

Invited Research Article

Ecosystem turnover in an urbanized subtropical seascape driven by climate and pollution

Yuanyuan Hong^{a,1,*}, Moriaki Yasuhara^{a,*}, Hokuto Iwatani^{a,b,1}, Anne Chao^{c,1}, Paul G. Harnik^{d,1}, Chih-Lin Wei^{e,1}

^a School of Biological Sciences, Division for Ecology & Biodiversity, Swire Institute of Marine Science, and State Key Laboratory of Marine Pollution, The University of Hong Kong, Pok Fu Lam Road, Hong Kong SAR, China

^b Department of Earth Sciences, College of Science, Graduate School of Sciences and Technology for Innovation, Yamaguchi University, Japan

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

^d Department of Geology, Colgate University, Hamilton, NY, USA

^e Institute of Oceanography, National Taiwan University, Taipei, 106, Taiwan

ARTICLE INFO

Keywords:

Conservation paleobiology
river discharge
East Asian Summer Monsoon
pollution
urban environment
Ostracoda

ABSTRACT

Natural and anthropogenic factors shape present-day benthic marine ecosystems. Understanding their combined influence on benthic communities is limited, however, by a lack of biological monitoring. Using a conservation paleobiology approach, this study establishes biological baselines and assesses the effects of natural and anthropogenic environmental change on benthic communities in an urbanized subtropical seascape. We compared subsurface ("past", covering approximately the last 50–100 years) and surface ("present", covering approximately the last 5 years) faunal assemblages in sediment grab samples in Hong Kong, one of the busiest ports and urbanized coastal areas in the world. Results show that both natural (climate, monsoon) and anthropogenic factors (metal pollution, damming) were associated with recent faunal changes (dissimilarities between subsurface and surface faunal assemblages). Changes in freshwater and sediment discharge from the Pearl River due to monsoon rains and dams produced a strong west-east gradient in the turnover of rare species. Pollution from metals resulted in the turnover of abundant and dominant species in the central part of Hong Kong. Examining these data in the context of published results from other urbanized coastal areas around the world suggests that metal pollution may be an important and understudied factor, responsible for benthic turnover in regions where pollution levels exceed thresholds for sediment toxicity.

1. Introduction

Hong Kong is among the most urbanized coastal areas in the world (Ng et al., 2017; Yeung, 2001). Human activities, including rapid industrialization, sewage discharge, trawling, dredging, land reclamation, and ship traffic have led to pronounced physical and chemical changes in coastal ecosystems (Astudillo et al., 2014; Blackmore, 1998; Hodgkiss and Yim, 1995; Hong et al., 2017; Hu et al., 2008; Morton, 1996; Morton and Blackmore, 2001; Owen and Sandhu, 2000; Tanner et al., 2000). Situated at the mouth of one of the largest rivers in Asia, the Pearl River, Hong Kong is also sensitive to monsoons and other climate variations (Lee et al., 2019). The region, at the northern edge of the Coral Triangle biodiversity hotspot, also sustains high marine

biological diversity (Duprey et al., 2016; Ng et al., 2017). The intersection of high biodiversity and elevated anthropogenic and climatic stressors makes Hong Kong's coastal waters a conservation priority. They are also a model case for evaluating ecosystem-level changes in other tropical and subtropical coastal regions.

Understanding and predicting biotic response to anthropogenic and climatic change has proven difficult, because biological monitoring generally postdates the onset of different human activities that concern scientists and/or society (Kosnik and Kowalewski, 2016). The emerging field of conservation paleobiology mitigates this problem by using data derived from subfossil and present-day assemblages to investigate changes in species, communities, and ecosystems over decadal to millennial time scales (Dietl et al., 2015). Comparisons between living

* Corresponding authors.

E-mail addresses: ooicrlr@gmail.com (Y. Hong), moriakiyasuhara@gmail.com (M. Yasuhara).

¹ Equal contribution

and historical (i.e., “dead”) assemblages of marine mollusks, for example, have found significantly weaker statistical agreement in taxonomic composition and species relative abundance in areas affected by eutrophication and bottom-trawling than in areas with negligible histories of human modification (Kidwell, 2007, 2009).

Live-dead mismatch is a powerful tool for identifying how human activities and recent climatic changes have altered shallow marine ecosystems (Kidwell, 2015). Most live-dead studies have focused on macrofossils (Harnik et al., 2017; Hyman et al., 2019; Kidwell, 2008; Leshno et al., 2015; Pearson, 1993; Tomašových and Kidwell, 2017). Microfossils, however, are useful for quantitative paleoecology because

of their small size, high abundance (even in a limited volume of sediment), and high preservation potential (Yasuhara et al., 2017). Ostracods, for example, are extensively used in paleoecological research (Chiu et al., 2017; Hong et al., 2017; Yasuhara et al., 2017), and are one of the microfossil groups with considerable potential for live-dead research.

This study investigates shallow-marine ostracods in surface sediments at 52 sites covering all Hong Kong marine waters (Fig. 1). Because of the low abundance of living specimens, we compared surface (top ~1 cm) and subsurface (~1–20 cm lumped) assemblages, in analogy with live-dead studies. We do not assume that samples of dead, empty shells in surface sediments represent the living assemblage at the

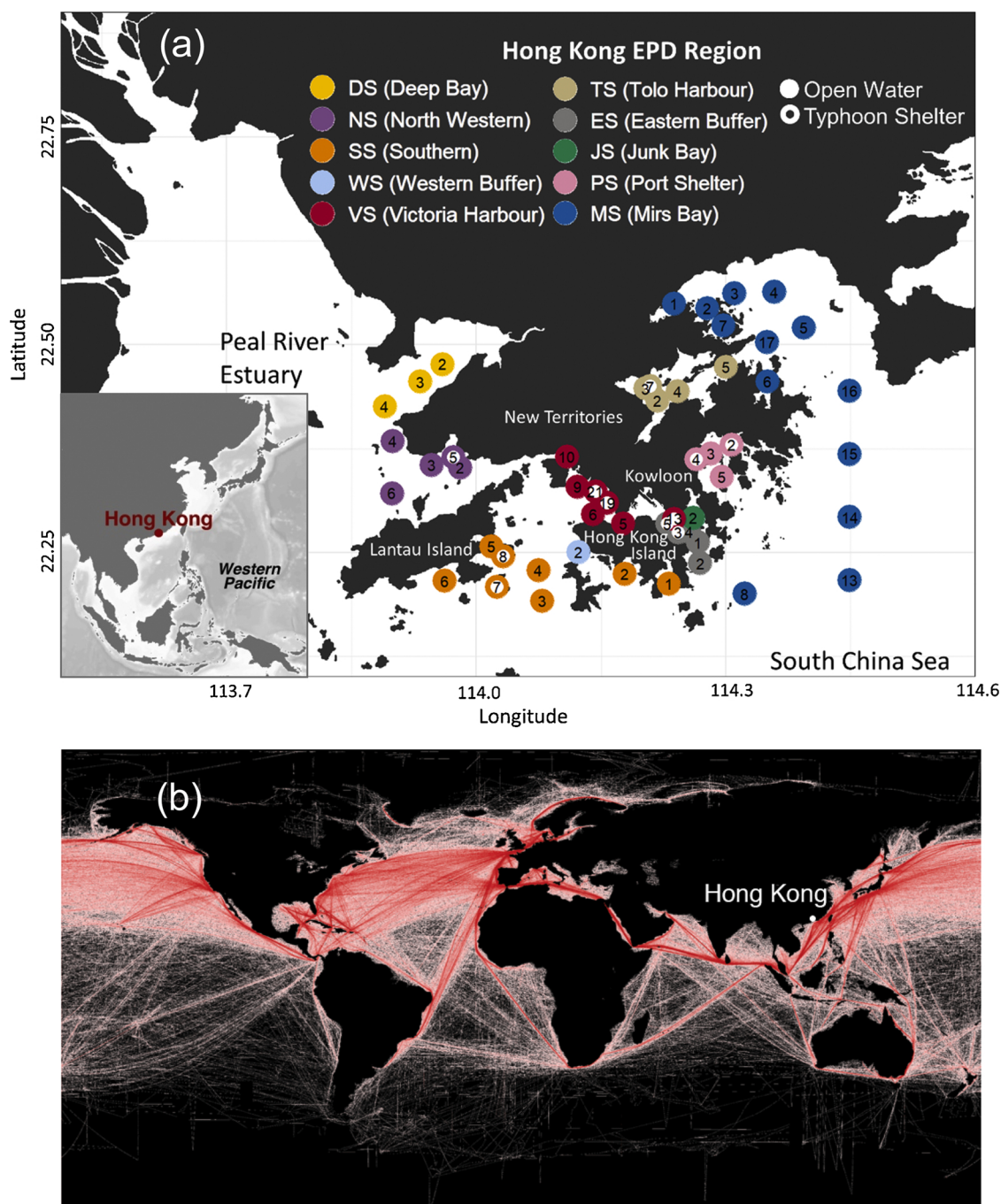


Fig. 1. Locality map and global shipping density data. (a) Sampling sites of the Environmental Protection Department marine water and sediment quality monitoring program in Hong Kong. Unique site identity is denoted by the combination of color and number (e.g., site SS1 is indicated by an orange circle and the number 1). An inserted map indicates the location of Hong Kong in East Asia. (b) Global shipping routes; red lines indicate ship tracks. Fig. 1b is from Wikimedia Commons (https://commons.wikimedia.org/wiki/File:Shipping_routes_red_black.png) and is based on data from Halpern et al. (2008).

moment of sampling. Rather, surficial dead assemblages provide information about "present-day" communities (Brunner et al., 2006; Cheung et al., 2019; Salvi et al., 2015) (i.e., the recent past), whereas skeletal remains buried in subsurface sediment retain a memory of past communities that extends further back in time (see the sedimentation section below for details). By quantitatively comparing surface-subsurface differences in marine ostracod assemblages, we aimed to identify any ecological changes that have occurred over the past 50–100 years in Hong Kong, and the main environmental drivers of those faunal changes. The key questions were: (1) How have natural climatic and anthropogenic environmental changes affected benthic communities, and (2) what is the relative importance of these two factors in benthic turnover in an urban subtropical seascape? We hypothesized that (1) monsoon precipitation and damming altered the extent of freshwater and sediment discharge from the Pearl River, resulting in changes in benthic ecosystems along a gradient extending away from the river's mouth; and (2) because metal pollution is toxic to many benthic organisms, areas with the greatest levels of pollution will exhibit substantial differences between past and present benthic communities. Following presentation of the study below, we discuss the broader implications of our findings for understanding the impacts of natural and anthropogenic environmental change in other regions of the world.

2. Materials and methods

2.1. Study area

Hong Kong, a coastal city extending over 2500 km² with a population of over 7 million people, is one of the densest urban habitats on Earth (Warren-Rhodes and Koenig, 2001). The main city's activities are concentrated along both sides of Victoria Harbour (Xu et al., 2011) (Fig. 1). With a subtropical climate, Hong Kong has western monsoons in the summer that produce hot and wet conditions from May to September, followed by a cool and dry winter season that extends from November to March (Fleddum et al., 2011; Hodgkiss, 1984), with April and October as transitional months. The hydrography of coastal Hong Kong is complex: western Hong Kong is affected by substantial inputs from the Pearl River, particularly in the summer months when heavy rainfall (Morton and Wu, 1975) lowers surface water salinity. Conversely, eastern Hong Kong waters are mainly influenced by oceanic water derived from the South China Sea (Hong et al., 2019). Overall, the waters of Hong Kong are highly eutrophic and polluted due to local sources and inputs from the Pearl River, whose watershed includes large cities such as Shenzhen, Guangzhou, and Zhuhai (Hu et al., 2008).

2.2. Samples and laboratory procedure

We conducted benthic sampling during January and July of 2011. A Van Veen Grab collected 100 ml of sediment from the uppermost cm (surface samples) and from ~1 cm down to the bottom of the grab (~1–20 cm lumped: subsurface samples). The fifty-two sites sampled in this study (Fig. 1; Appendix A) included 41 in open waters and 11 in typhoon shelters. Typhoon shelters are semi-enclosed areas of water designed to protect moored vessels in extreme weather (Environmental Protection Department, 2011). All sites are included in the Hong Kong Environmental Protection Department (EPD) marine water and sediment quality monitoring program, which has operated since 1986. The biweekly to monthly water, and biannually sediment, quality measurements made by the EPD provide a comprehensive and continuous long-term marine environmental dataset for Hong Kong. The EPD divides the coastal waters of Hong Kong into 10 regions (Fig. 1) (Environmental Protection Department, 2011).

We wet-sieved the sediments with a 63 µm mesh sieve, and air/oven dried them at 40 °C. We then dry-sieved the residue with a 150 µm mesh sieve. We picked the ostracod specimens from the >150 µm fraction; this is a standard sieve size for ostracod analyses (see Yasuhara et al., 2009

and Yasuhara et al., 2017 for more details). Generally, if samples contained ~200 or fewer specimens, we picked all individuals; if there were estimated to be much more than 200 specimens, we used a sample splitter and picked all ostracods from a split. We picked from multiple splits if a split contained < 200 specimens. We considered both an entire carapace or a single valve as one individual for counting, and these were identified to the species level when possible.

2.3. Environmental Variables

We selected environmental parameters from the EPD monitoring program dataset (Environmental Protection Department, 2011) for regression modeling (see below). These parameters included eutrophication- and pollution-related environmental factors, such as surface productivity (Chlorophyll-a, Chl; Fig. S1), bottom water dissolved oxygen (DO; Fig. S1), turbidity (Tur; Fig. S1), and metal concentrations (copper [Cu], zinc [Zn], and lead [Pb]; Fig. S1), as well as other major environmental parameters such as bottom-water salinity (Sal; Fig. S1) and mud content (MD; Fig. S1). Sea surface temperature was not part of our regression modeling because of very low variation across Hong Kong waters (Duprey et al., 2016). We analyzed mean values for these EPD data over the entire monitoring period (1986–2011). Bottom water DO is the average of the summer season (June–September), due to the potential importance of summer bottom water oxygen depletion on the benthos (Fleddum et al., 2011; Xu et al., 2011).

2.4. Quantifying diversity

The most intuitive and frequently used diversity measure is species richness (i.e., the number of species), but this metric ignores species abundances. Until fairly recently, how to integrate species richness and abundances when quantifying diversity was among the most controversial issues in ecology. A consensus has now emerged that Hill numbers (Hill, 1973) should be the diversity measure of choice (Ellison, 2010). We thus used Hill numbers to estimate ostracod diversity in surface and subsurface assemblages for each EPD region. The Hill number of order q (qD) is expressed as ${}^qD = (\sum_{i=1}^S p_i^q)^{1/(1-q)}$, $q \geq 0$ and $q \neq 1$, where S is the number of species and p_i denotes the relative abundance of species i , $i = 1, 2, \dots, S$. Here, the diversity order q controls the sensitivity of Hill numbers to species relative abundances.

Hill numbers for order $q \geq 0$ are all in the same units of "species". Hill numbers are interpreted as the effective number of species or species equivalents in the following sense: if ${}^qD = k$, then the diversity of order q of the focal assemblage is the same as the diversity of a simple reference assemblage with k equally abundant species. The Hill number of order $q = 0$ weights all species equally, and 0D is simply species richness. The Hill number of order $q = 1$ (the limit of qD when q approaches 1) is the Shannon diversity (i.e., the exponential of Shannon entropy) and weights species in proportion to their abundances (Chao et al., 2014a). Thus, 1D is interpretable as the effective number of abundant species. The Hill number of order $q = 2$ is known as the Simpson diversity (i.e., the inverse of Simpson concentration index) and weights species in proportion to their squared abundances. Thus, 2D is interpretable as the effective number of highly abundant or dominant species.

Observed diversity (including species richness) depends on sampling effort and sample completeness. Consequently, observed diversity based on incomplete sampling data is not directly comparable unless sampling effects are controlled through standardization. Size-based standardization (i.e., rarefying all samples to the same size) has been the traditional approach in ecology. Chao and Jost (2012) showed, however, that the magnitude of the difference in diversity among assemblages is much compressed under size-based standardization. Chao et al. (2014b) and Chao et al. (2020) provided a standardization approach via coverage-based rarefaction and extrapolation with Hill numbers. This approach compares diversity estimates for equally complete samples,

where sample completeness is measured by sample coverage (or simply coverage, i.e., a fraction of the assemblage's individuals that belong to the observed species). This concept was originally developed by Alan Turing and I. J. Good in their cryptographic analysis during the World War II (Chao et al., 2017; Good, 1953; Good, 2000). Chao et al. (2014b) demonstrated that sample-coverage-based rarefaction and extrapolation with Hill numbers allowed for better inference of the magnitude of the diversity differences among assemblages, compared to traditional sample-size-based rarefaction and extrapolation.

In this application, we focused on rarefaction and extrapolation with Hill numbers of order $q = 0, 1, 2$ up to a maximum value of sample coverage (Chao et al., 2020) among the samples and EPD regions. Specifically, we first extrapolated the Hill numbers of each sample or each region to two times the number of observed individuals. The maximum coverage used in our analysis was then the minimum among the coverage values obtained from those extrapolated samples, which was 93% based on our data. Although the data did not contain sufficient information to compare entire assemblages, coverage-based sampling curves enabled sensible inferences and fair comparisons for any standardized assemblage fraction up to 93%. We estimated the standard error and 95% confidence intervals of the Hill numbers for a rarefied or extrapolated sample by bootstrap resampling procedure that was repeated 1000 times; see Chao et al., 2014b; Chao et al. 2020) for further details.

2.5. Beta diversity and dissimilarity

In addition to comparing within-assemblage diversity (Section 2.4 for surface and subsurface assemblages), quantifying between-assemblage beta diversity is also imperative. In this context, beta diversity assesses the compositional difference between surface and subsurface ostracod assemblages. Compared to alpha diversity, quantifying beta diversity among assemblages is an even more complicated and extensively discussed issue (Ellison, 2010). We used diversity decomposition to calculate beta and dissimilarity measures. Based on a multiplicative decomposition of the Hill numbers (Jost, 2007), we partitioned gamma diversity (i.e., diversity of pooled surface and subsurface assemblages) into alpha (i.e., mean diversity of individual assemblages) and beta components (i.e., effective number of assemblages). The resulting beta-diversity was then transformed to obtain two general classes of abundance-based dissimilarity measures, namely the Jaccard-type and the Sørensen-type (Chao et al., 2014a). Since the two classes of measures yield consistent patterns of inferences, we only used the Sørensen-type dissimilarity measures, denoted as $1 - C_{qN}$ for diversity order q and N assemblages, based on the notation of (Chao et al., 2014a).

The measure $1 - C_{qN}$ quantifies the effective average proportion of non-shared species in an assemblage. Similar to Hill numbers, when the order q increases, the dissimilarity measure gives more weight to the dominant species. For $q = 0$, $1 - C_{0N}$ reduces to the classical richness-based Sørensen dissimilarity (Sørensen, 1948). In the special case of two assemblages (e.g., surface and subsurface, $N = 2$), $1 - C_{0N}$ reduces to the ratio of the number of un-shared species to the mean number of species in a single assemblage. For $q = 1$, $1 - C_{1N}$ reduces to Shannon-entropy-based Horn dissimilarity (Horn, 1966); for $q = 2$, $1 - C_{2N}$ reduces to Morisita-Horn dissimilarity (Morisita, 1959). These two measures intuitively quantify the compositional dissimilarity between two sets of species relative abundance vectors, respectively for abundant species and dominant species. Because undetected species should be present in nearly all surface and subsurface samples, we also adjusted for the effect of undetected species on the Sørensen-type dissimilarity measures (Chao and Jost, 2015). Although the adjusted classical Sørensen index ($q = 0$) may still be subject to some bias, the adjusted Horn ($q = 1$) and Morisita-Horn ($q = 2$) measures are generally nearly unbiased. We did not compute the Bray-Curtis dissimilarity metric, despite its wide use in ecology and environmental science, because this metric cannot statistically estimate and account for the

effect of un-detected species.

We identified species responsible for surface-subsurface dissimilarities using a jackknife re-sampling approach. We removed one species from a dissimilarity calculation and measured the difference between the surface-subsurface dissimilarities with and without that particular species. We repeated this procedure for all species, one by one. If omitting a species resulted in a large reduction in the surface-subsurface dissimilarity, then that species was a primary contributor to the observed difference (dissimilarity) between surface and subsurface assemblages.

2.6. Regression modeling

We determined the relationships between surface-subsurface ostracod dissimilarity ($1 - C_{qN}$) and environmental parameters using multiple linear regression modeling (Fig. S1). All environmental parameters were log-transformed, zero centered, and normalized (divided by the standard deviation). The faunal dissimilarities were logit transformed ($\log[x/(1 - x)]$) prior to analysis. We converted the concentrations of Cu, Pb, and Zn to orthogonal principal components (PCs) using principal component analysis (PCA) (Fig. S2). Together, PC1 and PC2 explain 96.9% of the total variation. PC1 explains 84.9% of the total variation and positively correlates with the concentrations of all metals. PC2 explains 12% of the total variation and is positively correlated with Cu, and negatively correlated with Pb concentrations. We used PC1 and PC2 in place of these metal concentrations to avoid collinearity in the regression analyses. Samples from brackish water sites (salinity < 25: DS2 and DS3) and samples with low abundance (< 50 specimens: ES5, VS21, VS5, VS6, VS13) were removed before regression modeling following Hong et al. (2019).

The best-fitting models were selected based on Akaike's Information Criterion (AICc) corrected for small sample size, in which the lower score indicates better model support considering both goodness-of-fit and model complexity (Anderson and Burnham, 2002). The Akaike weights summarize the relative support for all candidate models (Anderson et al., 2000). We considered parameter estimates averaged over all models, with the estimates generated by each model weighted by their relative support (Anderson et al., 2000). This approach accounted for the uncertainty in model selection and generated appropriate confidence intervals. The sum of Akaike weights of models that included the variables in question were used to quantify the relative importance of each variable (Burnham and Anderson, 2002).

We examined multicollinearity by computing variance inflation factors (VIF) (Legendre and Legendre, 1998) and pairwise correlations between predictor variables (Yasuhara et al., 2012b). The correlation coefficients among predictors in the model were between -0.55 and 0.67. The VIF of all 384 linear regression models was under 3.49.

We considered the degree of spatial autocorrelation in model residuals by calculating Moran's I for each regression model. The weights matrices for this calculation used the shortest distance among sampling sites that avoided all landmasses. No spatial autocorrelation was present ($p > 0.23$) in the residuals of all possible regression models for Sørensen dissimilarities. Only 2 of the 128 sets of model residuals for Horn dissimilarity and only 29 of the 128 sets of model residuals for Morisita-Horn dissimilarity were spatially autocorrelated ($p < 0.05$).

All analyses were implemented in RStudio (Team, 2016). We used 'iNEXT' to estimate ostracod diversity (Chao et al., 2014b; Hsieh et al., 2016), 'SpadeR' to calculate ostracod dissimilarity (Chao et al., 2016), 'nlme' (Pinheiro et al., 2019) and 'MuMIn' (Barton, 2013) for model averaging, 'gdistance' to compute the shortest distance among the sampling sites (Etten, 2017), and 'ape' to measure spatial autocorrelation (Paradis and Schliep, 2019). Figures and maps were constructed using 'ggplot2' (Wickham, 2012).

3. Results

3.1. Ostracod assemblages

In total, we identified 151 species of ostracods belonging to 77 genera in this study. We found 135 species belonging to 71 genera in the surface samples, and 130 species belonging to 71 genera were found in the subsurface samples. One hundred and sixteen species belonging to 65 genera occurred in both surface and subsurface samples. Dominant species (i.e., those found at more than 80% of sample sites) are very similar between subsurface and surface samples and are *Sinocytheridea impressa*, *Neomonoceratina delicata*, *Propontocypris* spp., *Pistocythereis bradyi*, *Bicornucythere bisanensis* s.l., and *Loxococoncha malayensis*. Appendix A contains the raw census data.

3.2. Diversity

Hill numbers of order $q = 0$ and 1 (0D , 1D) were significantly higher in surface and subsurface samples in the Eastern Buffer (ES) region than in other regions (i.e., non-overlapping 95% confidence interval, Fig. S3). The Hill number of order $q = 2$ (2D) in the ES region was significantly higher than other regions in the subsurface but not the surface samples (Fig. S3). In general, Tolo Harbour & Channel (TS), Junk Bay (JS), and Mirs Bay (MS) regions had the lowest 0D and 1D (Fig. S3).

Hill numbers for surface and subsurface assemblages were similar in most of the regions (overlapping 95% CI). The exceptions are the ES region (Eastern Buffer) where the 0D , 1D and 2D of the surface assemblages was significantly lower than those of the subsurface assemblages; VS (Victoria Harbour) and MS (Mirs Bay) regions where the 0D of the surface assemblages were significantly higher than those of the subsurface assemblages; and TS region (Tolo Harbour & Channel) where the 0D , 1D and 2D of the surface assemblages were significantly higher than those of the subsurface assemblages (Fig. 2). The highest local diversities occurred in the ES region (Eastern Buffer) and its surrounding areas (Fig. S4). The lowest local diversities occurred in the TS (Tolo Harbour & Channel) and northern part of the MS regions (Mirs Bay) (Fig. S4). No change was apparent in local 0D from subsurface to surface samples, except at a few sites in the PS (Port Shelter), MS (Mirs Bay), and NS (North Western) regions, which had more than 100% increase in diversity (Fig. 3). The 1D and 2D also increased at these sites, but these increases were less pronounced (Fig. 3). For the Hill numbers of higher

order q , 1D and 2D decreased from subsurface to surface assemblages in the ES (Eastern Buffer), JS (Junk Bay), and at a few sites in DS (Deep Bay), TS (Tolo Harbour & Channel) and northern MS (Mirs Bay) regions (Fig. 3).

3.3. Dissimilarity

Richness-based Sørensen dissimilarity between surface and subsurface samples increased toward the east side of the EPD regions (Figs. 4,5). The highest Sørensen dissimilarities occurred in the TS (Tolo Harbour & Channel), PS (Port Shelter), JS (Junk Bay), and MS (Mirs Bay) regions (Fig. 5). In contrast, no such longitudinal trend was observed in either Horn or Morisita-Horn dissimilarities (Fig. 5). Instead, Horn and Morisita-Horn dissimilarities showed the highest values on average in the ES region (Eastern Buffer) (Figs. 4,5), where metal concentrations were high (Figs S1, S2).

Multiple regression models and model averaging showed that turbidity, mud content and salinity were the most influential factors affecting Sørensen dissimilarity (Table 1, S1; Fig. 6). Only turbidity and mud content, however, had statistically significant effects (Table 1). The effect of salinity on Sørensen index was marginal ($p = 0.07$) (Table 1). Turbidity and metal PC1 were important for Horn and Morisita-Horn dissimilarities, but the turbidity effect was significant only for Horn dissimilarity and marginal for Morisita-Horn dissimilarity ($p = 0.09$) (Table 1; Fig. 6). Metal PC1 had marginal effects on both Horn ($p = 0.06$) and Morisita-Horn dissimilarities ($p = 0.07$) (Table 1). Turbidity had a greater effect on Sørensen dissimilarity than on Horn and Morisita-Horn dissimilarities (Table 1). The effect size of pollution-related parameters (metals and chlorophyll a) increased with order q from Sørensen to Horn and then Morisita-Horn indices (Table 1).

We estimated the top 10 species responsible for compositional dissimilarities between surface and subsurface assemblages for each region (Figs S5–S7). We also calculated the mean relative abundance change from subsurface to surface for these top 10 species in each EPD region (Figs S8–S10). For Sørensen dissimilarity, the removal of a single species generated up to a 6.7% reduction in the dissimilarity of subsurface and surface assemblages (i.e., *Cytherois* spp. and *Cytheropteron* cf. *ignobilis* in the DS region) (Fig. S5). In other EPD regions, *Tanella gracilis*, *Paradoxostomatid*, and *Pistocythereis bradyformis* contributed the most to the mean surface-subsurface dissimilarity in the TS region (i.e., dissimilarity decreasing by 2.3–3.3%), *Munseyella japonica*, *Callistocythere* sp. 1, and

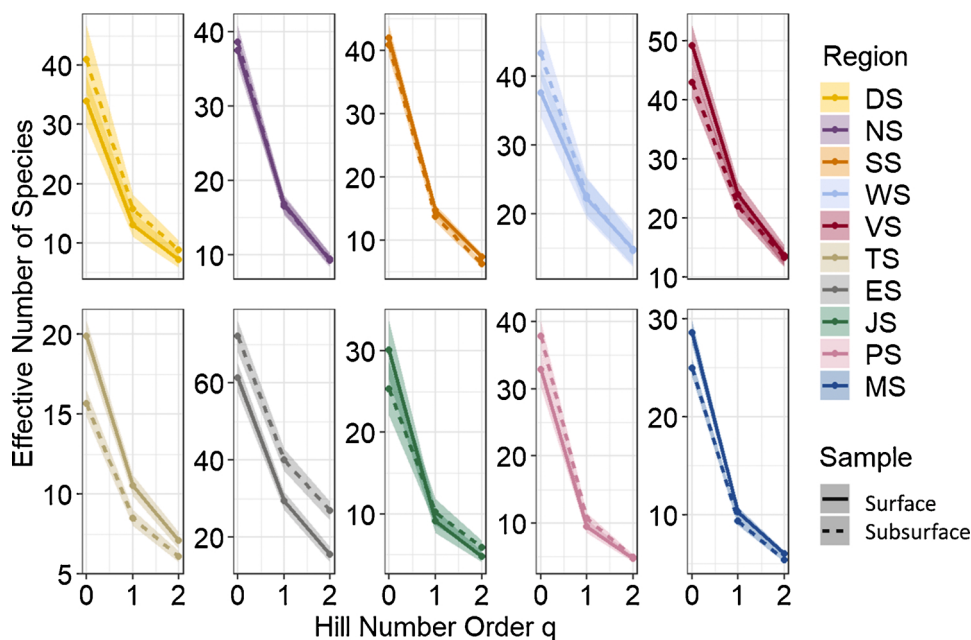


Fig. 2. Differences in diversity over time in different regions of Hong Kong. Panels show diversity profiles of the surface ("present", i.e., the average of the past 5 years) and subsurface ("past", i.e., past 50–100 years ago) samples based on standardized sample coverage (93%) for each region. The regions include: Deep Bay (DS), North Western Water (NS), Southern Water (SS), Western Buffer (WS), Victoria Harbour (VS), Tolo Harbour and Channel (TS), Eastern Buffer (ES), Junk Bay (JS), Port Shelter (PS), Mirs Bay (MS). Shaded area shows 95% confidence interval of the profile from 1000 bootstrap replicates. The overall elevation of the profile indicates the diversity based on Hill number (diversity index used in this study. See the materials and methods section) across different order q . 0D ($q = 0$) reflects species richness, and 1D ($q = 1$) and 2D ($q = 2$) reflect diversities of abundant and dominant species, respectively. Diversities between surface and subsurface samples are similar in most regions, except ES (subsurface higher), VS (surface higher in 0D), MS (surface higher in 0D), and TS (surface higher) that show significant differences.

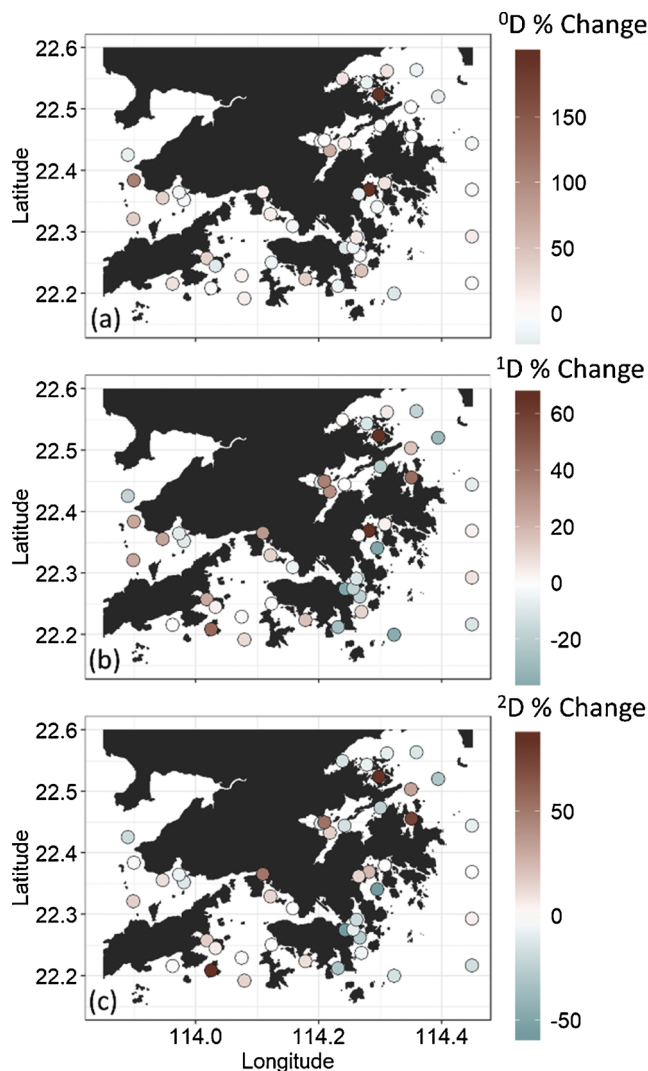


Fig. 3. Diversity change from subsurface ("past", i.e., past 50–100 years) to surface ("present", i.e., past 5 years; see the sedimentation section) sediment samples in Hong Kong. The percent changes were calculated by (surface-sub-surface)/subsurface*100. The panels (a), (b), and (c) show the percent changes (by color key) of ostracode diversity [Hill numbers of order $q = 0$ (0D), 1 (1D), and 2 (2D), respectively]. Surface-subsurface diversity changes are quite complex and do not show clear patterns (see the discussion section for details).

Stigmatocythere kingmai contributed the most to the mean surface-subsurface dissimilarity in the PS region (i.e., dissimilarity decreasing by 1.5–1.7%), *Pistocythereis euplectella*, *Loxoconcha zhejiangensis*, *Bythocythere* sp., *Alocopocythere goujoni*, *Munseyella japonica*, *Neocytheretta faceta*, and *Pontocythere* cf. *subjaponica* contributed the most to the mean surface-subsurface dissimilarity in the JS region (i.e., dissimilarity decreasing by 2.2%), and *Aurila* cf. *disparata*, *Pontocythere* cf. *subjaponica*, and *Pistocythereis euplectella* contributed the most to the mean surface-subsurface dissimilarity in the MS region (i.e., dissimilarity decreasing by 0.8–1.2%) (Fig. S5). The relative abundance of most of these species decreased from subsurface to surface samples (Fig. S8). For Horn and Morisita-Horn, *Sinocytheridea impressa*, *Neomonoceratina delicata*, and *Propontocypris* spp. contributed the most to surface-subsurface faunal dissimilarities in most EPD regions (Figs S6, S7, S9, S10). Omitting *Neomonoceratina delicata* led to 2.7% decrease of the Horn and 9.9% decrease of the Morisita-Horn dissimilarities in the ES region (Figs S6, S7), where the largest surface-subsurface dissimilarities were observed of all EPD regions (Figs S4, S5). In addition, the relative abundance of *Neomonoceratina delicata* increased by 10.1% from subsurface to surface

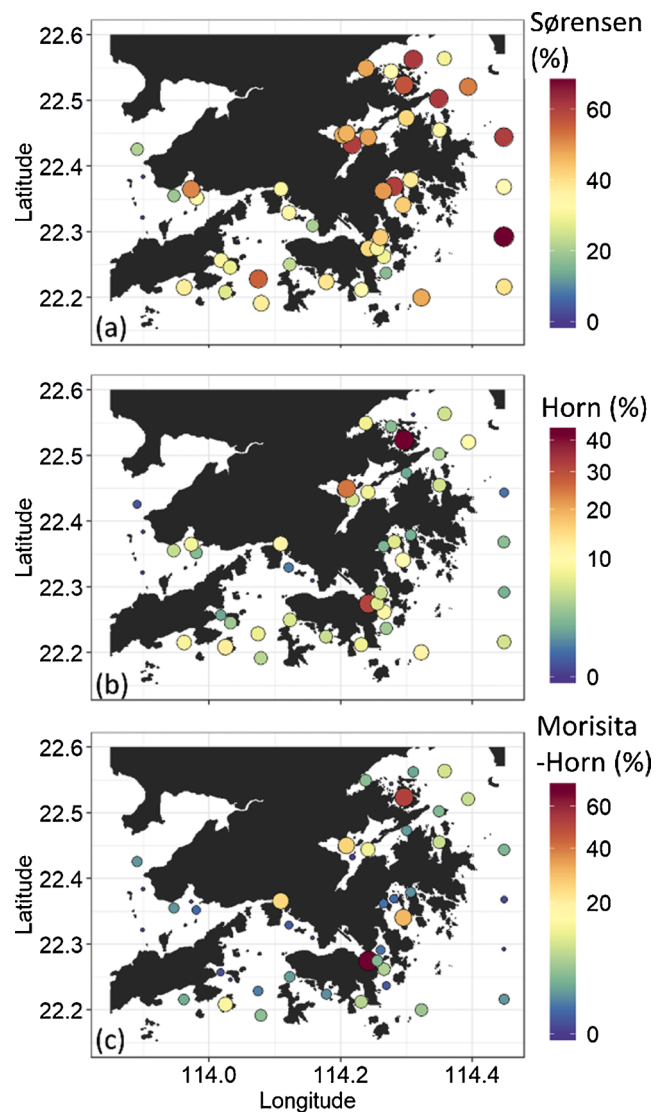


Fig. 4. Ostracode faunal difference between the past and the present in Hong Kong. Panels show ostracode faunal dissimilarity between subsurface ("past", i.e., past 50–100 years) and surface ("present", i.e., past 5 years; see the sedimentation section) sediments based on (a) Sørensen, (b) Horn and (c) Morisita-Horn dissimilarities. Symbol size and color key show the relative dissimilarity. For visualization purposes, the symbol size and color key in the panel (b) and (c) are on a square-root scale. The Sørensen (presence-absence) dissimilarity shows a clear west-to-east increase, whereas, the Horn (abundant species) and Morisita-Horn (dominant species) dissimilarities do not show a clear longitudinal gradient. Several sites in the central parts of Hong Kong show high values in Horn and Morisita-Horn.

samples (Figs S9, S10).

3.4. Sedimentation

Sedimentation rate varied among sites in Hong Kong. Overall, subsurface sediments (i.e., the top 20-cm of sediment in a grab sample) in Hong Kong were likely deposited within the past 50–100 years based on published estimates of sedimentation rates (Owen and Lee, 2004; Owen and Sandhu, 2000; Tang et al., 2008; Tanner et al., 2000; Wei et al., 2008). In turn, surface sediments (i.e., the top cm) likely represent up to the past 5 years. Previous studies have observed relatively higher sedimentation rates at Victoria Harbour and Easter Buffer (Fig. 7) compared to other waters in the region, indicating that subsurface samples in these areas likely span a much shorter interval of time than those from areas

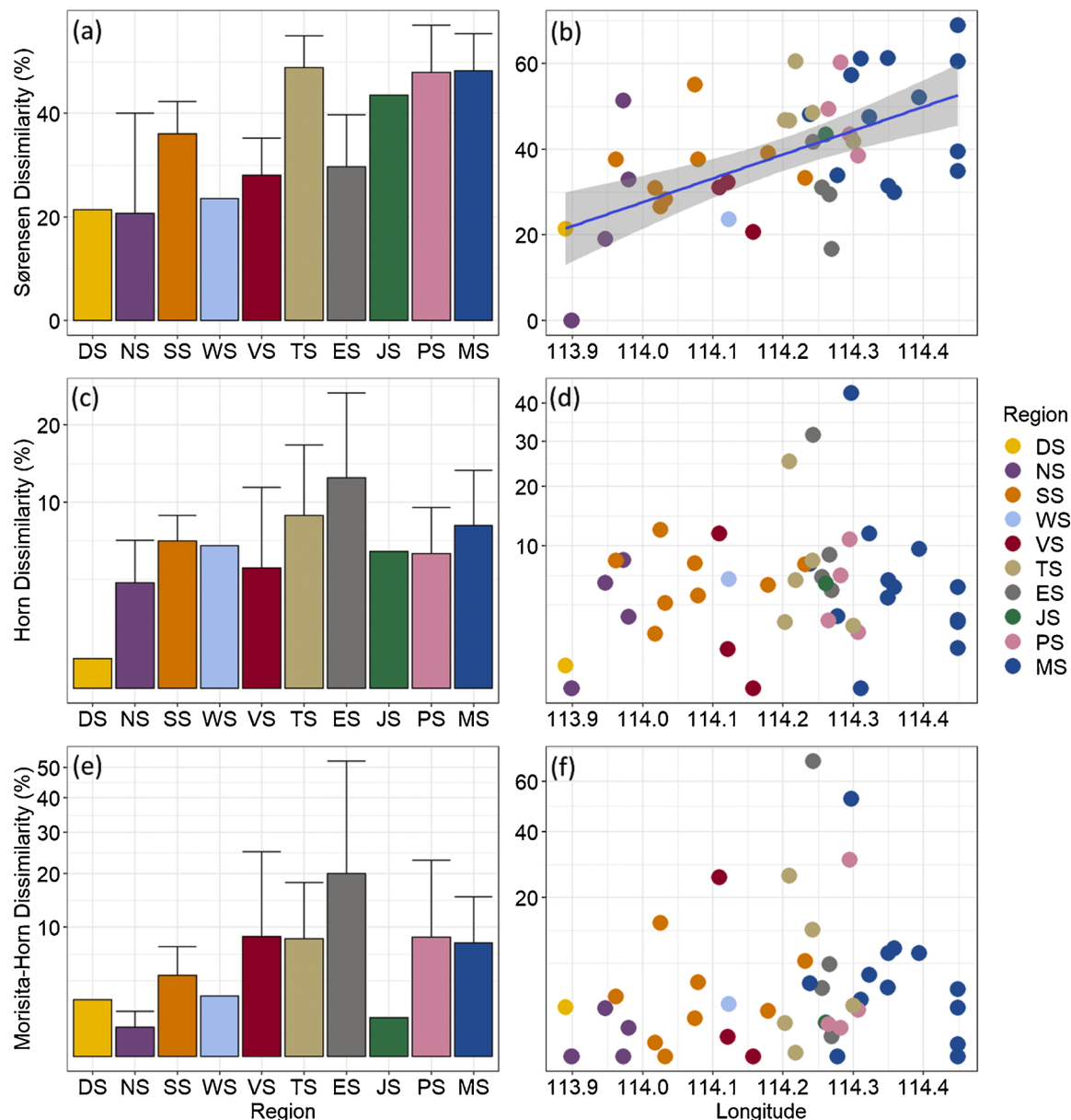


Fig. 5. Regional and longitudinal trends in ostracode faunal difference between the past and the present in Hong Kong. Dissimilarity between the subsurface ("past", i.e., past 50–100 years) and surface ("present", i.e., past 5 years; see the sedimentation section) sediments based on (a–b) Sørensen, (c–d) Horn, and (e–f) Morisita-Horn dissimilarity. The EPD regions are aligned by their average longitude (from west to east): Deep Bay (DS), North Western Water (NS), Southern Water (SS), Western Buffer (WS), Victoria Harbour (VS), Tolo Harbour and Channel (TS), Eastern Buffer (ES), Junk Bay (JS), Port Shelter (PS), and Mirs Bay (MS). Error bars are 95% confidence intervals. The colors indicate EPD regions. For visualization purpose, the y-axis in panels c–f is on a square-root scale. Solid line indicates significant linear relationship. Shaded areas are 95% confidence intervals. The Sørensen (presence-absence) dissimilarity shows a clear west-to-east increase, whereas, the Horn (abundant species) and Morisita-Horn (dominant species) dissimilarities do not show a clear longitudinal gradient but instead the central parts of Hong Kong exhibit the highest values, especially in Morisita-Horn.

with lower sedimentation rates. No evidence is present of a clear west-east trend in sedimentation rates in Hong Kong (Owen and Lee, 2004; Owen and Sandhu, 2000; Tang et al., 2008; Tanner et al., 2000; Wei et al., 2008). Physical disturbance is also intensive in the region, including reclamation and dumping (Fabricius and McCorry, 2006; Goodkin et al., 2011; Lai et al., 2016; Leung and Morton, 1997). High sedimentation rates and intensive sediment mixing in Hong Kong (Cheung et al., 2003; Tang et al., 2008) could blur the temporal separation of present (surface) and past (subsurface) ostracod assemblages, and thereby obscure any associations between environmental factors and benthic community change, but are unlikely to generate surface-subsurface compositional differences where none existed before. Furthermore, the lack of a west-east trend in sedimentation rates

indicates that the strong west-east trend in surface-subsurface Sørensen dissimilarity is not a sedimentation artefact. Similarly, the changing associations between environmental variables and Sørensen, Horn, and Morisita-Horn dissimilarities, respectively, strongly suggest that subsurface ostracod records in Hong Kong retain a paleobiological signal of past populations that can be used to detect recent community change.

4. Discussion

4.1. Faunal and diversity changes

We found a striking east-west trend in the recent turnover of benthic communities in Hong Kong (Figs. 4,5). The significant factors associated

Table 1

Environmental control of the compositional difference between past vs present ostracode assemblages in Hong Kong. Model averaging of multiple linear regressions of the subsurface ("past", i.e., 50–100 years) vs surface ("present", i.e., past 5 years; see the sedimentation section) dissimilarities and environmental factors. RI = relative importance. Asterisk shows significance ($Pr < 0.05$). Period shows marginal significance ($Pr = 0.05–0.10$).

Dissimilarity	Variable	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)	RI
Sørensen	(Intercept)	−0.53	0.09	0.09	5.83	0.00	*
	Tur	−0.47	0.11	0.12	4.09	0.00	*
	Mud	0.29	0.10	0.10	2.99	0.00	*
	Sal	0.24	0.13	0.14	1.78	0.07	.
	PC2	0.02	0.19	0.20	0.08	0.94	
	Chl	−0.01	0.12	0.12	0.04	0.97	
	O2	0.01	0.10	0.10	0.14	0.89	
	PC1	0.01	0.08	0.08	0.07	0.94	
							0.05
Horn	(Intercept)	−2.46	0.11	0.11	22.53	0.00	*
	Tur	−0.27	0.13	0.13	2.04	0.04	*
	PC1	0.15	0.08	0.08	1.90	0.06	.
	Sal	0.20	0.17	0.17	1.13	0.26	
	PC2	0.10	0.21	0.22	0.47	0.64	
	Chl	0.04	0.14	0.14	0.29	0.77	
	Mud	−0.08	0.12	0.12	0.68	0.49	
	O2	0.06	0.12	0.13	0.47	0.64	
							0.09
Morisita-Horn	(Intercept)	−2.61	0.17	0.17	15.09	0.00	*
	PC1	0.29	0.15	0.16	1.84	0.07	.
	Tur	−0.35	0.20	0.21	1.72	0.09	.
	Chl	−0.34	0.26	0.27	1.26	0.21	
	PC2	0.00	0.35	0.36	0.01	0.99	
	Sal	0.12	0.27	0.28	0.45	0.65	
	Mud	−0.17	0.19	0.20	0.84	0.40	
	O2	0.02	0.20	0.21	0.11	0.91	
							0.12

with this turnover primarily relate to sediment and freshwater discharge from the Pearl River (Table 1, S1; Fig. 6). Sediment discharge from the Pearl River has decreased since the 1990s, mainly as a result of the construction of reservoirs and dams (Zhang et al., 2008). Freshwater discharge is affected by regional precipitation and thus the East Asian

Summer Monsoon. The East Asian Summer Monsoon was stronger between approximately 1850 and 1950, which resulted in more precipitation and greater freshwater discharge at that time compared with the present-day (Cheung et al., 2018; Lee et al., 2019). High surface-subsurface Sørensen dissimilarities in the eastern waters of Hong

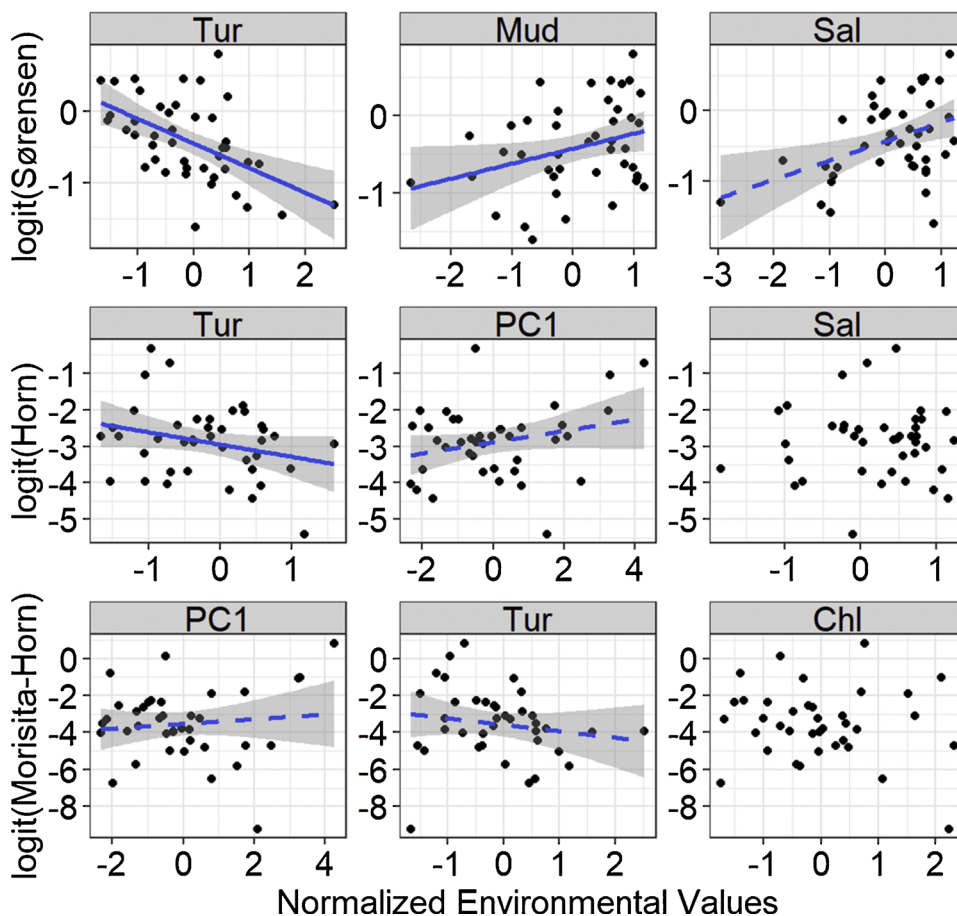


Fig. 6. Major environmental factors influencing compositional difference between past and present ostracode assemblages in Hong Kong. The variables were chosen from the environmental factors with highest relative importance from model averaging (i.e., $RI > 0.2$, Table 1) on the (a) Sørensen, (b) Horn, and (c) Morisita-Horn dissimilarity between subsurface ("past", i.e., past 50–100 years) and surface ("present", i.e., past 5 years; see the sedimentation section) ostracode assemblages. Solid line indicates significant effect and dashed line indicates marginal effects in the model averaging result (Table 1). Shaded area shows 95% confidence interval. Tur: turbidity; Mud: mud content; Sal: salinity; PC1: metal PC1; Chl: chlorophyll a. The Sørensen dissimilarity trend is related to turbidity, mud content, and salinity, whereas, the Horn and Morisita-Horn dissimilarities are related to pollution (PC1) in addition to turbidity (see Tables 1 and S1 for the regression modelling results).

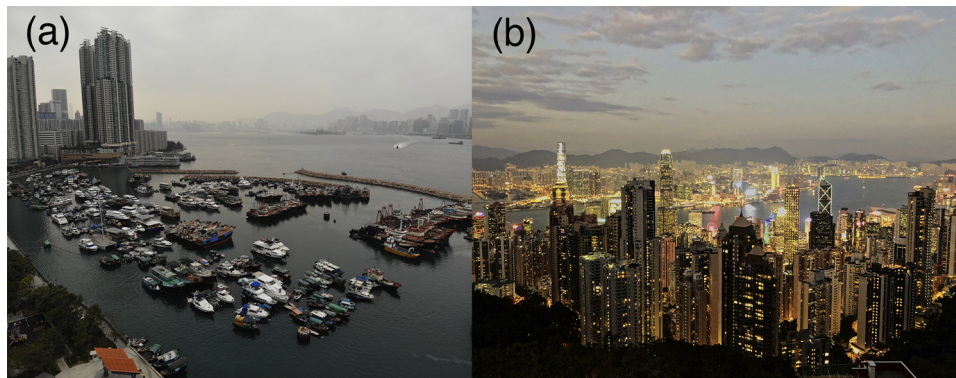


Fig. 7. Hong Kong's urbanized seascapes. Photographs of a typhoon shelter at Easter Buffer (a), and of Victoria Harbour (b), showing Hong Kong's high ship density and urban development.

Kong may reflect the recent weakening influence of the Pearl River on those benthic communities.

In contrast, the turnover of abundant and dominant species (Horn and Morisita-Horn) was greatest in the central parts of Hong Kong (Figs. 4, 5). In this region, pollution-related parameters (i.e., metals and chlorophyll *a*) played a greater role in community dissimilarities than environmental parameters associated with the Pearl River (i.e., turbidity, mud content, and salinity) (Tables 1, S1; Fig. 6). Copper, lead, and zinc are components in most marine antifouling paints and are known to be among the most toxic metals to marine invertebrates (Amara et al., 2018; Canning-Clode et al., 2011; Hall et al., 1998; Kwok and Leung, 2005; Turner, 2010). The central part of Hong Kong (e.g., Victoria Harbour; Fig. 7) is among the busiest ports in the world (Figs. 1, 7). Metal pollution in the central part of Hong Kong also results from the discharge of sewage, industrial inputs, and surface runoff (Tang et al., 2008; Tanner et al., 2000; Warren-Rhodes and Koenig, 2001; Zhou et al., 2007). According to the sediment guidelines of the U.S. Environmental Protection Agency (USEPA) regarding toxicological effects on marine organisms (Long et al., 1995), the ERL (Effect Range-Low) and ERM (Effect Range-Median) of copper, lead, and zinc are 34 and 270 mg/kg, 46.7 and 218 mg/kg, and 150 and 410 mg/kg, respectively. Higher concentrations than the ERL and ERM values indicate substantial pollution with significantly negative biological effects. Sediments in the central part of Hong Kong around Victoria Harbour (Fig. 7) have higher values of these metals, especially copper (e.g., at ES3: 330.98 mg/kg and ES5: 306.60 mg/kg; Appendix B; Fig. 7), than its ERL and ERM (Figs S1, S2), indicating that these sites are highly polluted, which supports our interpretation that these pollutants are responsible for recent faunal change. Grab samples from many Victoria Harbour sites (VS21, VS5, VS6 and VS13; 4 out of 7; see Appendix B; Fig. 7) contained limited numbers of ostracods and thus could not be included in our analyses, further indicating stressful environmental conditions for benthic organisms.

In contrast with compositional dissimilarities, changes in subsurface to surface diversity (Sørensen, Horn, and Morisita-Horn) do not show clear spatial patterns (Fig. 3). For example, diversity differences in central Hong Kong are no greater than in other regions, despite evidence that metal pollution has impacted benthic fauna in that area. These results suggest that higher compositional dissimilarities are driven by the turnover of species and environmental-filtering, and not by local extinction. Overall, diversities have tended to decrease in high diversity sites and increase in low diversity sites, thereby decreasing regional variation in biodiversity (Fig. S3). Diversities in the Eastern Buffer have recently declined whereas diversity in Tolo Harbour has increased relative to subsurface baselines for the past 50–100 years (Fig. 2; see the sedimentation section); Eastern Buffer and Tolo Harbour are the areas of highest and lowest diversity, respectively (Figs S3, S4).

Since faunal dissimilarity cannot be interpreted simply as a measure

of degradation or recovery, we identified the species that were most responsible for the surface-subsurface dissimilarities in different regions (Figs S5–S10). For the surface-subsurface dissimilarity of rare species (Sørensen), responsible species for faunal differences differ among regions (Figs S5, S8), with some species increasing in relative abundance from subsurface to surface and others decreasing (Fig. S8). Although the species that contributed the most to Sørensen dissimilarities varied among regions (Figs S5, S8), substantial Sørensen dissimilarity tended to be associated with a reduction in the abundance of certain species (e.g., *Tanella gracillis* in the TS region, *Munseyella japonica* in the PS region, *Pistocythereis euplectella* in the JS region, and *Aurila cf. disparata* in the MS region) from the subsurface to surface (see Section 3.3). Weakening of the East Asian Summer Monsoon and a reduction in river discharge (Cheung et al., 2019; Lee et al., 2019; Zhang et al., 2008) have caused eastern waters to become less estuarine and more oceanic over the past 50–100 years. Thus, the higher surface-subsurface Sørensen dissimilarity in eastern waters likely reflects the weakening influence of the Pearl River in that region, and a shift towards more fully marine benthic communities characterized by greater local-scale environmental heterogeneity than is observed in estuarine environments where salinity may be the dominant environmental control.

Sinocytheridea impressa, *Neomonoceratina delicata*, and *Propontocypris* spp. tend to be the species most responsible for the faunal dissimilarities of abundant (Horn) and especially dominant species (Morisita-Horn) (Figs S6, S7, S9, S10). The former two species are known to be resistant to anthropogenic pollution (*Sinocytheridea impressa* for eutrophication; *Neomonoceratina delicata* for metal pollution; Hong et al., 2019). In contrast, *Propontocypris* spp. prefers less eutrophic environments (Hong et al., 2019). *Neomonoceratina delicata* is more abundant in the regions where this species is responsible for surface-subsurface dissimilarities (e.g., the ES region), whereas the relative abundance of the other two species does not show clear regional trend (Figs S9, S10). Thus, high surface-subsurface Horn and Morisita-Horn dissimilarities reflect the impacts of metal pollution in the central parts of Hong Kong (i.e., areas adjacent to Victoria Harbour, such as Eastern Buffer; Fig. 7).

Comparing results from Hong Kong with similar paleoecological studies in other regions reveals a surprising contrast. Eutrophication and deoxygenation are often the main drivers of human-induced ecological degradation in marginal marine environments (Breitburg et al., 2018; Duprey et al., 2016; Kidwell, 2007, 2009; Yasuhara et al., 2012a), yet neither exhibit a dominant signal in this study (Table 1, S1). The impacts of eutrophication and deoxygenation on benthic communities are well documented in paleoecological and/or microfossil records from the Chesapeake Bay (Brush, 2009; Cooper, 1995; Cronin and Vann, 2003; Willard and Cronin, 2007), Baltic Sea (Andrén, 1999; Weckström et al., 2007), north European fjords (Alve, 1991; Clarke et al., 2006; Dale et al., 1999), Osaka Bay (Tsujimoto et al., 2006; Tsujimoto et al., 2008; Yasuhara and Yamazaki, 2005; Yasuhara et al., 2007), Gulf of Mexico

(Rabalais et al., 2007; Sen Gupta et al., 1996), Adriatic Sea (Tomašových et al., 2018; Tomašových et al., 2017), Yangtze River Estuary (Cheung et al., 2019), and other areas (Yasuhara et al., 2012a; Yasuhara et al., 2019). The relatively minimal effect of eutrophication in this study may be due in part to the adaptation of species in Hong Kong to the naturally eutrophic and turbid coastal environments of the South China Sea. Furthermore, deoxygenation in Hong Kong is not very prevalent (Fig. S1; Hong et al., 2019), in contrast with many of the regions cited above. The discrepancy may also be due, however, to studies in these other regions overlooking, or discounting, the impacts of metal pollution on the benthos. This omission may be because (1) metals have often not been considered in these types of paleoecological analyses, except in areas with significant metal pollution such as areas adjacent to mining sites (Alve, 1995; Yasuhara et al., 2012a; but see Alve et al., 2009; Dolven et al., 2013; Irizuki et al., 2015; Irizuki et al., 2018; Yasuhara et al., 2003), and (2) eutrophication/deoxygenation and metal pollution tend to show similar spatiotemporal trends because they are often linked to a common source [e.g., the river system entering a bay (e.g., Osaka Bay: Yasuhara et al., 2007)], and as a result it is difficult to distinguish their unique effects (Alve et al., 2009). In Hong Kong, metal pollution (Cu, Pb, Zn) and eutrophication/deoxygenation (chlorophyll a, dissolved oxygen) show different geographic patterns (i.e., multicollinearity is not high; see the materials and methods section; Fig. S1), because of the complexity of coastal geography (i.e., existence of multiple embayments, straits, and open ocean areas in this small region) and the multiple sources of pollutants (e.g., Pearl River, Victoria Harbour, Tolo Harbour). These spatial differences allow us to clearly detect the impacts of metals and distinguish those from any effects due to eutrophication/deoxygenation. In many urbanized coastal regions in the world, metal pollution levels are known to be higher than the ERL or ERM (Qian et al., 2015), indicating that metals may be more responsible for recent benthic changes than is currently recognized. Eutrophication does play a major role in the diversity and distribution of other marine organisms in Hong Kong. Ecological and paleoecological evidence indicate that eutrophication is a major driver of coral diversity and distribution in the region (Cybulski et al., 2020; Duprey et al., 2016). This difference between ostracods (this study) and corals is probably because corals prefer oligotrophic environments and are thus much more sensitive to eutrophication than soft sediment benthos.

5. Conclusions

This conservation paleobiology study revealed recent compositional changes in benthic assemblages that would otherwise have gone undetected due to limited biological monitoring. We found that these changes were associated with a combination of natural climatic and anthropogenic factors. Rare species were affected by reduced sediment and freshwater discharge from the Pearl River as a result of reservoir and dam constructions and weakened East Asian Summer Monsoon. In contrast, abundant and dominant species, especially in the central part of Hong Kong, were affected by anthropogenic pollutants from ships and urban effluents. Natural and anthropogenic environmental changes in the last 50–100 years led to changes in faunal compositional but not changes in species diversity. These results indicate that human activities (i.e., metal pollution) play a dominant role in structuring Hong Kong's benthic ecosystem along with natural climatic factors (i.e., East Asian Summer Monsoon). In addition, the East Asian Summer Monsoon's impact on rare species suggests that the monsoon is an important driver of overall marine biodiversity in the broader southeast Asian marine ecosystem, as these tropical environments are characterized by a tremendous number of rare species (Bouchet et al., 2002; Schlacher et al., 1998; Shin and Ellingsen, 2004; Zuschin and Graham Oliver, 2005).

Among urbanized seascapes around the world, it is well established that eutrophication and deoxygenation have resulted in ecological degradation and play dominant roles in current biodiversity structure,

for example, in the Chesapeake Bay, Osaka Bay, and Gulf of Mexico (Yasuhara et al., 2012a; Yasuhara et al., 2019). Results from Hong Kong indicate that the impacts of metal pollution may be overlooked or discounted in some of these places, especially when the metal pollution levels are higher than the guideline values for sediment toxicity (this study; Irizuki et al., 2018). This finding highlights the need for comprehensive studies of ecological degradation that consider simultaneously the roles of eutrophication and pollution. Most previous studies of historical ecological degradation have concentrated on urban seascapes in mid and high latitudes such as the Chesapeake Bay, Osaka Bay, and Baltic Sea, with very few studies in low latitudes for comparison (Yasuhara et al., 2012a). Investigating these questions in tropical and subtropical urban seascapes is critical because these areas support tremendous biodiversity (Duprey et al., 2016; Ng et al., 2017; Tao et al., 2018). They are impacted by pollution and eutrophication, for example, in southeastern Asia, Jakarta Bay and Manila Bay (Breckwoldt et al., 2016; Hosono et al., 2011; Hosono et al., 2010; Jacinto et al., 2006; Sotito et al., 2014; Todd et al., 2010). Historical and paleoecological investigations of human-induced ecological degradation remain rare in tropical and subtropical urban seascapes (Fauzielly et al., 2013; van der Meij et al., 2009). Assessing the efficacy of actions taken to remediate human impacts in urbanized seascapes requires a holistic approach that combines biological monitoring (e.g., Tao et al., 2020a; Tao et al., 2020b; Wang et al., 2021) with benthic baselines generated from paleoecological records (e.g., this study; Hong et al., 2017; Cybulski et al., 2020).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the Environmental Protection Department of Hong Kong, especially K. Yung, for sediment collection support; L. Wong, C. Law, M. Lo, R.P.P. Wong, F.Y.F. Chan and K.H.M. Wong for their technical support; B. Lin, S. Wang, R. Mak, and V. Wang for helping with sampling; T. Irizuki for valuable comments on taxonomic identification and an early version of this manuscript; and S.M. Kidwell for discussion. We also thank the editor Anne Chin and two anonymous reviewers for their valuable comments. All data analyzed for this study are included in the tables and supplements. The work described in this paper was partially supported by the Environment and Conservation Fund of Hong Kong (project code: 19/2012), grants from the Research Grants Council of Hong Kong (project codes: HKU 17303115, 17302518, C7013-19G), the Early Career Scheme of the Research Grants Council of Hong Kong (project code: HKU 709413P), the Marine Ecology Enhancement Fund of Hong Kong (MEEF2021001), the Small Equipment Grant of the University of Hong Kong, the Faculty of Science RAE Improvement Fund of the University of Hong Kong, the Seed Funding Programme for Basic Research of the University of Hong Kong (project codes: 20111159140, 201611159053), and the Seed Funding of the HKU-TCL Joint Research Centre for Artificial Intelligence (to MY); the National Science Foundation (NSF EAR-2041667) (to PGH), the Ministry of Science and Technology of Taiwan (MOST 108-2611-M-002-001 and 108-2119-M-001-019) (to CW); and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (grant No. 203108) and the 45th Round of the Post-doctoral Fellow Scheme of the University of Hong Kong (to YH).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <https://doi.org/10.1016/j.ancene.2021.100304>.

References

- Alve, E., 1991. Foraminifera, climatic change, and pollution: a study of late Holocene sediments in Drammensfiord, southeast Norway. *The Holocene* 1, 243–261.
- Alve, E., Lepland, A., Magnusson, J., Backer-Owe, K., 2009. Monitoring strategies for re-establishment of ecological reference conditions: possibilities and limitations. *Marine Pollution Bulletin* 59, 297–310.
- Amara, I., Miled, W., Slama, R.B., Ladhari, N., 2018. Antifouling processes and toxicity effects of antifouling paints on marine environment. A review. *Environmental toxicology and pharmacology* 57, 115–130.
- Anderson, D.R., Burnham, K.P., 2002. Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management* 66, 912–918.
- Anderson, D.R., Burnham, K.P., Thompson, W.L., 2000. Null hypothesis testing: problems, prevalence, and an alternative. *The journal of wildlife management* 64, 912–923.
- Andrén, E., 1999. Changes in the composition of the diatom flora during the last century indicate increased eutrophication of the Oder estuary, south-western Baltic Sea. *Estuarine, Coastal and Shelf Science* 48, 665–676.
- Astudillo, J.-C., Wong, J.C., Dumont, C.P., Bonebrake, T.C., Leung, K.M., 2014. Status of six non-native marine species in the coastal environment of Hong Kong, 30 years after their first record. *BioInvasions Records* 3, 123–137.
- Bartoń, K., 2013. MuMin: Multi-model inference. R package version 1.9.13. See: <https://CRAN.R-project.org/package=MuMin>.
- Blackmore, G., 1998. An overview of trace metal pollution in the coastal waters of Hong Kong. *Science of the Total Environment* 214, 21–48.
- Bouchet, P., Lozouet, P., Maestrati, P., Heros, V., 2002. Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society* 75, 421–436. <https://academic.oup.com/biolinnean/article/75/4/421/2639775?login=true>.
- Breckwoldt, A., Dsikowitzky, L., Baum, G., Ferse, S.C., van der Wulp, S., Kusumanti, I., Ramadhan, A., Adrianto, L., 2016. A review of stressors, uses and management perspectives for the larger Jakarta Bay Area, Indonesia. *Mar. Pollut. Bull.* 110, 790–794.
- Breitbart, D., Levin, L.A., Oschlies, A., Grégoire, M., Chavez, F.P., Conley, D.J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., Jacinto, G.S., Limburg, K.E., Montes, L., Naqvi, S.W.A., Pitcher, G.C., Rabalais, N.N., Roman, M.R., Rose, K.A., Seibel, B.A., Telszewski, M., Yasuhara, M., Zhang, J., 2018. Declining oxygen in the global ocean and coastal waters. *Science* 359, eaam7240.
- Brunner, C.A., Beall, J.M., Bentley, S.J., Furukawa, Y., 2006. Hypoxia hotspots in the Mississippi Bight. *The Journal of Foraminiferal Research* 36, 95–107.
- Brush, G.S., 2009. Historical land use, nitrogen, and coastal eutrophication: A paleoecological perspective. *Estuaries and Coasts* 32, 18–28.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York.
- Canning-Clode, J., Fofonoff, P., Riedel, G.F., Torchin, M., Ruiz, G.M., 2011. The effects of copper pollution on fouling assemblage diversity: a tropical-temperate comparison. *PLoS one* 6, e18026.
- Chao, A., Chiu, C.-H., Jost, L., 2014a. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual review of ecology, evolution, and systematics* 45, 297–324. <http://www.annualreviews.org/doi/10.1146/annurev-ecolsys-120213-091540>.
- Chao, A., Chiu, C.H., Colwell, R.K., Magnago, L.F.S., Chazdon, R.L., Gotelli, N.J., 2017. Deciphering the enigma of undetected species, phylogenetic, and functional diversity based on Good-Turing theory. *Ecology* 98, 2914–2929. https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecy.2000?casa_token=CciXuJ18pGAAAAA%3AMKRrVzRyWaeWLGwNFGGv6eA6L-a0hP1a3Bgrqv7PFu6U4wT1M-98Zub59yPPCAwzmC-JuKwRETB-VVA.
- Chao, A., Gotelli, N.J., Hsieh, T., Sander, E.L., Ma, K., Colwell, R.K., Ellison, A.M., 2014b. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological monographs* 84, 45–67. <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/13-0133.1>.
- Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93, 2533–2547. <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/11-1952.1>.
- Chao, A., Jost, L., 2015. Estimating diversity and entropy profiles via discovery rates of new species. *Methods in Ecology and Evolution* 6, 873–882. <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12349>.
- Chao, A., Kubota, Y., Zelený, D., Chiu, C.H., Li, C.F., Kusumoto, B., Yasuhara, M., Thorn, S., Wei, C.L., Costello, M.J., 2020. Quantifying sample completeness and comparing diversities among assemblages. *Ecological Research* 35, 292–314. <http://esj-journals.onlinelibrary.wiley.com/doi/10.1111/1440-1703.12102>.
- Chao, A., Ma, K., Hsieh, T., Chiu, C.-H., Chao, M.A., 2016. SpadeR: species-richness prediction and diversity estimation with R: an R package in CRAN. See: <https://CRAN.R-project.org/package=SpadeR>.
- Cheung, C.-W.R., Yasuhara, M., Iwatani, H., Wei, C.-L., Dong, Y.-W., 2019. Benthic community history in the Changjiang (Yangtze River) mega-delta: Damming, urbanization, and environmental control. *Paleobiology* 45, 469–483. <https://www.cambridge.org/core/journals/paleobiology/article/abs/benthic-community-history-in-the-changjiang-yangtze-river-megadelta-damming-urbanization-and-environmental-control/407C52B86A31ACC9DE32FFD6793D8303>.
- Cheung, C.-W.R., Yasuhara, M., Mamo, B., Katsuki, K., Seto, K., Takata, H., Yang, D.Y., Nakanishi, T., Yamada, K., Iwatani, H., 2018. Decadal-to Centennial-Scale East Asian Summer Monsoon Variability Over the Past Millennium: An Oceanic Perspective. *Geophysical Research Letters* 45, 7711–7718.
- Cheung, K., Wong, M.H., Yung, Y., 2003. Toxicity assessment of sediments containing tributyltin around Hong Kong harbour. *Toxicology letters* 137, 121–131. https://www.sciencedirect.com/science/article/pii/S0378427402003867?casa_token=1d3ud9LUJ2gAAAAA:nPf9YVToElsVVEmd4Cniw8Q23fp17HFwAsaVUCr5pjHjMRSIWOQhpsKwmhUmbtKw3G0BfnAJS8.
- Chiu, W.-T.R., Yasuhara, M., Iwatani, H., Kitamura, A., Fujita, K., 2017. Response of subtropical submarine-cave ecosystem to Holocene cave development and Asian monsoon variability. *Paleobiology* 43, 425–434.
- Clarke, A., Weckström, K., Conley, D., Anderson, N.J., Adser, F., Andrén, E., De Jonge, V., Ellegaard, M., Juggins, S., Kaupila, P., 2006. Long-term trends in eutrophication and nutrients in the coastal zone. *Limnology and Oceanography* 51, 385–397.
- Cooper, S.R., 1995. Chesapeake Bay watershed historical land use: impact on water quality and diatom communities. *Ecological applications* 5, 703–723.
- Cronin, T.M., Vann, C.D., 2003. The sedimentary record of climatic and anthropogenic influence on the Patuxent estuary and Chesapeake Bay ecosystems. *Estuaries* 26, 196–209. <https://link.springer.com/article/10.1007/BF02695962>.
- Cybulski, J.D., Husa, S.M., Duprey, N.N., Mamo, B.L., Tsang, T.P., Yasuhara, M., Xie, J.Y., Qiu, J.-W., Yokoyama, Y., Baker, D.M., 2020. Coral reef diversity losses in China's Greater Bay Area were driven by regional stressors. *Science advances* 6, eabb1046.
- Dale, B., Thorsen, T., Fjellsa, A., 1999. Dinoflagellate cysts as indicators of cultural eutrophication in the Oslofjord, Norway. *Estuarine, Coastal and Shelf Science* 48, 371–382.
- Dietl, G.P., Kidwell, S.M., Brenner, M., Burney, D.A., Flessa, K.W., Jackson, S.T., Koch, P. L., 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annual Review of Earth and Planetary Sciences* 43, 79–103.
- Dolven, J.K., Alve, E., Rygg, B., Magnusson, J., 2013. Defining past ecological status and in situ reference conditions using benthic foraminifera: a case study from the Oslofjord, Norway. *Ecological indicators* 29, 219–233.
- Duprey, N.N., Yasuhara, M., Baker, D.M., 2016. Reefs of tomorrow: eutrophication reduces coral biodiversity in an urbanized seascape. *Global change biology* 22, 3550–3565.
- Ellison, A.M., 2010. Partitioning diversity 1. *Ecology* 91, 1962–1963.
- Environmental Protection Department, H.K., 2011. Marine Water Quality in Hong Kong 2011. See: Environmental Protection Department, Hong Kong. <https://www.epd.gov.hk/epd/sites/default/files/epd/english/environmentinhk/water/hkwqrc/files/waterquality/annual-report/marinereport2011.pdf>.
- Etten, J.v., 2017. R package gdistance: distances and routes on geographical grids. *Journal of Statistical Software* 76, 1–21. <https://www.jstatsoft.org/article/view/3046>.
- Fabricius, K.E., McCorry, D., 2006. Changes in octocoral communities and benthic cover along a water quality gradient in the reefs of Hong Kong. *Marine Pollution Bulletin* 52, 22–33.
- Fauzielly, L., Irizuki, T., Sampei, Y., 2013. Vertical changes of recent ostracode assemblages and environment in the inner part of Jakarta Bay, Indonesia. *Journal of coastal development* 16, 11–24. <https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.859.4787&rep=rep1&type=pdf>.
- Fleddum, A., Cheung, S.G., Hodgson, P., Shin, P., 2011. Impact of hypoxia on the structure and function of benthic epifauna in Tolo Harbour, Hong Kong. *Marine pollution bulletin* 63, 221–229.
- Good, I.J., 1953. The population frequencies of species and the estimation of population parameters. *Biometrika* 40, 237–264.
- Good, I.J., 2000. Turing's anticipation of empirical Bayes in connection with the cryptanalysis of the naval Enigma. *Journal of Statistical Computation and Simulation* 66, 101–111.
- Goodkin, N.F., Switzer, A.D., McCorry, D., DeVantier, L., True, J.D., Hughes, K.A., Angelina, N., Yang, T.T., 2011. Coral communities of Hong Kong: long-lived corals in a marginal reef environment. *Marine Ecology Progress Series* 426, 185–196.
- Hall Jr, L.W., Scott, M.C., Killen, W.D., 1998. Ecological risk assessment of copper and cadmium in surface waters of Chesapeake Bay watershed. *Environmental Toxicology and Chemistry: An International Journal* 17, 1172–1189. https://setac.onlinelibrary.wiley.com/doi/full/10.1002/etc.5620170626?casa_token=eVd6Nace8OAAAAA%3ARq5CWB4gAmZMVA5nzDTUvQNLKQvMFS8X6-JlvXUojwCC2QGNiJlQc-F9tQZecQ-8p91rWvWb6Fo_WOpza.
- Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. A global map of human impact on marine ecosystems. *Science* 319, 948–952.
- Harnik, P.G., Torstenson, M.L., Williams, M.A., 2017. Assessing the effects of anthropogenic eutrophication on marine bivalve life history in the Northern Gulf of Mexico. *Palaios* 32, 678–688.
- Hodgkiss, I., Yim, W., 1995. A case study of Tolo Harbour, Hong Kong. In: McComb, A.J. (Ed.), *Eutrophic shallow estuaries and lagoons*. CRC Press, Boca Raton, Florida, USA, pp. 41–57.
- Hodgkiss, I.J., 1984. Seasonal patterns of intertidal algal distribution in Hong Kong. *Asian Mar. Biol.* 1, 49–57. https://books.google.com.hk/books?hl=zh-TW&lr=&id=aqMe0fwbXR0C&oi=fnd&pg=PA49&dq=Hodgkiss,+I.J.,+1984,+Seasonal+patterns+of+intertidal+algal+distribution+in+Hong+Kong&ots=FZ-snF5UWU&sig=By3REI0disb6473BQhjm0Plk4tC&redir_esc=y#v=onepage&q=Hodgkiss%2C%20I.J.%2C%201984.%20Seasonal%20patterns%20of%20intertidal%20algal%20distribution%20in%20Hong%20Kong&f=false.
- Hong, Y., Yasuhara, M., Iwatani, H., Mamo, B., 2019. Baseline for ostracod-based northwestern Pacific and Indo-Pacific shallow-marine paleoenvironmental reconstructions: ecological modeling of species distributions. *Biogeosciences* 16, 585–604. <https://bg.copernicus.org/articles/16/585/2019/>.

- Hong, Y., Yasuhara, M., Iwatani, H., Seto, K., Yokoyama, Y., Yoshioka, K., Mamo, B., 2017. Freshwater reservoir construction by damming a marine inlet in Hong Kong: Palaeoecological evidence of local community change. *Marine Micropaleontology* 132, 53–59. <https://www.sciencedirect.com/science/article/abs/pii/S0377839816301141>.
- Horn, H.S., 1966. Measurement of "overlap" in comparative ecological studies. *The American Naturalist* 100, 419–424. <https://www.journals.uchicago.edu/doi/abs/10.1086/282436>.
- Hosono, T., Su, C.-C., Delinon, R., Umezawa, Y., Toyota, T., Kaneko, S., Taniguchi, M., 2011. Decline in heavy metal contamination in marine sediments in Jakarta Bay, Indonesia due to increasing environmental regulations. *Estuarine, Coastal and Shelf Science* 92, 297–306. <https://www.sciencedirect.com/science/article/abs/pii/S0272771411000205>.
- Hosono, T., Su, C.-C., Siringan, F., Amano, A., Onodera, S.-i., 2010. Effects of environmental regulations on heavy metal pollution decline in core sediments from Manila Bay. *Marine Pollution Bulletin* 60, 780–785. <https://www.sciencedirect.com/science/article/abs/pii/S0025326X10000950>.
- Hsieh, T., Ma, K., Chao, A., 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7, 1451–1456. <https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12613>.
- Hu, J., Zhang, G., Li, K., Peng, P.A., Chivas, A.R., 2008. Increased eutrophication offshore Hong Kong, China during the past 75 years: evidence from high-resolution sedimentary records. *Marine Chemistry* 110, 7–17.
- Hyman, A.C., Frazer, T.K., Jacoby, C.A., Frost, J.R., Kowalewski, M., 2019. Long-term persistence of structured habitats: seagrass meadows as enduring hotspots of biodiversity and faunal stability. *Proc. R. Soc. B* 286, 20191861.
- Irizuki, T., Hirose, K., Ueda, Y., Fujiwara, Y., Ishiga, H., Seto, K., 2018. Ecological shifts due to anthropogenic activities in the coastal seas of the Seto Inland Sea, Japan, since the 20th century. *Marine pollution bulletin* 127, 637–653. <https://www.sciencedirect.com/science/article/abs/pii/S0025326X17310834>.
- Irizuki, T., Ito, H., Sako, M., Yoshioka, K., Kawano, S., Nomura, R., Tanaka, Y., 2015. Anthropogenic impacts on meiobenthic Ostracoda (Crustacea) in the moderately polluted Kasado Bay, Seto Inland Sea, Japan, over the past 70 years. *Marine pollution bulletin* 91, 149–159. <https://www.sciencedirect.com/science/article/abs/pii/S0025326X14008145>.
- Jacinto, G., Azanza, R., Velasquez, I., Siringan, F., 2006. Manila Bay: environmental challenges and opportunities. In: Wolanski, E. (Ed.), *The environment in Asia Pacific harbours*. Springer, Dordrecht, pp. 309–328.
- Jost, L., 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88, 2427–2439.
- Kidwell, S.M., 2007. Discordance between living and death assemblages as evidence for anthropogenic ecological change. *Proceedings of the National Academy of Sciences U. S. A.* 104, 17701–17706.
- Kidwell, S.M., 2008. Ecological fidelity of open marine molluscan death assemblages: effects of post-mortem transportation, shelf health, and taphonomic inertia. *Lethaia* 41, 199–217.
- Kidwell, S.M., 2009. Evaluating human modification of shallow marine ecosystems: mismatch in composition of molluscan living and time-averaged death assemblages. In: Dietl, G.P., Flessa, K.W. (Eds.), *Conservation Paleobiology: Using the Past to Manage for the Future*. Paleontological Society, The Paleontological Society Papers, pp. 113–139. [https://books.google.com.hk/books?hl=zh-TW&lr=&id=u-k5DwAAQBAJ&oi=fnd&pg=PA119&dq=Kidwell,+S.M.,+2009,+Evaluating+human+modification+of+shallow+marine+ecosystems+mismatch+in+composition+of+molluscan+living+and+time-averaged+death+assemblages.+In:+Dietl,+G.P.,+Flessa,+K.W.,+\(Eds.\),+Conservation+Paleobiology:+Using+the+Past+to+Manage+for+the+Future.+OnciBV7LV&sig=naOT76VR3kWLIVABVjKTSRSHo&redir_esc=y#v=onepage&q=Kidwell%2C%20S.M.%2C%202009.%20Evaluating%20human%20modification%20of%20shallow%20marine%20ecosystems%3A%20mismatch%20in%20composition%20of%20molluscan%20living%20and%20time-averaged%20death%20assemblages.%20In%3A%20Dietl%2C%20G.P.%2C%20Flessa%2C%20K.W.%20\(Eds.\)%2C%20Conservation%20Paleobiology%3A%20Using%20the%20Past%20to%20Manage%20for&f=false](https://books.google.com.hk/books?hl=zh-TW&lr=&id=u-k5DwAAQBAJ&oi=fnd&pg=PA119&dq=Kidwell,+S.M.,+2009,+Evaluating+human+modification+of+shallow+marine+ecosystems+mismatch+in+composition+of+molluscan+living+and+time-averaged+death+assemblages.+In:+Dietl,+G.P.,+Flessa,+K.W.,+(Eds.),+Conservation+Paleobiology:+Using+the+Past+to+Manage+for+the+Future.+OnciBV7LV&sig=naOT76VR3kWLIVABVjKTSRSHo&redir_esc=y#v=onepage&q=Kidwell%2C%20S.M.%2C%202009.%20Evaluating%20human%20modification%20of%20shallow%20marine%20ecosystems%3A%20mismatch%20in%20composition%20of%20molluscan%20living%20and%20time-averaged%20death%20assemblages.%20In%3A%20Dietl%2C%20G.P.%2C%20Flessa%2C%20K.W.%20(Eds.)%2C%20Conservation%20Paleobiology%3A%20Using%20the%20Past%20to%20Manage%20for&f=false).
- Kidwell, S.M., 2015. Biology in the Anthropocene: challenges and insights from young fossil records. *Proc. Natl. Acad. Sci. U.S.A.* 112, 4922–4929.
- Kosnik, M.A., Kowalewski, M., 2016. Understanding modern extinctions in marine ecosystems: the role of palaeoecological data. *Biology letters* 12, 20150951.
- Kwok, K., Leung, K., 2005. Toxicity of antifouling biocides to the intertidal harpacticoid copepod *Tigriopus japonicus* (Crustacea, Copepoda): effects of temperature and salinity. *Marine Pollution Bulletin* 51, 830–837.
- Lai, R.W., Perkins, M.J., Ho, K.K., Astudillo, J.C., Yung, M.M., Russell, B.D., Williams, G. A., Leung, K.M., 2016. Hong Kong's marine environments: History, challenges and opportunities. *Regional Studies in Marine Science* 8, 259–273.
- Lee, W.-M., Poon, K.-C., Kong, D., Sewell, R.J., Zong, Y., Zhang, Y., Liu, Z., 2019. Summer monsoon-induced upwelling dominated coastal sea surface temperature variations in the northern South China Sea over the last two millennia. *The Holocene* 29, 691–698.
- Legendre, P., Legendre, L., 1998. *Numerical ecology: second English edition*. Elsevier, Amsterdam, The Netherlands.
- Leshno, Y., Edelman-Furstenberg, Y., Mienis, H., Benjamini, C., 2015. Molluscan live and dead assemblages in an anthropogenically stressed shallow-shelf: Levantine margin of Israel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 433, 49–59.
- Leung, K., Morton, B., 1997. The impacts of dredging on the epibenthic molluscan community of the southeastern waters of Hong Kong: a comparison of the 1992 and 1995 trawl programmes. In: Morton, B. (Ed.), *Eighth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China*, Hong Kong 1995. Hong Kong University Press, Hong Kong, pp. 401–436. [https://books.google.com.hk/books?hl=zh-TW&lr=&id=YnVFBAAQBAJ&oi=fnd&pg=PA401&dq=Leung,+K.,+Morton,+B.,+1997,+The+impacts+of+dredging+on+the+epibenthic+molluscan+community+of+the+southeastern+waters+of+Hong+Kong:+a+comparison+of+the+1992+and+1995+trawl+programmes.+In:+Morton,+B.,+\(Ed.\),+Eighth+International+Marine+Biological+Workshop:+T&ots=GzXF27HhOB&sig=sZaACJZaeV7fOb7HNesZb_kMhVQ&redir_esc=y#v=onepage&q&f=false](https://books.google.com.hk/books?hl=zh-TW&lr=&id=YnVFBAAQBAJ&oi=fnd&pg=PA401&dq=Leung,+K.,+Morton,+B.,+1997,+The+impacts+of+dredging+on+the+epibenthic+molluscan+community+of+the+southeastern+waters+of+Hong+Kong:+a+comparison+of+the+1992+and+1995+trawl+programmes.+In:+Morton,+B.,+(Ed.),+Eighth+International+Marine+Biological+Workshop:+T&ots=GzXF27HhOB&sig=sZaACJZaeV7fOb7HNesZb_kMhVQ&redir_esc=y#v=onepage&q&f=false).
- Long, E.R., Macdonald, D.D., Smith, S.L., Calder, F.D., 1995. Incidence of adverse biological effects within ranges of chemical concentrations in marine and estuarine sediments. *Environmental management* 19, 81–97. <https://link.springer.com/article/10.1007%2BF02472006>.
- Morisita, M., 1959. Measuring of the dispersion of individuals and analysis of the distributional patterns. *Memoires of the Faculty of Science, Kyushu University. Series E. Biology* 2, 215–235. <https://ci.nii.ac.jp/naid/10016973008/>.
- Morton, B., 1996. The subsidiary impacts of dredging (and trawling) on a subtidal benthic molluscan community in the southern waters of Hong Kong. *Marine Pollution Bulletin* 32, 701–710.
- Morton, B., Blackmore, G., 2001. South China Sea. *Marine Pollution Bulletin* 42, 1236–1263.
- Morton, B., Wu, S., 1975. The hydrology of the coastal waters of Hong Kong. *Environmental Research* 10, 319–347.
- Ng, T.P., Cheng, M.C., Ho, K.K., Lui, G.C., Leung, K.M., Williams, G.A., 2017. Hong Kong's rich marine biodiversity: the unseen wealth of South China's megalopolis. *Biodiversity and conservation* 26, 23–36.
- Owen, R.B., Lee, R., 2004. Human impacts on organic matter sedimentation in a proximal shelf setting, Hong Kong. *Continental Shelf Research* 24, 583–602.
- Owen, R.B., Sandhu, N., 2000. Heavy Metal Accumulation and Anthropogenic Impacts on Tolo Harbour, Hong Kong. *Marine Pollution Bulletin* 40, 174–180.
- Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528.
- Pearson, M.P., 1993. The powerful dead: archaeological relationships between the living and the dead. *Cambridge Archaeological Journal* 3, 203–229. <https://www.cambridge.org/core/journals/cambridge-archaeological-journal/article/abs/powerful-dead-archaeological-relationships-between-the-living-and-the-dead/E32BD9EFC07AE2F776002722AF29A1E9>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.C., 2019. R Core Team. 2019. nlme: linear and nonlinear mixed effects models. R package version 3.1-141. See. <http://CRAN.R-Project.Org/Package=Nlme>.
- Qian, Y., Zhang, W., Yu, L., Feng, H., 2015. Metal pollution in coastal sediments. *Current Pollution Reports* 1, 203–219.
- Rabalais, N.N., Turner, R.E., Gupta, B.K.S., Platon, E., Parsons, M.L., 2007. Sediments tell the history of eutrophication and hypoxia in the northern Gulf of Mexico. *Ecological Applications* 17, S129–S143.
- Salvi, G., Buosi, C., Arbullo, D., Cherchi, A., De Giudici, G., Ibba, A., De Muro, S., 2015. Ostracoda and foraminifera response to a contaminated environment: the case of the Ex-Military Arsenal of the La Maddalena Harbour (Sardinia, Italy). *Micropaleontology* 61, 115–133. https://www.jstor.org/stable/24413751?casa_token=vFcbLh9k6PUAAAAA%3AeQBrxgRNvCriz2F4yds4xuXMx988ajea_4NoeUrVOJ4246H7XePWf5Cqiaq8i9EQVt-fH5o5YU36tP3Th8aQKbRncmZWJRRjhe6MaPzC86lxQGpk8gdw&seq=1#metadata.info_tav_contents.
- Schlacher, T., Newell, P., Clavier, J., Schlacher-Hoenlinger, M.A., Chevallon, C., Britton, J., 1998. Soft-sediment benthic community structure in a coral reef lagoon—the prominence of spatial heterogeneity and 'spot endemism'. *Marine Ecology Progress Series* 174, 159–174.
- Sen Gupta, B.K., Eugene Turner, R., Rabalais, N.N., 1996. Seasonal oxygen depletion in continental shelf waters of Louisiana: Historical record of benthic foraminifers. *Geology* 24, 227–230.
- Shin, P.K., Ellingsen, K.E., 2004. Spatial patterns of soft-sediment benthic diversity in subtropical Hong Kong waters. *Marine Ecology Progress Series* 276, 25–35.
- Sørensen, T.A., 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biol. krif.* 5, 1–34. <https://ci.nii.ac.jp/naid/10008878962/>.
- Sotto, L.P.A., Jacinto, G.S., Villanoy, C.L., 2014. Spatiotemporal variability of hypoxia and eutrophication in Manila Bay, Philippines during the northeast and southwest monsoons. *Marine pollution bulletin* 85, 446–454.
- Tang, C.W., Ip, C.C., Zhang, G., Shin, P.K.S., Qian, P.-y., Li, X.-d., 2008. The spatial and temporal distribution of heavy metals in sediments of Victoria Harbour, Hong Kong. *Marine Pollution Bulletin* 57, 816–825.
- Tanner, P.A., Leong, L.S., Pan, S.M., 2000. Contamination of heavy metals in marine sediment cores from Victoria Harbour, Hong Kong. *Marine Pollution Bulletin* 40, 769–779.
- Tao, L.S., Lau, D.C., Perkins, M.J., Hui, T.T., Yau, J.K., Mak, Y.K., Lau, E.T., Dudgeon, D., Leung, K.M., 2020a. Stable-isotope based trophic metrics reveal early recovery of tropical crustacean assemblages following a trawl ban. *Ecological Indicators* 117, 106610. https://www.sciencedirect.com/science/article/pii/S1470160X20305471?casa_token=jkfjKGLaF9oAAAAA:9HG6M9WYzAJXKqU5bNl4lv3HePdN7922PqKH9rmjUn4ef2KDKQqernPszkD3xtKUZjfgMmMoU.
- Tao, L.S., Lui, G.C., Wong, K.J., Hui, T.T., Mak, Y.K., C-t Sham, R., Yau, J.K., Cheung, W. W., Leung, K.M., 2020b. Does a Trawl Ban Benefit Commercially Important Decapoda and Stomatopoda in Hong Kong? *Ecosystems* 1–14. <https://link.springer.com/article/10.1007/s10021-020-00574-9>.
- Tao, L.S., Lui, K.K., Lau, E.T., Ho, K.K., Mak, Y.K., de Mitcheson, Y.S., Leung, K.M., 2018. Trawl ban in a heavily exploited marine environment: Responses in population

- dynamics of four stomatopod species. *Scientific reports* 8, 1–14. <https://www.nature.com/articles/s41598-018-35804-7>.
- Team, R., 2016. RStudio: Integrated development for R [Computer software]. RStudio, Inc, Boston, MA.
- Todd, P.A., Ong, X., Chou, L.M., 2010. Impacts of pollution on marine life in Southeast Asia. *Biodiversity and conservation* 19, 1063–1082.
- Tomašovič, A., Gallmetzer, I., Haselmair, A., Kaufman, D.S., Kralj, M., Cassin, D., Zonta, R., Zuschin, M., 2018. Tracing the effects of eutrophication on molluscan communities in sediment cores: outbreaks of an opportunistic species coincide with reduced bioturbation and high frequency of hypoxia in the Adriatic Sea. *Paleobiology* 44, 575–602. <https://www.cambridge.org/core/journals/paleobiology/article/tracing-the-effects-of-eutrophication-on-molluscan-communities-in-sediment-cores-outbreaks-of-an-opportunistic-species-coincide-with-reduced-bioturbation-and-high-frequency-of-hypoxia-in-the-adriatic-sea/D0664D450008B254D981A8B8DCBC6E68>.
- Tomašovič, A., Gallmetzer, I., Haselmair, A., Kaufman, D.S., Vidović, J., Zuschin, M., 2017. Stratigraphic unmixing reveals repeated hypoxia events over the past 500 yr in the northern Adriatic Sea. *Geology* 45, 363–366. <https://pubs.geoscienceworld.org/gsa/geology/article/45/4/363/195463/Stratigraphic-unmixing-reveals-repeated-hypoxia>.
- Tomašovič, A., Kidwell, S.M., 2017. Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. *Proc. R. Soc. B* 284, 20170328. <https://royalsocietypublishing.org/doi/full/10.1098/rspb.2017.0328>.
- Tsujimoto, A., Nomura, R., Yasuhara, M., Yoshikawa, S., 2006. Benthic foraminiferal assemblages in Osaka Bay, southwestern Japan: faunal changes over the last 50 years. *Paleontological Research* 10, 141–161.
- Tsujimoto, A., Yasuhara, M., Nomura, R., Yamazaki, H., Sampei, Y., Hirose, K., Yoshikawa, S., 2008. Development of modern benthic ecosystems in eutrophic coastal oceans: the foraminiferal record over the last 200 years, Osaka Bay, Japan. *Marine Micropaleontology* 69, 225–239.
- Turner, A., 2010. Marine pollution from antifouling paint particles. *Marine Pollution Bulletin* 60, 159–171.
- van der Meij, S.E., Moolenbeek, R.G., Hoeksema, B.W., 2009. Decline of the Jakarta Bay molluscan fauna linked to human impact. *Marine Pollution Bulletin* 59, 101–107.
- Wang, Z., Leung, K.M., Sung, Y.-H., Dudgeon, D., Qiu, J.-W., 2021. Recovery of tropical marine benthos after a trawl ban demonstrates linkage between abiotic and biotic changes. *Communications biology* 4, 1–8. <https://www.nature.com/articles/s42003-021-01732-y>.
- Warren-Rhodes, K., Koenig, A., 2001. Escalating trends in the urban metabolism of Hong Kong: 1971–1997. *AMBIO* 30, 429–438. <https://bioone.org/journals/ambio-a-journal-of-the-human-environment/volume-30/issue-7/0044-7447-30.7.429/Escalating-Trends-in-the-Urban-Metabolism-of-Hong-Kong/10.1579/0044-7447-30.7.429.short>.
- Weckström, K., Korhola, A., Weckström, J., 2007. Impacts of eutrophication on diatom life forms and species richness in coastal waters of the Baltic Sea. *AMBIO* 36, 155–160. [https://bioone.org/journals/AMBIO-A-Journal-of-the-Human-Environment/volume-36/issue-2/0044-7447\(2007\)36\[155:IOEODL\]2.0.CO;2/Impacts-of-Eutrophication-on-Diatom-Life-Forms-and-Species-Richness/10.1579/0044-7447\(2007\)36\[155:IOEODL\]2.0.CO;2.short](https://bioone.org/journals/AMBIO-A-Journal-of-the-Human-Environment/volume-36/issue-2/0044-7447(2007)36[155:IOEODL]2.0.CO;2/Impacts-of-Eutrophication-on-Diatom-Life-Forms-and-Species-Richness/10.1579/0044-7447(2007)36[155:IOEODL]2.0.CO;2.short).
- Wei, S., Wang, Y., Lam, J.C., Zheng, G.J., So, M., Yueng, L.W., Horii, Y., Chen, L., Yu, H., Yamashita, N., 2008. Historical trends of organic pollutants in sediment cores from Hong Kong. *Marine Pollution Bulletin* 57, 758–766.
- Wickham, H., 2012. reshape2: Flexibly reshape data: a reboot of the reshape package. R package version 1. <http://cran.ms.unimelb.edu.au/web/packages/reshape2/>.
- Willard, D.A., Cronin, T.M., 2007. Paleocology and ecosystem restoration: case studies from Chesapeake Bay and the Florida Everglades. *Frontiers in Ecology and the Environment* 5, 491–498. <https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/070015>.
- Xu, J., Lee, J.H., Yin, K., Liu, H., Harrison, P.J., 2011. Environmental response to sewage treatment strategies: Hong Kong's experience in long term water quality monitoring. *Marine pollution bulletin* 62, 2275–2287.
- Yasuhara, M., Hunt, G., Breitburg, D., Tsujimoto, A., Katsuki, K., 2012a. Human-induced marine ecological degradation: micropaleontological perspectives. *Ecology and Evolution* 2, 3242–3268. <https://onlinelibrary.wiley.com/doi/full/10.1002/ece3.425>.
- Yasuhara, M., Hunt, G., Cronin, T.M., Okahashi, H., 2009. Temporal latitudinal-gradient dynamics and tropical instability of deep-sea species diversity. *Proceedings of the National Academy of Sciences of the United States of America* 106, 21717–21720. <https://www.pnas.org/content/106/51/21717.short>.
- Yasuhara, M., Hunt, G., van Dijken, G., Arrigo, K.R., Cronin, T.M., Wollenburg, J.E., 2012b. Patterns and controlling factors of species diversity in the Arctic Ocean. *Journal of Biogeography* 39, 2081–2088. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1365-2699.2012.02758.x?casa_token=RY-yYrsl6MkAAAAA%3AkKf8ewlc72Zi50jE99Is4Go5n54-6Wb_5aDTEm-uA3tnCO6fKvh-UVNsau7aupSOJPOyqSkhQ_Y8E9qZg.
- Yasuhara, M., Rabalais, N., Conley, D., Gutierrez, D., 2019. Palaeo-records of histories of deoxygenation and its ecosystem impact. In: Laffoley, D., Baxter, J.M. (Eds.), *Ocean deoxygenation: Everyone's problem – Causes, Impacts, Consequences and Solutions*. IUCN, Gland, pp. 213–224. https://scholar.google.com.hk/scholar?hl=zh-TW&as_sdt=0%2C5&q=Palaeo-records+of+histories+of+deoxygenation+and+its+ecosystem+impact.+In%3A+Laffoley%2C+D.%2C+Baxter%2C+J.M.+%28Eds.%29%2C+Ocean+Deoxygenation%3A+Everyone'S+Problem++Causes%2C+Impacts%2C+Consequences+and+Solut&btnG=.
- Yasuhara, M., Tittensor, D.P., Hillebrand, H., Worm, B., 2017. Combining marine macroecology and palaeoecology in understanding biodiversity: microfossils as a model. *Biological Reviews* 92, 199–215. https://onlinelibrary.wiley.com/doi/full/10.1111/brv.12223?casa_token=hVjPvCvwwtUAAAAA%3A0F3nD-4Dwi_rxSiM5vyuKEoBmsqUxaFD2jG9c7NzGecdhlwvKQswiSQzu7L8Kj0McOn3XzGXeSEZUPSWA.
- Yasuhara, M., Yamazaki, H., 2005. The impact of 150 years of anthropogenic pollution on the shallow marine ostracode fauna, Osaka Bay, Japan. *Marine Micropaleontology* 55, 63–74. https://www.sciencedirect.com/science/article/pii/S0377839805000198?casa_token=anQBxmghAvMAAAAA:f9PX_XXCDkusoT7xgbmisxlzuTZWyh1o2hzcM0HrZGzDZoQOWD62m4FFAxutYFZvhXf_qfhWJE.
- Yasuhara, M., Yamazaki, H., Irizuki, T., Yoshikawa, S., 2003. Temporal changes of ostracode assemblages and anthropogenic pollution during the last 100 years, in sediment cores from Hiroshima Bay, Japan. *The Holocene* 13, 527–536. <https://journals.sagepub.com/doi/abs/10.1191/0959683603hl643rp>.
- Yasuhara, M., Yamazaki, H., Tsujimoto, A., Hirose, K., 2007. The effect of long-term spatiotemporal variations in urbanization-induced eutrophication on a benthic ecosystem, Osaka Bay, Japan. *Limnology and Oceanography* 52, 1633–1644. <https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.4319/lo.2007.52.4.1633>.
- Yeung, Y.-m., 2001. Coastal mega-cities in Asia: transformation, sustainability and management. *Ocean & Coastal Management* 44, 319–333.
- Zhang, S., Lu, X.X., Higgitt, D.L., Chen, C.-T.A., Han, J., Sun, H., 2008. Recent changes of water discharge and sediment load in the Zhujiang (Pearl River) Basin. *China. Glob. Planet. Change* 60, 365–380.
- Zhou, F., Guo, H., Liu, L., 2007. Quantitative identification and source apportionment of anthropogenic heavy metals in marine sediment of Hong Kong. *Environmental geology* 53, 295–305.
- Zuschin, M., Graham Oliver, P., 2005. Diversity patterns of bivalves in a coral dominated shallow-water bay in the northern Red Sea—high species richness on a local scale. *Marine Biology Research* 1, 396–410.