucythere bisanensis</i> s.l.													
1		<b>-0.09</b>		<b>-0.23</b>						<b>0.02</b>	0.60	-137.80	0.12
2		<b>-0.08</b>								<b>-0.01</b>	0.56	-136.77	0.07
3				<b>-0.29</b>				<b>0.18</b>		0.00	0.58	-136.77	0.05
<i>Nipponocythere bicarinata</i>													
1	<b>-0.07</b>		<b>-0.12</b>							<b>0.03</b>	0.43	-200.57	0.11
2	<b>-0.09</b>									<b>0.03</b>	0.39	-200.38	0.10
3	<b>-0.09</b>	-0.03	<b>-0.16</b>							<b>0.04</b>	0.45	-199.30	0.06
<i>Spinileberis quadriaculeata</i>													
1	0.06					<b>-0.09</b>				<b>-0.04</b>	0.63	-183.88	0.10
2		<b>-0.05</b>								<b>0.02</b>	0.60	-182.94	0.06
3	<b>0.08</b>					<b>-0.09</b>	-0.75			<b>-0.04</b>	0.65	-182.66	0.05
<i>Phlyctocythere japonica</i>													
1		<b>0.04</b>								0.00	0.28	-238.60	0.19
2		<b>0.03</b>			0.33					-0.02	0.30	-237.01	0.09
3		<b>0.03</b>						-0.02		0.00	0.27	-235.62	0.04
<i>Loxoconcha epeterseni</i>													
1		<b>0.03</b>			<b>-0.33</b>	<b>-0.03</b>				<b>0.01</b>	0.49	-288.61	0.11
2	<b>0.02</b>	<b>0.04</b>		<b>-0.04</b>	<b>-0.34</b>	<b>-0.04</b>				<b>0.00</b>	0.56	-287.76	0.07
3	0.02	<b>0.04</b>			<b>-0.34</b>	<b>-0.04</b>				0.00	0.51	-287.31	0.06
<i>Sinocytheridea impressa</i>													
1	<b>0.33</b>		<b>-1.47</b>	<b>0.75</b>	<b>-9.13</b>					<b>0.34</b>	0.55	-37.29	0.27
2	<b>0.41</b>		<b>-1.48</b>		<b>-8.75</b>					<b>0.37</b>	0.50	-35.24	0.10
3			<b>-1.12</b>	<b>0.94</b>	<b>-10.30</b>					<b>0.44</b>	0.49	-34.78	0.08
<i>Neomonoceratina delicata</i>													
1					<b>3.77</b>	<b>0.34</b>			<b>0.41</b>	<b>-0.13</b>	0.48	-82.57	0.29
2			0.43		<b>5.02</b>	<b>0.31</b>			<b>0.39</b>	<b>-0.20</b>	0.50	-81.21	0.15
3					<b>3.47</b>	<b>0.33</b>		-0.20	<b>0.55</b>	<b>-0.12</b>	0.48	-79.32	0.06
<i>Keijella kloempritisensis</i>													
1		<b>0.06</b>						<b>-0.06</b>		<b>-0.02</b>	0.56	-202.12	0.12
2		<b>0.08</b>								<b>-0.02</b>	0.53	-201.51	0.09
3		<b>0.06</b>		0.09				<b>-0.08</b>		<b>-0.02</b>	0.58	-200.86	0.06

Table 2. Continued.

Model	Chl	D	DO	MD	Sal	Tur	WT	Pb	Zn	R	R <sup>2</sup>	AIC	AW
<i>Neosinocythere elongata</i>													
1	<b>-0.02</b>					<b>0.09</b>				<b>-0.03</b>	0.76	-244.70	0.09
2				<b>-0.06</b>		<b>0.08</b>				<b>-0.03</b>	0.76	-244.42	0.08
3						<b>0.09</b>				<b>-0.03</b>	0.74	-244.15	0.07
<i>Stigmatocythere roesmani</i>													
1								<b>-0.08</b>		<b>0.00</b>	0.23	-225.23	0.07
2					0.36			<b>-0.07</b>		<b>-0.02</b>	0.25	-224.06	0.04
3			<b>0.10</b>		<b>0.67</b>			<b>-0.07</b>		<b>-0.03</b>	0.30	-224.03	0.04
<i>Hemicytheridea reticulata</i>													
1		<b>-0.03</b>						<b>-0.04</b>		<b>0.01</b>	0.23	-270.79	0.14
2	0.02	<b>-0.02</b>						<b>-0.04</b>		0.01	0.26	-269.44	0.07
3	<b>0.03</b>							<b>-0.03</b>		0.00	0.19	-268.64	0.05
<i>Loxoconcha malayensis</i>													
1		<b>-0.03</b>	<b>-0.14</b>	<b>-0.12</b>						<b>0.03</b>	0.55	-229.55	0.10
2	<b>0.04</b>		<b>-0.13</b>	<b>-0.12</b>						<b>0.02</b>	0.55	-229.42	0.09
3		<b>-0.04</b>	<b>-0.14</b>	<b>-0.10</b>				-0.04		<b>0.03</b>	0.57	-228.47	0.06
<i>Alocopocythere goujoni</i>													
1					<b>0.21</b>					<b>-0.04</b>	0.68	-331.97	0.09
2		<b>-0.01</b>			<b>0.28</b>				<b>-0.01</b>	<b>-0.04</b>	0.71	-330.52	0.05
3		<b>-0.01</b>			<b>0.27</b>			<b>-0.02</b>		<b>-0.04</b>	0.71	-330.45	0.04
<i>Hemikrithe orientalis</i>													
1		<b>0.03</b>					<b>0.46</b>			0.00	0.19	-249.44	0.11
2		<b>0.03</b>	<b>0.07</b>							0.00	0.18	-248.67	0.07
3		<b>0.04</b>	0.06				<b>0.42</b>			0.00	0.23	-248.60	0.07
<i>Propontocypris</i> spp.													
1	<b>-0.28</b>			<b>0.46</b>						<b>0.04</b>	0.20	-72.47	0.15
2	<b>-0.24</b>									<b>0.07</b>	0.13	-71.74	0.10
3	<b>-0.24</b>			<b>0.49</b>			-2.46			0.02	0.22	-70.76	0.06
<i>Neonesidea</i> spp.													
1	<b>-0.12</b>			<b>-0.25</b>					<b>0.19</b>	<b>0.05</b>	0.28	-149.00	0.09
2	<b>-0.11</b>		<b>0.33</b>	<b>-0.24</b>			-1.13		<b>0.20</b>	<b>0.05</b>	0.31	-147.86	0.05
3			0.21							0.02	0.08	-147.40	0.04
<i>Xestoleberis</i> spp.													
1		<b>0.04</b>	<b>0.15</b>	<b>-0.11</b>		<b>-0.08</b>		<b>0.05</b>		<b>-0.02</b>	0.62	-225.55	0.09
2		<b>0.03</b>	<b>0.15</b>	<b>-0.09</b>		<b>-0.09</b>				<b>-0.02</b>	0.59	-225.29	0.08
3				<b>-0.09</b>		<b>-0.06</b>				<b>0.00</b>	0.52	-224.60	0.06

ing to 76 genera (Supplement S1). Among them, 18 common taxa (mainly species, a few genera) of *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l., *Nipponocythere bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica*, *Loxoconcha epeterseni*, *Sinocytheridea impressa*, *Neomonocerotina delicata*, *Keijella kloempritis*, *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea retic-*

*ulata* *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*, *Propontocypris* spp., *Neonesidea* spp., and *Xestoleberis* spp. (Supplement S2) were used for regression modeling, and their relative abundances (to the total ostracod abundance in a sample) show significant relations to environmental parameters. The best three regression models are presented in Table 2 and the model-averaged parameter

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

Term	RI	Coefficient	Lower CI	Upper CI	Term	RI	Coefficient	Lower CI	Upper CI
<i>Pistocythereis bradyi</i>					<i>Bicornucythere bisanensis</i> s.l.				
R	1.00	-0.06	-0.15	0.04	R	1.00	0.01	-0.11	0.12
<b>Sal</b>	<b>1.00</b>	<b>2.71</b>	<b>1.53</b>	<b>3.88</b>	MD	0.63	-0.26	-0.52	0.00
<b>D</b>	<b>1.00</b>	<b>-0.12</b>	<b>-0.19</b>	<b>-0.06</b>	<b>D</b>	<b>0.62</b>	<b>-0.08</b>	<b>-0.16</b>	<b>0.00</b>
<b>Pb</b>	<b>0.97</b>	<b>-0.21</b>	<b>-0.32</b>	<b>-0.10</b>	Pb	0.38	0.14	-0.05	0.33
Tur	0.12	0.04	-0.07	0.15	DO	0.20	0.17	-0.15	0.48
Zn	0.11	-0.05	-0.23	0.13	Chl	0.19	0.06	-0.07	0.19
DO	0.10	0.06	-0.18	0.31	Tur	0.19	0.07	-0.08	0.22
WT	0.10	0.33	-0.98	1.64	Zn	0.16	-0.01	-0.28	0.25
Chl	0.09	0.02	-0.08	0.11	Sal	0.12	-0.02	-1.86	1.82
MD	0.08	-0.01	-0.20	0.18	WT	0.10	0.06	-1.80	1.92
<i>Nipponocythere bicarinata</i>					<i>Spinileberis quadriaculeata</i>				
R	1.00	0.02	-0.04	0.09	R		-0.01	-0.10	0.07
<b>Chl</b>	<b>0.92</b>	<b>-0.08</b>	<b>-0.14</b>	<b>-0.02</b>	<b>Tur</b>	<b>0.66</b>	<b>-0.09</b>	<b>-0.17</b>	<b>0.00</b>
DO	0.50	-0.14	-0.30	0.02	<b>Chl</b>	<b>0.54</b>	<b>0.06</b>	<b>0.00</b>	<b>0.13</b>
D	0.30	-0.03	-0.08	0.02	D	0.45	-0.05	-0.10	0.01
WT	0.25	-0.03	-0.08	0.02	WT	0.32	-0.76	-1.82	0.31
Sal	0.24	0.51	-0.35	1.36	DO	0.19	0.10	-0.10	0.30
Tur	0.19	-0.04	-0.11	0.04	MD	0.17	-0.07	-0.23	0.09
Zn	0.18	-0.04	-0.12	0.04	Pb	0.17	-0.05	-0.16	0.07
Pb	0.13	-0.03	-0.11	0.06	Zn	0.14	0.03	-0.09	0.15
MD	0.10	0.00	-0.13	0.13	Sal	0.13	0.11	-1.03	1.26
<i>Phlyctocythere japonica</i>					<i>Loxoconcha epeterseni</i>				
R	1.00	-0.01	-0.05	0.03	R	1.00	0.00	-0.02	0.03
<b>D</b>	<b>0.80</b>	<b>0.03</b>	<b>0.01</b>	<b>0.06</b>	<b>D</b>	<b>0.94</b>	<b>0.03</b>	<b>0.00</b>	<b>0.05</b>
Sal	0.42	0.46	-0.10	1.02	<b>Tur</b>	<b>0.76</b>	<b>-0.03</b>	<b>-0.06</b>	<b>0.00</b>
Pb	0.21	-0.03	-0.08	0.03	Sal	0.53	-0.30	-0.62	0.02
Zn	0.20	-0.02	-0.07	0.03	MD	0.38	-0.04	-0.08	0.01
WT	0.15	0.22	-0.38	0.81	Chl	0.30	0.02	-0.01	0.04
DO	0.14	0.03	-0.08	0.15	DO	0.26	0.04	-0.02	0.10
Tur	0.12	0.00	-0.05	0.05	Pb	0.17	0.01	-0.02	0.05
Chl	0.12	0.00	-0.04	0.05	WT	0.13	-0.13	-0.48	0.22
MD	0.11	0.00	-0.09	0.08	Zn	0.12	0.01	-0.03	0.04
<i>Sinocytheridea impressa</i>					<i>Neomonoceratina delicata</i>				
R	1.00	0.36	-0.09	0.81	R	1.00	-0.15	-0.42	0.12
<b>Sal</b>	<b>0.99</b>	<b>-9.26</b>	<b>-14.61</b>	<b>-3.91</b>	<b>Zn</b>	<b>0.94</b>	<b>0.41</b>	<b>0.11</b>	<b>0.70</b>
<b>DO</b>	<b>0.91</b>	<b>-1.42</b>	<b>-2.48</b>	<b>-0.37</b>	<b>Sal</b>	<b>0.93</b>	<b>4.06</b>	<b>1.00</b>	<b>7.13</b>
<b>MD</b>	<b>0.75</b>	<b>0.82</b>	<b>0.07</b>	<b>1.57</b>	<b>Tur</b>	<b>0.84</b>	<b>0.33</b>	<b>0.06</b>	<b>0.59</b>
<b>Chl</b>	<b>0.74</b>	<b>0.82</b>	<b>0.03</b>	<b>0.70</b>	DO	0.33	0.45	-0.17	1.06
WT	0.20	<b>0.82</b>	-2.34	8.89	Pb	0.17	-0.18	-0.67	0.30
Zn	0.13	<b>0.82</b>	-0.68	0.51	MD	0.14	0.25	-0.33	0.84
Tur	0.11	<b>0.82</b>	-0.61	0.30	D	0.11	-0.01	-0.22	0.20
D	0.11	<b>0.82</b>	-0.29	0.41	WT	0.11	-0.86	-4.32	2.60
Pb	0.10	<b>0.82</b>	-0.62	0.46	Chl	0.09	0.00	-0.24	0.23



Table 3. Continued.

Term	RI	Coefficient	Lower CI	Upper CI	Term	RI	Coefficient	Lower CI	Upper CI
<i>Keijella kloempritis</i>					<i>Neosinocythere elongata</i>				
R	1.00	-0.02	-0.09	0.04	R	1.00	-0.03	-0.07	0.00
<b>D</b>	<b>0.86</b>	<b>0.06</b>	<b>0.02</b>	<b>0.11</b>	<b>Tur</b>	<b>1.00</b>	<b>0.08</b>	<b>0.04</b>	<b>0.13</b>
Pb	0.58	-0.08	-0.17	0.01	MD	0.33	-0.05	-0.13	0.02
Sal	0.35	0.68	-0.21	1.58	Chl	0.30	-0.02	-0.05	0.01
MD	0.25	0.08	-0.05	0.21	WT	0.26	-0.33	-0.85	0.18
Tur	0.24	0.05	-0.03	0.14	Zn	0.21	-0.02	-0.06	0.02
Chl	0.22	-0.04	-0.11	0.03	Pb	0.19	-0.02	-0.07	0.02
Zn	0.17	0.02	-0.11	0.14	D	0.12	0.00	-0.03	0.03
WT	0.14	0.33	-0.55	1.22	DO	0.12	-0.02	-0.11	0.07
DO	0.11	0.03	-0.14	0.19	Sal	0.10	0.04	-0.40	0.49
<i>Stigmatocythere roesmani</i>					<i>Hemicytheridea reticulata</i>				
R	1.00	-0.01	-0.07	0.05	R	1.00	0.01	-0.02	0.03
Sal	0.61	0.62	-0.04	1.27	<b>Pb</b>	<b>0.67</b>	<b>-0.04</b>	<b>-0.07</b>	<b>0.00</b>
<b>Pb</b>	<b>0.61</b>	<b>-0.06</b>	<b>-0.12</b>	<b>0.00</b>	<b>D</b>	<b>0.66</b>	<b>-0.02</b>	<b>-0.04</b>	<b>0.00</b>
Tur	0.37	0.04	-0.01	0.10	Chl	0.49	0.03	0.00	0.05
Zn	0.31	-0.05	-0.11	0.02	WT	0.24	-0.24	-0.64	0.16
DO	0.31	0.09	-0.04	0.22	MD	0.23	-0.03	-0.09	0.02
MD	0.23	-0.06	-0.16	0.04	Zn	0.17	-0.01	-0.06	0.05
Chl	0.19	-0.02	-0.07	0.02	DO	0.13	0.02	-0.05	0.10
WT	0.19	0.35	-0.33	1.02	Tur	0.13	-0.01	-0.05	0.03
D	0.14	-0.01	-0.05	0.04	Sal	0.11	-0.05	-0.43	0.34
<i>Loxococoncha malayensis</i>					<i>Alocopocythere goujoni</i>				
R	1.00	0.02	-0.02	0.06	R	1.00	-0.03	-0.05	-0.02
<b>DO</b>	<b>0.87</b>	<b>-0.14</b>	<b>-0.25</b>	<b>-0.03</b>	<b>Sal</b>	<b>0.78</b>	<b>0.22</b>	<b>0.03</b>	<b>0.41</b>
<b>MD</b>	<b>0.85</b>	<b>-0.11</b>	<b>-0.20</b>	<b>-0.02</b>	D	0.46	-0.01	-0.02	0.00
D	0.48	-0.03	-0.06	0.00	DO	0.43	-0.03	-0.07	0.01
Chl	0.40	0.03	-0.01	0.08	Pb	0.31	-0.01	-0.03	0.01
Pb	0.29	-0.04	-0.10	0.02	Zn	0.29	-0.01	-0.03	0.01
WT	0.26	0.41	-0.21	1.03	WT	0.24	0.13	-0.08	0.33
Zn	0.20	-0.03	-0.10	0.04	Tur	0.18	0.01	-0.01	0.03
Sal	0.15	-0.26	-0.91	0.39	MD	0.14	-0.01	-0.04	0.02
Tur	0.11	-0.01	-0.07	0.05	Chl	0.11	0.00	-0.01	0.01
<i>Hemikritha orientalis</i>					<i>Propontocypris</i> spp.				
R	1.00	0.00	-0.04	0.03	R	1.00	0.05	-0.19	0.30
<b>D</b>	<b>0.77</b>	<b>0.03</b>	<b>0.00</b>	<b>0.05</b>	<b>Chl</b>	<b>0.80</b>	<b>-0.26</b>	<b>-0.47</b>	<b>-0.04</b>
WT	0.46	0.43	-0.07	0.93	MD	0.58	0.50	-0.03	1.03
DO	0.44	0.08	-0.02	0.17	WT	0.29	-2.60	-6.48	1.28
Sal	0.30	0.37	-0.17	0.90	Pb	0.19	-0.18	-0.55	0.20
Pb	0.22	-0.03	-0.08	0.02	Sal	0.17	-1.48	-4.88	1.92
Tur	0.17	0.02	-0.03	0.07	DO	0.15	-0.27	-0.99	0.45
Chl	0.14	-0.01	-0.05	0.03	Zn	0.14	-0.03	-0.48	0.41
Zn	0.11	0.00	-0.05	0.05	D	0.13	0.04	-0.17	0.26
MD	0.10	-0.01	-0.08	0.07	Tur	0.10	0.01	-0.29	0.32

Table 3. Continued.

Term	RI	Coefficient	Lower CI	Upper CI	Term	RI	Coefficient	Lower CI	Upper CI
<i>Neonesidea</i> spp.					<i>Xestoleberis</i> spp.				
R	1.00	0.02	−0.09	0.13	R	1.00	−0.01	−0.06	0.05
<b>DO</b>	<b>0.72</b>	<b>0.30</b>	<b>0.02</b>	<b>0.57</b>	<b>Tur</b>	<b>0.77</b>	<b>−0.07</b>	<b>−0.12</b>	<b>−0.01</b>
Zn	0.58	0.15	−0.01	0.31	<b>MD</b>	<b>0.66</b>	<b>−0.10</b>	<b>−0.19</b>	<b>0.00</b>
MD	0.46	−0.23	−0.49	0.03	<b>DO</b>	<b>0.63</b>	<b>0.13</b>	<b>0.00</b>	<b>0.26</b>
Chl	0.42	−0.09	−0.21	0.02	D	0.42	0.03	−0.01	0.07
WT	0.32	−1.13	−2.69	0.42	Pb	0.33	0.04	−0.02	0.11
Tur	0.24	−0.09	−0.22	0.05	Sal	0.27	0.46	−0.24	1.15
D	0.23	0.05	−0.04	0.15	WT	0.19	−0.37	−1.06	0.31
Pb	0.17	0.05	−0.13	0.24	Zn	0.14	0.00	−0.09	0.08
Sal	0.15	−0.60	−2.20	1.01	Chl	0.10	0.00	−0.05	0.05

Table 4. GVIF value for environmental variables. DoF, degrees of freedom; R, region. Other abbreviations are found in Table 1.

Environmental variables	GVIF	DoF	GVIF <sup>1/2DoF</sup>
Chl	7.40	1	2.72
D	6.41	1	2.53
DO	4.49	1	2.12
MD	3.72	1	1.93
Sal	9.43	1	3.07
Tur	6.67	1	2.58
Pb	9.98	1	3.16
Zn	10.05	1	3.17
WT	2.39	1	1.55
R	1266.30	9	1.49

estimates in Table 3. A small percentage of specimens of phytal genera (e.g., *Xestoleberis* spp., *Neonesidea* spp.) were contained in each sample, which are basically allochthonous specimens in bottom sediments transported from surrounding phytal environments. The value of allochthonous species to environmental interpretation is limited; however, most ostracod specimens in each sample are composed of benthic muddy sediment dwellers, which are considered autochthonous.

Ostracods were divided into four groups based on their geographic distributions: (a) widespread group; (b) temperate group; (c) subtropical group; (d) tropical group; and (e) globally distributed group (Fig. 4).

### 5.1 Widespread group

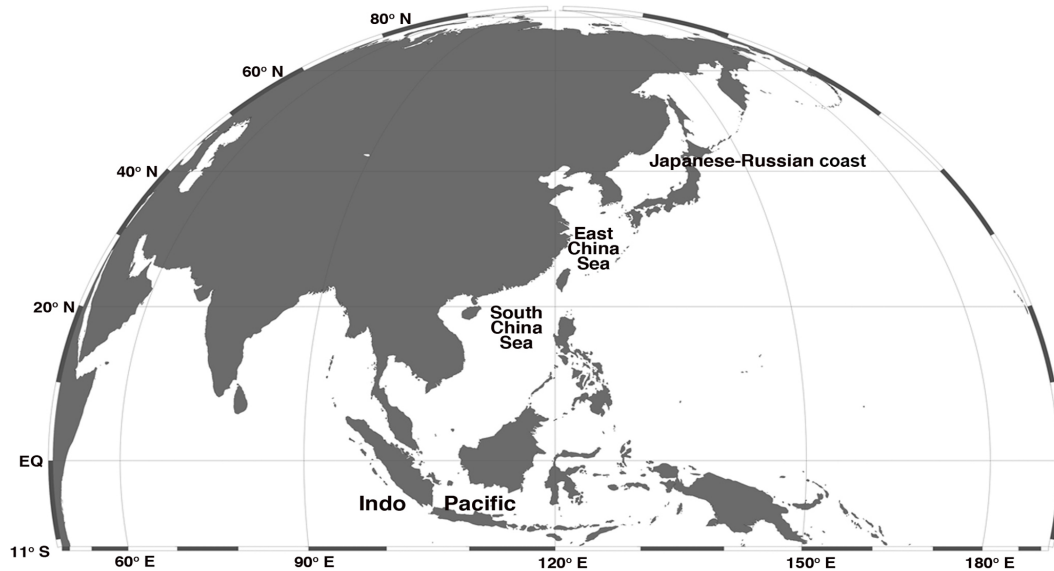
The widespread group constitutes only one species, *Pistocythereis bradyi*. *Pistocythereis bradyi* is widely distributed throughout the marginal marine environments of Japan, the East and South China Sea, and the Indo-Pacific (Fig. 4). Relative abundance of *P. bradyi* was highly correlated with salinity (positive), water depth (negative), and Pb (negative) (Ta-

bles 2 and 3). This indicates that the species prefers relatively shallow environments with high salinity (Figs. 2 and 5). In the Pearl River Delta and shallow South China Sea (Fig. 4), *P. bradyi* is dominant along the inner continental shelf at water depths < 100 m (mostly common between 10 and 50 m) and at salinities from 30–40 (Li, 1985; Zhao and Wang, 1990; Zhao et al., 1986). *Pistocythereis bradyi* is a typical middle muddy bay species in Japan (Irizuki et al., 2006; Yasuhara and Irizuki, 2001; Yasuhara and Seto, 2006), and known from open bays such as Gamagyang Bay in Korea (Abe, 1988) and Malacca Strait (Whatley and Zhao, 1988b). In these studies, *P. bradyi* prefers relatively high salinity and deeper water in the inner continental shelf. Our data agree as to the preference for high salinity, but are inconsistent with the literature regarding shallower water depths (Tables 2 and 3). Salinity may be more important than depth, but the restricted depth range of our sites ( $\leq 35$  m) may also be a reason for this inconsistency. Our results indicate that *P. bradyi* is sensitive to metal pollution (Tables 2 and 3).

### 5.2 Temperate group

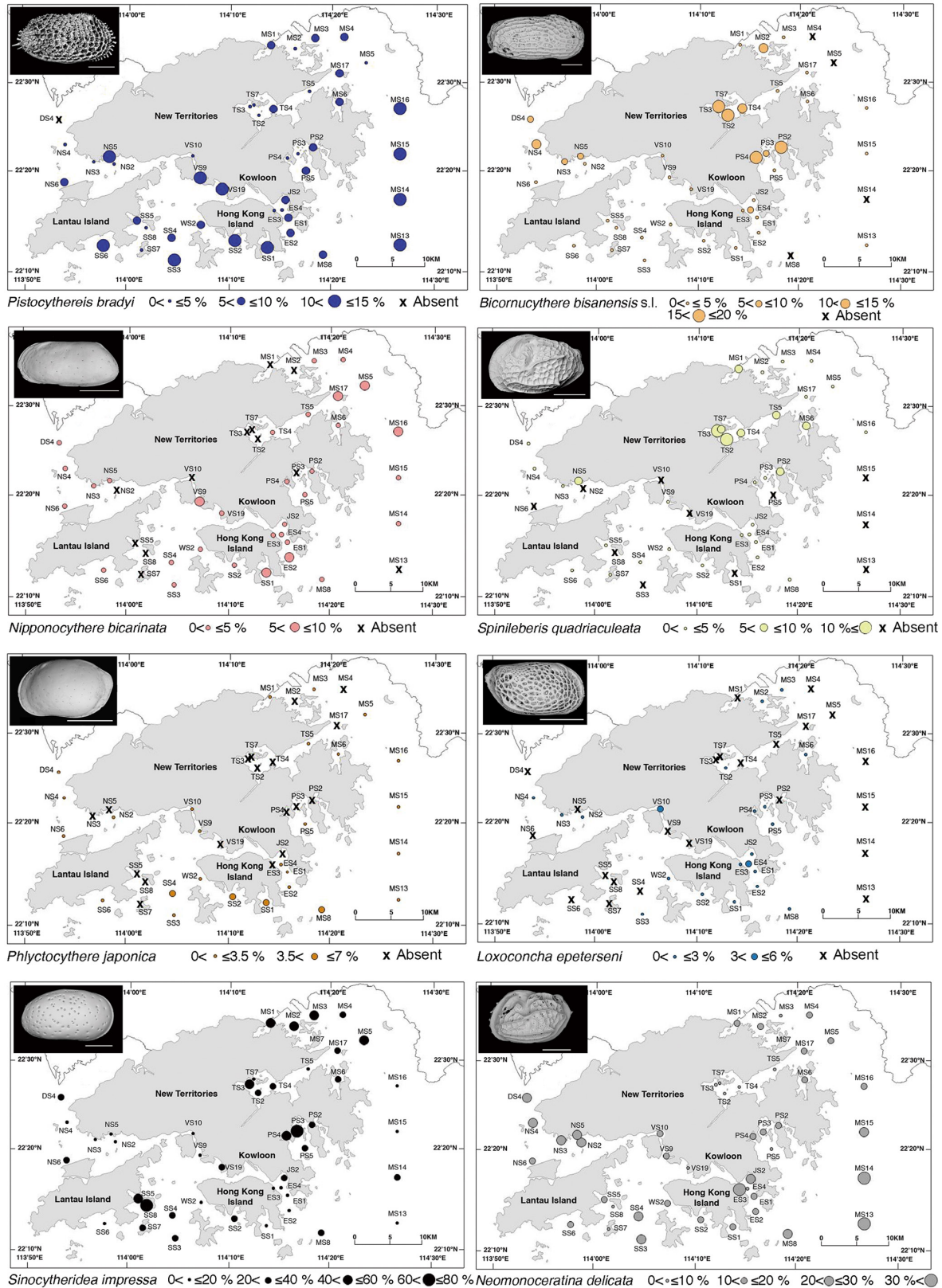
Five species including *Bicornucythere bisanensis* s.l., *Nipponocythere bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica*, and *Loxoconcha epeterseni* are distributed from the Japanese–Russian coast to the South China Sea.

*Bicornucythere bisanensis* s.l. is very common in most samples, the relative abundance of which was significantly correlated with water depth (negative) (Tables 2 and 3), and this species prefers shallower environments (Figs. 2 and 5). In Chinese and Japanese coastal areas, *B. bisanensis* s.l. is abundant in brackish water (salinity: 20–30) at depths less than 10 m (Ikeya and Shiozaki, 1993; Irizuki et al., 2006; Zhao et al., 1986). Our results confirm this preference for shallow depths. In Japan, *Bicornucythere bisanensis* is tolerant of anthropogenic impacts, especially eutrophication and the resulting bottom-water hypoxia (Irizuki et al., 2003, 2011, 2015a, 2018; Yasuhara et al., 2003, 2007,



Species	Indo-Pacific	South China Sea	East China Sea	Japanese-Russian coast
<i>Pistocythereis bradyi</i>	(a) _____			
<i>Bicornucythere bisanensis</i> s.l.		_____		
<i>Nipponocythere bicarinata</i>		_____		
<i>Spinileberis quadriaculeata</i>		(b) _____		
<i>Phlyctocythere japonica</i>		_____		
<i>Loxoconcha epeterseni</i>		_____		
<i>Sinocytheridea impressa</i>	_____			
<i>Neomonoceratina delicata</i>	_____			
<i>Keijella kloempritensis</i>	_____			
<i>Neosinocythere elongata</i>	(c) _____			
<i>Stigmatocythere roesmani</i>	_____			
<i>Hemicytheridea reticulata</i>	_____			
<i>Loxoconcha malayensis</i>	_____			
<i>Alocopocythere goujoni</i>	(d) _____			
<i>Hemikrithe orientalis</i>	_____			
<i>Propontocypris</i> spp.	_____			
<i>Neonesidea</i> spp.	(e) _____			
<i>Xestoleberis</i> spp.	_____			

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



**Figure 5.** Spatial distribution of the relative abundance for *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l., *Nipponocythere bicarinata*, *Spinileberis quadriaculeata*, *Phlyctocythere japonica*, *Loxoconcha epeterseni*, *Sinocytheridea impressa*, and *Neomonoceratina delicata* in Hong Kong. The scale bar is 200  $\mu$ m.

2012a). We did not see a significant relation between relative abundance and metal concentration, productivity, or dissolved oxygen. Possibly, the more dominant presence of *S. impressa* and *N. delicata*, which are neither dominant or distributed throughout most of Japan, could explain this difference. These species may have a higher tolerance than *B. bisanensis* s.l. Another explanation may be that different morphotypes have different ecological preferences (Abe, 1988), and only Form A is known to be tolerant to eutrophication and bottom-water oxygen depletion (Irizuki et al., 2011, 2015a, 2018; Yasuhara and Yamazaki, 2005; Yasuhara et al., 2007). Form A is less abundant in Hong Kong, and due to the difficulty of juvenile identification, we did not divide *B. bisanensis* into morphotypes. *Bicornucythere bisanensis* s.l. is widely distributed throughout marginal marine environments around Japan, Russia (Sea of Japan coast), and the East and South China Sea (Fig. 4).

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

The relative abundance of *S. quadriaculeata* correlated with productivity (positive) and turbidity (negative) (Tables 2 and 3). This is a typical inner muddy bay species in Japan (Irizuki et al., 2006), which prefers silty substrates in brackish waters at salinities from 20 to 30 and water depths of 2–7 m (Ikeya and Shiozaki, 1993). This study shows a preference for waters with higher productivity but relatively low turbidity (Tables 2 and 3) so that the species is abundant in Tolo Harbour (higher productivity, lower turbidity) but not in Deep Bay (higher turbidity) (Figs. 2 and 5). *Spinileberis quadriaculeata* is not tolerant to seasonal anoxia or oxygen depletion (0–1 mg L<sup>-1</sup>) in Uranouchi Bay, Japan (Irizuki et al., 2008), but we do not find a significant correlation with dissolved oxygen content, probably due to the relatively high bottom-water oxygen content (2.96–6.84 mg L<sup>-1</sup>) in Hong Kong (Fig. 2; Supplement S2). *Spinileberis quadriaculeata* is widely distributed in marginal marine environments around Japan, Russia (Sea of Japan coast), and the East and South China Sea (Fig. 4).

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

Similarly to *P. japonica*, the relative abundance of *L. epeterseni* correlated with water depth (positive) and turbidity (negative) (Tables 2 and 3). It occurs in the southern and

eastern, deeper, and less turbid regions of Hong Kong waters, but the trend is not very clear (Figs. 2 and 5). This species is also known from the deeper parts of Osaka Bay (Yasuhara and Irizuki, 2001) and marginal marine environments around Japan (Ishizaki, 1968), the East China Sea (Hou et al., 1982), and the South China Sea (Cao, 1998) (Fig. 4). This species is reported as *Loxoconcha modesta* in Hou and Gou (2007) and has also been misidentified as *Loxoconcha viva* and *Loxoconcha sinensis* (Hou and Gou, 2007). Ishizaki (1968) described *Loxoconcha laeta* and *Loxoconcha modesta*, but these are the females and males of the same species (Ikeya et al., 2003). Ishizaki (1981) gave the new species names *Loxoconcha epeterseni* and *Loxoconcha tosamodesta* for *Loxoconcha laeta* and *Loxoconcha modesta*, respectively, because these names were junior homonyms. Since *Loxoconcha laeta* (*epeterseni*) appears earlier than *Loxoconcha modesta* (*tosamodesta*) in the original description (Ishizaki, 1968), we use the name *Loxoconcha epeterseni* for this species (see, e.g., Ikeya et al., 2003).

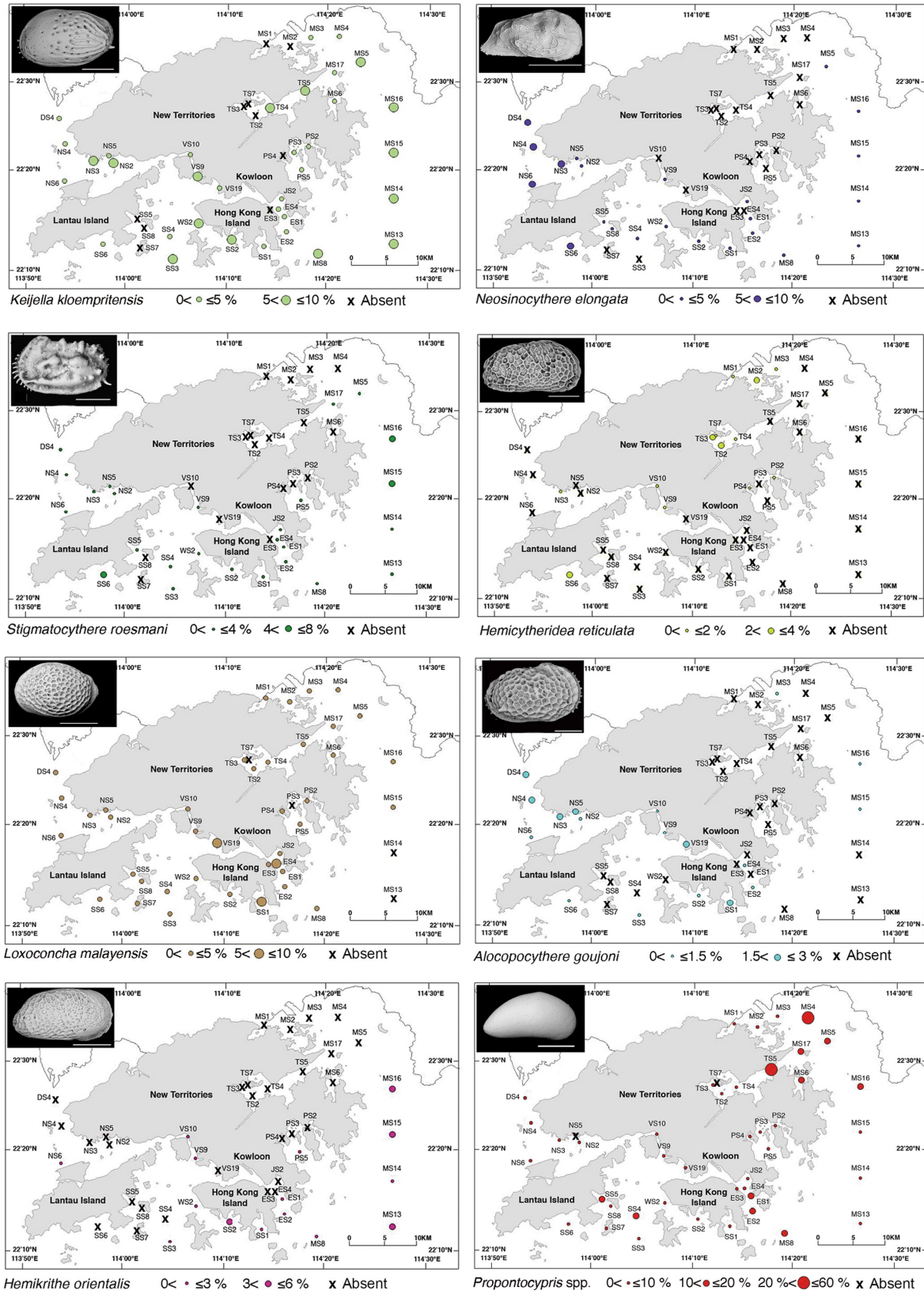
### 5.3 Subtropical group

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

*Sinocytheridea impressa* (*Sinocytheridea latiovata*; see Whatley and Zhao, 1988a) is the most dominant species in this study, the relative abundance of which is significantly correlated with salinity (negative), dissolved oxygen (negative), mud content (positive), and productivity (positive) (Tables 2 and 3). This species is noticeably dominant in areas characterized by a muddy bottom including northern Mirs Bay, Port Shelter, and coastal southern waters (Fig. 5). It is also abundant in Tolo Harbour, an area known for its summer hypoxia and eutrophication (Hu et al., 2001; Sin and Chau, 1992). These results are consistent with previous studies indicating that *S. impressa* is dominant in low-salinity, nutrient-rich, and turbid estuaries (Irizuki et al., 2005; Tanaka et al., 2011), but we did not see a significant relation with turbidity (Tables 2 and 3). *Sinocytheridea impressa* is known as a euryhaline species widely distributed throughout the East and South China Sea (abundant in water depths of < 20 m; Whatley and Zhao, 1988a) and the Indo-Pacific (Fig. 4).

*Neomonoceratina delicata* (*Neomonoceratina crispata*; see Hou and Gou, 2007) is very common in most of the samples, and the relative abundance significantly correlates with Zn (positive), salinity (positive), and turbidity (positive) (Tables 2 and 3). *Neomonoceratina delicata* is a nearshore species abundant at depths less than 30 m at relatively high salinities (> 30; Zhao and Wang, 1988b). It prefers the higher-salinity waters in Hong Kong (Figs. 2 and 5; Tables 2 and 3) and in view of its positive correlation with Zn and





**Figure 6.** Spatial distribution of the relative abundance for *Keijella kloempritis*, *Neosinocythere elongata*, *Stigmatocythere roesmani*, *Hemicytheridea reticulata*, *Loxoconcha malayensis*, *Alocopocythere goujoni*, *Hemikrithe orientalis*, and *Propontocypris* spp. in Hong Kong. The scale bar is 200 μm.



turbidity, is likely tolerant to human-induced environmental stress such as pollution and eutrophication. This species is widely known from nearshore and estuarine environments in the East and South China Sea and the Indo-Pacific (Fig. 4).

The relative abundance of *K. kloempritis* correlated only with water depth (positive) (Fig. 6; Tables 2 and 3). *Keijella kloempritis* is widely known from the tropical Indo-Pacific region and abundant along the inner continental shelf of the South and East China Sea (Fig. 4) at water depths ranging from 20 to 50 m and salinity close to normal marine (Zhao and Wang, 1990). Our modeling results are consistent with this, showing a preference for the relatively deeper waters in our study (Tables 2 and 3). Thus, this species is probably useful for reconstructing past sea-level changes in the broad tropical and subtropical Indo-Pacific and northwestern Pacific regions as a deeper water indicator.

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

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

#### 5.4 Tropical group

The three species *Loxoconcha malayensis*, *Alocopocythere goujoni*, and *Hemikrithe orientalis* are distributed from the South China Sea to the Indo-Pacific.

The relative abundance of *L. malayensis* correlated with dissolved oxygen (negative) and mud content (negative) (Tables 2 and 3). It is a typical tropical species known from the Indo-Pacific and the South China Sea (Fig. 4). We did not find a correlation with temperature, likely due to the small range of variation of bottom-water temperatures in Hong Kong (winter temperature: 19.10–21.49 °C). This species

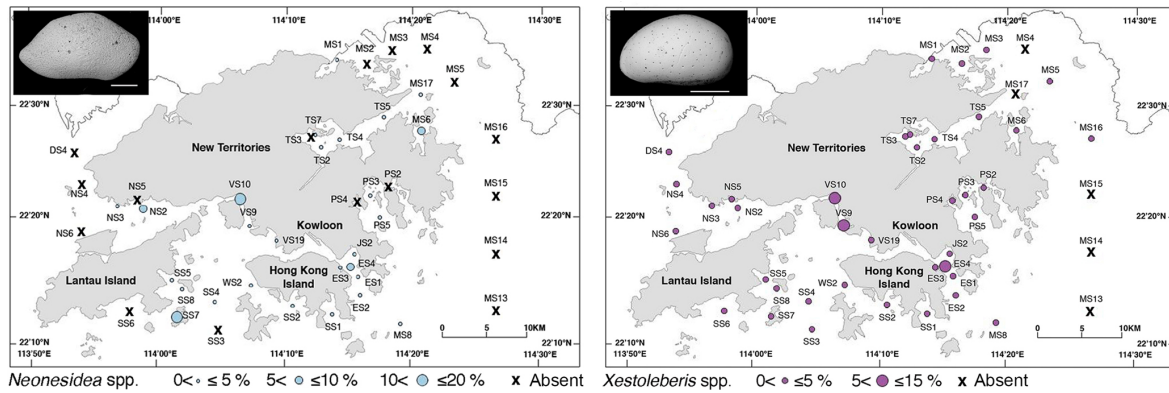
prefers coarse sediments and is resistant to low oxygen content (Table 2 and 3), as seen by its abundance in Victoria Harbour (Figs. 2 and 6).

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

#### 5.5 Globally distributed group

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

Phytoplankton genera including *Neonesidea* spp. and *Xestoleberis* spp. have a global distribution and are correlated with various environmental factors. The relative abundance of *Neonesidea* spp. correlated with dissolved oxygen (positive), as expected for a phytoplankton species (Smith and Kamiya, 2002; Yamada, 2007) (Tables 2 and 3; Fig. 7). Similarly, phytoplankton (Irizuki et al., 2008; Sato and Kamiya, 2007; Yasuhara et al., 2002) *Xestoleberis* spp. correlated with dissolved oxygen (positive), turbidity (negative), and mud content (negative) (Table 2 and 3; Fig. 7). This taxon's habitat preference, including clear water, coarse sediment, and high oxygen content, is reflected in our modeling. As mentioned above, the value of allochthonous phytoplankton species to environmental interpretation



**Figure 7.** Spatial distribution of the relative abundance for *Neonesidea* spp. and *Xestoleberis* spp. in Hong Kong. The scale bar is 200  $\mu$ m.

**Table 5.** Summary of autoecology for common ostracod taxa. Chl: chlorophyll *a*; D: water depth; DO: dissolved oxygen; MD: mud content; Sal: salinity; Tur: turbidity; WT: winter temperature; Pb: lead; Zn: zinc; R: region. The + and – marks indicate significant positive and negative correlations, respectively.

Taxa	Chl	D	DO	MD	Sal	Tur	WT	Pb	Zn	R
<i>Pistocythereis bradyi</i>		–			+			–		
<i>Bicornucythere bisanensis</i> s.l.		–								
<i>Nipponocythere bicarinata</i>	–					–				
<i>Spinileberis quadriculeata</i>	+									
<i>Phlyctocythere japonica</i>		+								
<i>Loxoconcha epeterseni</i>		+				–				
<i>Sinocythereidea impressa</i>	+		–	+	–					
<i>Neomonoceratina delicata</i>					+	+			+	
<i>Keijella kloempritenensis</i>		+								
<i>Neosinocythere elongata</i>						+				
<i>Stigmatocythere roesmani</i>									–	
<i>Hemicytheridea reticulata</i>		–							–	
<i>Loxoconcha malayensis</i>			–	–						
<i>Alocopocythere goujoni</i>					+					
<i>Hemikrithie orientalis</i>		+								
<i>Propontocypris</i> spp.	–									
<i>Neonesidea</i> spp.			+							
<i>Xestoleberis</i> spp.			+	–		–				

is limited, but they broadly reflect adjacent phytoplankton environments.

## 6 Summary

Benthic ostracods from Hong Kong marginal marine waters studied here include widespread (i.e., one species distributed throughout the northwestern Pacific–Indo-Pacific region), temperate (i.e., five species distributed from the South China Sea to Japan and Russia), subtropical (i.e., six species distributed from the Indo-Pacific to the East China Sea), and tropical (i.e., three species distributed in the Indo-Pacific and South China Sea) species and three globally distributed genera (Fig. 4). We provide a robust baseline of the autoecology for these common ostracod taxa based on rigorous statistical

modeling using comprehensive environmental data. We established reliable indicator taxa for water depth, mud content, salinity, turbidity, dissolved oxygen, heavy metal pollution (Pb and Zn), and eutrophication (chlorophyll *a*) (Table 5). Thus, our results are applicable for future ostracod-based paleoenvironmental studies in a wide range of localities from the tropics to the extratropics and from the Indian Ocean to the northwestern Pacific. We established pollution and eutrophication indicator species in tropical environments for the first time. Anthropocene paleoenvironmental and paleoecological studies in the tropics are urgently needed because (1) the tropics are seriously under-studied (Wilkinson et al., 2014; Yasuhara et al., 2012a), (2) tropical environments and ecosystems are vulnerable and sensitive to human influences (Jackson et al., 2001; Pandolfi et al., 2003), and (3) Indo-

Pacific tropical environments have been seriously degraded by human activity in rapidly developing countries (Bellwood et al., 2004; Jackson, 2008; Knowlton and Jackson, 2008). Our results provide useful and reliable tools for tropical Anthropocene research in the broad Indo-Pacific region.

**Data availability.** The data used are listed in the tables and the Supplement.

**Supplement.** The supplement related to this article is available online at: <https://doi.org/10.5194/bg-16-585-2019-supplement>.

**Author contributions.** MY and YH conceived and designed the research; YH, HI, MY, and BM performed the research; YH and MY analyzed the data; YH, MY, and BM wrote most of the paper.

**Competing interests.** The authors declare that they have no conflict of interest.

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