Evaluating the effects of aquaculture on the freshwater lake from the perspective of plankton communities: The diversity, co-occurrence patterns and their underlying mechanisms ☆

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ABSTRACT

Aquaculture has significant impacts on freshwater lakes, but plankton communities, as key components of the microbial food web, are rarely considered when assessing the impacts of aquaculture. Revealing the dynamics of plankton communities, including bacterioplankton, phytoplankton and zooplankton, under anthropological disturbances is critical for predicting the freshwater ecosystem functioning in response to future environmental changes. In the present study, we examined the impacts of aquaculture on water quality, plankton diversity and the co-occurrence patterns within plankton metacommunities in a shallow freshwater lake. The study zones are influenced by the 20-year historical intensive aquaculture, but now they are undergoing either ecological aquaculture or ecological restoration. Our results showed that ecological aquaculture was more efficient in nitrogen removal than ecological restoration. Moreover, lower bacterioplankton diversity but higher phytoplankton and zooplankton diversity were found in the ecological aquaculture and ecological restoration zones compared to the control zone. The lower network connectivity of the plankton metacommunities in the ecological aquaculture and ecological restoration zones indicated the decreasing complexity of potential microbial food web, suggesting a possible lower resistance of the plankton metacommunities to future disturbance. Furthermore, plankton communities of different trophic levels were driven under distinct mechanisms. The bacterioplankton community was primarily affected by abiotic factors, whereas the phytoplankton and zooplankton communities were explained more by trophic interactions. These results revealed the impacts of aquaculture on the plankton communities and their potential interactions, thereby providing fundamental information for better understanding the impacts of aquaculture on freshwater ecosystem functioning.

1. Introduction

Freshwater aquaculture plays a significant role in global food supply, which is predicted to be more and more important for providing an affordable, accessible and stable supply of aquatic food to vast numbers of consumers in the future (Zhang et al., 2022). However, intensive aquaculture through increasing use of pelleted feed as well as expansion of the aquaculture area induces the massive input of nitrogen and phosphorus (Lu et al., 2015), and results in eutrophication of the corresponding freshwater ecosystems (Edwards, 2015). Furthermore, the massive input of nutrients caused by the intensive aquaculture could change the compositions of plankton communities, including bacterioplankton (Wang et al., 2020), phytoplankton (Xu et al., 2010) and zooplankton (Lorenz et al., 2019), which play important roles in the flow of matter and energy throughout the microbial food web (Sarmento, 2012), thereby influencing the ecosystem functions. The increasing demand on freshwater aquaculture as well as the corresponding environmental issues required the transformation from the intensive aquaculture to ecological aquaculture by maximizing the use of natural resources as well as reducing the use of pelleted feed to balance the ecological and economic effects (Edwards, 2015; Costa-Pierce, 2008). Planting aquatic macrophytes is an important measure for restoring the

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shallow freshwater ecosystem (Zeng et al., 2017), which is also widely used in the ecological aquaculture. It has been reported that the macrophytes can reduce nutrient loading and stabilize clearwater conditions at the aquaculture-polluted sites (Li et al., 2021). Although the water quality might be improved when the intensive aquaculture is replaced by the ecological aquaculture, the impacts of aquaculture on the key components of the microbial food web acting as the important players in maintaining the ecosystem functioning, should be also included into the assessment for a better understanding of the impacts of aquaculture on the freshwater ecosystem.

The responses of the plankton communities to environmental changes, which may be regulated by their characteristics, including their life history, metabolism and physiology, could differ (Heino et al., 2015). Accordingly, we hypothesize that bacterioplankton, phytoplankton, and zooplankton communities could be affected differently under environmental changes induced by aquaculture. For instance, the organic matter derived from the feeding and excrement in aquaculture sites can affect the community compositions of bacterioplankton (Judd et al., 2006); the further release of nitrogen and phosphorus through mineralization of organic matter could be responsible for shifting phytoplankton populations (Vrede et al., 2009). The presence of aquatic macrophytes could lead to competition for nutrients with phytoplankton, thereby influencing the dynamics of phytoplankton community (Barrow et al., 2019). For the zooplankton community, lake primary productivity and the fish community (planktivores), which can also be influenced by aquaculture, are the major predictors of zooplankton diversity (Hessen et al., 2006). Nevertheless, multiple environmental variables, like nitrogen, phosphorus, and organic carbon input, which could be changed under aquaculture, can jointly contribute to the shift of plankton communities. The causal relationships between the environmental changes and plankton community shift are still unclear, thus limiting the comprehensive understanding of the impacts of aquaculture on the diversity and composition of different plankton communities. Furthermore, these plankton communities have been widely found to exhibit seasonal patterns in diversity, biomass and composition (Graham et al., 2004; Silva et al., 2014). Aquaculture activities as well as the growth of aquatic macrophytes are also associated with the seasonal changes. Therefore, seasonal variations should be considered when investigating the impacts of ecological aquaculture on plankton communities.

In addition to the effects of abiotic environment, the relationships between the different trophic levels within the microbial food web, including predation, competition and symbiosis, are also crucial for structuring plankton communities (Resetarits et al., 2005). For example, the grazing pressure from zooplankton is an important factor influencing phytoplankton communities (Havens et al., 2009). The dominance of small-bodied zooplankton can lead to strong grazing pressure on bacterioplankton (Jeppesen et al., 2007), and the dissolved organic matter released by zooplankton can also influence the corresponding decomposers (Johnston et al., 2021). In turn, phytoplankton and bacterioplankton taxa could also influence the zooplankton community by providing food. The relationships between phytoplankton and bacterioplankton could be more complicated (Seymour et al., 2017); at the simplest level, the relationship between these organisms is based on the provision of resources and can be either reciprocal or exploitative (Cole, 1982). The trophic interactions between these plankton communities control nutrient cycling and biomass production at the base of the food web, and thus represent a fundamental relationship in aquatic environments (Lima-Mendez et al., 2015). However, community-level trophic relationships are rarely considered into the investigation for revealing the mechanisms of plankton community assembly, especially when the ecosystem is disturbed by aquaculture. It will provide a more accurate assessment considering the joint effects of abiotic factors and biotic interactions on plankton community under the influence of aquaculture. Moreover, the potential interactions at a much lower taxonomic level than the community level, which can be explored through network analysis, can elucidate the ecologically meaningful interactions between taxa (Barberán et al., 2012). Network analysis would be a useful tool to reveal how aquaculture alters the potential interactions between different plankton taxa, which could provide insights into predicting the ecosystem functioning represented by the microbial food web.

In the present study, we conducted a seasonal survey on the water physiochemical characteristics and surface plankton community compositions across zones with different impacts of aquaculture in Eastern Lake Taihu, China. In this study, we aim to answer the following questions: (1) How do environmental parameters and plankton communities (diversity and composition) change with aquaculture? (2) Do potential interactions between plankton taxa change with aquaculture? (3) What are the mechanisms influencing the structures of the different plankton communities under the impacts of aquaculture?

2. Materials and methods

2.1. Sampling site

Eastern Lake Taihu is a shallow freshwater bay with the average depth of 1.6 m that has been influenced by the intensive aquaculture since the 1980s. However, since 2008, intensive aquaculture has been replaced by ecological aquaculture or ecological restoration where the area and density of cultivation have been reduced and aquatic macrophytes have been planted. Here we have defined the sampling sites into four zones, namely two ecological aquaculture zones (EA1 and EA2), one ecological restoration zone (ER) and one control zone (CK). These study zones were influenced by aquaculture activities and the construction of submerged macrophytes to different degrees. EA1, EA2 and ER zones were all used for intensive aquaculture for more than 20 years, which could be still affected by the legacy of historical aquaculture. Now EA1 and EA2 are being used for ecological aquaculture by planting submerged macrophytes and cultivating various aquatic animals. Pen fish culture is the main form of aquaculture in the EA zones. These farms cultivated mainly freshwater crab (*Eriocheir sinensis*) and shrimp (*Macrobrachium nipponense*). The dominant macrophyte in the EA zones is *Elodea nuttallii*. The ER zone is currently being ecologically restored by planting diverse aquatic macrophytes, of which the dominant macrophyte is *Potamogeton crispus*. The CK zone is not affected by historical aquaculture activities or current artificial management. For each zone, we set nine replicate sites, as shown in Fig. 1A.

We collected surface water samples at the depth of 50 cm for each sampling site in winter (February), spring (April) and summer (July) 2018. Therefore, the plankton communities mentioned in this study referred to the plankton communities of the surface water. All samples were preserved with ice bags and transported to the laboratory for further analyses.

2.2. The measurement of environmental parameters

Water temperature, dissolved oxygen (DO), electrical conductivity (EC), oxidation-reduction potential (ORP) and pH were determined *in situ* using a calibrated multifunction water quality sonde (YSI 6600, Yellow Springs, OH, USA). Total nitrogen (TN) and total phosphorus (TP) were measured with unfiltered water samples using the standard methods (Rice et al., 2012). Nitrate nitrogen (NO_3^--N) and ammonia nitrogen (NH_4^+-N) were measured through continuous flow analysis (Skalar SAN PLUS system, Skalar Analytical BV, Breda, Netherlands) after the water samples were filtered using the 0.22 μm pore-size polycarbonate membrane filter (47 mm diameter; Millipore). The filtered water samples were also used to measure dissolved organic carbon (DOC) with a TOC analyzer (Multi N/C 2100, Analytic Jena, Jena, Germany). Ethanol was selected to extract chlorophyll *a* (Chl-a) in the dark for 12 h, and then the concentrations of Chl-a were examined by spectrophotometry (Jespersen & Christoffersen, 1987).
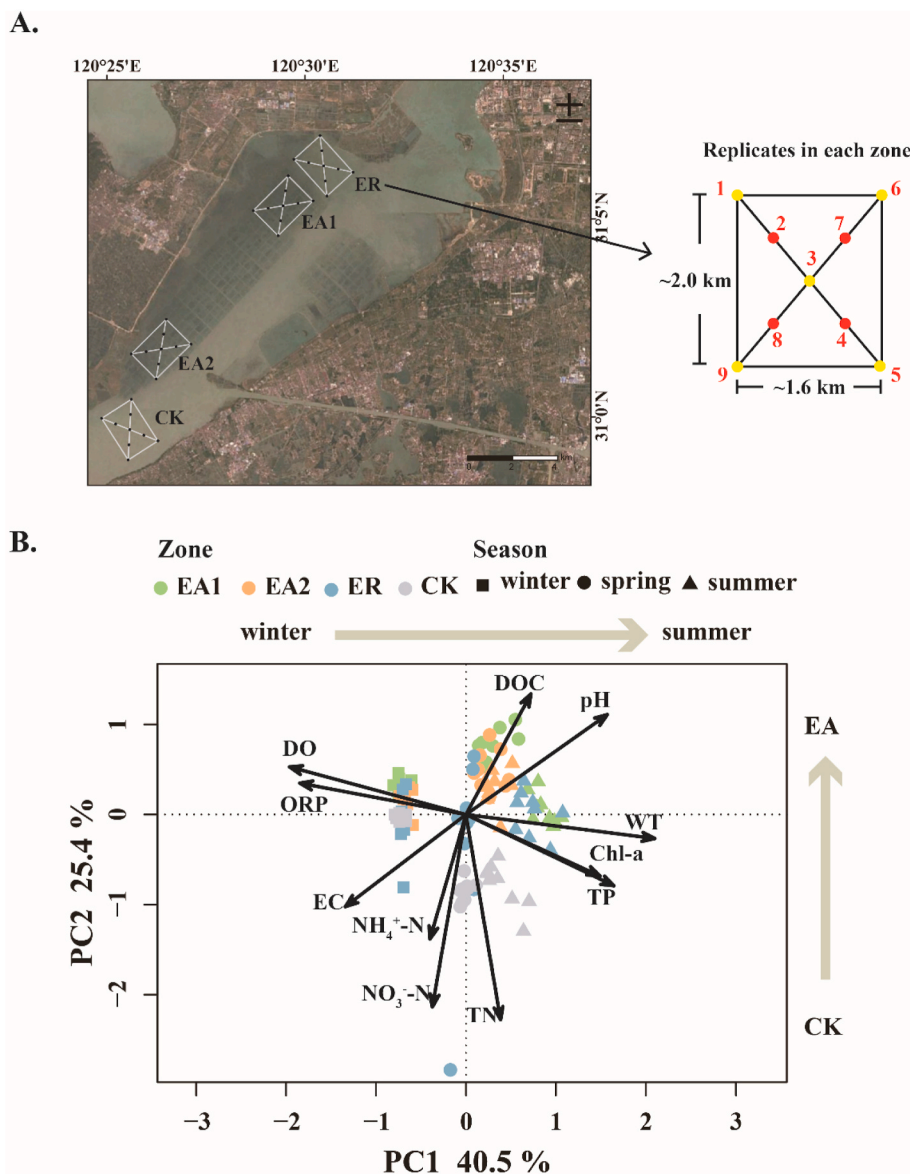
Fig. 1. The sampling design (A) and the principal components analysis (PCA) on the environmental parameters across seasons and zones. For A, the analyses of phytoplankton and zooplankton were only conducted in sites colored by yellow, whereas the bacterioplankton was analyzed in all replicate sites in each zone. For B, all the environmental parameters were measured in the current study. WT, water temperature; DO, dissolved oxygen; EC, electrical conductivity; ORP, oxidation-reduction potential; TN, total nitrogen; TP, total phosphorus; NO_3^--N, nitrate nitrogen; NH_4^+-N, ammonia nitrogen; DOC, dissolved organic carbon; Chl-a, chlorophyll *a*. EA, ecological aquaculture zone; ER, ecological restoring zone; CK, control zone. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.3. The morphological identification of phytoplankton and zooplankton

We analyzed the compositions of phytoplankton and zooplankton communities for five replicate sites in each zone (yellow nodes in Fig. 1A). To identify phytoplankton, water samples were first fixed with Lugol's iodine solution, then sedimented and concentrated for 48 h before phytoplankton cells were counted under the microscope using the separating funnel (Chen et al., 2003). The phytoplankton genera were identified according to Hu (2006). To identify zooplankton, water samples were filtered through a mesh of 64 μm and then preserved with 4% formalin. All samples were examined for Rotifera, Cladocera and Copepoda (Jiang and Du, 1979; Shen, 1979; Wang, 1961; Zhang and Huang, 1991) and counted under the microscope. The biovolumes of phytoplankton and zooplankton were calculated from the cell counts and cell size measurements. When converting to biomass, it is assumed that 1 mm³ volume corresponds to 1 mg fresh weight biomass.

We calculated the richness of the phytoplankton and zooplankton communities based on the number of genera identified in each sample. The Bray-Curtis distance was used to determine the beta diversity of the phytoplankton and zooplankton communities based on the relative biovolume data.

2.4. DNA extraction, PCR, high-throughput sequencing and sequencing processing for bacterioplankton

Water samples were filtered through the 0.22 μm pore-size polycarbonate membrane filter (47 mm diameter; Millipore) to collect the bacterial biomass. DNA was extracted using the E. Z.N.A. D5525-01 Water DNA Kit (Omega Bio-tek, Norcross, Georgia, USA). The V4 region of the 16S ribosomal RNA gene of the bacteria was amplified using primers 515F (5′-GTGCCAGCMGCCGCGG-3′) and 806R (5′- GGAC-TACNVGGGTWTCTAAT-3′) in a polymerase chain reaction (PCR) (Caporaso et al., 2012). The PCR reaction mixture and thermal cycling conditions were consistent with existing procedures (Zhao et al., 2017). For each sample, PCR was performed three times. The Illumina paired-end library was constructed and the amplicons were then sequenced using the Illumina HiSeq-PE250 platform (San Diego, CA, USA) at MAGIZENE Corporation Inc (Guangdong, China). The raw reads were submitted to the NCBI Sequence Read Archive (SRA) database (Accession ID: PRJNA605263) (Table S1).

The obtained paired-end raw data was processed according to our previous research (Jiao et al., 2021), which was described in the supporting information. The number of observed operational taxonomic

units (OTUs) was calculated as the richness of the bacterioplankton. The Bray-Curtis dissimilarity matrix was calculated as the beta diversity of the bacterioplankton community.

2.5. Statistical analysis

Two-way analysis of variance (ANOVA) was used to distinguish whether the environmental parameters, phyto/zooplankton cell density/biomass and richness of all plankton communities showed significant differences across seasons or zones. One-way ANOVA followed by Turkey's multiple comparison test was used to further identify the significant differences of these above indices between zones within each season. The significant differences in the dominant taxa of all plankton communities were also analyzed using the one-way ANOVA followed by Turkey's multiple comparison test. We used principal component analysis (PCA) to show the general trends of environmental parameters. Principal co-ordinates analyses (PCoA) and PERMANOVA tests were used to examine the differences in plankton communities across seasons and zones. The ANOVA tests were performed using the 'aov' command in R. The PCA, PCoA and PERMANOVA were all performed using the package 'vegan' in R (Oksanen et al., 2019). The average number and proportion of unique and shared taxa of plankton communities between different zones were represented by Venn diagrams.

Topological networks were constructed using Sparse Correlations for Compositional Data (SparCC) to reveal the potential interactions between taxa within the plankton metacommunities in each zone (Friedman and Alm, 2012). To enhance network reliability, we constructed them by selecting bacterial OTUs or phytoplankton/zooplankton genera that had an occurrence of >50% and a relative abundance of >0.05%. SparCC correlations having a coefficient of >0.7 or < −0.7 and identified as statistically significant ($p < 0.05$) were included in the construction of the network. Modules were separated from the networks using the fast greedy modularity optimization (Clauset et al., 2004). To describe the attributes of a network, indices including modularity, clustering coefficient, average path length, network diameter, average degree, and graph density were calculated using the package 'igraph' in R (Csardi 2006). A total of 1000 random networks of equal size were generated by using the 'igraph' package in R for each network analysis, and all of the indices of the random networks were calculated individually. A statistical Z test was used to verify whether the network indices between the observed and random networks were significantly different. Gephi (version 0.9.2) was used to depict the network analyses. The taxa with the degree ranking top 1% were determined as the 'keystone' taxa in the topological network (Hartman et al., 2018).

Structural equation models (SEMs) were constructed to separate the presumed direct and indirect effects of environmental factors and trophic interactions (at the community level) on bacterioplankton, phytoplankton and zooplankton community structures, respectively. SEM allows for both direct and indirect theoretical causal relationships between intercorrelated variables to be tested, and for potential multivariate relationships to be identified. First, we divided the environmental parameters into different groups, namely physical factors, nitrogen, phosphorus and carbon. The physical factors group included water temperature, DO, EC, pH and ORP. The group of nitrogen consisted of TN, NO_3^--N and NH_4^+-N, whereas the group of phosphorus consisted of TP only. The group of carbon contained DOC, and the group of primary productivity was represented by Chl-a. Then these groups of environmental parameters were converted to Euclidean dissimilarity after their normalization. Plankton community structures were calculated using Bray-Curtis dissimilarity. Pearson correlations were performed to test the relationships between the matrices before the SEMs were generated (Table S2; Fig. S1). The SEMs were created using the software IBM SPSS Amos (version: 26). The fitness of the model was tested the with comparative fit index (CFI) and the root mean square error of approximation (RMSEA). The ratio of chi-square to degree of freedom (chiq/df) was also calculated for each SEM.

3. Results

3.1. Environmental parameters across different seasons and zones

The PCA showed that the first component (PC1) explained 40.5% of the variance in the measured environmental factors among zones and seasons, which was much higher than the percentage explained by the second component (PC2) (25.4%) (Fig. 1B). Water temperature, DO, pH, EC, ORP, TP and Chl-a contributed more to PC1, whereas TN, NH_4^+-N, NO_3^--N and DOC showed more variations along PC2. Moreover, the seasonal variance of the measured environmental parameters was mainly represented by PC1, and their spatial differences were more represented by PC2, according to the distribution of the samples in the PCA plot (Fig. 1B). Additionally, the environmental dissimilarities between the zones were lower in winter than in spring and summer. According to the PCA plot, EA1, EA2 and ER zones had a higher similarity of the measured environmental parameters than CK zone (Fig. 1B).

We also compared the measured environmental parameters between zones within each season, as shown in Figs. S2 and S3. The concentration of Chl-a was the highest in the ER zone in winter and spring; however, EA1 and ER zones harbored similar concentrations of Chl-a in summer, which was significantly higher than the EA2 and CK zones (Fig. S3). In addition, the concentrations of TN and NO_3^--N were significantly lower in the EA zones than in ER and CK zones, regardless of the seasonal variation, but TP showed no significant differences between the different zones (Fig. S4). The concentration of DOC was consistently higher in the EA and ER zones than in the CK zone (Fig. S4).

3.2. The biomass and cell density of phytoplankton and zooplankton across different seasons and zones

Phytoplankton cell density showed significant seasonal differences (two-way ANOVA, $F = 23.65$, $P < 0.001$; Table S3), increasing from winter to summer, with remarkable differences between zones (Fig. S5A). Phytoplankton cell density was significantly higher in EA1 and ER zones compared to EA2 and CK zones in spring and summer (Fig. S5A). Phytoplankton biomass also showed significant differences across seasons (two-way ANOVA, $F = 11.35$, $P < 0.001$) and zones (two-way ANOVA, $F = 10.05$, $P < 0.001$). Additionally, phytoplankton biomass was consistently higher in the ER zone compared to the other three zones in all seasons (Fig. S5A).

The significant differences in cell density between seasons were also found in the zooplankton community (two-way ANOVA, $F = 9.18$, $P < 0.001$), whereas there were also significant differences between the different zones (two-way ANOVA, $F = 5.76$, $P < 0.01$), which was similar with phytoplankton cell density (Fig. S5B). However, the differences in zooplankton biomass were stronger between zones than between seasons (two-way ANOVA; zone: $F = 10.82$, $P < 0.01$; season: $F = 4.91$, $P < 0.05$; Fig. S5B), which was in contrast to the result of zooplankton cell density. Moreover, the zooplankton biomass in the CK zone was much higher compared to the other three zones in spring and summer.

3.3. The alpha diversity and compositions of bacterioplankton, phytoplankton and zooplankton communities in different zones across seasons

The results of two-way ANOVA indicated that the richness of bacterioplankton, phytoplankton and zooplankton communities differed significantly in different seasons and zones (Table S4). However, the richness of these plankton communities showed more significant differences between seasons than between zones, as indicated by higher F values. In winter and spring, the richness of bacterioplankton community was generally lower in EA zones than in ER and CK zones, but in summer, there were no significant differences in bacterioplankton richness between zones (Fig. 2A). Furthermore, we found no significant
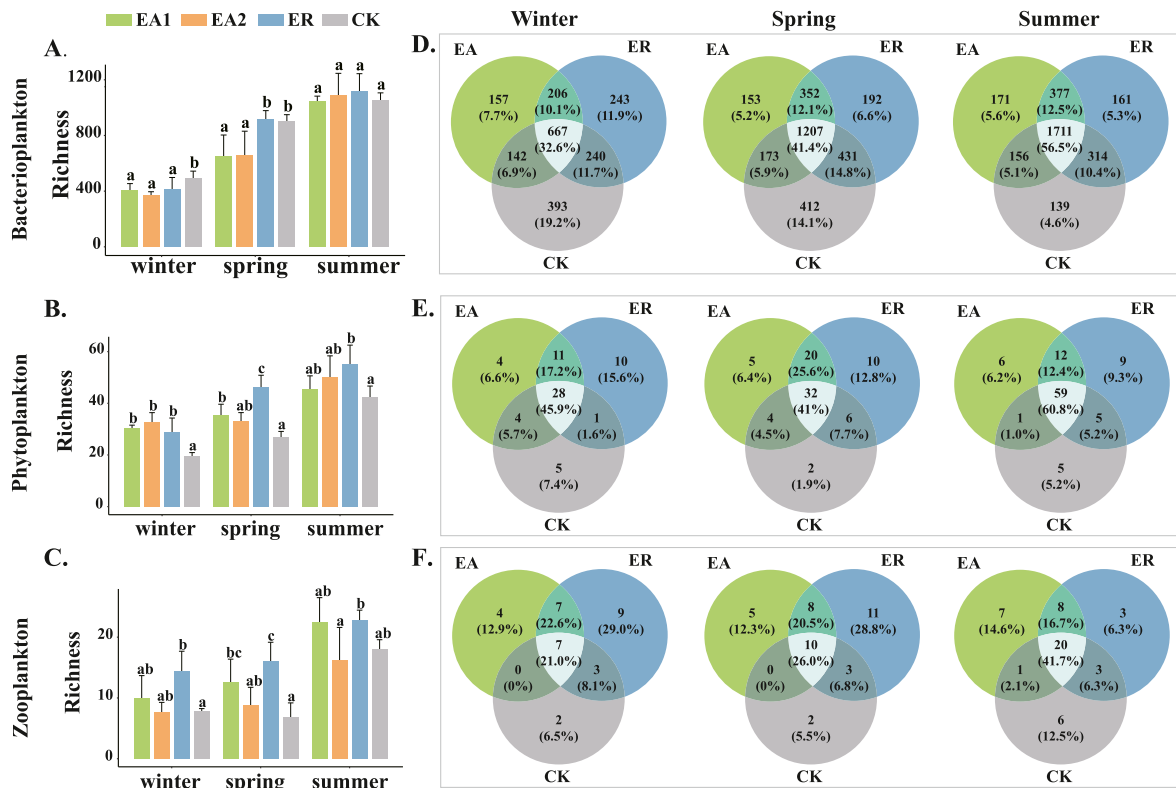
Fig. 2. The comparisons between number of total taxa (richness), unique taxa, and shared taxa of bacterioplankton, phytoplankton, and zooplankton communities across seasons and zones. For A-C, plots show the richness of bacterioplankton (A, OTU number, average value ± standard deviation, n = 9), phytoplankton (B, genus number, average value ± standard deviation, n = 5), and zooplankton (C, genus number, average value ± standard deviation, n = 5) communities. Different letters indicate significant differences (*P* < 0.05) between zones within single season. For D-F, Venn diagrams highlight the number and percentage of the unique and shared OTUs/genera of bacterioplankton (D), phytoplankton (E), and zooplankton (F) communities across different zones in each season. The results of Venn diagrams corresponding to the EA zones were averaged by EA1 and EA2 zones. EA, ecological aquaculture zone; ER, ecological restoring zone; CK, control zone.

differences in bacterioplankton richness between zones regardless of seasonal variation (Fig. S6A). Phytoplankton community richness was significantly higher in EA and ER zones than in CK zone in all seasons (Fig. 2B; Fig. S6B). The richness of the zooplankton community was generally higher in the EA1 and ER zones than in the EA2 and CK zones (Fig. 2C; Fig. S6C).

The Venn diagrams showed that the shared OTUs/genera among all zones increased from winter to summer for all plankton communities (Fig. 2D–F). The EA zones harbored fewer unique bacterial OTUs than the ER and CK zones did in both winter and spring; in summer, however, the number of unique bacterial OTUs of EA zones increased a bit when ER and CK zones both decreased (Fig. 2D). Moreover, ER zone showed higher overlapping in the bacterial OTUs with both EA and CK zones compared to those between EA and CK zones. The number of unique phytoplankton genera was consistently the highest in the ER zone in all seasons; furthermore, the ER zone harbored more shared phytoplankton genera with the EA zones than those with the CK zone (Fig. 2E). The Venn diagrams for the zooplankton taxa showed similar results with those for phytoplankton in winter and spring (Fig. 2F). In summer, the EA zones rather than the ER zone harbored the highest number of unique zooplankton taxa.

The bacterioplankton communities were gathered according to the seasons, and the bacterioplankton communities were also gathered according to their belonging zones within each season (Fig. S7A). Additionally, the PERMANOVA test showed that seasonal factors exhibited a much higher explanation for the bacterioplankton communities than the spatial differences (Table S4). The phytoplankton and zooplankton communities both showed significant community dissimilarities across seasons and zones, although it was difficult to distinguish their separated patterns among seasons and zones in the PCoA plots (Table S5;

Figs. S7B and C).

Ten phyla/classes, which mean relative abundance was >1%, were detected as the dominant taxa of the bacterioplankton community. The relative abundances of phylum Bacteroidetes and class Alphaproteobacteria were significantly higher in the EA and ER zones than that in the CK zone regardless of seasonal variation, whereas those of phyla Acidobacteria, Firmicutes and class Proteobacteria_unclassified decreased in the EA and ER zones compared to those in the CK zone (Fig. S8A). Diatom, Chlorophyta and Cyanophyta were the dominant taxa for the phytoplankton community. A higher relative abundance of Diatom but lower relative abundance of Chlorophyta were detected in the ER zone compared with those in the CK zone (Fig. S8B). Furthermore, taxa belonging to Rotifera dominated the zooplankton community in the EA and ER zones as the relative abundances were both higher than 80% (Fig. S8C). However, the relative abundance of Cladocera was significantly lower in the EA and ER zones than that in the CK zone (Fig. S8C).

3.4. The co-occurrence topological networks between taxa from bacterioplankton, phytoplankton and zooplankton communities in different zones

The co-occurrence topological networks between the taxa assigned to different plankton communities were constructed as a proxy of potential interactions within plankton communities of the microbial food web in the four zones (Fig. 3A). The topological parameters—including modularity, clustering coefficient, average path length and network diameter—were all significantly higher (*P* < 0.001) than those of random networks as estimated by Z-tests (Table 1), which indicated that all the topological networks were not randomly structured. The proportion of positive links were slightly higher than that of negative links
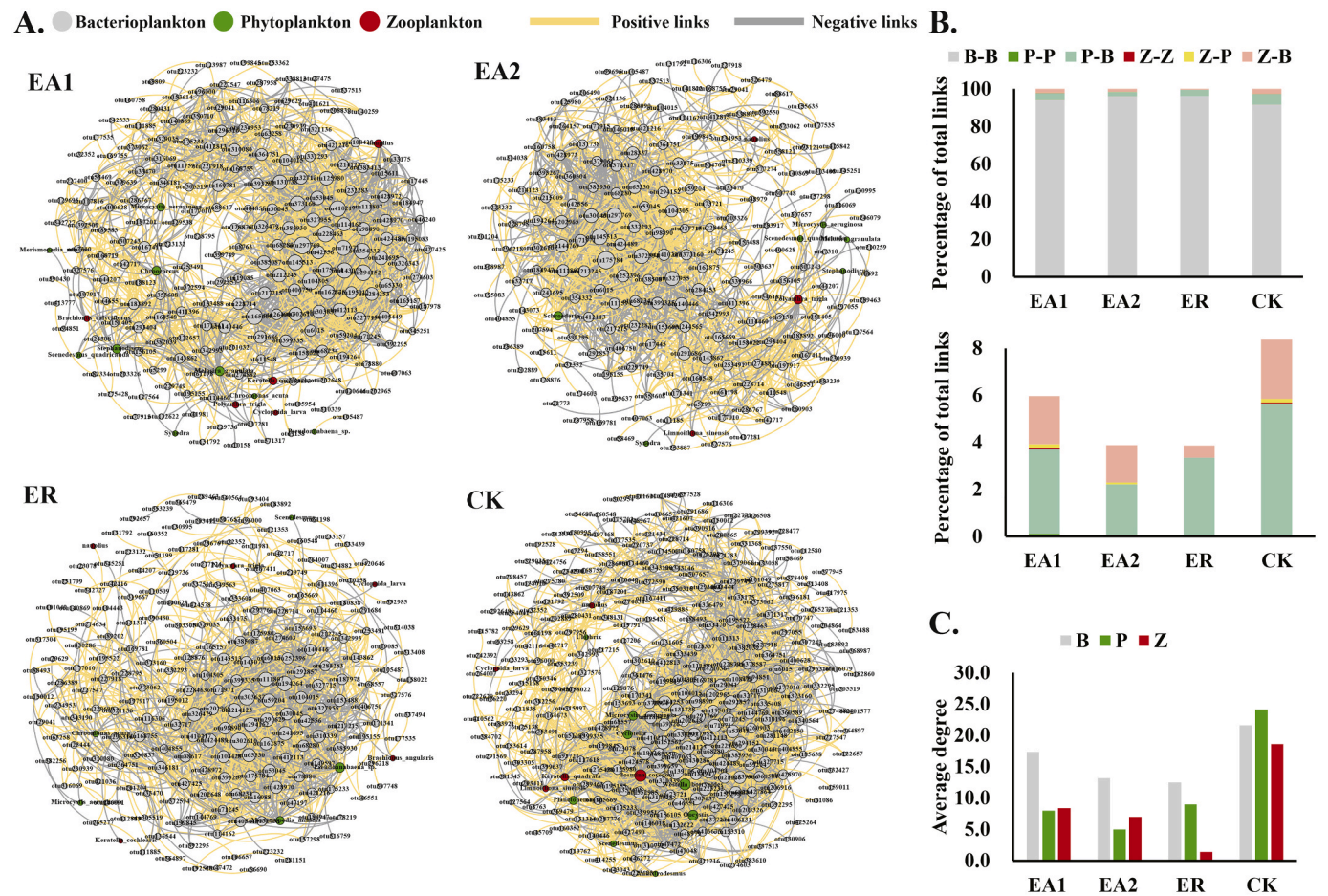
Fig. 3. Topological networks (A) derived from the plankton metacommunities and network characteristics (B, percentage of links between taxa intra/inter different plankton communities; C, average degree of the taxa belonging to different plankton communities) in the ecological aquaculture (EA), ecological restoration (ER), and control (CK) zones, respectively. For A, yellow edges indicate positive links, whereas grey edges indicate negative links. For B and C, the letter 'B' represents bacterioplankton; the letter 'P' represents phytoplankton; the letter 'Z' represents 'zooplankton'. Two letters connected by '-' mean the links between the taxa from the two plankton communities. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Topological properties of the empirical networks and their associated random networks in each zone. EA, ecological aquaculture zone; ER, ecological restoring zone; CK, control zone.

		Empirical network								Random network			
	Nodes	Edges		Average degree	Modularity	Clustering coefficient	Average path length	Network diameter	Graph density	Modularity (SD)	Clustering coefficient (SD)	Average path length (SD)	Network diameter (SD)
		Positive	Negative										
EA1	216/ 316	1054 58%	757 42%	16.77	0.371***	0.327***	2.66***	6***	0.078	0.196 (0.005)	0.078 (0.003)	2.17 (0.00)	3.17 (0.37)
EA2	197/ 327	763 60%	500 40%	12.82	0.319***	0.290***	2.91***	8***	0.065	0.231 (0.006)	0.066 (0.004)	2.34 (0.00)	4.00 (0.00)
ER	221/ 410	773 58%	571 42%	12.16	0.311***	0.255***	3.23***	10***	0.055	0.241 (0.005)	0.055 (0.003)	2.43 (0.00)	4.01 (0.08)
CK	304/ 460	1812 55%	1474 45%	21.62	0.240***	0.286***	2.81***	8***	0.071	0.172 (0.004)	0.071 (0.004)	2.13 (0.00)	3.01 (0.09)

***$P < 0.001$.

for all topological networks (Table 1). Furthermore, more than 90% of links of these topological networks represented potential interactions between bacterioplankton taxa (Fig. 3B). When the links intra bacterioplankton were excluded, lower proportion of links between taxa from different trophic levels was found in the EA and ER zones than the CK zone (Fig. 3B).

The index of average degree, which can represent the connectivity of the topological network, was lower in the EA and ER zones than the CK

zone (Table 1). Moreover, we compared the average degree of taxa between trophic levels (i.e., bacterioplankton, phytoplankton and zooplankton) (Fig. 3C). The average degree of taxa belonging to bacterioplankton was the highest in the EA and ER zones; besides, the average degree of taxa from phytoplankton and zooplankton were comparable between two EA zones, whereas the average degree of phytoplankton taxa was much higher than zooplankton taxa in the ER zone (Fig. 3C). On the contrary, the average degree of taxa from

phytoplankton was the highest in the CK zone, followed by bacterioplankton and then zooplankton.

We identified and defined keystone taxa for each topological network as those nodes within the top 1% of node degree values of each network. Therefore, nine OTUs from the bacterioplankton community were identified as the keystone taxa (Table S6). OTU 297769 and 104305, which were assigned to genus *Pseudomonas*, class Gammaproteobacteria and genus *Janthinobacterium*, class Betaproteobacteria, were detected as the keystone taxa in the topological network in the EA1 zone. OTU 175784 and 145513 belonging to genus *Sphingobacterium*, phylum Bacteroidetes and genus *Neorhizobium*, class Alphaproteobacteria were keystone taxa in the topological network of EA2 zone. The keystone taxa of the topological network of ER zone, OTU 302610 and 303637, were members of genus *Sporosarcina*, phylum Bacteroidetes and unclassified bacteria, respectively. For the topological network of CK zone, OTU 139106 (class Subdivision3, phylum Verrucomicrobia), 304704 (genus *Exiguobacterium*, phylum Firmicutes), and 68280 (genus *Flavobacterium*, phylum Bacteroidetes) were identified as the keystone taxa.

3.5. The forces of environmental dissimilarity and trophic interactions at the community level on driving bacterioplankton, phytoplankton and zooplankton communities

We performed SEM to investigate the mechanisms underlying the dissimilarity of these plankton communities. The CFI of all the models were higher than 0.9, and RMSRA was lower than 0.06, which indicated the fitness of our models was good (Fan et al., 2016). The physical factors ($P < 0.001$), phosphorus ($P < 0.001$) and primary productivity ($P < 0.001$) rather than nitrogen and carbon exhibited significant and direct effects on the bacterioplankton community (Fig. 4A). Furthermore, the composition of phytoplankton ($P < 0.001$) and zooplankton ($P < 0.001$) communities also exhibited significant effects on the bacterioplankton community. The physical factors, followed by the phytoplankton community, showed much higher effects on the bacterioplankton community than the other factors when evaluated by the total standardized effects (Fig. 4A). Phytoplankton community was directly and significantly driven by the physical factors ($P < 0.05$), nitrogen ($P < 0.05$), phosphorus ($P < 0.001$), carbon ($P < 0.05$), primary productivity ($P < 0.001$), bacterioplankton community ($P < 0.001$) and
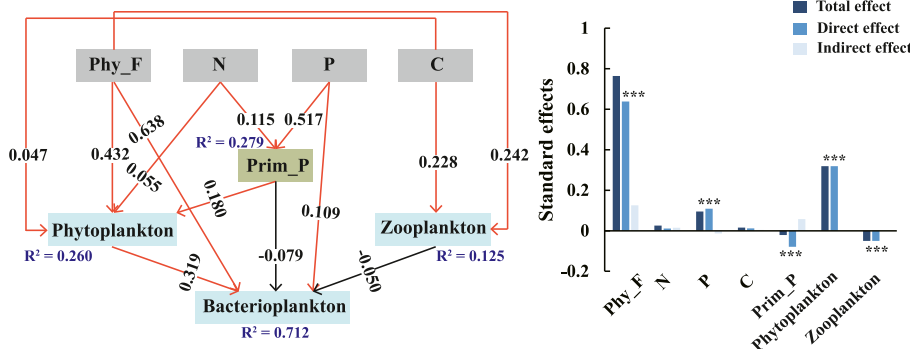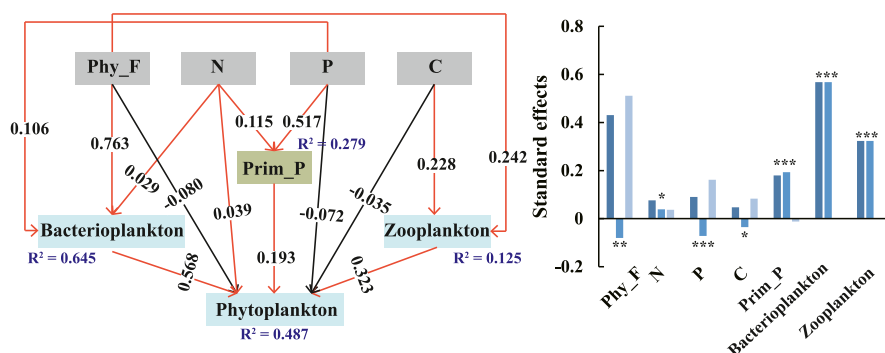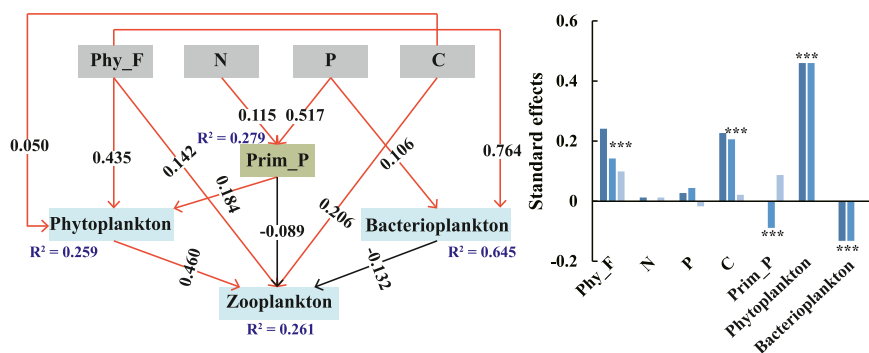

Fig. 4. Structural equation model (SEM) results for the bacterioplankton (A), phytoplankton (B), and zooplankton (C) communities. Standardized path coefficients are shown on the figure. Red arrows represent positive effects, whereas black arrows represent negative effects. Paths that were insignificant ($P > 0.05$) are not shown. The direct, indirect, and total effects of each factor on the bacterioplankton, phytoplankton, and zooplankton communities were also generated on the right panel. Phy_F, physical factors (including water temperature, dissolved oxygen, electrical conductivity, pH, and oxidation-reduction potential); N, nitrogen (including total nitrogen, nitrate nitrogen, and ammonia nitrogen); P, phosphorus (total phosphorus); C, carbon (dissolved organic carbon); Prim_P, primary productivity (chlorophyll *a*). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

zooplankton community ($P < 0.001$) (Fig. 4B). The major effects on structuring the phytoplankton community were contributed by direct effects of bacterioplankton and zooplankton communities and the indirect effect of physical factors (Fig. 4B). The zooplankton community was affected significantly and directly by physical factors ($P < 0.001$), carbon ($P < 0.001$), phytoplankton community ($P < 0.001$) and bacterioplankton community ($P < 0.001$) rather than nitrogen and phosphorus in our model (Fig. 4C); however, the major effects on structuring the zooplankton community were from the direct effect of phytoplankton community (Fig. 4C). Additionally, our models explained 71.2%, 48.7% and 26.1% of the variance of bacterioplankton, phytoplankton and zooplankton communities, respectively, when the trophic relationships were considered. The explanations of the models for these plankton communities were improved compared to the models without considering the trophic relationships.

4. Discussion

4.1. The effects of aquaculture on the ambient water quality

Historical intensive aquaculture has been responsible for the massive input of nutrients into the aquatic ecosystem, resulting in eutrophication (Lu et al., 2015). However, ecological aquaculture can be employed to keep the balance between the ecological and economic effects by artificial management, including planting submerged macrophytes (Li et al., 2021), regulating the structure of the food web (i.e., cultivating the aquatic products with different trophic levels) (Gamito et al., 2020) and rational feeding (Cho and Bureau, 2001). In the present study, the ecological aquaculture decreased the concentrations of TN and NO_3^--N compared to those in the CK zone regardless of seasonal variations. The aquatic macrophytes can absorb inorganic nitrogen for growth, which would also decrease the concentrations of TN and NO_3^--N. Additionally, the aquatic macrophytes can be efficient for nitrogen removal, especially for nitrate, as macrophytes can provide organic carbon and biofilm for the growth of denitrifying bacteria (Weisner et al., 1994; Zhang et al., 2016). However, the concentrations of TN, NO_3^--N and NH_4^+-N were higher in the ER zone than those in the EA zones, which suggested the effects of ecological restoration on the nitrogen removal was not as good as the ecological aquaculture. It implied that the aquatic macrophytes grown in the ER zone might be under degradation because of the lake eutrophication and lack of artificial management (Sayer et al., 2010). The highest phytoplankton biomass and diversity in the ER zone can also confirm that it could be shifting from the clear macrophyte-dominated to turbid phytoplankton-dominated state (Sayer et al., 2010). However, the cultivation of different aquatic animals (i.e., ecological aquaculture in the present study) could be beneficial for the reconstruction of the food web, which would be helpful for the restoration via trophic cascades in the aquaculture-influenced sites (Zanden et al., 2016). Although the nitrogen was removed remarkably by the ecological aquaculture, the concentration of DOC was consistently higher in the EA and ER zones compared with the CK zone. Considering the similarity between the EA and ER zones, the higher DOC concentration with few seasonal variations could be related to the historical aquaculture. Our previous study found that the total carbon was significantly higher in the sediment of aquaculture-influenced zones than in the CK zone (Qin et al., 2020; Qin et al., 2022). The organic matter in the sediment could be released from the solid phase and subsequently diffused to the water column (Peter et al., 2017), which reflected a long-term effect of historical intensive aquaculture on the lake environment.

4.2. Distinct effects of aquaculture on the plankton diversity and potential interactions between taxa of plankton metacommunities

The biotic parameters—the diversity of plankton communities—also varied across seasons and zones. Our results showed that the proportion

of the shared taxa among different zones rather than the unique taxa increased evidently from cold to warm seasons, which suggested that the seasonal changes could overwhelm the differences in species richness induced by aquaculture (Zeng et al., 2019). However, it was interesting that the number of the unique bacterial OTUs did not decline in the EA zones alongside the seasonal changes as those in ER and CK zones. This result supported that aquaculture could develop habitat-specific species, thereby forming distinct biogeochemical processes from the other zones (Wei et al., 2021). On the contrary, the ER zone harbored the highest numbers of unique taxa for the phytoplankton and zooplankton communities compared with those in the other two zones. Diverse submerged macrophytes were widely planted in the ER zone to improve water quality. Generally, phytoplankton and submerged macrophytes are competitors for light and nutrients, and submerged macrophytes could control phytoplankton by producing allelochemicals that suppress phytoplankton growth rates (Vanderstukken et al., 2014). However, the long-term eutrophication in the shallow Eastern Lake Taihu could induce a gradual process of macrophyte degradation and thereby increase the richness of phytoplankton (Sayer et al., 2010; Xu et al., 2010).

The species interactions are also important factors influencing the ecosystem functioning (Duffy, 2003). In the present study, we constructed topological networks containing taxa of bacterioplankton, phytoplankton and zooplankton to further reveal potential interactions among these plankton taxa and how this pattern would be affected by the aquaculture. The connectivity of the topological networks (i.e., average degree) was much lower in the EA and ER zones than that in the CK zone. Furthermore, lower proportions of inter-kingdom links were found in the EA and ER zones than in the CK zone, mainly referring to the associations of bacterial OTUs with taxa belonging to phytoplankton and zooplankton. These results suggested that the potential interactions between taxa from different trophic levels were weakened whatever the site was under ecological aquaculture or restoration. The more complex networks with a high number of interconnections are more likely to resist a disturbance, which is predicted by the seminal theoretical work in ecology that first emerged from MacArthur's early work (MacArthur, 1955; Philippot et al., 2021). Shade et al. (2011) also proposed that a more complex network of trophic interactions may buffer response to environmental changes. Thus, the lower network connectivity could imply a lower resistance of the plankton metacommunities to future disturbances in the EA zones than in the CK zone. Furthermore, the 'keystone' taxa in the topological networks identified in the EA zones were affiliated with genera *Pseudomonas*, *Janthinobacterium*, *Sphingobacterium* and *Neorhizobium*, respectively. Members of the genus *Pseudomonas*, which are capable of versatile metabolism and adapting to fluctuating environmental conditions, are generally related to plant, insect and human pathogens and environmental saprophytes (Silby et al., 2011). Species of genus *Janthinobacterium* have been isolated from the aquaculture sites and associated with the nitrite removal (Neissi et al., 2020). Moreover, members of the genus *Sphingobacterium* were also previously isolated from aquaculture water (Zhang et al., 2021). These results indicated that these aquaculture-related taxa acted as the keystone taxa could exhibit central impacts maintaining the potential species interactions in the EA zones, which might further reflect the influences of aquaculture on the potential microbial food web and the corresponding ecosystem functioning. However, it should be noted that these topological networks are statistically determined associations among the relative abundances of various OTUs/genera, which can only indicate potential positive or negative interactions. Further targeted studies are required to test whether these interactions would occur at microsite scales under field conditions.

4.3. Different mechanisms driving the structure of bacterioplankton, phytoplankton and zooplankton communities under the seasonal variations and aquaculture activities

Bacterioplankton, phytoplankton and zooplankton communities,

which play different trophic roles in the microbial food web, can be assembled under different mechanisms. We constructed SEMs to reveal how the measured environmental factors and trophic relationships worked jointly to drive the different planktonic communities. The bacterioplankton community was mainly regulated by the direct effect of the physical factors, followed by the direct effect of the phytoplankton community. It could explain the strong seasonality of bacterioplankton community compositions as these physical factors, like water temperature and DO, exhibited strong seasonality. It has been widely reported that the bacterioplankton community showed seasonality (Zeng et al., 2019). Moreover, the phytoplankton community composition was the second most important factor controlling the bacterioplankton community. Phytoplankton can shape the biochemistry of the water column by utilizing inorganic nutrients, fixing carbon (photosynthesis) and releasing dissolved organic matter (DOM) (Seymour et al., 2017). These DOM released by the phytoplankton during their growth can provide a series of ecological niches for bacterioplankton and lead to changes in bacterial growth rate and community composition (Camarena-Gómez et al., 2018). However, the quantity and quality of DOM may differ, depending on species-specific properties and the physiological status of the algae. Hence, the influences of phytoplankton community composition on the bacterioplankton community could be attributed to the different DOM pools derived from different phytoplankton taxa. Furthermore, the primary productivity (referred to Chl-a in our analyses), which could be more affected by the biomass of phytoplankton and macrophytes, showed few effects on driving the bacterioplankton community. This result suggested that the quality/source of the DOM could be more important than the quantity for the bacterioplankton community composition in the present study.

According to our model, the phytoplankton community was primarily affected by the bacterioplankton community, which also brought the indirect effect of the physical factors, nitrogen, and phosphorus. However, the direct effects of physical factors on the phytoplankton community was much lower than that on the bacterioplankton community. Liu et al. (2015) previously reported that the environmental changes showed higher explanation on the phytoplankton community compared to that on the bacterioplankton community, which was inconsistent with our results; meanwhile, the high explanation on the phytoplankton community in their study was primarily contributed by eutrophic factors, which ranged from middle eutrophic to oligo-mesotrophic levels. In the present study, however, the trophic state of the water environment did not change so much at both temporal and spatial scales compared to Liu et al. (2015). Moreover, most research only focused on the effects of phytoplankton on the bacterial community (Camarena-Gómez et al., 2018); how the bacterial community composition reversely affects the phytoplankton community is rarely reported. Bacteria can provide limiting inorganic nutrients for the growth of phytoplankton cells by mineralizing organic matter (Legendre and Rassoulzadegan, 1995). When the allochthonous supply of nutrients is low, phytoplankton growth is predicted to particularly benefit from bacterial delivery of regenerated nitrogen and phosphorus (Seymour et al., 2017). Consistently, in our study, the nitrogen and phosphorus both showed low effects on the phytoplankton, whereas the bacterioplankton community composition was the most critical factor influencing the phytoplankton community. Furthermore, growing evidence showed that phytoplankton could acquire vitamins (i.e., vitamin B12) and re-mineralized micronutrient (i.e., Fe) from the bacterial synthesis processes (Amin et al., 2009; Croft et al., 2005), which enhanced the phytoplankton-bacterioplankton mutualism.

The trophic interactions with phytoplankton mainly drove the composition of the zooplankton community. This result was not surprising because the phytoplankton can supply food for the zooplankton (Alcaraz and Calbet, 2003). Additionally, we found that carbon (referred to DOC) showed relatively higher effects on the zooplankton community than other environmental parameters. A previous study also found that the zooplankton community structure significantly shifted in response to DOC amendments in a mesocosm experiment (Mitrovic et al., 2014). The allochthonous DOC has been suggested to act as a basal resource that accounts for up to 70% of the carbon utilized by zooplankton (Cole et al., 2011). Although we cannot distinguish between allochthonous and autochthonous DOC in the present study, the impacts of DOC on the zooplankton community structure were still supported by both the literature and our model. Furthermore, the higher DOC concentration in the EA and ER zones could significantly affect the zooplankton community compositions in these zones.

5. Conclusions

This study investigated the impacts of aquaculture on water quality and plankton communities in the lake polluted by the historical intensive aquaculture. We found that TN and NO_3^--N was lower in the EA zones than that in the ER and CK zones. However, DOC was significantly higher in the EA and ER zones compared with the CK zone regardless of ecological aquaculture or ecological restoration were conducted. These results implied that ecological aquaculture could be better for reducing the nitrogen loading in the water body influenced by historical intensive aquaculture than the ecological restoration. Furthermore, aquaculture activities significantly shifted the compositions of all plankton communities. Generally, the lower richness of bacterioplankton but higher richness of phytoplankton and zooplankton was detected in the EA and ER zones compared with CK zone. Moreover, the network connectivity of plankton metacommunities was lower in the zones influenced by the historical intensive aquaculture than the CK zone, no matter ecological aquaculture or ecological restoration were conducted. The aquaculture-related bacterial taxa played as 'keystone' taxa maintaining the topological networks of plankton metacommunities in the EA zones. The bacterioplankton, phytoplankton and zooplankton communities were structured under distinct mechanisms. The bacterioplankton community was primarily driven by the physical factors, whereas the phytoplankton and zooplankton communities were more explained by the trophic relationships. These results demonstrated the effects of aquaculture on the water quality, the plankton communities and the potential species interactions of the plankton metacommunities, which provided new insights into evaluating the ecological impacts of aquaculture on the freshwater ecosystem.

Credit author contribution statement

Huimin Xu: Investigation, Writing – original draft preparation, Formal analysis, Visualization. Dayong Zhao: Conceptualization, Methodology, Resources, Writing-Reviewing and Editing, Funding acquisition, Supervision. Jin Zeng: Conceptualization, Investigation, Writing-Reviewing and Editing, Supervision, Funding acquisition. Zhigang Mao: Writing-Reviewing and Editing. Xiaohong Gu: Writing-Reviewing and Editing. Qinglong L. Wu: Conceptualization, Funding acquisition.

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.

Data availability

Our data has been submitted to the NCBI Sequence Read Archive (SRA) database (Accession ID: PRJNA605263)

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2022.119741.

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