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Eutrophication causes invertebrate biodiversity loss and decreases cross-taxon congruence across anthropogenically-disturbed lakes

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ABSTRACT

Eutrophication is a major problem currently impacting many surface water ecosystems. Impacts of increased nutrient concentrations on biodiversity may differ between different scales, different organism groups, and different trophic states. Surveys at different spatial scales have suggested that biodiversity of different taxa may exhibit significant cross-taxon congruence. In our study, we examined the diversity of zooplankton and zoobenthos across 261 lakes in the Lake Taihu watershed, an area that is undergoing a severe eutrophication process. We tested the cross-taxon congruence in species richness and Shannon-Wiener diversity between zooplankton and zoobenthos along a nutrient gradient across the lakes. Our findings were consistent with the intermediate disturbance hypothesis, considering nutrient input as the disturbance. Also, we found significant cross-taxon congruence between zooplankton and zoobenthos diversities. Our results confirmed that excess nutrient levels resulted in diversity loss and community simplification. Zoobenthos were more sensitive to nutrient increases compared with zooplankton, which decreased cross-taxon congruence because these organism groups did not respond similarly to the anthropogenic disturbance.

1. Introduction

Eutrophication resulting from increasing nitrogen and phosphorus levels caused by human activities is a primary problem impacting aquatic ecosystems worldwide in recent decades (Smith and Schindler, 2009; Alexander et al., 2017; Van Beusekom, 2018). Increased nutrient inputs through increased biomass of algae further affects the diversity of plants and animals (Bunting et al., 2016). Effects of increased nutrient concentrations on biodiversity may differ between trophic levels depending on trophic states (Barnett and Beisner, 2007; Rosset et al., 2014). For instance, changes in nutrient availability affect the community structure of aquatic organisms both directly and indirectly (Bini et al., 2014; Zhang et al.. 2014; Azevêdo et al., 2015). On the one hand, different taxa may be directly filtered through the changing environmental conditions, and different taxa have different tolerance to nutrient concentration (Smith et al., 1999; Lin et al., 2017; Zhang et al., 2019). On the other hand, eutrophication-driven changes affecting the producers and decomposers (Interlandi and Kilham, 2001; Gianuca et al., 2017) may cascade through the food chain indirectly affecting consumers (Heip, 1995; Binzer et al., 2016), called the bottom-up effect (Pace et al., 1999). The effect of nutrients on species diversity may exhibit a unimodal pattern, where diversity first increases, then attains a maximum, and finally starts to decrease with increasing nutrient levels (Abrams, 1995). When the nutrient level is relatively low, the primary productivity of both the plankton and the benthos increases with increasing nutrient levels (Sarnelle et al., 1998). At higher nutrient levels, however, increased nutrient concentrations may lead to less light reaching the lower strata, increasing planktonic yield and reducing benthic yield (Vadeboncoeur et al., 2003; Vasconcelos et al., 2019).

Coupling effects occur when both planktonic and benthic diversities are driven by nutrients and undergo simultaneous and consistent changes (Trigal et al., 2014). In contrast, uncoupling effects occur when planktonic and benthic diversities are driven in different ways, to different degrees, or non-synchronously with changing nutrient levels

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(Azevêdo et al., 2015). Eutrophication has been related to the change of energy transfer of benthic food links in shallow lakes, with a shift in primary productivity from benthic systems to pelagic systems mainly associated with the loss of light, which is associated with the increase of phytoplankton (Vadeboncoeur et al., 2001; Vadeboncoeur et al., 2003; Vasconcelos et al., 2019). This effect can in turn cascade through the food web producing shifts in trophic links of primary consumers. For example, in shallow lakes shifts from periphyton to phytoplankton are common under eutrophic conditions (Vadeboncoeur et al., 2003). Thus, consumers of benthic and pelagic organisms can respond to nutrient enrichment and may alter the autotrophic response (Leibold and Wilbur, 1992; Blumenshine et al., 1997).

Research conducted in aquatic systems on the relationships between primary consumer diversity and different degrees of eutrophication are underrepresented, but most studies suggest a unimodal, bell-shaped pattern of taxonomic richness along the nutrient enrichment gradient (Leibold, 1999; Jeppesen et al., 2000; Barnett and Beisner, 2007). This is because increased nutrients may be considered both as an increase in productivity and as an anthropogenic disturbance (Huston, 1994). When increased nutrients enhance productivity in the surface water ecosystems, they show a positive correlation with primary consumers, such as the increase in the diversity of zooplankton and zoobenthos often reported in originally oligotrophic lakes under increasing nutrient availability (Barnett and Beisner, 2007; Hart, 2011; Korhonen et al., 2011). There is a large body of literature on responses of zooplankton and zoobenthos under eutrophic conditions (Jeppesen et al., 2000; Bini et al., 2014; Gianuca et al., 2017; Zhang et al., 2019). However, as argued by Azevêdo et al. (2015), the evidence is not always consistent. For example, the species richness of zooplankton can increase in the hypereutrophic state due to the increase of small, pollution-resistant rotifers. Nevertheless, many studies often report a humped relationship between zooplankton diversity and total phosphorus concentrations, as shown by both crustaceans and rotifers (Leibold, 1999; Jeppesen et al., 2000), or by just crustaceans (Barnett and Beisner, 2007). Consequently, most of the literature still supports the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978), according to which the highest species richness is maintained at intermediate levels of nutrient enrichment.

A significant spatial correlation of biodiversity has often been found between different taxonomic groups, which is known as cross-taxon congruence (Gaston, 2000; Su et al., 2004; Heino, 2010; de Morais et al., 2018). Strong cross-taxon congruence can be used to identify protected areas, assess ecological effects, and facilitate finding efficient environmental indicators (Heino et al., 2009; Devictor et al., 2010; Namba et al., 2020). Özkan et al. (2014) found that cross-taxon congruence in lakes was not dependent on environmental gradients. However, strong cross-taxon congruence cannot be taken for granted in aquatic ecosystems (Heino, 2010; de Morais et al., 2018), because of among-study differences in trophic levels of the organism groups in question and differences between the spatial scales examined (Heino et al., 2009; Heino, 2010; Trigal et al., 2014). As a result, contradictory evidence exists for whether the diversities of pelagic and benthic primary consumers are congruent because they represent different trophic levels (Azevêdo et al., 2015) and because studies have been conducted at different spatial scales (Zhang et al., 2019).

To elucidate the response of lake biodiversity and cross-taxon congruence to eutrophication, it is necessary to study the effects of different trophic states on the diversity of primary consumers (Azevêdo et al., 2015; Stewart et al., 2018). While earlier studies have examined the effect of environmental gradients on taxonomic richness within and across lakes (Stendera et al., 2012; Özkan et al., 2014; Vilmi et al., 2016; Tolonen et al., 2020), our understanding of the relationships of cross-taxon congruence between zooplankton and zoobenthos with nutrient enrichment gradients is still limited. Here, we addressed this knowledge gap by studying the cross-taxon congruence between primary planktonic and benthic consumers across 261 water bodies of the Lake Taihu watershed in China, which is a region that has been under chronic nutrient enrichment for years (Stendera et al., 2012). We tested the cross-taxon congruence in species richness and Shannon-Wiener index indices between zooplankton and zoobenthos along a nutrient gradient across the lakes. Since energy is rapidly transferred to the planktonic chain during eutrophication (Vasconcelos et al., 2019), it is assumed that responses of zooplankton to nutrient enrichment should be lagging compared to those of zoobenthos (Fig. 1a). In addition, we hypothesized two scenarios, one in which the diversities of zooplankton and zoobenthos peak at a similar nutrient range with an almost complete overlap (left panel in Fig. 1a where the two groups have similar responses along the nutrient gradient), and the other in which the two primary consumers peak at a very different nutrient range with little overlap (central and right panels in Fig. 1a where the two groups have distinct responses along the nutrient gradient). Based on these individual response curves, we hypothesized that congruence between zooplankton and zoobenthos will follow (Fig. 1b) (1) a unimodal pattern with a congruence peak at intermediate nutrient concentrations and decreasing congruence towards the extremes of the gradient (left panel in Fig. 1b); (2) a monotonic increase or decrease in congruence where diversities of zooplankton and zoobenthos declined together or increased together as a result of achieving their diversity peaks at very different nutrient ranges (second and third panels in Fig. 1b).

2. Methods

2.1. Study area

The study was conducted in the Lake Taihu basin during September 2016. A total of 261 lakes were sampled (Fig. 2a), with the average area of lakes being 2.7 km^2. Located in the Yangtze River Delta, the basin accounts for 0.4% of China's land area and 4.4% of its population, but contributes about 9.8% of China's gross domestic product (GDP) (http://www.tba.gov.cn), making it the most industrialized region in China. High-density population and rapid economic development have caused chronic eutrophication in the Taihu Lake Basin, with increasing efforts devoted to ecosystem restoration.

2.2. Sampling methods, chemical analysis and eutrophication level groups

Triplicate water samples were collected near the shore at each lake at the upper (0.5 m from surface), middle (half way between the surface and the bottom) and lower (0.5 m above bottom) layers. Water samples were then used for subsequent analyses of water quality and zooplankton community. Because the water quality within lakes in the Taihu Basin is largely homogeneous (Gao et al., 2012), we focus on differences in the driving forces of eutrophication between lakes and ignore minor differences within lakes. The contents of total nitrogen (TN) and total phosphorus (TP) in each sample were analyzed by spectrophotometer after persulphate digestion (Ebina et al., 1983).

Sediment grabber sampler (ZH2988 CHINA) was used to sample the 0–10 cm surface sediments. The contents of TP and TN were analyzed by secondary sampling. After drying, grinding and sieving, and persulphate digestion, the total nitrogen and total phosphorus were determined by spectrophotometer (Ebina et al., 1983).

Nutrient status of each lake was then determined according to the oligotrophic, mesotrophic, eutrophic and hypertrophic categories defined by OCDE (1982) and Wetzel (1983).

2.3. Identification and counting of zooplankton and zoobenthos

The zooplankton/microcrustacean (Cladocera and Copepoda) were filtered (64-μm plankton net) and preserved (5% formalin) in 10-L water samples before identification and counting (Huang et al., 1999). Cladocera and Copepoda were counted and identified to the lowest possible taxonomic level (Smirnov and Timms, 1983; Einsle, 1993) under 40 ×

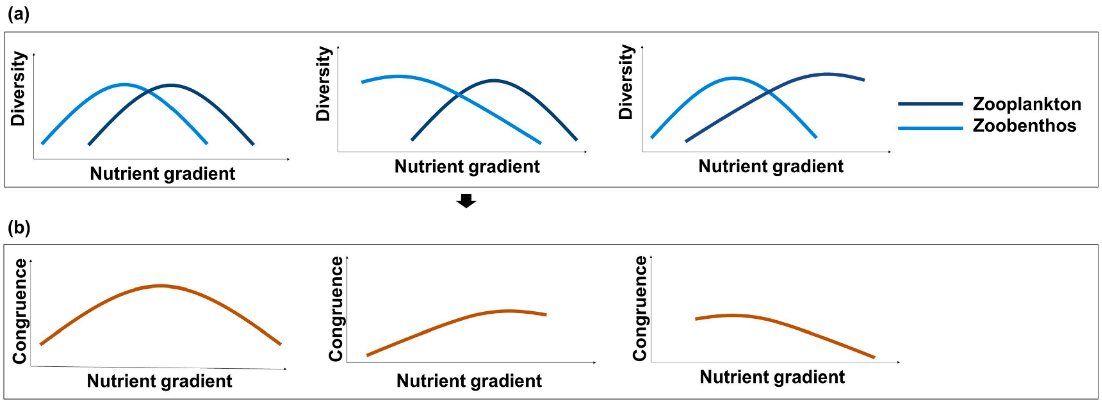


Fig. 1. Conceptual diagrams showing the hypothesized expected diversity and congruence responses of zooplankton and zoobenthos to nutrient enrichment gradients. (a) Zooplankton or zoobenthos diversity are expected to vary with nutrient gradient, subject to sampling time and regional constraints. We hypothesized two scenarios, one in which the diversities of zooplankton and zoobenthos peak at a similar nutrient range with an almost complete overlap (left panel), and the other in which the two primary consumers peak at a very different nutrient range with little overlap of their diversity peaks (central and right panels). (b) The resulting congruence follows then different patterns: (1) an unimodal congruent diversity patterns peaking at intermediate nutrient concentrations along the gradient (left panel); (2) a monotonic increase or decrease in congruence (central and right panels).

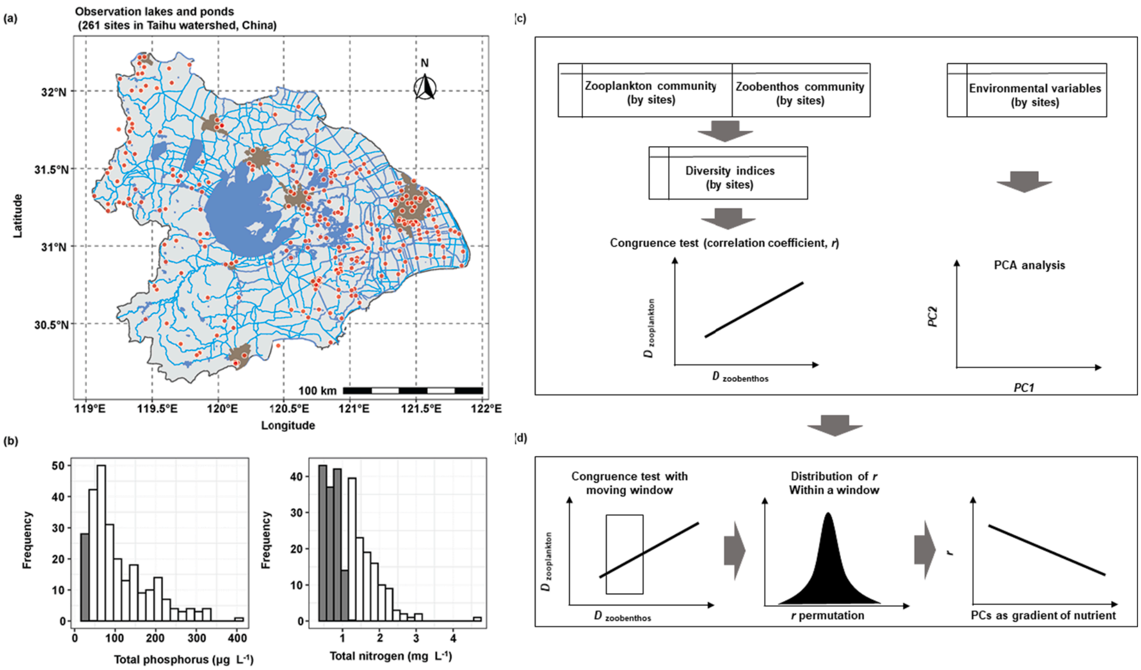


Fig. 2. Study area, nutrient gradients and analytical methods. (a) Location of the 261 lakes sampled within the Taihu watershed, China. (b) histograms of the nutrient levels in the lakes with their eutrophic status shown by the colour of the bars (mesotrophic lakes shown in grey, eutrophic and hypertrophic lakes in white). (c) Flow diagram of the analytical method of cross-taxon congruence test between diversity indexes of zooplankton and zoobenthos (d) A schematic representation of the analytical method used for testing the correlation coefficients of each species diversity index and the two independent variables (PC1 for water column and PC2 for sediments).

magnification (Olympus CX21 microscope). Using the methods described by Huang et al. (1999), the body lengths of at least 30 random individuals of each species were measured and the biomass of each plankton species was calculated as wet weight.

The zoobenthos were captured by a sediment grab, screened and cleaned in situ, and then put into containers for refrigerated transportation to the laboratory. After the zoobenthos were picked out on the white disk, they were preserved with 7% formalin solution. Finally, stereoscopic microscopy (MBS-10) was used for classification and identification to reach the lowest possible classification level utilizing available keys for this region (Morse et al., 1994; Wang, 2002).

2.4. *Statistical analyses*

Principal Component Analysis (PCA) was used on TP and TN in surficial sediment and water column across the 261 sampled lakes to visualize ordination patterns of zoobenthos and zooplankton in nutrient space according to the eutrophic status of the water bodies. The first and second principal components (PCs), which explained 62% of total variation (supplementary information Fig. S1), were used to represent the water and sediment nutrient enrichment status, respectively.

To measure how the diversity of the two key primary consumer communities, i.e. zooplankton and zoobenthos, was affected by nutrient enrichment gradients, we first calculated species richness (S) and Shannon-Wiener index (*H'*) as diversity descriptors of a community for a given lake. Species richness was calculated as the number of species in a community. The Shannon-Wiener index was calculated as $H' = -\Sigma P_i \ln P_i$, where P_i represents the proportion of total abundance belonging to species *i*. Multiple quadratic regressions were then used to explain the relationship between each biodiversity index for each primary consumer, as response variables, and nutrient enrichment status using the two PCs as synthetic predictor variables.

Overall cross-taxon congruence between the two primary consumer communities was tested using simple linear regression for each biodiversity index on the observed paired values for each primary consumer at each sampling site, and calculated the coefficient of correlation and the significance level ($\alpha = 0.05$). The effect of nutrient enrichment on cross-taxon congruence between the two consumer communities was then analyzed using a rolling-window analysis as proposed by Zivot and Wang (2003), which consisted of four main steps: selection of regression algorithm, finding an optimal window size, estimation of the regression using each rolling window subsamples, and the analysis of the series of resulting regression coefficients. A rolling window analysis is typically used in time series analysis to assess the stationarity or temporal stability of the model's coefficients over time (Zivot and Wang, 2003). Here, however, we used this approach to assess the stability of our congruence model's parameters across the nutrient enrichment gradient.

First, the selection of the regression algorithm was performed using bootstrapping (Efron and Tibshirani, 1994) to calculate the coefficient of determination as an index of the strength of cross-taxon congruence of diversity between zooplankton and zoobenthos. Bootstrapping was used to produce a distribution of coefficient of determination to compare with the actual observed coefficient of determination. For each rolling window, we bootstrapped the whole dataset with replacement 999 times to generate the underlying distribution of the model coefficient of determination (Fig. 2c).

Second, given that the accuracy of the fitted model generally improves as the size of the rolling window increases (Xu et al., 2018), we based the choice of the optimal rolling window size on a stability criterion, which is achieved at a point where increasing further the size of the window produces only small changes in the model estimates. Since we used two PCA-based nutrient gradients to predict cross-taxon congruence and to have adequate numbers of samples to compute estimates correctly, we initially used window sizes greater than 60 samples (about 1/4 of the whole dataset), and increased window sizes to 130 samples (about 1/2 of the whole dataset). The stability criterion was achieved when the window sizes were larger than 80 samples. Thus, we chose the window size of 90 samples (about 1/3 of the whole dataset) (Table S1) and rolled the window from low to high values of both first and second PCAs.

Finally, using a series of correlation coefficients and the means of the values of both first and second PCAs corresponding to the lakes that the observations within each rolling window corresponded to, we used multiple linear quadratic regressions to explain the relationship between correlation coefficients of each species diversity index and the two independent variables (i.e. mean values of the first and second axes of PCA). This approach helps understanding how the strength of cross-taxon congruence of species diversity between zooplankton and zoobenthos was affected by nutrient gradients (Fig. 2d).

All statistical analyses were produced within the vegan R package (Oksanen et al., 2013) in version R 3.5.1 (R Development Core Team, 2019).

3. Results

The lakes we studied ranged from mesotrophic to hypertrophic (Fig. 2b). TP and TN concentration in the water column varied from 0.017 to 0.391 mg L^{-1} and 0.301 to 4.696 mg L^{-1} with respective mean values of 0.103 mg L^{-1} and 1.106 mg L^{-1}. TP and TN concentrations in the sediment varied from 101 to 3645 mg kg^{-1} and 253 to 11251 mg kg^{-1} with mean values of 636 mg kg^{-1} and 2710 mg kg^{-1}.

A total of 15 zooplankton groups were found across all sampled lakes, including 7 Cladoceras and 8 Copepods. Zoobenthos diversity accounted for a total of 74 taxa, including 21 Mollusca, 25 Annelida and 28 Insecta taxa. The mean species richness and Shannon-Wiener index of zooplankton and zoobenthos across the 261 lakes were 6.6 and 4.4, 0.54 and 0.51, respectively. The diversity indexes (species richness and Shannon-Wiener index) of zooplankton and zoobenthos were best accounted for by the quadratic models along the nutrient gradients (PC1 and PC2) (mean $r = 0.56$ and 0.63, respectively; Fig. 3 and Table S1).

The response of zooplankton diversity (both species richness and Shannon-Wiener index) to eutrophication in water (PC1) decreased exponentially, while the response to the nutrient increase in sediment (PC2) followed a unimodal curve (Fig. 3a,c). On the contrary, benthos diversity showed an opposite response: an exponentially decreasing response to the nutrient increase in sediment and a unimodal response to the eutrophication of the water (Fig. 3b,d). Zooplankton were more strongly affected by the eutrophication level in the water column (PC1), while zoobenthos were more affected by sediment nutrient enrichment (PC2) (Fig. 3 and Table S1). In general, both species richness and Shannon-Wiener indexes of zooplankton and zoobenthos showed an exponential decay pattern (Fig. 3), and our results thus matched the posterior portion of the intermediate disturbance hypothesis that alpha diversities were asymptotically decreasing with increasing disturbance levels (Hypotheses Fig. 1a). Zoobenthos diversities followed a more consistent decreasing pattern, whereas zooplankton diversity showed initially an increasing response, followed by a decline (Fig. 3). This finding proved that zoobenthos diversity decreased before zooplankton diversity (Hypotheses Fig. 1a first figure).

The five dominant species were *Diaphanosoma brachyurum* (relative abundance 41.34%), *Bosminopsis deitersi* (12%), *Moina micrura* (11.61%), *Ceriodaphnia cornuta* (8.23%), and *Thermocyclops taihokuensis* (7.88%) for zooplankton, as well as *Microchironomus tabarui* (13.88%), *Tanypus chinensis* (13.85%), *Limnodrilus hoffmeisteri* (12.06%), *Branchiura sowerbyi* (8.23%), and *Chironomus semireductus* (8.05%) for zoobenthos (Table S3). The diversities of zooplankton and zoobenthos, measured by different indexes, were significantly positively correlated (mean $r = 0.37$, $P < 0.001$, Fig. 4).

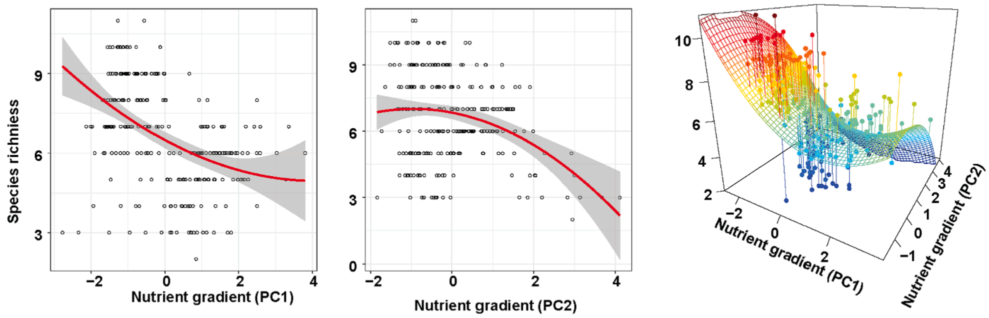
Results from the tests of cross-taxon congruence using moving windows (raw points and quadratic models) of correlation coefficients between zooplankton and zoobenthos diversity indexes provided relevant insights (Fig. 5 and Table S4). These models showed that the correlation coefficient was negatively associated with nutrient gradient (mean $r = 0.74$, $P < 0.001$). This proved that the overall positive correlation between the diversity of the two organism groups was weakened by increasing nutrient levels, which is consistent with the intermediate disturbance hypothesis (first panel of Fig. 1b).

4. Discussion

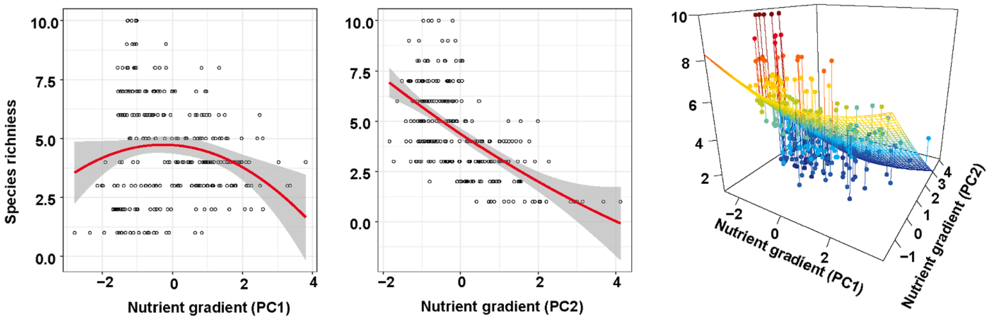
Our results confirmed that all sampled lakes in the Lake Taihu basin are already at a stage exceeding mesotrophic conditions (Peng et al., 2018) and are thus experiencing a period of declining species diversity (Zhang et al., 2014). We also observed significant decreases in the diversity of both zooplankton and zoobenthos along nutrient gradients. Similar patterns of decreasing species diversity with increasing productivity were also found in various aquatic ecosystems in previous studies (Jeppesen et al., 2000; Worm et al., 2002; Stomp et al., 2011). Our findings thus suggest that the diversity responses of zooplankton and zoobenthos to eutrophication are similar, implying relatively strong cross-taxon congruence along nutrient gradients. The Lake Taihu basin has experienced serious development and environmental destruction, which may be an important reason for the decrease of congruence as a reflection of the characteristics of this basin.

Compared with the diversities of zooplankton and zoobenthos detected in previous research (Guan et al., 2011; Cai et al., 2012; Chen et al., 2012), we found diversity of Lake Taihu basin reduced, evidencing

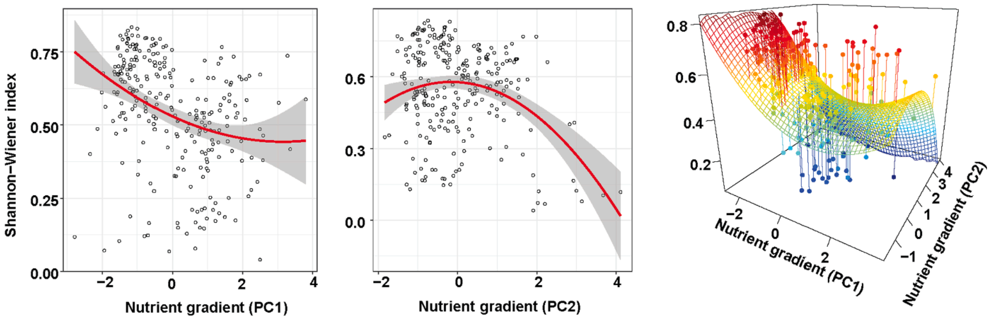
(a) Zooplankton



(b) Zoobenthos



(c) Zooplankton



(d) Zoobenthos

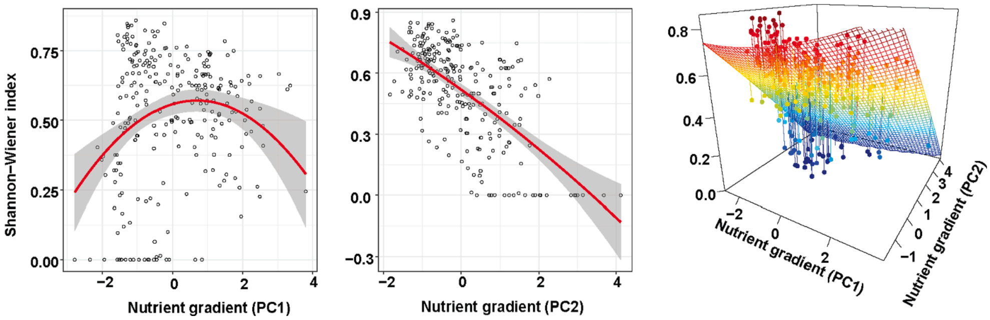


Fig. 3. The quadratic models of diversity indexes of zooplankton and zoobenthos along the nutrient gradient (PC1 for water column and PC2 for sediments). Panels: (a) species richness of zooplankton; (b) species richness of zoobenthos; (c) Shannon-Wiener index of zooplankton; (c) Shannon-Wiener index of zoobenthos.

that biodiversity is now in a declining stage. Whereas *Bosmina* sp. and *Mesocyclops* sp. represented the dominant species of zooplankton in these lakes back in 2009 (Chen et al., 2012), and the most common zoobenthos taxa were found to be *Limnodrilus hoffmeisteri*, *Branchiura sowerbyi*, *Corbicula fluminea* and *Gammarus* sp. during February 2007 to November 2008 (Cai et al., 2012), in our study we found that current dominant groups have shifted towards species better adapted to highly eutrophic water bodies (Yang et al., 1998; Barnett and Beisner, 2007). Other than direct effects of nutrient enrichments on these species, competitive exclusion can also be responsible for the observed differences in taxonomic composition. For example, *Diaphanosoma brachyurum* and *Moina micrura* are more tolerant to high nutrient and low oxygen levels and are thus stronger competitors than *Bosmina* sp. and *Mesocyclops* sp. (Yang et al., 1998). Under the intensification of

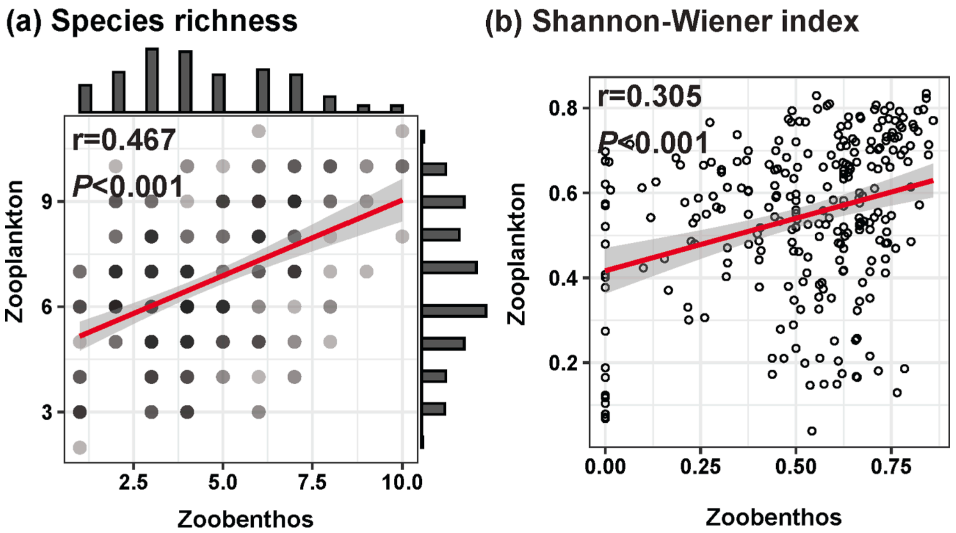


Fig. 4. The congruence test of diversity indexes of zooplankton and zoobenthos for (a) species richness, where the transparency and marginal historgams shows the density of overlapping points; and (b) Shannon-Wiener index. Red lines in the panels represent the linear regression trends.

eutrophication, the pollution-tolerant taxa (e.g. *Microchironomus tabarui* and *Tanypus chinensis*) should gradually take advantage over more sensitive taxa (Zhang et al., 2019).

Our findings show that excess nutrient levels have resulted in biodiversity loss in highly eutrophic lakes, following the hump-shaped model of disturbance-diversity response. Although the diversity peaks of zooplankton and zoobenthos appeared in the near nutrient range, the diversities of zooplankton and zoobenthos still showed a similar decreasing trend, which may be related to the different tolerances of plankton and benthos to nutrient enrichment (Blumenshine et al., 1997; Jäger and Diehl, 2014). Each species of zooplankton and zoobenthos has a competitive advantage over the resources in certain conditions, and a weaker competitor can sometimes co-exist with a stronger one, eventually even excluding superior competitors if conditions change (Jäger and Diehl, 2014). As expected under the intermediate disturbance hypothesis, the initial increase in nutrient levels favours both zooplankton and benthic organisms but further increases in phytoplankton eventually alter light and other conditions, blocking the benthic chain and triggering a turning point (Jäger and Diehl, 2014). It is precisely because planktonic primary consumers and benthic primary consumers prefer different levels of nutrients that they exhibit different biological rates and processes. Whereas the benthic chain is more affected by nutrient availability, the planktonic chain is more dependent on light conditions (Vasconcelos et al., 2019; Wang et al., 2020). Under the long-term and chronic eutrophication process of the Taihu Basin, the energy of the water system is transferred to the plankton chain, which may lead to an earlier collapse of the benthic community (Vadeboncoeur et al., 2001; Vadeboncoeur et al., 2003; Vasconcelos et al,. 2019).

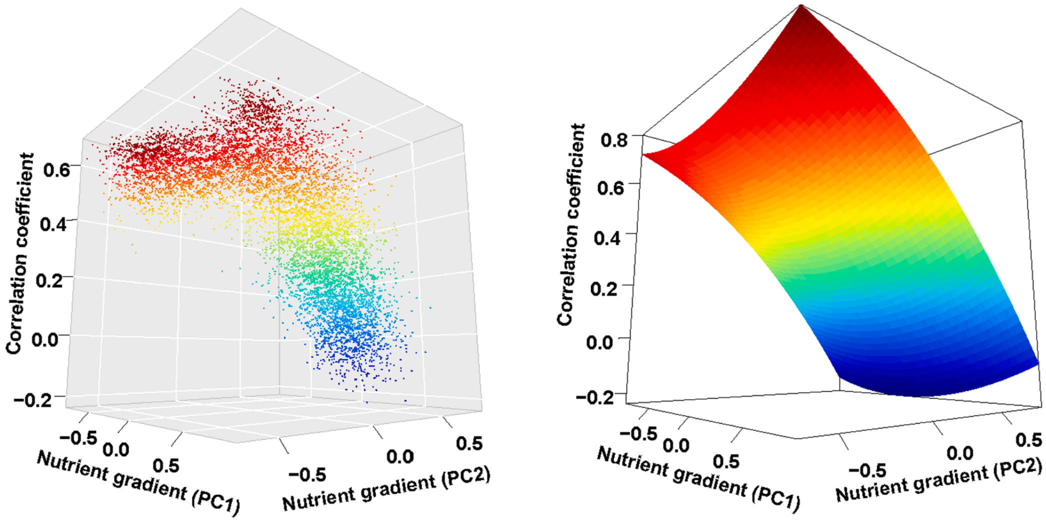
The diversities of both zooplankton and zoobenthos peaked at moderate levels of nutrients, whereas dominance by a few species characterized lakes with high levels of nutrients. The bottom-up effect on organisms in eutrophic lakes is a common finding (Matsuzaki et al., 2018), as nutrients promote the large biomass of planktonic algae and degraded organic matter as carbon sources for primary consumers (Anderson et al., 2002). Eutrophication thus plays a key role in structuring zooplankton and zoobenthos communities (Snickars et al., 2015, Binzer et al., 2016, Alexander et al., 2017), through being associated with wave disturbance and sediments in lake environments and through determining the amount of light and primary productivity (Striebel et al., 2012). Therefore, the bottom-up linkages from nutrients to zooplankton and zoobenthos can drive variation in their diversity in eutrophic lakes. Similar to our results, recent studies have also indicated a decline in alpha or beta diversity with increasing nutrient levels (Jeppesen et al., 2000; Bini et al., 2014; Gianuca et al., 2017; Zhang et al., 2019). This could be associated with the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978), suggesting that excessive nutrient-related disturbances can eliminate the category of species being in competitive disadvantage, resulting in decreased biodiversity.

Our study adds to the evidence of the role of eutrophication as an important driver of cross-taxon congruence (Heino, 2010; Özkan et al., 2014). Our results thus corroborate previous studies documenting significant congruence in species diversity across lakes (Striebel et al., 2012; Tisseuil et al., 2013). We found clear congruence of species diversity between planktonic primary consumer (zooplankton) and benthic primary consumers (zoobenthos) across lakes in the Lake Taihu watershed. The diversities of zooplankton and zoobenthos responded similarly to the nutrient gradients, which is consistent with findings from previous studies (Özkan et al., 2014). As primary consumers in two different food chains (i.e. pelagic vs benthic), zooplankton and zoobenthos communities may not necessarily exhibit strong food-web interactions (Snickars et al., 2015; Matsuzaki et al., 2018).

Although we found significant positive correlations between zooplankton and zoobenthos diversities, there may be differences in their responses to eutrophication. Our results indicate that although eutrophication may decrease average species diversity in eutrophic lakes (Interlandi and Kilham, 2001; Gianuca et al., 2017), it can also decrease the strength of cross-taxon congruence. Therefore, zooplankton and zoobenthos communities might provide distinct information regarding ecological quality assessment in nutrient-rich conditions (Azevêdo et al., 2015). Our study also demonstrated that eutrophication may have asynchronous effects on the diversities of zooplankton and zoobenthos, which may be intensified as eutrophication progresses.

The response of zoobenthos diversity and zooplankton diversity to eutrophication was exponential in our study, and zoobenthos diversity decreased before zooplankton diversity did. This suggests that the diversity of zoobenthos is more sensitive to eutrophication compared with the diversity of zooplankton. In other words, zoobenthos diversity declined first, as has also been found previously (Azevêdo et al., 2015). Zoobenthos may be thus a better indicator group than zooplankton for assessing lake eutrophication (Pinel-Alloul et al., 1996; Friberg et al., 2011). Our results also indicate that zooplankton were mainly affected by the nutrient level of water column, while zoobenthos were more affected by the nutrient level of sediments. Cross-taxon congruence in species richness and Shannon-Wiener indexes were both more strongly affected by sediment nutrients. This suggests that the decline of cross-congruence was affected by the exposure of zoobenthos to sediment

(a) Species richness



(b) Shannon−Wiener index

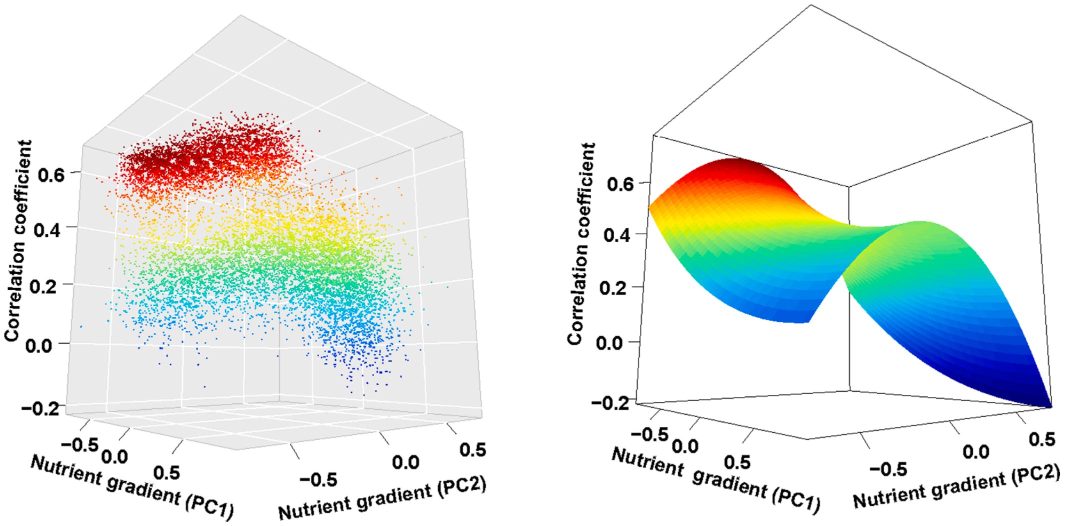


Fig. 5. Results from the moving window congruence test for the raw points (left panels) and quadratic (right panels) models of diversity correlation coefficient between zooplankton and zoobenthos along the nutrient gradient (PC1 for water column and PC2 for sediments). Panels: (a) species richness; (b) Shannon-Wiener index.

nutrients (Azevêdo et al., 2015).

Our study provides evidence for significant cross-taxon congruence between zooplankton and zoobenthos. However, increasing nutrient levels decreased the cross-taxon congruence of zooplankton and zoobenthos. This finding corroborates those of recent studies that have shown clear responses of primary consumers to environmental variation (Azevêdo et al., 2015; Snickars et al., 2015). In addition, along with intensifying eutrophication, the diversities of zooplankton and zoobenthos could be further reduced. On the other hand, our results contribute to assessing which organism groups could be used as indicators of eutrophication in freshwater ecosystems.

5. Conclusion

The key finding of our study is that zooplankton and zoobenthos showed significant cross-taxon congruence in species diversity. However, it should be emphasized that increasing degrees of eutrophication decreased the congruence between zooplankton and zoobenthos. In addition, if the aim is to monitor the eutrophication process, careful selection of a group of organisms for different phases of the process in space and time should be considered. Sustainable management of freshwater ecosystems therefore requires a better understanding of the complex interrelationships between biodiversity and among-taxon congruence and how they are affected by eutrophication. The reliability of the surrogacy approach may decrease when the eutrophic gradient is intensifying. Knowledge of the differences in responses among taxonomic groups and between habitats to disturbance related to increased nutrient levels can be used to design more cost-effective monitoring programs.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envint.2021.106494.

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